Red Knot *Calidris canutus roselaari* migration connectivity, abundance and non-breeding distribution along the Pacific coast of the Americas

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Red Knots Calidris canutus roselaari occur along the Pacific coast of the Americas and may use as few as four stopover or staging sites during spring migration. There are key information gaps regarding this population's status and non-breeding distribution because of its localized distribution during migration, relatively small population size (estimated population of 17,000) and a poor understanding of the location of major overwintering sites. Based on resightings of marked birds, we assessed migratory connectivity of Red Knots along the Pacific coast. Knots captured and marked at two sites in NW Mexico have been observed at several locations, including migration areas in coastal Washington and the Yukon-Kuskokwim Delta in W Alaska and breeding areas in NW Alaska. The greatest connectivity was between Guerrero Negro/Ojo de Liebre and Golfo de Santa Clara, Mexico, and during northbound migration, between those two sites and coastal Washington, USA. Much less is known about the southbound migration; comparatively few marked knots have been resighted north of Mexico during autumn. We reviewed scientific literature and consulted eBird data to compile observational records of Red Knots along the Pacific coast. Records from mainland NW Mexico document substantial aggregations (hundreds or thousands) of Red Knots at several locations during the non-breeding season. Connectivity involving locations in mainland NW Mexico may be demonstrated with more field effort. Additional records along the Pacific coast south of Mexico, which involved far fewer birds, extended to extreme southern Chile near the documented winter range of the *rufa* subspecies. The available information suggests the possibility of an area of overlap in the non-breeding range of roselaari and rufa in southern Mexico; the southernmost distribution of roselaari remains incompletely known. Comprehensive conservation assessments will require additional investigation to identify important stopover and overwintering sites.

INTRODUCTION

Understanding the seasonal geographic structure of migratory bird populations is an essential element of applied conservation (Martin *et al.* 2007). In this regard it is important to know not only where populations are distributed throughout the annual cycle but also how individuals within or among populations are linked to seasonal sites (Boulet & Norris 2006, Webster & Mara 2005, Webster *et al.* 2005). Undertaking assessments of migratory connectivity for

shorebirds is particularly challenging because of the number of species having polytypic forms, many with complex geographic structure (Engelmoer & Roselaar 1998, Gill et al. 2013). An exemplar of this is the Red Knot Calidris canutus, a Holarctic-breeding species having as many as six subspecies (Buehler & Baker 2005). Two of these (C. canutus rufa [hereafter, rufa] and C. c. roselaari [hereafter, rose*laari*]) have both significant breeding and overwintering areas in the Western Hemisphere on the Atlantic and Pacific coasts, respectively (Harrington 2001). While some aspects of the movement ecology of rufa are generally known (Niles et al. 2010), movement ecology of roselaari is fragmentary at best. We know that roselaari migrate along the Pacific coast of the Americas (Buehler & Piersma 2008, Patten et al. 2003, Tomkovich 1992) and that during the post- and non-breeding seasons they have been recorded at several sites in this region, ranging from W Alaska south possibly to Ecuador (Carmona et al. 2006, Chappell 2005, Gill & Handel 1981, Gill & Handel 1990, Harrington 2001, Niles et al. 2008). Lacking for roselaari, however, is a basic understanding of seasonal distribution and abundance, use of sites, and migratory connectivity. In this paper we address these gaps through (1) an assessment of banding and resighting data obtained from capture efforts at sites along the Pacific coast since 1988, and (2) a compilation of historic and current records of the occurrence and abundance of knots along the Pacific coast from Russia to Chile.

MATERIALS AND METHODS

Study area

We marked knots at several sites along the Pacific coast from Russia to Baja California Sur, Mexico (Table 1). Several detailed descriptions of these sites have been published for sites in Russia, Tomkovich & Dondua (2008); for Alaska, Gill & Handel (1981, 1990), Johnson & Connors (2010), Johnson et al. (2011), McCaffery et al. (2008) and Tomkovich & Dementyev (2006); for Washington, Buchanan (2008) and Buchanan et al. (2010, 2011); for Mexico, Carmona et al. (2008) and CONANP (2007); and for Texas, Newstead et al. (2013).

Capture, marking and resighting

We used bow traps to capture nesting adults and mist-nets and cannon and rocket nets to capture birds outside of the breeding season. With the exception of knots captured on Wrangel Island, Russia, all birds received colored leg flags inscribed with unique numeric or alphanumeric codes to facilitate resightings (Clark et al. 2005). Birds captured in Russia and the United States (but not Mexico) also received a uniquely numbered metal band. Efforts to resight marked knots were coordinated among investigators and projects, including those on the Yukon-Kuskokwim Delta, Alaska,

Table 1. Summary of banding effort at study sites in Russia, USA and Mexico where Red Knots were marked 1988–2012.

Location/Year	Season	Status	Number marked (totals)
Russia			
Wrangel Island (71°20'N, 17	79°30'W)		
1988	Summer	Breeding	2
1995	Summer	Breeding	5
2006	Summer	Breeding	3
2007	Summer	Breeding	45
Subtotal			(55)
United States			
Western Alaska (64°56'N, 10	65°38'W)		
2010	Spring/summer	Breeding	40
2011	Spring/summer	Breeding	28
2012	Spring/summer	Breeding	41
Subtotal			(109)
Yukon-Kuskokwim Delta, A	laska (61°14'N, 165°38'W)		
2006	Spring	Passage	19
Grays Harbor, Washington (46°58'N, 124°04'W)		
2011	Spring	Passage	162
Mexico			
Golfo de Santa Clara (31°40)'N, 114°30'W)		
2010	Spring	Passage	6
2011	Spring	Passage	59
2012	Spring	Passage	24
Subtotal			(89)
Guerrero Negro (27°35'N, 1	14°06'W)		
2006	Autumn	Passage	195
2007	Autumn/winter	Passage/resident	128
2008	Autumn/winter/spring	Passage/resident	195
2009	Autumn/winter/spring	Passage/resident	90
2010	Autumn/winter/spring	Passage/resident	45
2011	Winter	Resident	1
2012	Autumn/winter	Resident/passage	162
Subtotal			(816)
Total			1,250

between 2004 and 2012, at Grays Harbor and Willapa Bay, Washington, between 2007 and 2013, and intensively in 2009–2010 (Buchanan *et al.* 2012), at Guerrero Negro/Ojo de Liebre (hereafter, Guerrero Negro), Mexico, from 2006 to spring 2013 (Arce 2011), Golfo de Santa Clara, Mexico, during spring 2010–2013 (Hernández-Alvarez 2013) and at North Padre Island, Texas, during several recent migration seasons (Newstead *et al.* 2013). Observations at other locations were incidental or involved lesser levels of effort. Because efforts among sites did not always coincide in years and seasons, we acknowledge a likely spatiotemporal bias in resightings, but nevertheless feel the data provide new and much-needed information on distribution and migratory connectivity for the *roselaari* subspecies.

Records of distribution and abundance

To construct historic and contemporary records of the distribution and abundance of *roselaari*, we conducted an extensive review of the ornithological literature pertinent to the Pacific coast from Russia to Chile since the mid-1850s. We supplemented sources in the published literature, particularly those pertinent to sites in temperate western North America, by including data collected during Christmas Bird Counts (CBC; *http://netapp.audubon.org/cbcobservation/Historical/SpeciesData.aspx*) and records posted on eBird (*http://eBird.org*). We reference all data from the perspective of northern hemisphere seasons in which winter or the non-

breeding season encompasses September to April, spring or northward migration the period from May to early June, breeding during June and July, and autumn or southward migration from late July throughout August.

RESULTS

Capture and marking

Between 1988 and 2012, we captured and marked 1,250 Red Knots at six different sites along the Pacific Flyway (Table 1); 1,195 of these (96%) carried uniquely coded leg flags. Most birds (72%) were marked in Mexico at Guerrero Negro, Baja California Sur, and Golfo de Santa Clara, Sonora (Table 1), followed by those marked in Washington (13%), Alaska (10%) and Russia (4%). From the pool of marked birds, we received >2,500 reports of our birds away from marking areas (as of May 2013). These included 949 individuals seen at multiple sites. After eliminating potential duplicate records of the same individuals, the number was reduced to 649, for a minimum resighting rate of 51.9%.

Connectivity (distribution of resightings)

Resightings of Red Knots marked during this study established links between known breeding areas and sites used during migration and winter. Birds captured and marked at Wrangel Island were seen at stopover sites in Washington and

Table 2. Number of Red Knot resightings by banding/marking and resighting (or re-capture) locations. None of 515 Red Knots banded at North Padre Island, Texas, have been observed at sites listed in this table.

		Resighting location												
Banding location	Total banded	Wrangel Island, Russia	Chukotka, Russia	Breeding areas, Alaska, USA	Yukon-Kuskokwim River estuary, Alaska, USA	Copper River Delta, Alaska, USA	Gustavus, Alaska, USA	Washington, USA	Oregon, USA	Coastal California, USA	North Padre Island, Texas, USA	Golfo de Santa Clara, Sonora, Mexico	Guerrero Negro, Baja California, Mexico	Total resighted
Wrangel Island, Russia	55		1					2ª				6ª	5 ^a	_a
Seward Peninsula, Alaska, USA	109					2		4 ^b		1		9	6	20
Yukon-Kuskokwim River estuary, Alaska, USA	19							1°					2	2
Washington, USA	162							40			1	16	18	62
Golfo de Santa Clara, Sonora, Mexico	89						1	15				59	14	57
Guerrero Negro, Baja California, Mexico	816			6	4	2		272	1	6	1	150	304	508
Totals	1250	0	1	6	4	4	1	334	1	7	2	240	349	

^a There were 17 observations of Wrangel Island knots in Washington, 16 at Golfo de Santa Clara and 21 at Guerrero Negro. Although values in the table represent tallies of known or probable individual birds, we were unable to determine the total numbers resigned because the birds were marked with cohort flags and were not individually identifiable.

^b A fifth bird may also have been present.

° No codes were read; one sighting (partial flag code read) in 2008 and two in 2010.



Fig. 1. Migratory connectivity of Red Knots as represented by resightings of marked birds between 2006 and 2013. Lines connect sites, and arrows indicate the site at which the marked bird was seen. Lines having arrows at both ends indicate an exchange of sightings of marked birds. Dashed lines indicate 1–5 resightings between two sites, thin solid lines represent 6–10 resightings and heavy solid lines indicate >10 resightings. Lines do not depict migration routes between sites. Bandon Marsh is in Oregon, USA, and Mission Bay is in California, USA. The link between Mustang and Padre Islands, Texas and Laguna Superior, Oaxaca, Mexico, involved Red Knots of the *rufa* subspecies.

throughout the winter at sites in Mexico (Fig. 1, Table 2). Similarly, birds (n = 20) marked at nesting sites in W Alaska were resighted during passage on the Copper River Delta, Alaska, and at Grays Harbor, Washington, and during autumn and winter at Guerrero Negro, Mexico. One knot banded in Alaska was observed in both Washington and Guerrero Negro. The W Alaska-Guerrero Negro link was also confirmed by birds marked in autumn and winter at Guerrero Negro being seen on W Alaska nesting grounds (Fig. 1, Table 2).

Resighting of marked birds established links between or among several sites during the non-breeding period. Some of the most prominent of these were between sites in Washington and Mexico (Fig. 1, Table 2) where, for example, almost 32% (288 of 905) of birds marked in Mexico were seen at sites in Washington, while almost 20% of the birds marked in Washington (32 of 162) were subsequently resighted in Mexico (Fig. 1, Table 2).

Birds marked on spring passage on the outer Yukon-Kuskokwim Delta, Alaska, were seen in both Washington (passage) and Mexico (autumn, winter; Fig. 1, Table 2). Unexpectedly, putative *roselaari* marked in the Pacific Flyway in Washington and Mexico were linked to sites in the Central Flyway along the coast of Texas. Finally, resightings revealed strong interchange of marked birds at local scales, including between Golfo de Santa Clara and Guerrero Negro in Mexico (Fig. 1, Table 2). Combined, these resightings establish a complex pattern of migratory connectivity by *roselaari* throughout the Pacific Flyway (Fig. 1).

Non-breeding distribution

Our data, primarily compiled from CBC and eBird sources, indicate that as a species Red Knots occur during migration and as winter residents along the Pacific coast from Russia to S Chile. This distribution includes the roselaari subspecies that occupies the northern portion of the range from Wrangel Island, Russia, to Guerrero Negro, Mexico. [Note, however, that since our analyses were completed we have learned that a Red Knot marked during spring migration in Washington in 2011 has been seen at Las Garzas, Navarit, Mexico, about 1,000 km south of Guerrero Negro.] The southern portion of the range from at least S Mexico to S Chile is occupied by the *rufa* subspecies, but there remains a 1,300 km gap between the Nayarit observation of roselaari and S Mexico (Oaxaca) records of rufa (D. Newstead, unpubl. data) for which the subspecies distribution needs resolving. In addition, single knots that we marked at Guerrero Negro and Washington were subsequently observed in coastal Texas (Fig. 1; D. Newstead, unpubl. data) in what was previously presumed to be the nonbreeding range of the *rufa* subspecies; information on those sightings will be presented elsewhere.

Abundance

Our compilation of abundance data revealed nothing that would appreciably alter the currently accepted population levels for either *roselaari* or *rufa*. Specifically, we found no records of previously unknown large aggregations in the portion of the range that appears to be largely occupied by *rufa* (Central America south to S Chile). Similarly, abundance of putative *roselaari* Red Knots at 'new' sites in Mexico and elsewhere were consistent with estimates of population size for this subspecies. We did, however, find numerous sites among the various regions and countries that were not previously known to support birds during migration or winter. This information is summarized below.

United States and Canada

Unpublished CBC and eBird records helped clarify the abundance of Red Knots at sites along the Pacific coast of the Americas. Observations of small numbers (often 1–2 birds) were reported from >200 locations from the western United States and Canada, but very few sites had high counts of at least 20 (Fig. 2). Not surprisingly, we found no records of sites that supported at least 1,000 Red Knots that were not previously known to us through other sources of information. In California, multiple locations in the vicinity of San Francisco and San Diego supported collective totals that approached (San Diego: 935) or exceeded (San Francisco: 1,011) 1,000 birds.

Mexico

Survey efforts in parts of Mexico, by birdwatchers or professional biologists, have been much less intensive than in coastal areas of the United States. Counts of >100 Red Knots were reported on eBird from several sites: Ensenada and Estero Punta Banda, Baja California Norte; Costa Azul and La Reforma, Sinaloa; and Laguna Superior, Oaxaca (Fig. 3). In addition, 2,025 Red Knots were reported at Las Garzas, Nayarit, in February 2010. eBird records of Red Knots were generally scarce south of Nayarit, with the exception of Santa María Xadani, Oaxaca, where a high count of 300 was recorded.

Guatemala to Panama

We found numerous eBird records from Costa Rica and Panama, but there were no records from other Central American countries. Most records involved very small (typically 1–2 birds) or unreported numbers of knots, and all four counts of ≥ 20 knots were from Golfo Nicoya in Costa Rica (Fig. 3).

South America

Review of eBird records indicated that Red Knots occurred along much of the Pacific coast of South America (Fig. 4). Of the 95 eBird records of Red Knots from the Pacific coast of South America, 63 were recorded during winter (Nov– Feb) and 32 during migration periods. Only three records exceeding 20 knots were reported during migration (Paraiso, Peru, and two counts at Bahía de Caulín, Chile), but none exceeded 150. In contrast, there were 23 counts of \geq 20 knots from five sites during winter, none of which exceeded 150: Manglares de San Pedro de Vice, Peru; and Putemún, Bahía de Caulín, Bahía Pullao and Estación Esturial de Quempillén, Chile.

DISCUSSION

Connectivity

Resightings of Red Knots marked during this study have greatly clarified the movement ecology of C. c. roselaari in the Pacific Flyway. The greatest connectivity documented to date is between Guerrero Negro and the coast of Washington. A lesser degree of connectivity has been documented between Guerrero Negro and Golfo de Santa Clara, and between the latter site and coastal Washington. Observations of marked knots and count data indicate that a segment of the Guerrero Negro population moves northward to Golfo de Santa Clara from mid-March to late-April (Hernández-Alvarez 2011, Soto-Montoya et al. 2009), but part of the increase in abundance at Golfo de Santa Clara could also represent knots moving north from other sites on the northwest mainland coast of Mexico. With the exception of sites on the mainland coast of Mexico, there are few other areas south of Alaska (e.g. San Francisco Bay and southern California in autumn) that support large numbers of knots. However, observer effort has been far greater at Mexico banding sites and stopover areas in Washington compared to other areas along the Pacific coast. There may well be substantial connectivity involving other sites (e.g. Yukon-Kuskokwim River Delta, Copper River Delta, sites on the mainland coast of Mexico) that has yet to be documented, considering that some of these sites are difficult to access or have received little attention.

Golfo de Santa Clara and Guerrero Negro appear to be used differently by Red Knots. In particular, knots at Golfo de Santa Clara feed on gulf grunion *Leuresthes sardina* eggs during spring and undergo prealternate molt and increase body mass there - the latter evidenced by abdominal profiles (Hernández-Alvarez 2011) - which suggests that for migrant knots the site may function as a staging area (Warnock 2010). This site likely does not function as a staging area for some knots as it is the only documented aggregation of knots during summer in the Pacific Flyway south of breeding areas (Soto-Montoya et al. 2009). Red Knots do not migrate north to breeding areas until they are ≥ 2 years of age (Harrington 2001); therefore the large summer aggregations at Golfo de Santa Clara may be dominated by sub-adult birds. It seems likely that this age structure in population may influence the age structure of migratory cohorts that stopover at sites such as Grays Harbor, Washington. This is a logical explanation for differing resighting rates: in coastal Washington during spring, only 16.9% of knots marked at Golfo de Santa Clara were resighted, compared to 33.3% of those marked at Guerrero Negro.

The passage of spring migrants in both coastal Washington (Buchanan *et al.* 2011) and Golfo de Santa Clara (Carmona *et al.* 2012, Hernández-Alvarez 2013) have been characterized as having a later, secondary peak of abundance

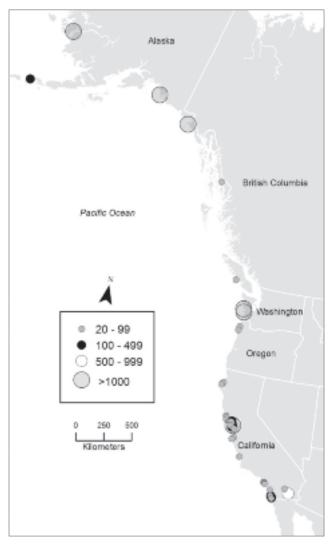


Fig. 2. Abundance of Red Knots at Pacific coast locations of Alaska, British Columbia (Canada) and the conterminous USA during migration and winter. Information was derived from published sources, Christmas Bird Count data, eBird, our own records and personal communications with colleagues.

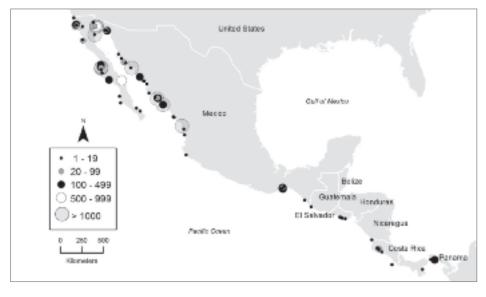


Fig. 3. Abundance of Red Knots at Pacific coast locations of Mexico, Guatemala, El Salvador, Nicaragua, Costa Rica and Panama during migration and winter. Information was derived from published sources, eBird, our own records and personal communications with colleagues.

that appears to involve fewer birds than the earlier, primary peak. Because of the comparatively low connectivity between Guerrero Negro and Golfo de Santa Clara, it is likely that the composition of late-arriving migrants at Golfo de Santa Clara includes knots from sites in northwestern mainland Mexico. Moreover, the population estimate calculated for spring migrants at Grays Harbor and Willapa Bay (Andres *et al.* 2012) exceeds the number of knots documented to occur on the Baja California peninsula, which suggests that knots from mainland Mexico also stopover in Washington during migration. Further investigation should clarify connectivity across the network of sites.

Some aspects of migratory connectivity movement ecology of roselaari remain unknown. It is unclear whether reports of knots south of Las Garzas, the southernmost record of roselaari occurrence, refer to birds that use the North American Pacific, Central or Atlantic flyways and, consequently, which subspecies are represented; rufa knots have been reported in southern Mexico, Panama and Chiloe Island, Chile (Buehler 2002; P. González, pers. comm.; D. Newstead, unpubl. data; L. Niles, unpubl. data). Resightings thus far confirm an exchange of *rufa* between Texas and Oaxaca in southern Mexico, and of *roselaari* between banding sites in both Baja California Sur and Washington on the Pacific Flyway and resighting sites in coastal Texas on the Central Flyway (Fig. 3). Flyway-switching by Red Knots has been documented in other regions (Wilson et al. 2010). The status of the connections between Texas and the Pacific Coast and consequently of subspecific status - is unclear. There has been no dedicated resighting effort south of Guererro Negro, Mexico, including mainland NW Mexico where considerable numbers of Red Knots occur during migration. Red Knots (n=29) were banded in NW Costa Rica in the 1970s (Smith & Stiles 1979) and a single Red Knot was banded on the Pacific coast of Colombia in 2008 (Ruiz-Guerra 2011), but none of these birds were color-marked and to our knowledge there were no recoveries.

Non-breeding distribution and abundance

North of Mexico

The abundance of spring migrant Red Knots north of Mexico

has been fairly well documented. Substantial aggregations (thousands) of birds have been documented in coastal Washington (Buchanan 2008, Buchanan et al. 2011) and in Alaska at Seal Creek/Ahrnklin River (Andres & Brown 1998), Copper River (Isleib 1979) and Yukon-Kuskokwim River deltas (Gill & Handel 1981, Gill & Handel 1990, McCaffery et al. 2008, McCaffery et al. 2009; P. Tomkovich, unpubl. data; Fig. 2). Lesser numbers (hundreds) of birds have been reported from San Francisco Bay and Salton Sea, California. Migration counts at Humboldt Bay, California, generally involved <50 birds (Colwell 1994). Except for two sites, Grays Harbor and Willapa Bay in coastal Washington, aggregations of ≥ 20 Red Knots during spring are rarely encountered between N California and the Seal Creek/Ahrnklin River, Alaska (Campbell et al. 1990, Chappell 2005, McGie 2003, Paulson 1993).

The largest aggregations of Red Knots along the Pacific Flyway occur in coastal Alaska, where they stop at both the Copper River Delta and the Yukon-Kuskokwim Delta. Peak daily counts of 40,000 and 110,000 were recorded on 11 May 1975 and 21 May 1980, on the Copper River Delta and at the mouth of the Tutakoke River on the Yukon-Kuskokwim Delta, respectively (Gill & Handel 1990, Kessel & Gibson 1978); at the time, however, at least the latter total was considered an anomaly (Gill & Handel 1990) relative to much lower counts in previous years at the same site. Over the last three decades, comparable numbers have not been recorded again at either site; the maximum daily count at the Copper River Delta was 6,000 birds on 12 May 2013 (M. Burcham & P. Mikelson, pers. comm.) and maximum daily counts at any one site on the central Yukon-Kuskokwim Delta have never exceeded 6,400 birds (Mc-Caffery et al. 2009). Only a small portion of these deltas' coastlines have ever been surveyed at that time of year, and it is possible that substantial numbers of knots were missed in previous surveys (M. Burcham & P. Mikelson, pers. comm.; McCaffery et al. 2008). Given the incomplete survey coverage to date and unknown levels of turnover, Tomkovich & Dementyev's (2006) suggestion that the Yukon-Kuskokwim Delta may support at least 10,000 knots on passage is not unreasonable.

The post-breeding movements of Red Knots at the

northern end of the Pacific Flyway remain a mystery. Most knots appear to largely bypass both the Copper River Delta and the Yukon-Kuskokwim Delta during autumn migration (Gill & Handel 1990, R. Gill & B. McCaffery, unpubl. data, Isleib & Kessel 1973). The absence of aggregations at the sites used during spring migration suggests that most knots leaving their breeding grounds on Wrangel Island and NW Alaska might: (1) overfly the major spring sites en route to stopovers south of Alaska, (2) congregate at other Alaskan sites not yet identified as important to post-breeding knots, or (3) have a southward passage that is very dispersed spatially and temporally, without conspicuous aggregations.

Red Knots are not abundant in coastal Washington during autumn and they are similarly uncommon or rare elsewhere along the Pacific coast from British Columbia south to N California (Paulson 1993). The northernmost location – outside of Alaska – where appreciable numbers (>1,000) of knots have been regularly documented is San Francisco Bay. This suggests the possibility of a minimum southbound flight for most Red Knots departing Alaska that exceeds the length of the northbound flight during spring from Washington to Alaska. That the other areas of significant Red Knot aggregations are the two intensively monitored sites in Mexico (Golfo de Santa Clara and Guerrero Negro; Table 2) suggests that Red Knots are equally or even more spatially limited in their site use during autumn compared to spring, or that other sites are yet to be documented.

Mexico

For over a decade, at least hundreds of Red Knots have been known to overwinter in coastal NW Mexico (Harrington 2001). In recent years, two important areas were identified in that region: Guerrero Negro, Baja California Sur, which is used as a wintering site (Arce 2011, Carmona et al. 2006, Carmona et al. 2008) and Golfo de Santa Clara, Sonora (on the northwestern mainland), a site used in spring and summer (Hernández-Alvarez 2011, Soto-Montoya et al. 2009; Fig. 2). Guerrero Negro was first identified as an important site for Red Knots in 1994 when about 1,000 knots were documented (Page et al. 1997), and this site now supports the largest overwintering population of roselaari knots. Ongoing monitoring indicates that the number of knots that use the complex has remained relatively constant since 2006 (Arce 2011). At Golfo de Santa Clara, flocks of 200-1,400 knots in March and April (2000 and 2001) were reported. Up to 4,500 Red Knots have been reported there in spring (Carmona et al. 2012) and slightly less than 2,000 in June/July (Soto-Montoya et al. 2009).

Only a small number of sites on the Baja California Peninsula have records of knots and Guerrero Negro is the only location known to regularly support large numbers. Very early records come from Grinnell (1928), who cited two knots collected at La Paz in September 1923 (cited from Lamb 1925), and three observed on 2 April 1926, one of which was collected and one of which was observed again on 7 April at San Felipe (cited from Huey 1927). At Ensenada de La Paz, Red Knots are considered occasional visitors in autumn, winter and spring (Carmona *et al.* 2008b). Red Knots have not been encountered, or have been encountered only in very small numbers, at numerous other sites where shorebird surveys have been conducted (Appendix A).

Elsewhere in NW Mexico, Red Knots have been encountered at numerous sites, a few with substantial numbers. In Sonora, Russell & Lamm (1978) reported seeing hundreds of knots during spring migration at Puerto Peñasco, and Van Rossem (1945) reported flocks of hundreds at Tóbari Bay. Engilis *et al.* (1998) reported 1,705 at Bahía Santa Maria, Sinaloa, and eBird data indicate a high count of 2,025 at Las Garzas, Nayarit. Ten sites were visited (April–September 2007) south of Nayarit by Molina (2008) and no knots were reported. Similarly, no knots were detected by Hernández (2005) at 12 sites on the coast of Jalisco (November 1998 to October 1999). Surveys of shorebirds at additional sites in NW Mexico have produced no records or very small numbers of birds (Appendix A) and general assessments of status indicate locally common occurrence (Appendix B).

In Mexico, Red Knots appear to be most abundant in Baja California and northwestern mainland Mexico. Seven sites there have had high counts of $\geq 1,000$ birds: San Felipe, Baja California; Guerrero Negro, Baja California Sur; Golfo de Santa Clara and Guaymas, Sonora; Bahia Santa Maria and Ensenada Pabellones, Sinaloa; and Las Garzas, Nayarit. Additional sites in NW Mexico supported smaller numbers of Red Knots; counts of 100-999 were reported from Estero Punta Banda, Baja California Norte (Erickson & Howell 2001); El Coyote (R. Carmona, unpubl data) and San Ignacio Lagoon (Mendoza & Carmona 2013), Baja California Sur; and Puerto Peñasco (Russell & Lamm 1978) and Tobari Bay (Van Rossem 1945), Sonora (Fig. 2). Most of the sites in NW Mexico have not been regularly monitored, but the magnitude of the counts suggests that NW Mexico may, in one or more seasons, support a large proportion of the flyway population, which has recently been updated to approximately 17,000 birds based on mark-resighting data from Grays Harbor and Willapa Bay in coastal Washington, United States (Andres et al. 2012).

Guatemala to Panama

Red Knots have generally been considered uncommon spring and autumn migrants through coastal areas of Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica and Panama (Appendix B). Aspects of the occurrence and abundance of knots were not well understood until documentation of <500 birds during winter at Golfo Nicoya, Costa Rica (Smith & Stiles 1979) and 200 in Panama (Buehler 2002). Knots have also been observed during summer months in Panama (Angehr & Dean 2010), with highest counts exceeding 200 birds. Knots appeared to use few sites in this region (see Fig. 3; Smith & Stiles 1979); they were not detected by Schneider & Mallory (1982) or Delgado & Butler (1993).

Morrison *et al.* (1998a) conducted aerial surveys along the Pacific coast of Panama in February 1988, October 1991 and January 1993. They did not detect knots from the air, but encountered numerous unidentified medium-sized shorebirds. In 1988, there were 3,115 unidentified medium-sized birds between Rio Ia Maestra and Panama City; in 1991 there were 1,027 between Isla Majagual and Rio Ia Maestra; and in 1993 there were 800 at Bahia de Chame, 1,400 between Isla Chepillo and Panama City, and 4,350 between Punta de Piedra and Chitre Point (Morrison *et al.* 1998b). Red Knot records posted on eBird were noted from some of these localities (e.g. Panama Bay in autumn and winter, Chitre in spring).

South America

Most general sources have considered this species a migrant along the Pacific coast of South America (Appendix B).

Similarly, Hughes (1979) did not consider Red Knot a regular winter resident in Peru. Although Morrison and Ross (1989a, 1989b) did not observe Red Knots along the Pacific coast of South America during aerial surveys conducted in January 1985 and February 1986, they observed substantial numbers of unidentified medium-sized shorebirds at several localities: 4,992 in Colombia, including 2,648 at the mouth of Rio Guapi and 1,055 between Tumaco and the Rio Patia mouth (Morrison et al. 1989a); and 2,335 at Lima, 6,393 at Mollendo and 14,204 at Chiclayo, Peru (Morrison et al. 1989c). There were no similar-sized aggregations of unidentified shorebirds in Ecuador, where the highest count was 1,334 in the Gulf of Guayaquil and near Muisne (Morrison et al. 1989b), or Chile (Morrison et al. 1989d) north of Tierra del Fuego, where numbers of *rufa* are substantial (Harrington 2001, Morrison et al. 1989d). There were few records of Red Knots from Ecuador (Donahue 1986).

Some eBird records were from areas such as Chiloé Island, Chile and Virrila, Peru, where large numbers of unidentified medium-sized shorebirds were reported in prior aerial surveys (Morrison & Ross 1989, Morrison *et al.* 1989a, 1989b). Published records included 82 at Mollendo, Peru, in 1971 (date[s] not reported, and no observations in 1972–1975; Hughes 1979) and observations in coastal Colombia on at least 12 dates in 2007–2011 (high counts: 30 in autumn, 31 in winter, 16 in spring; Ruiz-Guerra 2011). Small numbers of Red Knots occurred along the coast of South America (see Fig. 4).

Subspecies distribution

Our data and other sources of information suggest that the distribution of Red Knots along the Pacific coast of the Americas can be separated according to the known distribution of the *roselaari* and *rufa* subspecies. The northern part of this distribution extends south from breeding areas on Wrangel Island, Russia, and NW Alaska, to Nayarit, Mexico, and represents the documented distribution of the *roselaari* subspecies. Approximately 1,000 km south of that documented distribution is the northernmost observation of *rufa* (D. Newstead, unpubl. data), which has been observed – based on banding data - southward along the Pacific coast at sites in Panama and Chile (Buehler 2002; P. González, pers. comm.) with some documented movement from these areas to the Atlantic coast (L. Niles, unpubl. data). Although our subspecies distribution assessment is preliminary and will be refined with additional information, we suspect it is reasonably correct given the clustering of sites in NW Mexico that appear to support numbers of knots consistent with the recently updated population estimate for roselaari (Andres et al. 2012), the lack of large aggregations along the Pacific coast south of NW Mexico, and the documentation of *rufa* as far north as Laguna Superior, Oaxaca, Mexico. We expect that further information may reveal a degree of overlap in the distribution of the two subspecies along the coast of Mexico and perhaps south of there, as originally posited by Roselaar (1983).

Migration of Red Knots

Our work indicates that the migration strategies of Pacific Flyway Red Knots may have attributes similar to those of *rufa* knots in the Atlantic and Central flyways. The available information – including records we presented and other sources of information – indicates that *roselaari* is distributed

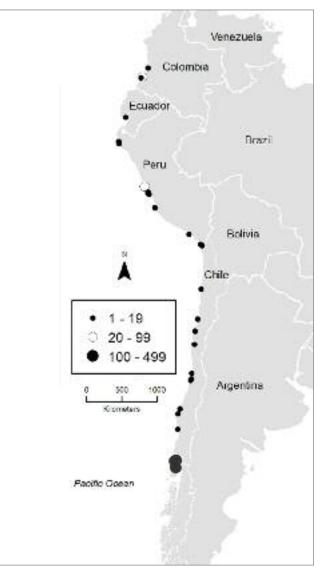


Fig. 4. Abundance of Red Knots observed at Pacific coast locations in Colombia, Ecuador, Peru and Chile during migration and winter. Information was derived from published sources, eBird and personal communications with colleagues.

during migration at a few key stopover sites and consequently flies longer distances between sites than most other shorebird species, similar to *rufa* Red Knots (Niles *et al.* 2008). With the exception of monitoring data from Golfo de Santa Clara and Guerrero Negro (Carmona *et al.* 2008, Soto-Montoya *et al.* 2009), we lack information to substantially understand Red Knot occurrence and use of other areas in NW Mexico where large aggregations of knots have been reported in at least one season. Nonetheless, knots use few estuaries in appreciable numbers (thousands) north of Mexico during migration (San Francisco Bay, Willapa Bay, Grays Harbor, Seal Creek/Ahrnklin River, Copper River Delta, Yukon–Kuskokwim River Delta).

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Appendix A. Published studies of shorebirds in Mexico where Red Knots were not encountered or were found only in small numbers during taxa- or area-intensive surveys.

Site	Notes	Citation	
Baja California Peninsula			
Estero de Punta Banda	Listed as occurring Not listed as occurring Listed as occurring 47 on 22 Feb 1992	Escofet <i>et al.</i> 1988 Palacios <i>et al.</i> 1991 Massey & Palacios 1994 Unitt <i>et al.</i> 1995	
Small coastal wetlands of NW Baja California	Not listed as occurring	Ruiz-Campos et al. 2005	
Punta Cabra, Baja California	None recorded	López-Uriarte et al. 1997	
Bahía de San Quintín	None observed (aerial survey) Listed as occurring 18 on 28 Mar 1993 3 in Jan 1991, 29 in Jan 1992	Schick <i>et al.</i> 1984 Massey & Palacios 1994 Unitt <i>et al.</i> 1995 Page <i>et al.</i> 1997	
Guerrero Negro lagoon complex	One seen during limited ground-based effort	Schick et al. 1984	
Guerrero Negro saltwork	10 in May 1996	Danemann et al. 2002	
Esteros El Coyote and La Bocana	None observed	Danemann & Carmona 1993	
San Ignacio lagoon	No data None observed	Schick <i>et al.</i> 1984 Danemann & Guzman Poo 1992	
Bahía Magdalena	None recorded No data (aerial survey) Listed as occurring None recorded	Amador-Silva 1985 Schick <i>et al.</i> 1984 Massey & Palacios 1994 Zárate-Ovando <i>et al.</i> 2006	
Ensenada de La Paz	One in Nov 1995; 7 in Jan 1996; 1 in Feb 1996 56 in 1994 26 in Feb 1997	Carmona-Islas 1997 Carmona 1999 Carmona <i>et al.</i> 2008b	
Estero de San José del Cabo	Not listed as occurring	Guzmán et al. 1994	
Mainland Coast Delta del Río Colorado	12 in winter 1993–1994 (ground survey); 40 in Mar 1994 (aerial survey) None recorded	Mellink <i>et al.</i> 1997 Hinojosa-Huerta <i>et al.</i> 2004	
Bahía Adair, Sonora	53 in 2005	Gómez-Sapiens & Soto-Montoya 2006	
Estero Santa Cruz, Sonora	None recorded	Fleischner & Gates 2009	
Bahía Kino, Sonora	Not listed as occurring	Fleischner & Riegner 1993	
Bahía Santa María, Sinaloa	None recorded	Carmona 1996	
Nayarit area	Listed as occurring	Escalante 1988	
South Coast Nayarit	None recorded	Molina 2008	
Jalisco Coast	None recorded	Hernández 2005	
South Chiapas	None recorded	Becerril 2011	

Appendix B. The general status of Red Knots at sites along the Pacific coast between Mexico and Chile.

Country / Region	Abundance / occurrence	Source
Mexico	Rare spring and fall transient	Grinnell (1928)
	Reported from Baja California (2 records, Apr & Sep), Sonora (Tóbari Bay, abundant	Van Rossem (1945), Friedmann
	26 Apr-1 May 1930) and Sinaloa (common, Reforma, May 1938; specimen[s])	<i>et al.</i> (1950), Blake (1953)
	Irregular migrant; local on both Pacific coasts but not often reported	Peterson & Chalif (1973)
	Uncommon migrant and winter visitor, usually in small numbers locally; 12 records listed from 9 sites	Wilbur (1987)
	Uncommon transient spring migrant in coastal Oaxaca. Possibly also a fall migrant and winter resident Uncommon to fairly common transient and local winter visitor (Aug–May)	Binford (1989) Howell & Webb (1995)
	Fairly common transient and winter resident, found on beaches and tidal flats all along the	Russell & Lamm (1978) in:
	Sonoran coast of the Gulf of California. Sometimes it is quite numerous	Russell & Monson (1998)
Guatemala	Not reported	Salvin (1865)
	Not reported	Griscom (1932)
	Transient; seen on the Pacific coast in Sep & Oct	Land (1970)
	Visitor; abundance < 50	Eiserman (2006)
El Salvador	See Ridgely & Gwynne (1989) and Howell & Webb (1995) elsewhere in this table	-
Honduras	Only one record from the Pacific coast: two present (one of them collected) on 9 Oct 1962 near Cedeño	Monroe (1968)
	See Ridgely & Gwynne (1989) and Howell & Webb (1995) elsewhere in this table	-
Nicaragua	No confirmed records. A mounted specimen was referenced from the Ponsol collection, but there are no supporting data	Martínez-Sánchez & Will (2010)
	See Ridgely & Gwynne (1989) and Howell & Webb (1995) elsewhere in this table	-
Costa Rica	Locally common migrant and winter resident in Golfo de Nicoya; elsewhere on Pacific coast a very	
	uncommon migrant, mainly in fall	Stiles & Skutch (1989)
Panama	The only records from Panama are two immature males in winter plumage taken by Wedel, at Puerto Obaldía, San Blas, 12 & 22 Sep 1934, preserved now in the United States National Museum	Wetmore (1965)
	Rare transient (from Sep to Oct and from Mar to Apr); a few birds present in winter and summer	Angehr & Dean (2010)
Central America	Uncommon visitant to both coasts, though more regular and in larger numbers on Pacific; greatest	
Central America	numbers are recorded during periods of transience (especially Sep–Oct & Mar–Apr), but a few are now	
	wintering and oversummering regularly (especially in the Juan Diaz/Panama City and Aguadulce areas)	Ridgely & Gwynne (1989)
	Uncommon to fairly common transient and local winter visitor (Aug-May)	Howell & Webb (1995)
Colombia	Four knots at Buenaventura Bay on 9 Feb 1984 are the only records from the Pacific coast	Hilty et al. (1986)
	Fairly common vagrant with records in both Pacific and Caribbean	McMullen et al. (2010)
	No information	Villegas (2011)
Ecuador	Not reported	Chapman (1926)
	Not reported	Lévêque (1964)
	Rare transient and boreal winter visitant along the southern coast. Documented only at western Guayas	
	(Ecuasal lagoons), but likely occurs at Gulf of Guayaquil. Records include six on Guayas coast on 9 Jan 1976 (Levêque 1977), one on 3 Aug 1980, one on 19 Jan 1991, one on 10 Apr 1991 (captured), one on	
	11 Aug 1991 and a second bird, based on plumage differences, on 13 Aug 1991, seven on 1 Dec 1995	
	and 20 on 9 Dec 1995	Ridgely & Greenfield (2001a)
	A very rare migrant on south-west coast (Aug & Jan). Noted singly or in at most small groups, often associating with other smaller shorebirds [volume 2]	Ridgely & Greenfield (2001b)
Peru	Migrant; fairly common (seen or heard daily in small numbers)	Parker <i>et al.</i> (1982)
	Uncommon boreal migrant (Sep-May) a few may oversummer. Uncommon; "easily can be missed	
	at a site, even during several days of observation, but should be encountered during longer stays of	
	a week or more"	Schulenberg et al. (2010)
Chile	Not mentioned	Hellmayr (1932)
	Apparently rarely encountered; author specifically mentioned observing one Red Knot on coast of Santiago Province	Johnson (1965)
	Rare visitor in austral summer. Specimens and sightings from Arica; mouths of the Huasco River	
	(Atacama) and Maipo River (Valparaíso); Yali Riverlet (Valparaíso); and Tierra del Fuego. One sight record from Montemar (Valparaíso) in Sep 1979	Araya & Chester (1993)
	Rare in most of Chile	Jaramillo (2003)
South America	Winters on seashore (map indicates range is coastal areas in southern Peru and central Chile)	De La Peña & Rumboll (2001)
(Pacific Coast)	miners on seasifiere (map indicates range is coastar areas in southern r eru and contrar cliffe)	250 Eu Fena & Kumbon (2001)