research paper *Wader Study* 122(1): 37–53. doi: 10.18194/ws.00005

Estimating sustainable mortality limits for shorebirds using the Western Atlantic Flyway

Bryan D. Watts[1,*], Eric T. Reed[2] & Courtney Turrin[1]

[1]*Center for Conservation Biology, College of William and Mary and Virginia Commonwealth University, Williamsburg, VA 23187-8795, USA*
[2]*Canadian Wildlife Service, Environment Canada, Gatineau, Quebec, K1A 0H3, CA*
**Corresponding author: bdwatt@wm.edu*

Watts, B.D., Reed, E.T. & Turrin, C. 2015. Estimating sustainable mortality limits for shorebirds using the Western Atlantic Flyway. *Wader Study* 122(1): 37–53.

Of the 35 shorebird populations using the Western Atlantic Flyway for which trend data are available, more than 65% are experiencing declines. Due to their low reproductive potential, many shorebirds are vulnerable to perturbations in adult survival rates, and contemporary hunting pressure is emerging as a potential population-level constraint for some species. A central question is how much mortality these populations are capable of sustaining while maintaining population sizes sufficient to meet biological and social needs. We used estimates of population parameters within a harvest-theoretic framework to estimate sustainable mortality limits for shorebird populations using the flyway (N = 37). Such limits varied over five orders of magnitude among populations, from less than 70 to more than 490,000 individuals and from 1 to 20% of the population estimate. Sustainable mortality limits were sensitive to adult survival and age at first reproduction. These relationships reflect the underlying slow-fast continuum in life-history strategies and suggest that species with long generation times and high adult survival are most vulnerable to elevated mortality rates. Shorebird hunting continues to be legal within many jurisdictions throughout the flyway, but flyway-wide harvest is virtually unknown for any species. Fragmentary information suggests that current harvest levels could contribute to observed declines for some species. Assessment of potential harvest impacts would be greatly enhanced by further defining those shorebird populations that actually use the flyway, improving confidence in demographic parameter estimates, and coordinating a flyway-wide estimate of harvest levels.

Keywords

demography

hunting

mortality limits

population

potential biological removal

shorebirds

Western Atlantic Flyway

INTRODUCTION

Shorebird populations are declining on a global scale (International Wader Study Group 2003, Morrison *et al.* 2001b, Nebel *et al.* 2008). Of the 237 populations with trend data, 52% are thought to be declining and only 8% are thought to be increasing (Wetlands International 2006). Declines have been particularly dramatic for populations using the Western Atlantic Flyway. Of the 35 populations with trend data that regularly utilize this migratory corridor, 65% are declining whereas 11% are increasing (Andres *et al.* 2012). Although the underlying causes for the majority of these declines are poorly understood, the fact that declining species breed in different locations, depend on different resources, and have varied winter ranges implies many species-specific causes acting in concert, broad causal factors across species, or issues along shared migration routes.

Due to their low reproductive potential, many shorebird populations are vulnerable to perturbations in adult survival rates. Shorebird populations that depend on the Western Atlantic Flyway are subjected to direct anthropogenic mortality through harvest (e.g. subsistence, recreational, or market hunting) or through incidental take (e.g. oil spills, collisions with buildings, power lines, or wind turbines). Although hunting pressure on shorebirds within the flyway is poorly understood (outside the US and Canada), the annual harvest is emerging as a potential population-level constraint for some species. A survey of biologists within the Caribbean Basin in 2010 determined that considerable hunting pressure continues on at least

Guadeloupe, Martinique, Barbados, and Trinidad and Tobago, and to a lesser extent Puerto Rico, as well as other jurisdictions within northern South America (Andres 2011). The collective annual harvest of passage shorebirds within this region may be of the order of 200,000 individuals, with particular species shouldering the bulk of the pressure (Andres 2011, E.T. Reed unpubl. data, Hutt 1991, Ottema & Spaans 2008). Efforts are currently underway to estimate annual harvest and to clarify hunting policy throughout the flyway (Andres 2011).

From a population perspective, the central question is not how many individuals are killed annually but whether the focal population has the capacity to absorb the mortality incurred and still reach management objectives. Sustained levels of take have the potential to drive populations towards extinction, to hold populations below carrying capacity, or to change recovery trajectories. Understanding the relationship between realized mortality rates and sustainable mortality limits serves to focus management actions on appropriate causes. Potential Biological Removal (PBR) is a harvest-type model designed to estimate the level of take that will not jeopardize a focal population (Wade 1998). The PBR model has been used as a framework for estimating sustainable limits of human-caused mortality and has been applied to bird species of conservation concern (e.g. Dillingham & Fletcher 2008, Runge *et al.* 2004, 2009, Watts 2010). This method is particularly appealing for use with migratory shorebirds because (1) it is based on a limited number of parameters that can be estimated, (2) it incorporates safeguards against uncertainties in the data, (3) it is compatible with performance criteria needed to evaluate the success of management schemes, and (4) it utilizes an approach that may be easily explained to constituencies. The incorporation of uncertainties into the approach is particularly critical because tools used to set limits on take should be precautionary to protect populations against severe declines.

Current national (Brown *et al.* 2001, Donaldson *et al.* 2000) and regional (e.g. Clark & Niles 2000, Hunter 2002) shorebird conservation plans provide population trends and species-specific goals and conservation scores. However, these broad goals must be translated into specific demographic objectives in order to develop effective targeted actions. Without specific demographic objectives, we have no way to measure the success of management actions implemented to positively affect population change. Sustainable mortality limits represent specific demographic objectives that inherently lead to targeted management actions. Here, our objectives are (1) to utilize the best available estimates of population parameters within a PBR framework to estimate sustainable mortality limits for shorebird populations using the Western Atlantic Flyway, and (2) to conduct a sensitivity analysis to assess the impacts of uncertainty in parameter estimates on the estimates of sustainable mortality limits and to provide interpretational context for these estimates.

METHODS

Shorebird populations

Population exposure to a hazard is the extent to which a population is expected to interact with and be impacted by the hazard. This includes the extent to which the population spatially overlaps with the hazard and the conditional probability that if it does overlap, it will be impacted. Similarly, mortality experienced within a migration flyway exclusively impacts those individuals using the flyway. Correct assignment of this impact requires an understanding of population connectivity. However, our understanding of connectivity between shorebird breeding populations and the Western Atlantic Flyway is incomplete. The association between a breeding population and the flyway varies from exclusive to minor. For example, the entire life cycles of Atlantic Coast populations of Piping Plovers *Charadrius melodus melodus* and American Oystercatchers *Haematopus palliatus palliatus* are carried out within the flyway (American Oystercatcher Working Group *et al.* 2012). In contrast, only small portions of the Western Sandpiper *Calidris mauri* and Western Willet *Tringa semipalmatus inornatus* populations use the flyway during the non-breeding season (Lowther *et al.* 2001). For several species, the association is poorly understood and may represent a complex mixture of populations (e.g. Gratto-Trevor *et al.* 2012, Tibbitts & Moskoff 2014).

We used the best available information describing connectivity to assign breeding populations to the flyway in order to estimate mortality limits (Appendix 1). We chose not to split available population estimates. When available, we used independent population estimates for populations known to use the flyway. We used species-level, continental population estimates for (1) populations known to use the flyway but for which no independent population estimates are available, or (2) species that have poorly understood associations with the flyway. It should be noted that the impact of using the broader, less-refined estimate is that the inference of mortality limits is on the species level rather than the level of specific populations associated with the flyway. Our ability to link human-caused mortality to the dynamics of particular populations, as well as our ability to set appropriate mortality limits, will improve with time as our understanding of the connectivity between breeding populations and the flyway advances.

Potential biological removal models

We used estimates of population size, maximum annual recruitment rate ($r_{\max}$), and a management objective F_r to estimate PBR in units of number of birds taken for shorebirds using the Western Atlantic Flyway according to the following formulation:

$$PBR_t = \frac{r_{\max} F_r}{2} N_{\min,t} \quad (1)$$

where $r_{\max}$ is the intrinsic rate of natural increase under optimal conditions, $N_{\min,\,t}$ is a conservative estimate of population size at time t, and F_r is a recovery factor between 0 and 2 (i.e. harvest rate between zero and $r_{\max}$) that represents the management objective (Runge *et al.* 2009). Any value in this range can produce a sustainable harvest strategy. When F_r is near zero, little take is allowed and the population is expected to equilibrate near its carrying capacity. When $F_r = 1$, the strategy seeks to maintain the population near maximum sustainable yield, at half the carrying capacity. With values of F_r close to 2, the harvest rate is near $r_{\max}$ and the population is held at a small fraction of its carrying capacity. In general, strategies designed to maintain a population below half of its carrying capacity involve more risk and are unsuitable for conservation objectives.

We used the 'demographic invariant approach' to estimate $r_{\max}$ (Niel & Lebreton 2005), using the following formulations:

$$r_{\max} = \lambda_{\max} - 1 \quad (2)$$

and

$$\lambda_{\max} \approx \frac{(S\alpha - S + \alpha + 1) + \sqrt{(S - S\alpha - \alpha - 1)^2 - 4S\alpha^2}}{2\alpha} \quad (3)$$

where $\lambda_{\max}$ is the maximum annual growth rate of the population, S represents adult survival, and α is the age at first reproduction. These parameters should reflect optimal conditions (i.e. optimal environmental conditions, no anthropogenic mortality, and minimal density dependence). We explicitly accounted for uncertainty in parameter estimates used in the calculation of PBR by describing each parameter with a probability distribution (derivation of distributions described below). We then used simulations to sample from those distributions independently, solved equations 3 and 1 numerically, and used the results from 10,000 replicates to describe uncertainty in PBR.

Parameter estimates

We extracted parameter estimates from the shorebird literature (Appendix 1). The availability of estimates for critical demographic parameters is very limited for many shorebird species within the Western Hemisphere. We used the 'best available information' approach to estimate parameters, giving preference to estimates from shorebird populations using the Western Atlantic Flyway. When these specific estimates were unavailable, we used estimates derived from other North American breeding populations. When no estimates were available for North American populations we (1) used estimates from the Eastern Hemisphere for shared species, or (2) used 'surrogate' estimates (Appendix 2). As surrogates, we calculated mean estimates from as many congeners as were available.

Population size (N_{min}). We used the most recent size estimates of North American shorebird populations (Andres *et al.* 2012). As outlined in both Andres *et al.* (2012) and earlier treatments (Morrison *et al.* 2006), the origin of current estimates varies from expert opinion to statistically sound sampling design with variance estimates. For estimates based on statistically sound sampling, we report a point estimate with one standard deviation unit and describe uncertainty with a corresponding normal distribution. Population estimates derived from a number of independent monitoring programs or expert opinion are usually regarded as conservative population size estimates because they are often based on the maximum number of individuals observed at one point in time or space. Most population estimates in this category have increased through revisions or addition of data over time (see Andres *et al.* 2012, Appendix), indicating that they likely represent minimum estimates of population and that true population size is more likely to be larger than smaller. For those, we report a point estimate with no estimate of the variance, and we chose to represent uncertainty using a uniform distribution spanning a range of plausible values bounded by a minimum (-25%) and maximum (+50%).

Recovery factor (F_r). As envisioned by Wade (1998) and applied within an increasing number of conservation settings (e.g. Dillingham & Fletcher 2008, Niel & Lebreton 2005, Taylor *et al.* 2000), F_r is a recovery factor usually ranging from 0.1 to 1.0 that reflects management objectives and the status of a population relative to recovery goals. A value of 0.1 is often used for highly imperiled species in order to afford the population the greatest opportunity to recover and to minimize risk of extinction. Higher values are used for populations that are close to or have achieved conservation goals, and can be as high as 1.0 for species for which monitoring and management efforts are high (Johnson *et al.* 1997). We used conservation scores assigned to shorebird species within the Canadian and United States shorebird conservation plans (Brown *et al.* 2001, Donaldson *et al.* 2000, U.S. Shorebird Conservation Plan 2004) to derive F_r values. Assignment of conservation scores is consistent between the two plans for most species. Where there were discrepancies, we were conservative in using the lower value. We chose an F_r value of 0.5 for species of 'low concern' and 'moderate concern', $F_r = 0.3$ for species of 'high concern', and $F_r = 0.1$ for 'highly imperiled' species. It should be noted that for most species, conservation scores provided in the country plans reflect continental trends and threats. Although these values often align with trends for populations tied to the Western Atlantic Flyway, there are some species for which this may not be true. Relevant population-specific conservation scores were given priority when provided in the conservation plan (Brown *et al.* 2001). As population-specific scores become available and information on connectivity improves, recovery factors should be adjusted accordingly.

Adult survival (S). Published survival estimates currently available for shorebirds have been derived from a wide range of sample sizes using a variety of techniques. We report the estimate and sample size and refer the reader to references provided for the underlying techniques. We used the highest survival estimate reported for a species to conform to the optimal values required under the

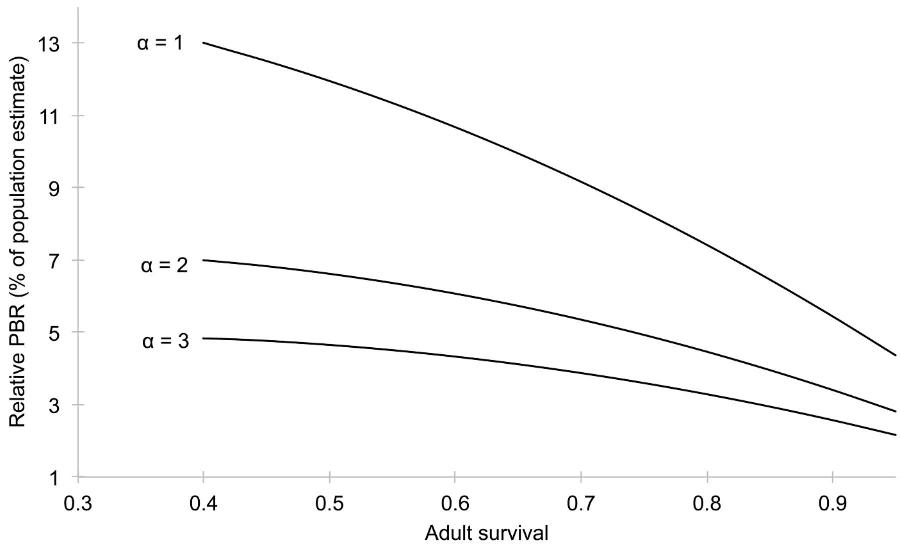

Fig. 1. Sensitivity of PBR to the range of age at first reproduction (α) and adult survival (S) observed in shorebird populations using the Western Atlantic Flyway.

Demographic Invariant Method. It should be noted that these estimates were not made in the absence of harvest. However, all available estimates of shorebird survival were derived from mark-recapture studies that don't distinguish between mortality and emigration and thus represent apparent survival, which is likely biased toward lower values by unmeasured emigration from the study area. When available, we report variance estimates as one standard deviation unit and describe uncertainty with a beta distribution, which is naturally bounded between 0 and 1. Parameters defining the beta distribution were estimated using the method of moments (Morris & Doak 2002) using species-specific mean and variance estimates. When no variance estimate was available, we described uncertainty with a uniform distribution spanning a range of ±10% of the estimate.

Age at first reproduction (α). Age at first reproduction is an important parameter that has received limited direct investigation for most shorebird species. Most treatments consider the parameter to be a static life-history trait. We report the best available information on the expected age at first reproduction. We described uncertainty in age at first reproduction with a uniform distribution that spanned the range of published values (min. α, max. α) when more than one estimate was reported for a species.

Sensitivity analysis

We performed a sensitivity analysis in order to evaluate the influence of inaccuracies in parameter estimates on PBR results. Due to the mathematical structure of PBR models, the influence of both population size and the recovery factor (F_r) on estimates of sustainable mortality are straightforward. Increasing F_r across the range (0.1–0.5) of values used here results in a five-fold increase in PBR. The influences of the demographic parameters age at first reproduction (α) and adult survival (S) on PBR estimates are less clear. We examined the influence of variation in these parameters on PBR results using a hypothetical shorebird with a population estimate of 500,000 and an assigned F_r value of 0.3. We then varied age at first reproduction (1–3) and adult survival (0.4–0.95) independently across the range of values reported for shorebird populations using the Western Atlantic Flyway (Appendix 1). We then evaluated the influence of these parameters on both PBR and $r_{\max}$.

RESULTS

Demographic parameters were available for the majority (76%) of the 37 shorebird populations that regularly use the Western Atlantic Flyway (Appendix 1). Congener surrogates (n = 1–13 surrogates for each species) were used to estimate values for remaining species (Appendix 2).

PBR values varied greatly among species and ranged over five orders of magnitude from more than 490,000 to less than 80 individuals (Table 1). Several species stand out as having sustainable mortality limits below 500 individuals, including the Atlantic Coast populations of Wilson's Plovers *Charadrius wilsonia*, Piping Plovers, American Oystercatchers, and the *rufa* population of Red Knots *Calidris canutus*. Seven populations have estimated sustained mortality limits above 200,000 individuals. These species have large population sizes (N_{min} > 1,000,000), begin reproducing at an early age (α = 1 or 1-2), and have relatively low adult survival ($S \leq 0.8$).

Relative PBR (expressed as % of population estimate) is sensitive to variation in age at first reproduction and adult survival (Fig. 1). Sensitivity was highest under low parameter values and lowest under high parameter values. For example, shifts in age at first reproduction when adult survival is low resulted in a 2.8-fold increase in relative PBR compared to a 2.2-fold increase when adult survival is high. A similar sensitivity response results when the influence of adult survival is assessed as a function of shifts in age at first reproduction.

DISCUSSION

A fundamental problem when attempting to manage a population subject to direct human-induced mortality is determining the acceptable level of take. Without some defensible, population-relevant benchmark, information about human-induced mortality rates provides no clear management directive. Currently, demographic data are limited for the majority of shorebird populations within the Western Atlantic Flyway. Because it relies on relatively few demographic parameters, PBR provides an accessible approach to estimate sustainable take that is easily adjusted as management circumstances and/or information improves. From a practical perspective, PBR also provides an approach for directing resources toward the most vulnerable species or prioritizing research towards key demographic uncertainties.

A population's capacity to sustain mortality reflects its underlying demographic traits (Russell 1999, Stearns 1992). Shorebird species using the Western Atlantic Flyway showed a diversity of life histories that translated into a wide variation of PBR estimates. Some of this variation was also related to differences in population size. PBR when expressed as a percentage of the population estimate was sensitive to both adult survival and age at first reproduction. This pattern reflects the slow-fast continuum in life-history strategies from 'highly reproductive' or r-selected species on one end to 'survivor' or K-selected species on the other end (MacArthur & Wilson 1967, Saether 1988, Saether & Bakke 2000). Species with short generation times generally have high growth potential and high relative PBR estimates. In contrast, species with long generation times tend to have lower growth potential and low relative PBR estimates. The relationship provides insight into which populations are most vulnerable to elevated mortality rates and guidance for prioritizing the establishment of mortality limits.

PBR estimates by themselves allow a coarse evaluation of potential impacts of anthropogenic take on shorebird populations. Four species had PBR estimates that were below 1,000 individuals and one of them, the Red Knot, can be legally hunted in some countries (e.g. Barbados, where hunters generally avoid the species) or has only recently been afforded protection in others (e.g. Guadeloupe in 2012). With such a small potential to sustain harvest and ranges that span the Americas, it is clear that these four species require effective protection from hunting and other sources of anthropogenic mortality. On the other hand, seven species had PBR estimates that were above 200,000 individuals, including American Woodcock *Scolopax minor* and Wilson's Snipe *Gallinago delicata*, which are legally hunted in Canada and the United States. These species can sustain higher levels of take than most, although a careful management of that take is required to ensure that it does not exceed sustainable levels at the hemispheric scale.

On a flyway scale, shorebird harvests are poorly documented. However, some fragments of information are suggestive of potential problem areas. The species complex including Whimbrel *Numenius phaeopus*, Lesser Yellowlegs *Tringa flavipes*, and American Golden-plover *Pluvialis dominica* that departs from northeastern North America to make a transoceanic flight east of the West Indies to South America is subject to hunting pressure when grounded by tropical storms on Barbados, Guadeloupe, Martinique, and Trinidad and Tobago. The estimated sustainable mortality limit for the Hudson Bay population of Whimbrel was just over 1,200 individuals. This population has been declining at an annual rate of approximately 4% (1994–2009) within a mid-Atlantic staging area (Watts & Truitt 2011) and within its primary winter site (Morrison *et al.* 2012). The annual harvest of Whimbrel on Barbados alone ranges from 100 to 160 individuals (E.T. Reed unpubl. data), likely representing birds from both the Hudson Bay and Mackenzie Delta populations. Whimbrel harvest within the French West Indies is unknown, but more than 100 individuals were taken from a single swamp in 2013 (A. Lévesque unpubl. data). Due to its size, the species is preferred by hunters within all other hunting areas. For Lesser Yellowlegs, PBR is more than 79,000 individuals (using continental population estimate). Lesser Yellowlegs using Ontario (1974–2009) have experienced a 6.9% annual rate of decline (Ross *et al.* 2012). Surveys in the largest winter site in South America documented an 80% decline between the 1970s and the early 2000s (Ottema & Ramcharan 2009). Lesser Yellowlegs is likely the most widely hunted species throughout the flyway. The annual harvest on Barbados alone ranges from 5,700 to 19,900 (Hutt 1991, E.T. Reed unpubl. data), and harvest on Guadeloupe likely exceeds 8,000 birds annually (B. Andres, pers. comm.), representing 35% or more of PBR in years of high harvest. No harvest estimates are available from other jurisdictions, but Lesser Yellowlegs are known to also be an important species in the harvest in other localities. For American Golden-plover, PBR is 17,500 (using continental population estimate). Bart *et al.* (2007) reported a decline in the number of birds staging along the North Atlantic, but reports of population trends are conflicted (Clay *et al.* 2010), possibly reflecting the lack of population differentiation. The annual harvest on Barbados ranges from 600 to 1,800 individuals (Hutt 1991, E.T. Reed unpubl. data). No estimates are available from other jurisdictions. However, in the two days following the passage of Tropical Storm Maria in September of 2011, an estimated 2,000 individuals (11% of PBR) were taken in a single plowed field on Guadeloupe (A. Lévesque, unpubl. data). Semipalmated Sandpipers *Calidris pusilla* appear to be hunted primarily on the winter grounds in northern South America. PBR is more than 68,000 individuals (using eastern and central population

Table 1. Input parameter estimates and the resulting r_{max} and PBR values for shorebird species using the Western Atlantic Flyway. The best available information approach was used for adult survivorship (S) and age at first reproduction (α). Where available, variance associated with *S* estimates is reported as SD. Where variance was not available, values represent upper and lower limits of the point estimate of *S* ± 10%. Population size estimates were taken from Andres *et al.* (2012) unless otherwise indicated. Where available, variance associated with population size estimates is reported as SE. Recovery factor (F_r) scores were assigned based on recommendations from Canadian and United States shorebird plans (Donaldson *et al.* 2000, Brown *et al.* 2001, United States Shorebird Conservation Plan 2004). Specific subspecies and population/geographic area designations are provided in Appendix I.

Common name	*S*	α	Population size	F_r	r_{max} mean ± SD	PBR mean ± SD	PBR 90% CI
Black-necked Stilt	(0.68, 0.83)[c]	2	175000 ± 12755	0.1	0.294 ± 0.022	2574 ± 267	(2139–3019)
American Avocet	(0.76, 0.93)[a]	2	(337500, 675000)	0.5	0.239 ± 0.034	30290 ± 7275	(19075–43238)
American Oystercatcher	(0.80, 0.98)[a]	3	11000 ± 153	0.3	0.152 ± 0.033	251 ± 55	(149–324)
Black-bellied Plover	(0.77, 0.95)[b]	2–3	(75000, 150000)	0.5	0.196 ± 0.035	5484 ± 1464	(3318–8103)
American Golden-Plover	(0.36, 0.44)[a]	1–2	208570 ± 54228	0.3	0.560 ± 0.101	17530 ± 5611	(9230–27719)
Wilson's Plover	(0.81, 0.99)[a]	1	(6450, 12900)	0.3	0.303 ± 0.090	440 ± 157	(188–710)
Semipalmated Plover	(0.64, 0.78)[a]	2–3	(150000, 300000)	0.5	0.267 ± 0.029	15000 ± 3303	(9979–20631)
Piping Plover	0.73 ± .07[a]	1–2	(2736, 5472)	0.1	0.385 ± 0.075	79 ± 22	(48–118)
Killdeer	(0.72, 0.88)[a]	1	(1500000, 3000000)	0.5	0.445 ± 0.052	250100 ± 57031	(163181–350014)
Spotted Sandpiper	(0.57, 0.69)[a]	1–2	(495000, 990000)	0.5	0.451 ± 0.076	83960 ± 21559	(52466–123975)
Solitary Sandpiper	(0.72, 0.89)[c]	1 - 2[e]	(141750, 283500)	0.3	0.334 ± 0.062	10640 ± 2868	(6567–15899)
Greater Yellowlegs	(0.72, 0.89)[c]	2	(102750, 205500)	0.5	0.265 ± 0.028	10210 ± 2234	(6780–14042)
Willet (Western)	(0.77, 0.95)[a]	2–3	(120000, 240000)	0.5	0.196 ± 0.035	8834 ± 2332	(5385–13045)
Willet (Eastern)	(0.77, 0.94)[a]	2–3	(67500, 135000)	0.5	0.202 ± 0.034	5131 ± 1325	(3157–7472)
Lesser Yellowlegs	(0.60, 0.74)[a]	1–2	(495000, 990000)	0.5	0.428 ± 0.072	79450 ± 20562	(49522–117114)
Upland Sandpiper	0.38 ± 0.04[a]	1–2	(562500, 1125000)	0.3	0.566 ± 0.104	71380 ± 18981	(43924–106609)
Whimbrel	0.89 ± 0.03[b]	2–3	(30000, 60000)	0.3	0.179 ± 0.025	1210 ± 287	(783–1718)

Common name	S	α	Population size	F_r	r_{max} mean ± SD	PBR mean ± SD	PBR 90% CI
Hudsonian Godwit	(0.80, 0.97)[c]	2	(42000, 84000)	0.3	0.206 ± 0.046	1945 ± 573	(1056–2944)
Marbled Godwit (Great Plains)	(0.86, 0.99)[a]	2	(127500, 255000)	0.3	0.166 ± 0.043	4783 ± 1571	(2305–7519)
Ruddy Turnstone	(0.77, 0.94)[b]	2	(135000, 270000)	0.3	0.235 ± 0.035	7124 ± 1761	(4448–10276)
Red Knot	0.92 ± 0.001[a]	2–3	(31500, 63000)	0.1	0.161 ± 0.013	382 ± 80	(261–517)
Stilt Sandpiper	(0.66, 0.81)[a]	2	1244000 ± 420889	0.5	0.303 ± 0.020	94300 ± 32781	(40796–148800)
Sanderling	(0.75, 0.91)[b]	2	(74250, 148500)f	0.3	0.249 ± 0.031	4168 ± 959	(2693–5834)
Dunlin	(0.75, 0.92)[b]	1–2	450000 ± 116667	0.3	0.310 ± 0.062	20860 ± 6894	(10929–33105)
Purple Sandpiper	(0.72, 0.88)[b]	1–2	(18750, 37500)	0.5	0.340 ± 0.062	2388 ± 636	(1476–3550)
Least Sandpiper	(0.49, 0.59)[a]	1	(525000, 1050000)	0.5	0.678 ± 0.023	133400 ± 26408	(92850–175598)
White-rumped Sandpiper	(0.69, 0.85)[c]	1	1694000 ± 578512	0.5	0.479 ± 0.046	203300 ± 72880	(86958–325775)
Buff-breasted Sandpiper	0.76 ± 0.03[a]	1	56000 ± 10969	0.1	0.490 ± 0.033	1371 ± 282	(921–1847)
Pectoral Sandpiper	(0.69, 0.84)[c]	1	432767 ± 125503	0.5	0.481 ± 0.046	51780 ± 15861	(26289–78464)
Semipalmated Sandpiper	(0.59, 0.72)[a]	2	810000 ± 170036	0.5	0.337 ± 0.015	68200 ± 14479	(44628–92074)
Western Sandpiper	(0.64, 0.78)[a]	1–2	(2625000, 5250000)	0.3	0.404 ± 0.068	238600 ± 61783	(149077–354335)
Short-billed Dowitcher	(0.68, 0.84)[d]	1–2	(58500, 117000)	0.3	0.369 ± 0.064	4847 ± 1252	(3038–7171)
Long-billed Dowitcher	(0.68, 0.84)[d]	1–2[e]	(375000, 750000)	0.5	0.371 ± 0.064	52420 ± 13717	(32586–77214)
Wilson's Snipe	(0.45, 0.55)[a]	1	(1500000, 3000000)	0.5	0.708 ± 0.020	398100 ± 77983	(278059–520131)
American Woodcock	0.71 ± 0.009[a]	1	(2625000, 5250000)	0.3	0.541 ± 0.008	318700 ± 60939	(224674–414479)
Red-necked Phalarope	(0.45, 0.55)[a]	1	(1875000, 3750000)	0.5	0.704 ± 0.021	493600 ± 96116	(345832–644624)
Red Phalarope	(0.62, 0.76)[c]	1	1620000 ± 244898	0.5	0.557 ± 0.036	225600 ± 36514	(166945–287244)

[a] Estimate based on a North American population
[b] Estimate based on a European population
[c] Estimate based on mean maximum survivorship in within-genus surrogate species
[d] Estimate based on list-wide mean maximum survivorship with study species as surrogates
[e] Estimate based on mean age at first reproduction in within-genus surrogate species
[f] Estimate taken from Donaldson *et al.* (2000) and Morrison *et al.* (2001a)

estimate). Semipalmated Sandpipers have declined (1974–2009) within North Atlantic staging areas (Morrison & Hicklin 2001, Ross *et al.* 2001) and by 79% (1982–2011) on their primary winter grounds in the Guianas (Morrison *et al.* 2012). Harvest throughout the core of the winter grounds along the northern South American coast is mostly undocumented. Harvest within the Suriname portion is estimated broadly in the tens of thousands (Ottema & Spaans 2008).

Illegal hunting of shorebirds likely occurs within most jurisdictions throughout the Western Atlantic Flyway and remains difficult to quantify. In the majority of locations, harvest likely amounts to no more than low-level subsistence hunts. An important exception appears to be Suriname, Guyana, and Brazil, which lie within the heart of one of the largest shorebird winter sites in the Western Hemisphere (Morrison & Ross 1989). Illegal harvest in Guyana and Brazil remains undocumented. Illegal harvest in Suriname is estimated in the several tens of thousands, essentially including all shorebird species, and is exacerbated by an illegal trade of shorebirds to local markets (Ottema & Spaans 2008). A large portion of this harvest is focused on Semipalmated Sandpipers and Lesser Yellowlegs. Some aboriginal subsistence harvest occurs in Alaska and Canada. Though species-specific subsistence harvest estimates are available (2004–2012) for shorebirds in Alaska (Naves 2010a, 2010b, 2011, 2012, 2014; Naves & Braem 2014), confidence is low for many species and we lack information on species affected and numbers harvested in Canada.

As with all models, PBR is sensitive to errors in input parameters. For many shorebird species and populations, estimates of demographic parameters are currently of poor quality or lacking (Appendix 1). All survival estimates available from the literature were derived from mark-recapture or mark-resight studies conducted in a specific area of the species range. Estimates of survival derived from such a study design produce apparent survival estimates that in most cases will be biased low by emigration from the study area. Therefore, the estimates of survival used here are likely lower than true survival. Published estimates of age at first reproduction are also possibly biased. This parameter has been grossly understudied within this taxonomic group and is well known to have a significant influence on population growth potential (Stearns 1992). Most researchers consider this parameter to be a static life-history trait with relatively few studies that provide a more comprehensive assessment (e.g. Hicklin & Gratto-Trevor 2010, Oring *et al.* 1983). In the configuration used here, relative PBR estimates (expressed as % of population estimate) were most sensitive when both age at first reproduction and adult survival were within the lower extremes of their ranges. This result is encouraging because, according to the model's prediction, species with these life history traits are capable of sustaining the highest mortality rates. On the other extreme, relative PBR estimates were the least sensitive when both of these parameters were near their higher extremes, suggesting that estimates were the most robust for species that are typically of the highest conservation concern.

Despite these weaknesses, PBR is a useful tool for evaluating the sustainability of the shorebird harvest in the Western Atlantic Flyway. It provides a simple model that requires only two demographic parameters to be known. It also provides a benchmark for testing hypotheses concerning the decline of shorebirds and evaluating whether uncontrolled harvest may be contributing to observed declines. Finally, it can be used in an adaptive resource management approach (Lancia *et al.* 1996) through a regular updating of model parameters as new or more accurate information emerges. This approach has been successfully used to evaluate the sustainability of the harvest for a variety of birds (Dillingham & Fletcher 2008, Niel & Lebreton 2005, Runge *et al.* 2009) and has been used effectively to assess the status of marine mammal populations (Lonergan 2011, Wade 1998).

There are several lines of evidence needed to fully assess the possible contribution of hunting to population declines for shorebirds using the Western Atlantic Flyway. In many cases, data suggesting declines are based on a time series of surveys for staging or winter areas within the flyway. However, population estimates are often continental in scope. This disconnect can result in an inflation of PBR and associated underestimate of the influence of hunting on observed declines. Gaps in knowledge of connectivity must be filled in order to allow estimates of PBR and harvest to be on a common scale. Currently, basic demographic data are lacking for many species. Some, such as the Pectoral Sandpiper *Calidris melanotos*, are harvested in large numbers in some areas (e.g. Hutt 1991). Quantifying survival and age at first reproduction should be a research priority for those species. Finally, flyway-wide hunting pressure is virtually unknown for any species. It will not be possible to either evaluate the population-level impacts of hunting or to introduce appropriate policies without adequate assessments of harvest.

ACKNOWLEDGEMENTS

We thank Fletcher Smith for assistance with compiling demographic estimates. Brad Andres and two anonymous reviewers provided comments on an earlier draft of this manuscript. This project was supported by the U.S. Fish and Wildlife Service, the Canadian Wildlife Service, and The Center for Conservation Biology at the College of William and Mary and Virginia Commonwealth University.

REFERENCES

Almeida, J.B. 2009. *Wintering ecology of Buff-breasted Sandpipers (*Tryngites subruficollis*) in southern Brazil.* Ph.D. Dissertation, University of Nevada, Reno.

American Oystercatcher Working Group, E. Nol & R. C. Humphrey. 2012. American Oystercatcher (*Haematopus palliatus*). No. 082 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New

York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/082.*

Andres, B. 2011. Shorebird hunting in the Caribbean. Symposia Report form Western Hemisphere Shorebird Group, Fourth Meeting. *Wader Study Group Bulletin* 118: 198–199.

Andres, B.A., P.A. Smith, R.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(3): 178–192.

Badzinski, D.S. 2000. *Population dynamics of Semipalmated Plovers (*Charadrius semipalmatus*) breeding at Churchill, Manitoba*. M.Sc. Thesis, Trent University, Peterborough, Ontario, Canada.

Baker, A., P. Gonzalez, R.I.G. Morrison & B.A. Harrington. 2013. Red Knot (*Calidris canutus*). No. 563 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/563.*

Bart, J., S. Brown, B. Harrington & R.I.G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *Journal of Avian Biology* 38: 73–82.

Bergman, G. 1946. Der Steinwalzer, *Arenia i. interpres* (L.), in seiner Beziehung zur Umwelt [The Turnstone, *Arenaria interpres* (L.), in its relationship to the environment]. *Acta Zoologica Fennica* 47: 1–151. [In German.]

Brown, S., C. Hickey, B. Harrington & R. Gill (Eds). 2001. *United States Shorebird Conservation Plan, Second Edition.* Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Burton, N.H.K., M.M. Rehfisch, N.A. Clark & S.G. Dodd. 2006. Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *Journal of Applied Ecology* 43: 464–473.

Clark, K.E. & L.J. Niles. 2000. *Northern Atlantic Regional Shorebird Plan: Version 1.1.* The US Shorebird Conservation Plan. Accessed July 2014 at: *http://www.shorebirdplan.org/regional-shorebird-conservation-plans/secpcrrev02.*

Clay, R.P., A.J. Lesterhuis & O. Johnson. 2010. *Conservation Plan for the American Golden-Plover (*Pluvialis dominica*).* Version 1.1. Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Colwell, M.A. & L.W. Oring. 1989. Return rates of prairie shorebirds: sex and species differences. *Wader Study Group Bulletin* 55: 21–24.

Cooper, J.M. 1993. *The breeding biology of the Least Sandpiper on the Queen Charlotte Island.* M.S. Thesis. University of Victoria, British Columbia, Canada.

del Hoyo, J., A. Elliott & J. Sargatal (Eds). 1996. *Handbook of the Birds of the World.* Volume 3, Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

Department of the Environment. 2014a. *Calidris ruficollis.* Species Profile and Threats Database, Department of the Environment, Canberra, Australia. Accessed July 2014 at: *http://www.environment.gov.au/sprat.*

Department of the Environment. 2014b. *Tringa stagnatilis.* Species Profile and Threats Database, Department of the Environment, Canberra, Australia. Accessed July 2014 at: *http://www.environment.gov.au/sprat.*

Dierschke, V. 1998. Site fidelity and survival of Purple Sandpipers *Calidris maritima* at Helgoland (SE North Sea). *Ringing & Migration* 19: 41–48.

Dillingham, P.W. & D. Fletcher. 2008. Estimating the ability of birds to sustain additional human-caused mortalities using simple decision rule and allometric relationships. *Biological Conservation* 141: 1783–1792.

Donaldson, G., C. Hyslop, G. Morrison, L. Dickson & I. Davidson (Eds). 2000. *Canadian shorebird conservation plan.* Canadian Wildlife Service, Ottawa, Canada.

Elliott-Smith, E. & S.M. Haig. 2004. Piping Plover (*Charadrius melodus*). No. 002 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/002.*

Elphick, C.S. & T.L. Tibbitts. 1998. Greater Yellowlegs (*Tringa melanoleuca*). No 355 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/355.*

Evans, P.R. & M. Pienkowski. 1984. Population dynamics of shorebirds. Pages 83-123 in: *Shorebirds: breeding behavior and populations* (J. Burger & B. L. Olla, Eds.) Plenum Press, New York.

Farmer, A., R.T. Holmes & F.A. Pitelka. 2013. Pectoral Sandpiper (*Calidris melanotos*). No. 348 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/348.*

Figuerola, J. 2007. Climate and Dispersal: Black-Winged Stilts Disperse Further in Dry Springs. *PloS One* 2(6): E539. DOI: 10.1371/journal.pone.0000539.

Flynn, L., E. Nol & Y. Zharikov. 1999. Philopatry, nest-site tenacity and mate fidelity of Semipalmated Plovers. *Journal of Avian Biology* 30: 47-55.

Franks, S., D.B. Lank & W.H. Wilson. 2014. Western Sandpiper (*Calidris mauri*). No. 090 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/090.*

Garnett, S., J. Szabo & G. Dutson. 2011. *The Action Plan for Australian Birds 2010.* CSIRO Publishing, Collingwood, Australia.

Grant, M.C. 1991. Nesting densities, productivity and survival of breeding Whimbrel *Numenius phaeopus* in Shetland. *Bird Study* 38(3): 160–169.

Gratto-Trevor, C.L. 2000. Marbled Godwit (*Limosa fedoa*). No. 492 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/492.*

Gratto-Trevor, C.L., R.I.G. Morrison, D. Mizrahi, D.B. Lank, P. Hicklin & A.L. Spaans. 2012. Migratory connectivity of semipalmated sandpipers: winter distribution and migration routes of breeding populations. *Waterbirds* 35: 96–105.

Groen, N.M. & L. Hemerik. 2002. Reproductive success and survival of Black-tailed Godwits *Limosa limosa* in a declining local population in the Netherlands. *Ardea* 90(2): 239–248.

Hicklin, P. & C.L. Gratto-Trevor. 2010. Semipalmated Sandpiper (*Calidris pusilla*). No. 006 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/006.*

Hildén, O. 1979. Territoriality and site tenacity of Temminck's Stint *Calidris temminckii*. *Ornis Fennica* 56: 56–74.

Hildén, O. & S. Vuolanto. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. *Ornis Fennica* 49: 57–85.

Houston, C.S., C.R. Jackson & D.E. Bowen, Jr. 2011. Upland Sandpiper (*Bartramia longicauda*). No. 580 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/580.*

Howe, M.A. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). *Auk* 99: 88–102.

Hunter, W.C. 2002. *Southeastern Coastal Plains-Caribbean Regional Report*. The U.S. Shorebird Conservation Plan. Accessed July 2014 at: *http://www.shorebirdplan.org/regional-shorebird-conservation-plans/secpcrrev02.*

Hutt, M.B. 1991. Shooting of migrating shorebirds in Barbados. Pages 77-91 in: *Conserving migratory birds* (T. Salathe, Ed.). International Council for Bird Preservation Technical Publication 12, Cambridge, U.K.

International Wader Study Group. 2003. Waders are declining worldwide. Conclusions from the 2003 International Study Group Conference, Cadiz, Spain. *Wader Study Group Bulletin* 101: 8–12.

Jackson, B.J. & J.A. Jackson. 2000. Killdeer (*Charadrius vociferus*). No. 517 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/517.*

Jehl, Jr., J.R. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. *Wilson Bulletin* 85: 114–147.

Jehl, Jr., J.R., J. Klima & R.E. Harris. 2001. Short-billed Dowitcher (*Limnodromus griseus*). No. 564 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/564.*

Johnson, F.A., C.T. Moore, W.L. Kendall, J.A. Dubovsky, D.F. Caithamer, J.R. Kelley & B.K. Williams. 1997. Uncertainty and the management of mallard harvests. *Journal of Wildlife Management* 61: 202-216.

Johnson, M., D.R. Ruthrauff, B.J. McCaffery, S.M. Haig & J.R. Walters. 2010. Apparent survival of breeding Western Sandpipers on the Yukon-Kuskokwim River Delta, Alaska. *Wilson Journal of Ornithology* 122: 15–22.

Johnson, O.W. 1979. Biology of shorebirds summering on Enewetak Atoll. *Studies in Avian Biology* 2: 193-205.

Johnson, O.W. & P.G. Connors. 2010. American Golden-Plover (*Pluvialis dominica*). No. 201 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/201.*

Jönsson, P.E. 1991. Reproduction and survival in a declining population of the southern Dunlin *Calidris alpina schinzii*. *Wader Study Group Bulletin* 6 (Supplement): 56–68.

Lancia, R.A., C.E. Braun, M.W. Collopy, R.D. Dueser, J.G. Kie, C.J. Martinka, J.D. Nichols, T.D. Nudds, W.R. Porath & N.G. Tilghman. 1996. ARM! For the future: adaptive resource management in the wildlife profession. *Wildlife Society Bulletin* 24: 436–442.

Lanctot, R.B. & C.D. Laredo. 1994. Buff-breasted Sandpiper (*Calidris subruficollis*). No. 091 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/091.*

Lonergan, M. 2011. Potential biological removal and other currently used management rules for marine mammal populations: A comparison. *Marine Policy* 35: 584–589.

Lowther, P.E., H.D. Douglas III & C.L. Gratto-Trevor. 2001. Willet (*Tringa semipalmata*). No. 579 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/579.*

MacArthur, R.H. & E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

Macwhirter, B., P. Austin-Smith, Jr., & D. Kroodsma. 2002. Sanderling (*Calidris alba*). No. 653 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/653.*

McAuley, D.G., D.M. Keppie & R.M. Whiting, Jr. 2013. American Woodcock (*Scolopax minor*). No. 100 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/100.*

McAuley, D.G., J.R. Longcore, D.A. Clugston, R.B. Allen, A. Weik, S. Williamson, J. Dunn, B. Palmer, K. Evans, W. Staats, G.F. Sepik & W. Halteman. 2005. Effects of hunting on survival of American Woodcock in the Northeast. *Journal of Wildlife Management* 69(4): 1565–1577.

McGowan, C.P., J.E. Hines, J.D. Nichols, J.E. Lyons, D.R. Smith, K.S. Kalasz, L.J. Niles, A.D. Dey, N.A. Clark, P.W. Atkinson, C.D.T. Minton & W. Kendall. 2011. Demographic consequences of migratory stopover: Linking Red Knot survival to horseshoe crab spawning abundance. *Ecosphere* 2(6): Art. 69.

Metcalfe, N.B. & R.W. Furness. 1985. Survival, winter population stability and site fidelity in the Turnstone. *Bird Study* 32: 207–214.

Miller, E.H. 1983. Habitat and breeding cycle of the Least Sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia. *Canadian Journal Zoology* 61: 2880–2898.

Moitoret, C.S., T.R. Walker & P.D. Martin. 1996. *Predevelopment surveys of nesting birds at two sites in the Kuparuk Oilfield, Alaska, 1988-1992.* U.S. Fish and Wildlife Service, Northern Alaska Ecological Services.

Mong, T.W. & B.K. Sandercock. 2007. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. *Journal of Wildlife Management* 71(3): 971–980.

Morris, D.F. & D.F. Doak. 2002. *Quantitative conservation biology: theory and practice of population viability analysis.* Sinauer Associates, Sunderland, Massachusetts.

Morrison, R.I.G., Y. Aubry, R.W. Butler, G.W. Beyersbergen, G.M. Donaldson, C.L. Gratto-Trevor, P.W. Hicklin, V.H. Johnston & R.K. Ross. 2001b. Declines in North American shorebird populations. *Wader Study Group Bulletin* 94: 34–38.

Morrison, R.I.G., R.E. Gill, Jr., B.A. Harrington, S. Skagen, G.W. Page, C.L. Gratto-Trevor & S.M. Haig. 2001a. *Estimates of shorebird populations in North America.* Occasional Paper No. 104, Canadian Wildlife Service, Ottawa, Ontario.

Morrison, R.I.G. & P. Hicklin. 2001. Recent trends in shorebird populations in the Atlantic Provinces. *Bird Trends* 8: 16–19.

Morrison, R.I.G., B.J. McCaffery, R.E. Gill, S.K. Skagen, S.L. Jones, G.W. Page, C.L. Gratto-Trevor & B.A. Andres. 2006. Population estimates of North American shorebirds, 2006. *Wader Study Group Bulletin* 111: 66–-84.

Morrison, R.I.G., D.S. Mizrahi, R.K. Ross, O.H. Ottema, N. Pracontal & A. Narine. 2012. Dramatic declines of semiplamated sandpipers on their major wintering areas in the Guianas, northern South America. *Waterbirds* 35: 120–134.

Morrison, R.I.G. & R.K. Ross. 1989. *Atlas of Nearctic shorebirds on the coast of South America*. Canadian Wildlife Service Special Publication, Ottawa, Ontario.

Mueller, H. 1999. Wilson's Snipe (*Gallinago delicata*). No. 417 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/417.*

Naves, L.C. 2010a, revised [2009]. *Alaska Subsistence Harvest of Birds and Eggs, 2004-2007, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 349, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/TP349_revised.pdf.*

Naves, L.C. 2010b. *Alaska Subsistence Harvest of Birds and Eggs, 2008, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 353, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/08%20Final%20Report_TP353.pdf.*

Naves, L.C. 2011. *Alaska Subsistence Harvest of Birds and Eggs, 2009, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 364, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/2009%20Final%20Harvest%20Report.pdf.*

Naves, L.C. 2012. *Alaska Subsistence Harvest of Birds and Eggs, 2010, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 376, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/TP%20376.pdf.*

Naves, L.C. 2014. *Alaska Subsistence Harvest of Birds and Eggs, 2011, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 395, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/AMBCC%202011%20Report.pdf.*

Naves, L.C. & N.M. Braem. 2014. *Alaska Subsistence Harvest of Birds and Eggs, 2012, Alaska Migratory Bird Co-Management Council.* Alaska Department of Fish and Game Division of Subsistence, Technical Paper Number 397, Anchorage, Alaska. Accessed 6 January 2015 at: *http://www.fws.gov/alaska/ambcc/ambcc/Harvest/TP397.pdf.*

Nebel, S., J.L. Porter & R.T. Kingsford. 2008. Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation* 141: 971–980.

Niel, C. & J. Lebreton. 2005. Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology* 19: 826–835.

Oring, L.W., D.B. Lank & S.J. Maxson. 1983. Population studies of the polyandrous spotted sandpiper. *Auk* 100(2): 272–285.

Ottema, O.H. & S. Ramcharan. 2009. Declining numbers of Lesser Yellowlegs *Tringa flavipes* in Suriname. *Wader Study Group Bulletin* 116: 87–88.

Ottema, O.H. & A.L. Spaans. 2008. Challenges and advances in shorebird conservation in the Guianas, with a focus on Suriname. *Neotropical Ornithology* 19: 339–346.

Pain, D., R. Green & N. Clark. 2011. Bird on the edge: can the Spoon-billed Sandpiper *Eurynohynchus pygemeus* be saved? *BirdingASIA* 15: 26–35.

Parmelee, D.F. 1992. White-rumped Sandpiper (*Calidris fuscicollis*). No. 029 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/029.*

Payne, L.X. & E.P. Pierce. 2002. Purple Sandpiper (*Calidris maritima*). No. 706 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/706.*

Ray, K.L. 2011. *Factors affecting Wilson's Plover (*Charadrius wilsonia*) demography and habitat use at Onslow Beach, Marine Corps Base Camp Lejeune, North Carolina.* Ph.D. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg.

Reed, J.M., C.S. Elphick & L.W. Oring. 1998. Life-history and viability analysis of the endangered Hawaiian stilt. *Biological Conservation* 84: 35–45.

Reed, J.M. & L.W. Oring. 1993. Philopatry, site fidelity, dispersal, and survival of Spotted Sandpipers. *Auk* 110: 541–551.

Reynolds, J.D. 1987. Mating system and nesting biology of the Red-necked Phalarope *Phalaropus lobatus*: What constrains polyandry? *Ibis* 129: 225–242.

Robinson, J.A. & L.W. Oring. 1997. Natal and breeding dispersal of American Avocets. *Auk* 114(3): 416–430.

Robinson, J.A., J. M. Reed, J.P. Skorupa & L.W. Oring. 1999. Black-necked Stilt (*Himantopus mexicanus*). No. 449 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/449.*

Robinson, R.A. 2005a. Green Sandpiper *Tringa ochropus*. In: *BirdFacts: profiles of birds occurring in Britain & Ireland.* BTO Research Report 407. BTO, Thetford, U.K. Accessed July 2014 at: *http://blx1.bto.org/birdfacts/results/bob5480.htm.*

Robinson, R.A. 2005b. Greenshank *Tringa nebularia*. In: *BirdFacts: profiles of birds occurring in Britain & Ireland* (BTO Research Report 407). BTO, Thetford, U.K. Accessed July 2014 at: *http://blx1.bto.org/birdfacts/results/bob5480.htm.*

Roche, E.A., J.B. Cohen, D.H. Catlin, D.L. Amirault-Langlais, F.J. Cuthbert, C.L. Gratto-Trevor, J. Felio & J.D. Fraser. 2010. Range-Wide Piping Plover Survival: Correlated Patterns and Temporal Declines. *Journal of Wildlife Management* 74(8): 1784–1791.

Ross, R.K., J. Pedlar & R.I.G. Morrison. 2001. Trends in shorebird populations migrating through southern Ontario. *Bird Trends* 8: 24–25.

Ross, R.K., P.A. Smith, B. Campbell, C.A. Friis & R.I.G. Morrison. 2012. Population trends of shorebirds in southern Ontario, 1974-2009. *Waterbirds* 35: 15–24.

Runge, M.C., W.L. Kendall & J.D. Nichols. 2004. Exploitation. Pages 303-328 in: *Bird ecology and conservation: a handbook of techniques* (W.J. Sutherland, I. Newton & R.E. Green, Eds.). Oxford University Press, Oxford, U.K.

Runge, M.C., J.R. Sauer, M.L. Avery, B.F. Blackwell & M.D. Koneff. 2009. Assessing allowable take of migratory birds. *Journal of Wildlife Management* 73: 556–565.

Russell, R.W. 1999. Comparative demography and life history tactics of seabirds: Implications for conservation and marine monitoring. Pages 51-69 in: *Life in the slow lane: ecology and conservation of long-lived marine animals* (J. A. Musick, Ed.). American Fisheries Society, Bethesda, Maryland.

Ryabitsev, V.K. 2000. On the population ecology of the gray plover in the northern Yamal Peninsula. *Russian Journal of Ecology* 31(2): 108–112.

Saether, B-E. 1988. Pattern of covariation between life history traits of European birds. *Nature* 331: 616–627.

Saether, B-E. & O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–-653.

Sandercock, B.K., D.B. Lank, R.B. Lanctot, B. Kempenaers & F. Cooke. 2000. Ecological correlates of mate fidelity in two Arctic-breeding sandpipers. *Canadian Journal of Zoology* 78(11): 1948–1958.

Schamel, D. & D.M. Tracy. 1991. Breeding Site Fidelity and Natal Philopatry in the Sex Role-Reversed Red and Red-Necked Phalaropes. *Journal of Field Ornithology* 62: 390–398.

Simons, T.R. & S. Schulte. 2010. *American Oystercatcher (*Haematopus palliatus*) research and monitoring in North Carolina*. Final report. USGS North Carolina Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh.

Skeel, M.A. & E.P. Mallory. 1996. Whimbrel (*Numenius phaeopus*). No. 219 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/219.*

Smith, K.W., J.M. Reed & B.E. Trevis. 1992. Habitat use and site fidelity of Green Sandpipers *Tringa ochropus* wintering in southern England. Bird Study 39(3): 155–164.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, U.K.

Taylor, B.L., P.R. Wade, D.P. DeMaster & J. Barlow. 2000. Incorporating uncertainty into management models for marine mammals. *Conservation Biology* 14: 1243–1252.

Thompson, D.B.A., P.S. Thompson & D. Nethersole-Thompson. 1986. Timing of breeding and breeding performance in a population of Greenshanks (*Tringa nebularia*). Journal of *Animal Ecology* 55: 181–199.

Thompson, M.C 1973. Migration patterns of Ruddy Turnstones in the central Pacific region. *Living Bird* 12: 5-23.

Thompson, P.S. & W.G. Hale. 1991. Age-related reproductive variation in the redshank *Tringa totanus*. *Ornis Scandinavica* 22(4): 353–359.

Tibbitts, T.L. & W. Moskoff. 2014. Lesser Yellowlegs (*Tringa flavipes*). No. 427 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/427.*

Tomkovich, P.S. 1994. Site fidelity and spatial structure of population in the Rock Sandpiper *Calidris ptilocnemis* and Dunlin *Calidris alpina* on Chukotsky Peninsula. *Russian Journal of Ornithology* 3: 13–30.

Tomkovich, P.S. 1996. A third report on the biology of the Great Knot *Calidris tenuirostris* on the breeding grounds. *Wader Study Group Bulletin* 81: 88–90.

Tracy, D.M., D. Schamel & J. Dale. 2002. Red Phalarope (*Phalaropus fulicarius*). No. 698 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/698.*

Tuck, L.M. 1972. *The snipes: a study of the genus* Capella. No. 5. Canadian Wildlife Service, Ottowa, Ontario.

United States Shorebird Conservation Plan. 2004. *High Priority Shorebirds – 2004*. Unpublished Report, U. S. Fish and Wildlife Service, Arlington, Virginia.

Wade, P.R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnepeds. *Marine Mammal Science* 14: 1–37.

Walker, B.M., N.R. Senner, C.S. Elphick & J. Klima. 2011. Hudsonian Godwit (*Limosa haemastica*). No. 629 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/629.*

Warnock, N.D. & R.E. Gill. 1996. Dunlin (*Calidris alpina*). No. 203 in: *The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Accessed July 2014 at: *http://bna.birds.cornell.edu/bna/species/203*.

Watts, B.D. 2010. *Wind and waterbirds: Establishing sustainable mortality limits within the Atlantic Flyway.* Center for Conservation Biology Technical Report Series, CCBTR-10-05. College of William and Mary/Virginia Commonwealth University, Williamsburg, Virginia.

Watts, B.D. & B.R. Truitt. 2011. Decline of whimbrels within a mid-Atlantic staging area (1994-2009). *Waterbirds* 34: 347–351.

Wetlands International. 2006. *Waterbird Population Estimates, fourth edition*. Wetlands International, Wageningen, The Netherlands.

Zdravkovik, M.G. 2013. *Conservation plan for the Wilson's Plover* (Charadrius wilsonia). Version 1.0. Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Appendix 1. List of shorebird species and populations that regularly use the Western Atlantic Flyway along with demographic parameter estimates and sources used in PBR modeling. Preference was given to source estimates extracted from the literature in the following order: 1) populations known to use the flyway, 2) estimates from North American populations, 3) estimates from other populations. Estimates of adult survivorship (*S*) and age at first reproduction (α) are reported. When multiple *S* estimates were reported in the literature for a single species or population, we used the maximum *S* estimate. Population size estimates were taken from Andres *et al.* (2012) unless otherwise indicated.

Common name	Species name	Subspecies/ population	Population/ Geographic area	*S* mean ± SD (n)	*S* Citation	α (yr)	α Citation	Population mean ± SE
Black-necked Stilt	*Himantopus mexicanus*	*mexicanus*	North America	no dataa		usually 2	Robinson *et al.* 1999	175000 ± 12755
American Avocet	*Recurvirostra americana*		North America	0.83–0.86 (19)	Robinson & Oring 1997	usually 2	Robinson & Oring 1997	450,000
American Oystercatcher	*Haematopus palliatus*	*palliatus*	North America	0.89	Simons & Schulte 2010	usually 3	American Oystercatcher Working Group *et al.* 2012	11000 ± 153
Black-bellied Plover	*Pluvialis squatarola*	*cynosurae*	Canadian Arctic	0.86	Evans & Pienkowksi 1984	2 to 3	Ryabitsev 2000	100,000
American Golden-plover	*Pluvialis dominica*		Canadian Arctic	0.40 (10)	Moitoret *et al.* 1996	1 to 2	Johnson & Connors 2010	208570 ± 54228
Wilson's Plover	*Charadrius wilsonia*	*wilsonia*	North America	0.90 (20)	Ray 2011	1	Zdravkovic 2013	8,600
Semipalmated Plover	*Charadrius semipalmatus*		North America	0.71 (256)	Badzinski 2000	2 to 3	Flynn *et al.* 1999	200,000
Piping Plover	*Charadrius melodus*	*melodus*	North Atlantic Coast	0.73 ± 0.07 (2040)	Roche *et al.* 2010	1 to 2	Elliott-Smith & Haig 2004	3,648
Killdeer	*Charadrius vociferus*	*vociferus*	North America	0.80 (5)	Colwell & Oring 1989	1	Jackson & Jackson 2000	2,000,000
Spotted Sandpiper	*Actitis macularius*		North America	0.63 (92)	Reed & Oring 1993	usually 1 to 2	Oring *et al.* 1983	660,000
Solitary Sandpiper	*Tringa solitaria*	*solitaria and cinnamomea*	North America	no data[a]		no datac		189,000
Greater Yellowlegs	*Tringa melanoleuca*		North America	no data[a]		presumed 2	Elphick & Tibbitts 1998	137,000
Willet (Western)	*Tringa semipalmata*	*inornata*	Interior North America	0.76–0.96 (110)	Lowther *et al.* 2001	2 to 3	Lowther *et al.* 2001	160,000
Willet (Eastern)	*Tringa semipalmata*	*semipalmata*	Atlantic Coast	0.85 (93)	Howe 1982	2 to 3	Lowther *et al.* 2001	90,000
Lesser Yellowlegs	*Tringa flavipes*		North America	0.67 (100)	Tibbitts & Moskoff 2014	1 to 2	Tibbitts & Moskoff 2014	660,000
Upland Sandpiper	*Bartramia longicauda*		North America	0.38 ± 0.04 (189)	Mong & Sandercock 2007	1 to 2	Houston *et al.* 2011	750,000
Whimbrel	*Numenius phaeopus*	*hudsonicus*	Hudson Bay	0.89 ± 0.03 (120)	Grant 1991	2 to 3	Skeel & Mallory 1996	40,000
Hudsonian Godwit	*Limosa haemastica*		Hudson Bay	no data[a]		2	Walker *et al.* 2011	56,000

Common name	Species name	Subspecies/ population	Population/ Geographic area	*S* mean ± SD (n)	*S* Citation	α (yr)	α Citation	Population mean ± SE
Marbled Godwit	*Limosa fedoa*	*fedoa*	Great Plains	0.96 (57)	Gratto-Trevor 2000	presumed 2	Gratto-Trevor 2000	170,000
Ruddy Turnstone	*Arenaria interpres*	*morinella*	Canadian Arctic (central)	0.85 (123)	Metcalfe & Furness 1985	usually 2	Bergman 1946, Thompson 1973, Johnson 1979	180,000
Red Knot	*Calidris canutus*	*rufa*	Canadian Arctic (central)	0.916 ± 0.001 (16572)	Mcgowan *et al.* 2011	2 to 3	Johnson 1979, Baker *et al.* 2013	42,000
Stilt Sandpiper	*Calidris himantopus*		North America	0.73 (41)	Jehl 1973	2	Jehl 1973	1244000 ± 420889
Sanderling	*Calidris alba*		Atlantic Coast (winter)	0.83	Evans & Pienkowski 1984	presumed 2	Macwhirter *et al.* 2002	99,000[d]
Dunlin	*Calidris alpina*	*hudsonia*	Hudson Bay	0.83 (396)	Jönsson 1991	1 to 2	Warnock & Gill 1996	450000 ± 116667
Purple Sandpiper	*Calidris maritima*	*belcheri* and *maritima*	Canadian Arctic	0.8 (152)	Dierschke 1998	1 to 2	Payne & Pierce 2002	25,000
Least Sandpiper	*Calidris minutilla*		North America	0.54 (50)	Miller 1983	1	Cooper 1993	700,000
White-rumped Sandpiper	*Calidris fuscicollis*		Canadian Arctic	no data[a]		presumed 1	Parmelee 1992	1694000 ± 578512
Buff-breasted Sandpiper	*Calidris subruficollis*		North America	0.76 ± 0.03 (163)	Almeida 2009	presumed 1	Lanctot & Laredo 1994	56000 ± 10969
Pectoral Sandpiper	*Calidris melanotos*		Canadian Arctic	no data[a]		1	Farmer *et al.* 2013	432767 ± 125503
Semipalmated Sandpiper	*Calidris pusilla*		Canadian Arctic (central and eastern)	0.66 (230)	Sandercock *et al.* 2000	usually 2	Hicklin & Gratto-Trevor 2010	810000 ± 170036
Western Sandpiper	*Calidris mauri*		North America	0.71 (533)	Johnson *et al.* 2010	1 to 2	Franks *et al.* 2014	3,500,000
Short-billed Dowitcher	*Limnodromus griseus*	*griseus* and *hendersoni*	Canadian Arctic (central and eastern)	no data[b]		1 to 2	Jehl *et al.* 2001	78,000
Long-billed Dowitcher	*Limnodromus scolopaceus*		North America	no data[b]		no data[c]		500,000
Wilson's Snipe	*Gallinago delicata*		North America	0.5	Tuck 1972	1	Mueller 1999	2,000,000
American Woodcock	*Scolopax minor*		North America	0.707 ± 0.009 (430)	McAuley *et al.* 2005	1	McAuley *et al.* 2013	3,500,000
Red-necked Phalarope	*Phalaropus lobatus*		North America	0.50 (209)	Schamel & Tracy 1991	1	Hildén & Vuolanto 1972, Reynolds 1987, Schamel & Tracy 1991	2,500,000
Red Phalarope	*Phalaropus fulicarius*		North America	no data[a]		presumed 1	Tracy *et al.* 2002	1620000 ± 244898

[a] A surrogate *S* estimate was made based on average maximum adult survivorship for all other species within the genus for which survival estimates were available. These data are presented in Appendix 2.
[b] In the case of Long- and Short-billed Dowitchers, no adult survival estimates were available for any species within the genus; thus, we used the list-wide average survivorship of all the study species as the surrogate *S* estimate for dowitchers.
[c] Age at first reproduction estimate was made using within-genus average α as a surrogate. These data are presented in Appendix 2.
[d] Population estimate was taken from Donaldson *et al.* (2000) and Morrison *et al.* (2001a).

Appendix 2. List of shorebird species and populations used as 'surrogates' for species in Appendix 1 that lacked estimates for demographic parameters needed for PBR modeling. Surrogate parameters were extracted from studies of congeners. We used the maximum adult survival (*S*) estimate for each species. When multiple survival estimates were presented in a study, we took the weighted average as the overall estimate. For both *S* and age at first reproduction (α), we used a midpoint when ranges were presented. Means of all available congener values were calculated and used as surrogates in Table 1.

Species name	Subspecies	Common name	*S*	α	*S* Citation	α Citation
Himanoptus himantopus		Black-winged Stilt	0.70 ± 0.05		Figuerola 2007	
Himanoptus mexicanus	*knudseni*	Hawaiian Stilt	0.81		Reed *et al.* 1998	
Tringa ochropus		Green Sandpiper	0.84	2	Smith *et al.* 1992	Robinson 2005a
Tringa brevipes		Grey-tailed Tattler		2		Garnett *et al.* 2011
Tringa melanoleuca		Greater Yellowlegs		2		Elphick & Tibbetts 1998
Tringa nebularia		Common Greenshank	0.70–0.94	2	Thompson *et al.* 1986	Robinson 2005b
Tringa semipalmata		Willet	0.76–0.96	2–3	Lowther *et al.* 2001	Lowther *et al.* 2001
Tringa flavipes		Lesser Yellowlegs	0.67	1–2	Tibbetts & Moskoff 2014	Tibbetts & Moskoff 2014
Tringa stagnatilis		Marsh Sandpiper		1		Department of the Environment 2014b
Tringa glareola		Wood Sandpiper		1		del Hoyo *et al.* 1996
Tringa totanus		Common Redshank	0.84	1–2	Burton *et al.* 2006	Thompson & Hale 1991
Limosa limosa		Black-tailed Godwit	0.81		Groen & Hemerik 2002	
Limosa lapponica		Bar-Tailed Godwit	0.88		Evans & Pienkowski 1984	
Limosa fedoa		Marbled Godwit	0.96		Gratto-Trevor 2000	
Calidris tenuirostris		Great Knot	0.92		Tomkovich 1996	

Appendix 2, continued

Species name	Subspecies	Common name	*S*	α	*S* Citation	α Citation
Calidris canutus		Red Knot	0.92 ± 0.05		McGowan *et al.* 2011	
Calidris temminckii		Temminck's Stint	0.76		Hildén 1979	
Calidris pygmea		Spoon-billed Sandpiper	0.76		Pain *et al.* 2011	
Calidris ruficollis		Red-necked Stint	0.75		Department of the Environment 2014a	
Calidris alba		Sanderling	0.83		Evans & Pienkowski 1984	
Calidris alpina	*schinzii*	Dunlin	0.83		Jönsson 1991	
Calidris ptilocnemis		Rock Sandpiper	0.74		Tomkovich 1994	
Calidris maritima		Purple Sandpiper	0.8		Dierschke 1998	
Calidris minutilla		Least Sandpiper	0.54		Miller 1983	
Calidris pusilla		Semipalmated Sandpiper	0.66 ± 0.06		Sandercock *et al.* 2000	
Calidris mauri		Western Sandpiper	0.71		Johnson *et al.* 2010	
Calidris subruficollis		Buff-breasted Sandpiper	0.76 ± 0.09		Almeida 2009	
Limnodromus griseus		Short-billed Dowitcher		1–2		Jehl *et al.* 2001
Phalaropus tricolor		Wilson's Phalarope	0.87		Colwell & Oring 1989	
Phalaropus lobatus		Red-necked Phalarope	0.5		Schamel & Tracy 1991	