# Humboldt Bay, California is more important to spring migrating shorebirds than previously recognized

Mark A. Colwell\* & Elizabeth J. Feucht

Wildlife Department, Humboldt State University, Arcata, CA 95521, USA

Colwell, M.A. & E.J. Feucht. 2018. Humboldt Bay, California is more important to spring migrating shorebirds than previously recognized. *Wader Study* 125(2): xx–xx.

An important first step in conservation is recognition of critical habitats worthy of protection. Both the Ramsar Convention and Western Hemisphere Shorebird Reserve Network (WHSRN) gauge wetland importance based on total shorebird abundance or percentage of a flyway population using a site. In 1998, WHSRN designated Humboldt Bay, California, USA a site of International Importance based on estimated use by >100,000 shorebirds. Here, we provide data from a recent survey effort to show that the bay and surrounding habitats are used by >500,000 shorebirds of ~26 species during spring migration alone; most observations were of Western Sandpipers *Calidris mauri*. These data indicate that Humboldt Bay, at least in some years, is more important than previously recognized and, therefore, worthy of elevated WHSRN status as a Hemispheric site.

### Keywords

abundance

diversity

habitat quality

Pacific Americas Flyway

Western Hemisphere Shorebird Reserve Network

Western Sandpiper

# **INTRODUCTION**

Worldwide, many shorebird populations are in decline (Nebel et al. 2008, Delaney et al. 2009, Andres et al. 2012). An important conservation approach addresses such trends by recognizing and protecting habitats. For shorebirds, the 'staging paradigm' (Myers 1983, Myers et al. 1987) highlights key wetlands or landscapes along flyways that connect populations moving between breeding and nonbreeding ranges. Moreover, the importance of a site (e.g. Hemispheric, International or Regional designation under the Western Hemisphere Shorebird Reserve Network, WHSRN) is gauged by either total abundance or percentage of a flyway population that uses a wetland complex. For example, Delaware Bay is a WHSRN Hemispheric site because >500,000 shorebirds occur there annually during spring migration (Clark et al. 1993). WHSRN designations also apply to breeding areas such as the coastal plain of the Arctic National Wildlife Refuge, Alaska (Brown et al. 2007) or wintering locales such as The Grasslands of California's Central Valley (e.g. Shuford et al. 1998). Accordingly, the importance of a site requires accurate estimates of abundance in order to ascertain the percentage of a flyway population that uses a site. Often, however, estimates are derived from single surveys, which may not accurately represent abundances, especially during short intervals when many individuals are moving rapidly between sites along a flyway.

At present, WHSRN recognizes over 100 sites within 16 countries, of which 22 sites are of highest importance (i.e. Hemispheric; https://www.whsrn.org/). Humboldt

Bay, on the Pacific coast of northern California, USA, was recognized as a WHSRN site of International Importance in 1998 (Page et al. 1999) based on estimates of shorebird abundance collected over a quarter century ago (Senner & Howe 1984, Colwell 1994). Threats to shorebird populations at Humboldt Bay have increased, principally owing to loss and degradation of intertidal habitats. Spilled oil from two shipping accidents (1997) and 1999) damaged habitats, sea level rise is forecast to reduce the extent of intertidal foraging habitats (Galbraith et al. 2002), and proposals exist to expand leases for the cultivation of oysters (Crassostrea, Ostrea). Each of these activities compromises foraging habitats or directly causes mortality, which affect populations. Here, we present evidence that Humboldt Bay and adjacent habitats host >500,000 shorebirds of 26 species during spring migration alone, raising its importance to migratory shorebirds along the Pacific Americas Flyway and warranting increased conservation efforts.

#### **METHODS**

# Study area

Humboldt Bay (Fig. 1) is the second largest estuary in California; it consists of two large, shallow basins (Arcata Bay, 4,103 ha; South Bay, 1,797 ha; Mathis *et al.* 2006) connected by a narrow shipping channel to the ocean. Immediately west of the bay lies ~20 km of sandy, ocean-fronting beach, separated by rocky north and south jetties.

<sup>\*</sup>Corresponding author: mac3@humboldt.edu





Fig. 1. Humboldt Bay, California (★), is located at 40°N along the Pacific Americas Flyway (left). The arrows indicate the migratory paths of species breeding in the mid-continent (temperate) and arctic/boreal regions. The study area (right) shows the 15 survey areas. Opportunistic observations occurred from the NE corner of Arcata Bay (★), 19–27 April.

The bay has a mixed semi-diurnal tidal cycle (i.e. two unequal highs and lows in ~24 hr). At mean low tide, ~61 km² of intertidal flats provide foraging habitat for shorebirds (Barnhart *et al.* 1992). The substrates exposed at low tide offer diverse sediments varying in size from fine, clayey silts to coarse sands, which host rich invertebrate populations as prey for shorebirds (Danufsky & Colwell 2003). The inner reaches of Arcata Bay and South Bay support dense stands of Common Eelgrass *Zostera marina*, which are exposed at lower tides. Based on research of roosting shorebirds on the bay (see Colwell *et al.* 2003, Conklin & Colwell 2007) and reconnaissance during the month prior to the start of surveys, we established 15 survey routes around the periphery of the bay (Fig. 1).

## Field methods

We recruited 15 highly qualified and experienced shorebird fieldworkers and assigned each observer to a single survey route to standardize effort. We provided them with a high resolution, color image of their area, discussed where they were likely to encounter roosts (Colwell *et al.* 2003), and how to move efficiently within their areas to locate roosts within the 3-hr window of observation bracketing high tide. Lastly, we reviewed methods of flock size estimation, and each observer trained on software to facilitate their ability to estimate flock sizes.

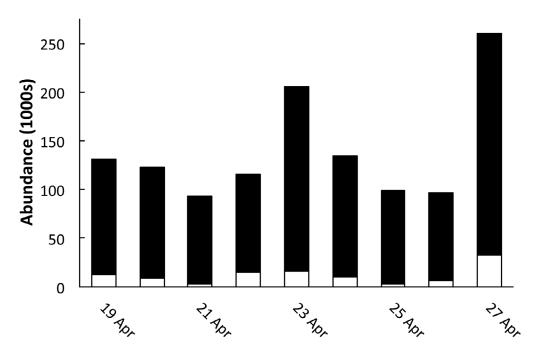
We undertook four surveys (Table 1) spaced at ~14-d intervals over 46 days coinciding with peak spring migration (April). For each survey date, we instructed observers to be in position to start their survey 1.5 hrs prior to the time of predicted high tide. Although the timing of high tide across the bay varies by as much as 45 mins (Barnhart *et al.* 1992), we started all surveys 1.5 hrs before predicted high tide for the North Spit tide gauge (Fig. 1), which lies along the shipping channel mid-way between Arcata and South bays. Each observer walked, drove or boated through their area for ~3 hrs, recording all observations and estimates of shorebirds. These data provided a single count total for each species within a survey area.

Survey conditions varied across the four observation days (Table 1). On three surveys (31 March, 14 April and 13 May), partly to mostly cloudy skies and calm to light winds made for ideal observations; on 28 April, intermittent rain and light winds created challenging survey conditions. High tides ranged from 1.77–2.16 m, all of which inundated foraging habitats and forced birds to roost.

A few days after the second survey, there was a large influx of shorebirds. We therefore supplemented roost surveys with observations conducted from the northeast corner of Arcata Bay (Fig. 1) to ensure we did not miss

Table 1. Estimates of shorebird abundances based on four surveys during spring 2018 at Humboldt Bay, CA.

Species	31 March	14 April	28 April	13 May	Maximum count	Summed count	Previous estimate
a) Local breeders			<u>I</u>				
Black Oystercatcher Haematopus bachmani	4	6	5	5	6	_	19
Killdeer <i>Charadrius vociferus</i>	11	10	23	10	23	-	9
Snowy Plover <i>Charadrius nivosus</i>	0	7	5	1	7	_	19
Spotted Sandpiper Actitis macularius	0	0	0	5	5	_	4
Total					41		
b) Temperate/interior breeders							
American Avocet Recurvirostra americana	37	28	9	1	37	_	74
Long-billed Curlew Numenius americanus	351	189	90	65	351	_	399
Marbled Godwit <i>Limosa fedoa</i>	8,580	6,797	1,530	767	8,580	_	6,900
Willet <i>Tringa semipalmata</i>	1,377	751	287	100	1,377	-	348
Total					10,345		
c) Boreal/arctic breeders							
Black-bellied Plover <i>Pluvialis squatarola</i>	2,896	3,686	280	339	_	7,201	293
Semipalmated Plover Charadrius semipalmatus	2	118	154	76	-	350	500
Whimbrel <i>Numenius phaeopus</i>	70	271	118	311	_	770	223
Ruddy Turnstone <i>Arenaria interpres</i>	1	0	1	7	-	9	9
Black Turnstone Arenaria melanocephala	78	74	47	5	_	204	75
Red Knot <i>Calidris canutus</i>	2	1	1	98	-	102	55
Surfbird <i>Calidris virgata</i>	10	17	1	7	_	35	23
Sanderling <i>Calidris alba</i>	207	1,154	484	330	-	2,175	725
Dunlin <i>Calidris alpina</i>	7,824	12,960	5,449	120	_	26,353	23,303
Rock Sandpiper <i>Calidris ptilocnemis</i>	0	1	0	0	-	1	-
Least Sandpiper <i>Calidris minutilla</i>	5,088	4,904	347	39	_	10,378	1,047
Western Sandpiper <i>Calidris mauri</i>	6,063	15,910	95,709	211	-	117,893	9,732
Small calidridine sandpiper	9,127	7,948	1,809	76	_	18,960	37,565
Long-billed Dowitcher Limnodromus scolopaceus	181	93	466	17	-	757	_
Short-billed Dowitcher <i>Limnodromus griseus</i>	33	1,184	2,590	26	_	3,833	-
Dowitcher <i>Limnodromus</i> spp.	450	1,695	1,278	38	-	3,461	2,979
Wilson's Snipe <i>Gallinago delicata</i>	23	5	2	0	_	30	2
Red-necked Phalarope <i>Phalaropus lobatus</i>	0	0	0	59	-	59	-
Wandering Tattler <i>Tringa incana</i>	1	1	8	8	_	18	15
Greater Yellowlegs <i>Tringa melanoleuca</i>	183	150	39	7	-	393	40
Large sandpiper	70	950	10	0	_	-	2,590
Total						192,982	
Diversity (S)	22	23	23	24	26		
Total abundance	42,669	58,910	110,742	2,728	203,368		
High tide (m)	2.16	1.92	1.89	1.77			
Time of high tide	12:51	11:49	11:58	11:34			



**Fig. 2.** A summary of maximum shorebird abundance estimated at the Arcata Marsh and Wildlife Sanctuary in April 2018 (see Fig. 1) with totals for Western Sandpipers (■) and all other species combined (□).

the main pulse of migrants. We conducted these observations in the late afternoon/early evening coinciding with a flooding tide that inundated tidal flats and pushed large flocks toward observer(s) positioned on a levee adjacent to the bay. We summarized these data separately from the high-tide roost surveys.

#### Data summary and analysis

For each of the four surveys, we collated data by species as the total number of individuals observed within each survey route. Next, we summed these maxima across the 15 survey routes to derive a bay-wide estimate of total abundance for each species within each survey period (Table 1). Finally, we used two different approaches (single maximum count or summed maxima) to derive a total estimate of a species' abundance during the 46-d window. We based these alternatives on the migration patterns and breeding locations of three groups: 1) local breeders (4 species); 2) species that breed in temperate regions of the continental interior (4); and 3) boreal/arctic breeding species (18). For local and temperate breeders, we used the maximum of the four counts to represent abundance, whereas we summed the counts for the boreal/arctic breeders. For the latter group, we assumed that species moved rapidly along the Pacific Americas Flyway such that the duration of stay of individuals at Humboldt Bay was limited to a few days. For example, Dunlins and Western Sandpipers, which breed in western Alaska, have been shown to stop for approximately 3–4 d at Humboldt Bay, with individuals transiting between San Francisco Bay and arctic breeding sites in approximately two weeks (Warnock & Bishop 1998, Warnock et al. 2004). Therefore, given the 2-week interval between consecutive surveys,

we summed counts of the four individual surveys to derive a total abundance estimate for boreal/arctic species. Similarly, we used the opportunistic observations conducted over a 9-d interval between the 14 and 28 April surveys to calculate a maximum number using Arcata Bay alone. Humboldt Bay is also an important wintering location for nine species that either breed locally (e.g. Black Oystercatchers, Snowy Plovers) or migrate comparatively short distances to breed in the Great Basin or prairies (e.g. Long-billed Curlews, Willets). These short-distance migrants depart during late March or April, with no evidence that they stage at Humboldt Bay. For example, several hundred American Avocets, Long-billed Curlews, and Willets winter on Humboldt Bay (Colwell et al. 2001, Mathis et al. 2006); they depart in a northeasterly direction for temperate breeding areas (e.g. MAC heard Longbilled Curlews as they passed from the bay over his house at 22:00 hrs on 3 April 2018 and Willets departed at a similar time on 1 May). For these temperate-breeding species, we used the single maximum count from the four surveys to represent total abundance.

#### **RESULTS**

#### **Diversity and abundances**

In total, we detected 26 species, with 22–24 observed on any one survey. Species' abundances varied over six orders of magnitude (Table 1). Western Sandpipers and Dunlins were numerically dominant, with estimates from individual surveys representing 14–86% and 5–22%, respectively, of total shorebirds. In total, 203,368 shorebirds used the bay, based on the combination of summed and maximum counts conducted at 14-day intervals.

#### Western Sandpipers

On the 14 and 28 April surveys, observers estimated that bay-wide shorebirds numbered 58,910 and 110,742, respectively. Shortly after the 14 April survey, a large influx of Western Sandpipers occurred; accordingly, we surveyed the Arcata Marsh and Wildlife Sanctuary on nine successive days (19-27 April). We estimated that on any one day 93,466–260,662 shorebirds were present in that area alone; most (90,000–228,000; 87–96%) were Western Sandpipers (Fig. 2). We used the opportunistic observations conducted from 19–27 April to supplement the data from the four surveys and provide an estimate of Western Sandpiper abundance during the migration peak. Using a 3-d interval (19, 22 and 25 April), the summed total of observations suggested that 313,750 Western Sandpipers were present; using a 4-d interval (19, 23 and 27 April), we estimated a total of 536,750 Western Sandpipers.

#### **DISCUSSION**

In total, we detected 26 species, which is similar to that reported during spring surveys a quarter century ago (Colwell 1994). During the same interval, birders reported to eBird (https://ebird.org/home) two additional species (Solitary Sandpiper *Tringa solitaria*; Lesser Yellowlegs *T.* flavipes). At 40°N latitude, the bay lies near the northern limit of the winter range of several species (e.g. American Avocet, Long-billed Curlew, Marbled Godwit, Willet) that breed at temperate latitudes of the continental interior; it also sits squarely within the winter range of many boreal/arctic breeding taxa (e.g. Dunlin, Western Sandpiper, Sanderling). Collectively, these species comprise most of the non-breeding assemblage of the bay, supplemented by several species that breed locally. A second factor contributing to the bay's high diversity is the juxtaposition of varied habitat types, including rocky intertidal, sandy ocean-fronting beaches, expansive and unconsolidated substrates of intertidal flats, freshwater wetlands, and riverine reaches (Colwell 1994). Habitat diversity begets species diversity. These diverse habitats also provide rich food resources for non-breeding shorebirds year-round.

Our survey effort provides new perspectives on the importance of Humboldt Bay to shorebirds along the Pacific Americas Flyway, and it highlights how the timing and frequency of surveys can influence estimates of abundance. In particular, our use of four surveys spaced at 2-week intervals during spring migration increased the estimate of abundance for most arctic/boreal species compared with a single count. For example, our estimate for Blackbellied Plover (7,201) was an order of magnitude higher than that based on any of the three late April surveys in 1991–1993 (118–293; Colwell 1994), illustrating how the use of a single count outside the period of peak migration may under-represent abundances. Highest counts for Black-bellied Plover occurred on 31 March and 14 April, which appears to bracket the peak time of passage for this species. Other species reached maximum abundance later in the spring. The Western Sandpiper was the most abundant species during mid-April, and summation of the totals from the four surveys indicated that it dominated the shorebird assemblage. Compared with arctic/boreal species, the use of a single maximum count provided estimates of abundance for local breeders and those species breeding in the temperate interior that were similar (i.e. same order of magnitude) to those reported by Colwell (1994).

In most cases, our updated estimates of abundance for spring migration far surpass published accounts, especially for Western Sandpiper (Table 1). For example, Senner & Howe (1984) suggested that "over 100,000" shorebirds used the bay during migration based on extrapolated data (Colwell 1994). Ten years later, a coordinated, baywide survey conducted in late April tallied a maximum of 83,647 shorebirds, of which 83% were small calidridine sandpipers (Colwell 1994). In this effort, we used multiple, coordinated surveys to estimate that 313,750-536,750 Western Sandpipers alone used the bay during a 2-week period. If we add to this total the maximum counts for the other species, then Humboldt Bay easily hosts half a million shorebirds during spring migration alone. We think this increase in estimated shorebird use more accurately represents the importance of Humboldt Bay because the multiple coordinated counts account for the phenology of migration that is not addressed by one-time surveys (Colwell 1994).

#### **Survey methods and limitations**

The challenges of monitoring shorebirds based on migration counts have been addressed by others (Rappoldt et al. 1985, Elphick 2008). Briefly, for many species accurate estimates of abundance are difficult to obtain owing to the patchy distribution of shorebirds responding to prey (Colwell & Landrum 1993), localized movements prompted by predators (Conklin et al. 2008), somewhat unpredictable phenology of migration, and varying lengths of stay at staging sites. Single survey efforts conducted within a migration season (e.g. Colwell 1994) may miss peak passage for some migrants; our effort used multiple counts and a well-defined protocol to better capture the dynamics of shorebird abundances over the spring passage. With prior knowledge of the bay and roosting habitats (see Colwell 1994, Colwell et al. 2003, Conklin & Colwell 2007), we adopted a high-tide survey protocol designed to minimize double-counting shorebirds. To improve on these efforts would require knowledge of the stopover duration of marked birds, and even more effort. Another challenge of migration counts is the ability to identify species and accurately estimate the size of flocks. We specifically selected observers based on their expertise and ability in these areas; we also provided a brief training on estimating large flock sizes. Finally, weather conditions were favorable for surveying on three of the four observation dates. Each of these issues contributes to annual and seasonal variation in shorebird abundance, albeit the magnitude of the variation remains unknown. As a result, in most instances it is difficult to address whether or not populations using Humboldt Bay have increased or decreased. However, it appears American Avocet numbers have decreased substantially since the early 1990s, when ~1,000 wintered on the bay (Colwell *et al.* 2001).

## **Conservation implications**

Humboldt Bay has been recognized as an important site for Nearctic shorebirds (Senner & Howe 1984, Colwell 1994, Page et al. 1999). The bay is currently designated as a site of International Importance under WHSRN based on the criterion of its use by >100,000 shorebirds; the bay has not been nominated for inclusion in the list of Ramsar sites but it clearly is worthy of recognition. Our data from a series of coordinated surveys highlight the importance of the bay within the Pacific Americas Flyway (see Page et al. 1999). During spring migration, the estimate of >500,000 shorebirds justifies elevating the status of the bay to one of Hemispheric Importance under WHSRN; we are preparing a proposal to do so. Almost certainly individual species totals further support this heightened recognition of the bay to shorebirds. Although it is challenging to apply the criterion of percentage of a flyway population to our individual species totals owing to imprecision in many population estimates (Andres et al. 2012), several species deserve comment: 1) Western Sandpiper, >10% of 3.5 million; 2) Shortbilled Dowitcher, 5% of 75,000 for L. g. caurinus; and 3) pacifica subspecies of Dunlin, 4% of 550,000 (Fernández et al. 2010). Lastly, two Marbled Godwit subspecies (mid-continent, L. f. fedoa and Alaska, L. f. beringiae) winter on Humboldt Bay, based on morphometric data (Gibson & Kessel 1989) and movements of marked individuals (Ruthrauff & Tibbitts in press). Although we do not know the composition of the local wintering population (5,000-10,000; Colwell 1994 and Table 1), Humboldt Bay and San Francisco Bay must collectively host the majority of the Alaskan subspecies (2,000–3,000 population size; Andres et al. 2012) given its limited winter range (Ruthrauff & Tibbitts in press) and the general absence of large numbers of godwits at other estuaries within the region (Page et al. 1999; eBird).

The importance of Humboldt Bay to Nearctic shorebirds highlights various threats to their populations posed by human activities (Colwell 1994). As a major port, habitat loss and degradation associated with shipping (e.g. dredging, pollution) has altered the quality of intertidal habitats. Oil spills (1997 and 1999) have occasionally compromised bay habitats and wildlife populations. Within Arcata Bay, recent proposals to expand oyster cultivation may threaten to degrade critical foraging habitats (Kelly et al. 1996). In addition, projected sealevel rise will greatly reduce the area of intertidal habitat available to foraging shorebirds (Galbraith et al. 2002, 2014). Over a century ago, European-American settlers built levees that currently constrain the upper limits of tidal influence. Recently, however, levees have been breached to enhance the area and quality of habitat associated with upper reaches of intertidal habitats. In fact, the observation point for our opportunistic surveys (19– 27 April) was immediately south of a newly restored intertidal wetland that clearly benefits tens of thousands

of shorebirds during the peak of migration. Restoration continues to be the most productive means by which habitat can be enhanced within the Humboldt Bay estuary such that it continues to provide the food resources essential to fuel the individual needs of shorebirds along the Pacific Americas Flyway.

#### **ACKNOWLEDGEMENTS**

For fieldwork, we thank: Cedric Dulhade, David Fix, Rob Fowler, Gary Friedrichsen, Deven Kammerichs-Berke, Tony Kurz, Fanter Lane, Tom Leskiw, Nora Papian, Jeremy Pohlman, Jude Power, Katie Raby, Casey Ryan, Keith Slauson, Khara Strum, Kayla Welser, and Andrew Wiegardt. Gary Friedrichsen, James Ray, and Steve Wilson provided logistical support for boat-based surveys. Audubon California, California Department of Fish and Wildlife, March Conservation Fund, Redwood Region Audubon Society, Sequoia Zoo Conservation Fund, and the United States Fish and Wildlife Service supported the project.

#### **REFERENCES**

- Andres, B.A., P.A. Smith, R.I.G. Morrison, C.L. Gratto-Trevor, S.C. Brown & C.A. Friis. 2012. Population estimates of North American shorebirds, 2012. *Wader Study Group Bulletin* 119: 178–194.
- Barnhart, R.A., M.J. Boyd & J.E. Pequegnat. 1992. *The ecology of Humboldt Bay, California: an estuarine profile.* United State Fish & Wildlife Service Biological Report. Arcata, CA, USA.
- Brown, S., J. Bart, R.B. Lanctot, J.A. Johnson, S. Kendall, D. Payer & J. Johnson. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. *Condor* 109: 1–14.
- **Clark, K.E., L.J. Niles & J. Burger.** 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95: 694–705.
- **Colwell, M.A.** 1994. Shorebirds of Humboldt Bay, California: abundance estimates and conservation implications. *Western Birds* 25: 137–145.
- **Colwell, M.A. & S.L. Landrum.** 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. *Condor* 95: 94–103.
- Colwell, M.A., T. Danufsky, R.L. Mathis & S.W. Harris. 2001. Historical changes in the abundance and distribution of the American Avocet at the northern limit of its winter range. *Western Birds* 32: 1–12.
- Colwell, M.A., T. Danufsky, N. Fox-Fernandez, J.E. Roth & J.R. Conklin. 2003. Variation in shorebird use of diurnal high-tide roosts: How consistently are roosts used? *Waterbirds* 26: 484–493.
- Conklin, J.R. & M.A. Colwell. 2007. Diurnal and nocturnal roost site fidelity of Dunlin (*Calidris alpina*) at Humboldt Bay, California. *Auk* 124: 677–689.
- Conklin, J.R., M.A. Colwell & N.W. Fox-Fernandez. 2008. High variation in roost use by Dunlin wintering in California: Implications for habitat limitation. *Bird Conservation International* 18: 275–291.

- **Danufsky, T. & M.A. Colwell**. 2003. Winter shorebird communities and tidal flat characteristics at Humboldt Bay, California. *Condor* 105: 117–129.
- **Delaney, S., T. Dodman & D.A. Stroud** (Eds.). 2009. *An atlas of wader populations in Africa and western Eurasia.* Wetlands International, Wageningen, The Netherlands.
- **Elphick, C.S.** 2008. How you count counts: the importance of methods research in applied ecology. *Journal of Applied Ecology* 45: 1313–1320.
- Fernandez, G., J.B. Buchanan, R.E. Gill, Jr., R. Lanctot & N. Warnock. 2010. Conservation plan for Dunlin breeding populations in North America (Calidris alpina arcticola, C. a. pacifica, and C. a. hudsonicus). Version 1.1. Manomet Center for Conservation Sciences, Manomet, MA, USA.
- Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington & G. Page. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* 25: 173–183.
- Galbraith, H., D.W. DesRochers, S. Brown & J.M. Reed. 2014. Predicting vulnerabilities of North American shorebirds to climate change. *PloS ONE* 99: e108899.
- **Gibson, D.D. & B. Kessel.** 1989. Geographic variation in the Marbled Godwit and description of an Alaskan subspecies. *Condor* 91: 436–443.
- Kelly, J.P., J.G. Evens, R.W. Stallcup & D. Wimpfheimer. 1996. Effects of aquaculture on habitat use by wintering shorebirds in Tomales Bay, California. *California Fish & Game* 82: 160–174.
- Mathis, R.L., M.A. Colwell, L.W. Leeman & T.S. Leeman. 2006. Long-billed Curlew distributions in intertidal habitats: scale-dependent patterns. *Western Birds* 37: 156–168.
- **Myers, J.P.** 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. *American Birds* 37: 23–25.

- Myers, J.P., R.I.G. Morrison, P.Z. Antas, B.A. Harrington, T.E. Lovejoy, M. Sallaberry, S.E. Senner & A. Tarak. 1987. Conservation strategy for migratory species. *American Scientist* 75: 19–26.
- Nebel, S., J.L. Porter & R.T. Kingsford. 2008. Long-term trends in shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation* 141: 971–980.
- Page, G.W., L.E. Stenzel & J.E. Kjelmyr. 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific coast of the contiguous United States. *Condor* 101: 461–471.
- Rappoldt, C., M. Kersten & C. Smit. 1985. Errors in largescale shorebird counts. Ardea 73: 49–61.
- **Ruthrauff, D.R. & T.L. Tibbitts.** In press. Flexible timing of annual movements across consistently used sites by Marbled Godwits breeding in Alaska. *Auk.* doi: 10.1642/AUK-18-82.1
- Senner, S.E. & M.A. Howe. 1984. Conservation of Nearctic shorebirds. Pp. 379–421 in: Shorebirds: Breeding Behavior and Populations (J. Burger & B. Olla, Eds.). Plenum Press, New York, NY, USA.
- **Shuford, W.D., G.W. Page & J.E. Kjelmyr.** 1998. Patterns and dynamics of shorebird use of California's Central Valley. *Condor* 100: 227–244.
- **Warnock, N. & M.A. Bishop.** 1998. Spring stopover ecology of migrant Western Sandpipers. *Condor* 100: 456–467.
- Warnock, N., J. Takekawa & M.A. Bishop. 2004. Migration and stopover strategies of individual Dunlin along the Pacific coast of North America. *Canadian Journal Zoology* 82: 1687–1697.