



RESEARCH ARTICLE

Seasonal variation in mortality rates for Whimbrels (*Numenius phaeopus*) using the Western Atlantic Flyway

Bryan D. Watts,^{1*} Fletcher M. Smith,¹ Diana J. Hamilton,² Tim Keyes,³ Julie Paquet,⁴ Lisa Pirie-Dominix,⁵ Jennie Rausch,⁶ Barry Truitt,⁷ Brad Winn,⁸ and Paul Woodard⁶

¹ Center for Conservation Biology, College of William & Mary and Virginia Commonwealth University, Williamsburg, Virginia, USA

² Mount Allison University, Sackville, New Brunswick, Canada

³ Georgia Department of Natural Resources, Wildlife Resources Division, Non-game Conservation Section, Brunswick, Georgia, USA

⁴ Canadian Wildlife Service, Environment and Climate Change Canada, Sackville, New Brunswick, Canada

⁵ Canadian Wildlife Service, Environment and Climate Change Canada, Iqaluit, Nunavut, Canada

⁶ Canadian Wildlife Service, Environment and Climate Change Canada, Yellowknife, Northwest Territories, Canada

⁷ The Nature Conservancy's Virginia Coast Reserve, Nassawadox, Virginia, USA

⁸ Manomet Inc., Manomet, Massachusetts, USA

* Corresponding author: bdwatt@wm.edu

Submitted December 22, 2017; Accepted September 23, 2018; Published February 5, 2019

ABSTRACT

For most shorebird species, our understanding of the basic limiting factors and when or where they operate during the annual cycle is currently inadequate to either understand ongoing declines or effectively allocate conservation resources for recovery. Whimbrels (*Numenius phaeopus*) exhibit delayed recruitment and have low fecundity, and populations with such life-history traits are often vulnerable to increases in adult mortality. We tracked 33 adult Whimbrels with satellite transmitters for 12,802 bird-days to investigate patterns in survival and recorded 16 probable and 5 confirmed mortalities. We used Cox's proportional hazards model to estimate daily hazard rates by season and a Kaplan-Meier product limit estimator to estimate monthly survival. Daily hazard rates varied by season and were 5 times higher during migratory periods (fall and spring migration) compared to stationary periods (winter and breeding). Estimated annualized survivorship was 0.54 ± 0.21 (SE) and on the lower end of the range of 0.8–0.9 believed to be required to maintain a stable population. More than half of the mortality recorded during the study occurred during the fall hunting season and within the last remaining area throughout the Western Hemisphere where significant legal and illegal hunting occurs. One-third of mortality occurred during spring migration either within terminal staging sites or as birds made final movements to breeding grounds. Survival during the migratory periods may have been influenced by the use of transmitters.

Keywords: adult survival, hunting, *Numenius phaeopus*, satellite tracking, seasonality, Western Atlantic Flyway, Whimbrel

Variation saisonnière des taux de mortalité chez *Numenius phaeopus* utilisant la voie de migration de l'Atlantique Ouest

RÉSUMÉ

Pour la plupart des espèces de limicoles, notre compréhension des facteurs limitants de base et du moment ou de l'endroit où ils opèrent au cours du cycle annuel est insuffisante à l'heure actuelle pour bien comprendre les déclinés en cours ou allouer des ressources en conservation pour leur rétablissement. *Numenius phaeopus* est une espèce qui présente un recrutement à retardement et une faible fécondité; les populations ayant de telles caractéristiques d'histoire naturelle sont souvent vulnérables aux augmentations de la mortalité des adultes. Nous avons suivi 33 adultes de cette espèce avec des émetteurs satellite pendant 12,802 oiseaux-jours afin d'étudier les patrons de survie et nous avons enregistré 16 mortalités probables et 5 confirmées. Nous avons utilisé le modèle à risques proportionnels de Cox pour estimer les taux de risques quotidiens par saison et l'estimateur produit-limite de Kaplan-Meier afin d'estimer la survie mensuelle. Les taux de risques quotidiens ont varié d'une saison à l'autre et étaient 5 fois plus élevés au cours des périodes migratoires (migration automnale et printanière) comparativement aux périodes stationnaires (hiver et reproduction). Le taux de survie annualisé a été estimé à 0.54 ± 0.21 (erreur-type) et se trouvait dans la limite inférieure de la plage allant de 0.8 à 0.9 considérée comme requise pour maintenir une population stable. Plus de la moitié de la mortalité enregistrée au cours de l'étude s'est produite au cours de la saison de chasse automnale et à l'intérieur de la dernière zone restante de l'hémisphère occidental où une importante chasse légale et illégale a lieu. Le tiers de la mortalité s'est produit au cours de la migration printanière, soit dans les dernières haltes ou pendant que les oiseaux

faisaient leurs derniers déplacements vers les sites de reproduction. La survie au cours des périodes migratoires peut avoir été influencée par l'utilisation des émetteurs.

Mots-clés: chasse, *Numenius phaeopus*, saisonnalité, suivi par satellite, survie des adultes, voie de migration de l'Atlantique Ouest

INTRODUCTION

An alarming percentage of the world's shorebird species are experiencing population declines (International Wader Study Group 2003, Wetlands International 2006, Piersma 2007, Nebel et al. 2008). For species in the Western Hemisphere, evidence of ongoing declines is geographically widespread. There is documentation from the breeding grounds (e.g., Pattie 1990, Gratto-Trevor et al. 2001, Jehl 2007), wintering grounds (e.g., Morrison et al. 2004, Ottema and Ramcharan 2009, Morrison et al. 2012), and migratory staging sites (e.g., Butler and Lemon 2001, Watts and Truitt 2011, Ross et al. 2012). Many factors have been hypothesized as causes for declines in shorebird populations, including habitat loss and degradation (e.g., Vickery et al. 1999, Galbraith et al. 2002), human disturbance within staging sites (e.g., Burger 1986, Foster et al. 2009), reductions in critical prey populations (e.g., Baker et al. 2004, Escudero et al. 2012), climate change (Meltofte et al. 2007), recovery of predator populations (e.g., Ydenberg et al. 2002, Lank and Ydenberg 2003), and hunting (Hutt 1991, Andres 2017, Watts et al. 2015b).

A population's resilience to perturbations reflects its underlying demographic traits (Stearns 1992, Russell 1999), and understanding the demographic changes that underpin population trends is fundamental to effective management. For most shorebird species, our understanding of the basic limiting factors and when or where they operate during the annual cycle is currently inadequate to either understand declines or effectively allocate conservation resources for recovery. Identifying causal factors that are driving population declines is particularly challenging for this group because many species breed in the High Arctic and migrate between multiple jurisdictions over large geographic areas, potentially becoming exposed to a wide range of hazards. Ideally, management actions should be based on well-documented demographic information. Due to their relatively low fecundity (Maclean 1972), most shorebird species have limited capacity to compensate for increases in adult mortality, suggesting that achieving an understanding of survival patterns should be a priority for research investment.

Whimbrels (*Numenius phaeopus*) exhibit delayed recruitment into the breeding population, are single brooded, and have small broods (Grant 1991, Skeel and Mallory 1996), making populations vulnerable to elevations in adult mortality. Between 1994 and 2009, Whimbrels staging during spring migration along the lower Delmarva

Peninsula in Virginia declined by 50%, for an average annual rate of 4% (Watts and Truitt 2011). Previous evidence from the breeding grounds (Jehl and Lin 2001, Ballantyne and Nol 2015) and other migration areas (Howe et al. 1989, Bart et al. 2007) indicates that the eastern population has been in decline since the mid-1970s. Aerial surveys of the most significant wintering area for this population (as delineated in the early 1980s; Morrison and Ross 1989) indicate a 4% average annual rate of decline (Morrison et al. 2012). As a consequence of these patterns and relatively small population sizes, Whimbrels have been assigned high conservation scores by both the United States and Canadian shorebird conservation plans (Donaldson et al. 2000, Brown et al. 2001).

Understanding bottlenecks in survival is essential to making decisions on how to strategically mobilize limited conservation resources to effect recovery. In this study, we used satellite transmitters to track adult Whimbrels throughout their annual cycle. Our objectives included (1) documenting seasonal movements to delineate major stages of the annual cycle, (2) examining seasonal variation in mortality, (3) estimating annualized survival rates, and (4) exploring the relationship between seasonal activity and mortality.

METHODS

Study Species and Demographic Rates

Whimbrels are large, highly migratory, Holarctic waders with 4 recognized subspecies including 3 Eurasian forms and 1 Nearctic form (*N. p. hudsonicus*) (Cramp and Simmons 1983). The New World subspecies has disjunct eastern and western breeding ranges (Skeel and Mallory 1996). Age at first reproduction is at least 3 yr. Mean clutch size is highly consistent across years and among different breeding areas, ranging from 3.6 to 3.9 (Skeel and Mallory 1996, Ballantyne 2009, Perz 2014). Nesting success exhibits considerable year-to-year variation (Perz 2014), and successful pairs produce a single brood per year (Skeel and Mallory 1996). The species is believed to require high adult survival for population maintenance, and the current longevity record for North America is 16 yr (Klima et al. 2013).

For comparative purposes, we may consider the adult survival required for population stability under an optimistic scenario. If S_a is adult survival, S_1 is first-year survival, S_2 is second-year survival, S_3 is third-year survival, and β is annual fecundity, then $S_a = 1 - (S_1 S_2 S_3) \beta$ (Pulliam 1988).

Grant (1991), working in Shetland, United Kingdom, recorded the highest reproductive rates for the species to date as 0.75, 0.90, and 0.91 fledged young per pair in 1986, 1987, and 1988, respectively, for a 3-yr mean of 0.85 (0.43 per adult female). First-year survival rates are not available for Whimbrel but a value of 47% (Bainbridge and Minton 1978) was estimated for the closely related Eurasian Curlew (*Numenius arquata*) and is generally consistent with a range of 55–65% reported for other wader species (e.g. Peach et al. 1994, Sandercock 2003). Rates of after-first-year survival for *Numenius* spp. estimated using mark–recapture techniques generally fall within the 0.85–0.90 range (Sandercock 2003, Mendez et al. 2018). If we consider an optimistic survival rate for years 1 to 3 as 0.6, 0.9, and 0.9, respectively, to reach recruitment age, then the adult survival rate required for maintenance of the Shetland population would be 0.79. Based on return rates, the minimum adult survival rate for this population was estimated as 0.89.

Although fledging rates are not available for most North American breeding populations, a considerable amount of information is available on nest success or apparent nest survival, including a chronosequence within the Churchill portion of the Hudson Bay breeding population (Jehl 1971, Skeel 1983, Perz 2014). Jehl (1971) reported a 49% hatching rate. After adjusting for exposure days, Skeel (1983) estimated that apparent nest survival ranged from 54% to 86% (1973–1974), depending on habitat type, with a mean of 73%. More recently, Perz (2014) estimated a range of 18% to 74% (2011–2013), with a mean of 43%. The latter range is comparable to the range (19% to 69%) reported within the Mackenzie River population (Pirie 2008). The Skeel (1983) and Perz (2014) estimates would result in hatching rates of 1.23 and 0.72 young per female, respectively. Only 2 fledging rates are available. In western Alaska, 71% of nests were found to hatch (1989–1990) but only 13% of pairs fledged young (McCaffery 1996, Skeel and Mallory 1996). In Shetland, Grant (1991) recorded a 49% loss of young from hatching to fledging. Applying a midpoint (32%) of these 2 estimates to hatching rates, the Skeel (1983) and Perz (2014) studies would result in an estimated 0.40 and 0.23 young per female at the time of fledging, respectively. Applying the optimistic survival rates to recruitment presented above, the Skeel (1983) and Perz (2014) reproductive rates would require adult survival rates of 0.81 and 0.89, respectively, to achieve stability.

Field Methods

We captured 42 Whimbrels between 2008 and 2016 on migration staging sites along the lower Delmarva Peninsula in Virginia, USA ($n = 15$; 37.398°N, 75.865°W), along the coast of Georgia, USA ($n = 8$; 31.148°N, 81.379°W), along the Acadian Peninsula in New Brunswick, Canada ($n = 6$; 47.973°N, 64.509°W), as well as on the nesting ground near the Mackenzie River, Northwest Territories, Canada

($n = 13$; 69.372°N, 134.894°W) (Figure 1). Birds were captured using rocket nets ($n = 17$), noose lines ($n = 12$), and nest traps ($n = 13$). All birds were aged as adults by plumage (Prater et al. 1977) and were banded with U.S. Geological Survey tarsal bands and coded leg flags. Sex of captured birds was not determined.

We fitted all birds with satellite transmitters called Platform Transmitter Terminals (PTTs) using a modification of the leg-loop harness (Rappole and Tipton 1991, Sanzenbacher et al. 2000). Instead of elastic cord, we used Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA) that was fastened with brass rivets or crimps (Watts et al. 2008). We glued transmitters to a larger square of neoprene to elevate it above the body and prevent the bird from preening feathers over the solar panels. The transmitter package was below 3% of body mass (measured at the time of deployment) for all individuals tracked in this study.

Known-fate models assume that marking does not affect an individual's survival, fates of individuals are independent, and censoring is unrelated to mortality (White and Burnham 1999). We excluded 4 individuals from analysis for which transmitters may have influenced their loss to predators shortly after deployment. These exclusions included one Whimbrel confirmed to have been taken by a locally nesting Gyrfalcon (*Falco rusticolus*) on the Mackenzie River breeding grounds. We excluded 3 additional individuals from analysis because their failure to migrate away from the deployment location may have been influenced by the transmitters. Finally, we excluded 2 individuals that experienced early harness failure. Because all other birds ($n = 33$) migrated away from capture sites over great distances, we judged that the assumption of independent fate was met and we included them in analyses. The PTTs used in this study were 9.5 g PTT-100 ($n = 21$) or 5.0 g PTT-100 ($n = 12$) solar-powered units produced by Microwave Telemetry (Columbia, Maryland, USA).

The analyzed sample of birds included individuals from breeding populations from the Mackenzie River ($n = 15$), Hudson Bay ($n = 11$), and Barren Grounds, Northwest Territories, Canada ($n = 2$), as well as individuals ($n = 5$) for which tracking did not extend to the breeding grounds (Table 1). All but one of the birds whose wintering area was determined ($n = 26$) spent the winter months along the northern coast of South America. The majority (84%) of these birds wintered around the mouth of the Amazon River in Brazil and the remaining individuals were in nearby Guyana and Suriname.

Tracking Data

Birds were located using satellites of the National Oceanic and Atmospheric Administration and the European Organization for the Exploitation of Meteorological Satellites with onboard tracking equipment operated by Collecte Localisation Satellites (CLS America, Largo, Maryland, USA; Fancy

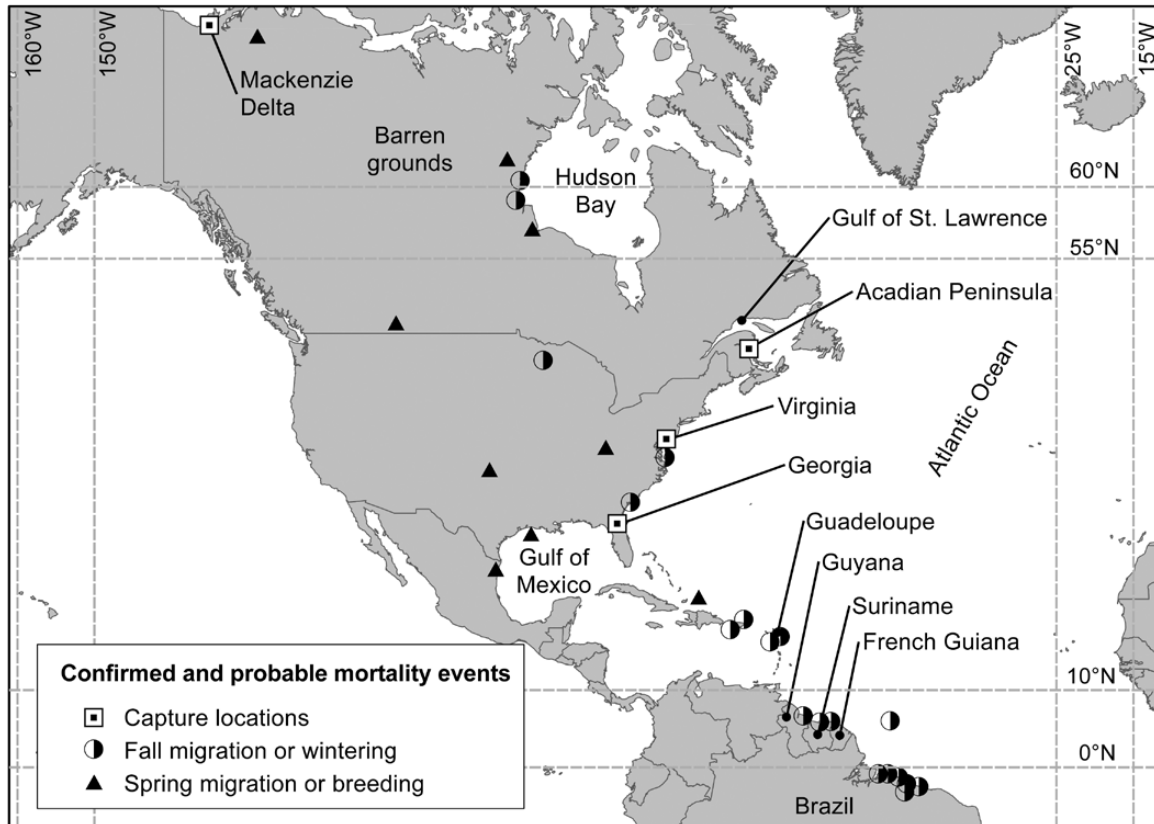


FIGURE 1. Locations where Whimbrels were originally captured and fitted with satellite transmitters (squares) and locations of subsequent confirmed and probable mortality events, based on the last signals received from transmitters. Half-shaded circles denote events that occurred during fall migration and winter; filled triangles denote events that occurred during spring migration and the breeding period.

et al. 1988). Transmitters were programmed to operate with a duty cycle of 24 hr off and 5 hr on ($n = 15$) or 48 hr off and 10 hr on ($n = 18$). Locations in latitude and longitude decimal degrees, date, time, and location error were received from CLS America within 24 hr of satellite contact with PTTs. Locations were estimated by the Advanced Research and Global Observation Satellite (ARGOS) system (www.Argos-system.org), which uses a Doppler shift in signal frequency and calculates a probability distribution within which the estimate lies. The standard deviation of this distribution gives an estimate of the location accuracy and assigns it to a “location class” (LC): LC3 ≤ 150 m, LC2 = 150–350 m, LC1 = 350–1000 m, LC0 $> 1,000$ m, LCA = location based on 3 messages and has no accuracy estimate, LCB = location based on 2 messages and has no accuracy estimate, and LCZ = location process failed. We used LC classes 1–3 to track Whimbrel locations and included LC classes 0, A, and B for “time stamps” only.

Seasonality

We used tracking data to subdivide the annual cycle into 4 seasons, including fall migration, winter, spring migration, and breeding. We delineated the length of each season, in days, for individuals based on their dates of arrival and de-

parture to and from breeding and wintering grounds each year, and calculated summary statistics across all individuals and years. We assessed arrival and departure when birds settled in or moved away from their stationary winter or breeding territories. These transitions were clear and abrupt except for the transition between fall migration and winter. Following long transoceanic flights, individuals made landfall on the northern coast of South America over a wide area from Venezuela to Brazil. Most birds landing to the west slowly made their way along the coast to Brazil where they settled on winter territories. We considered birds to have arrived on winter territories (end of fall migration and beginning of winter) when birds ceased directional movements along the coast and were resident for >1 week. Variation in landfall position and the length of time from landfall to final winter destination contributed to variation in the length of the fall migration period. We recorded no “false starts” of birds leaving breeding or wintering areas and then returning before resuming migration.

Mortality

For each bird we determined the probable cause of tracking termination (death of the bird or transmitter failure) using

TABLE 1. Summary information for adult Whimbrels tracked with satellite transmitters throughout the Western Atlantic Flyway (2008–2017). Numbers denote how many years for which each individual was tracked during a given season.

| Whimbrel | Transmitter size (g) | Breeding location | Winter location | Fall | Winter | Spring | Breeding |
|----------|----------------------|-------------------|-----------------|------|--------|--------|----------|
| 103520 | 5.0 | Mackenzie River | Brazil | 2 | 2 | 2 | 2 |
| 103521 | 5.0 | Mackenzie River | Brazil | 1 | 1 | 1 | 1 |
| 103522.1 | 5.0 | Mackenzie River | Brazil | 2 | 2 | 1 | 2 |
| 123745 | 5.0 | Mackenzie River | Brazil | 2 | 1 | 1 | 2 |
| 123746 | 5.0 | Mackenzie River | Brazil | 1 | 1 | 1 | 1 |
| 123748 | 5.0 | Mackenzie River | Brazil | 2 | 2 | 2 | 2 |
| 128483 | 5.0 | Hudson Bay | Unknown | 1 | 0 | 1 | 1 |
| 133734 | 5.0 | Mackenzie River | Brazil | 1 | 1 | 0 | 1 |
| 133735 | 5.0 | Mackenzie River | Brazil | 4 | 4 | 3 | 4 |
| 133736 | 5.0 | Mackenzie River | Brazil | 1 | 1 | 0 | 1 |
| 162868 | 5.0 | Barren Grounds | Brazil | 2 | 2 | 1 | 1 |
| 74854 | 5.0 | Mackenzie River | Brazil | 2 | 2 | 1 | 1 |
| 103522 | 9.5 | Mackenzie River | Brazil | 2 | 2 | 1 | 1 |
| 105874 | 9.5 | Hudson Bay | Brazil | 4 | 4 | 4 | 4 |
| 105875 | 9.5 | Mackenzie River | Unknown | 0 | 0 | 1 | 0 |
| 117299 | 9.5 | Hudson Bay | Suriname | 2 | 1 | 2 | 2 |
| 117300 | 9.5 | Hudson Bay | Brazil | 1 | 1 | 2 | 1 |
| 128484 | 9.5 | Hudson Bay | Unknown | 1 | 0 | 1 | 1 |
| 40166 | 9.5 | Unknown | Guyana | 1 | 1 | 0 | 0 |
| 50121 | 9.5 | Hudson Bay | Brazil | 1 | 1 | 1 | 1 |
| 74854.1 | 9.5 | Hudson Bay | Brazil | 3 | 2 | 2 | 2 |
| 74854.2 | 9.5 | Mackenzie River | Brazil | 2 | 1 | 1 | 2 |
| 74855 | 9.5 | Mackenzie River | Unknown | 1 | 0 | 1 | 1 |
| 84206 | 9.5 | Hudson Bay | Suriname | 2 | 2 | 2 | 2 |
| 88039 | 9.5 | Hudson Bay | Unknown | 1 | 0 | 1 | 1 |
| 88040 | 9.5 | Unknown | Suriname | 1 | 1 | 0 | 0 |
| 88042 | 9.5 | Hudson Bay | Unknown | 0 | 0 | 1 | 1 |
| 88043 | 9.5 | Unknown | Brazil | 1 | 1 | 1 | 0 |
| 88043.1 | 9.5 | Mackenzie River | St. Croix | 4 | 4 | 4 | 4 |
| 88044 | 9.5 | Barren Grounds | Unknown | 1 | 0 | 1 | 1 |
| 88045 | 9.5 | Unknown | Brazil | 1 | 1 | 1 | 0 |
| 88046 | 9.5 | Unknown | Brazil | 1 | 1 | 0 | 0 |
| 98354 | 9.5 | Hudson Bay | Brazil | 2 | 1 | 1 | 1 |

criteria similar to those in recent studies of avian mortality based on tracking data (e.g., Hupp et al. 2008, Klaassen et al. 2014). Contact was lost with 29 transmitters and 4 remain active at the time of writing (November 30, 2017).

Probable transmission failure ($n = 6$): Loss of contact with the transmitter was preceded by poor or intermittent transmitter performance and/or low battery voltage.

Confirmed transmission failure ($n = 2$): Transmitter behavior was as described above but the bird was subsequently identified alive. One bird lost a transmitter antenna, was subsequently resighted and recaptured, and its transmitter was removed. The second bird was resighted with an inactive transmitter.

Probable death of bird ($n = 16$): Loss of contact was abrupt despite good transmitter and battery performance or the transmitter was consistently or intermittently transmitting from a stationary position without indicating movement (activity counter stopped on 9.5-g transmitters) and the bird did not migrate during the next season.

Confirmed death of bird ($n = 5$): Tracking data is as described above but mortality was confirmed or inferred with a high level of confidence. This category includes 2

birds that were shot by hunters and whose transmitters were subsequently recovered, one transmitter that was recovered from the roof of a building with leg loops intact and presumed to be taken by a predator, and 2 birds that were lost at sea near the end of long transoceanic flights.

Statistical Analyses

We estimated survival rates in 2 ways to elucidate significant patterns. First, we estimated daily survival rates based on each individual's seasonal schedule so that we could provide estimates for discrete segments of the annual cycle (fall migration, winter, spring migration, and breeding) and test for effects of breeding origin, transmitter size, and season. In the second analysis, we estimated monthly survival rates for all birds combined regardless of where individuals were during their annual cycles so that we could examine population-level patterns and estimate an annual rate of survival.

To estimate daily survival rates, we considered exposure (days) to be a continuous variable and seasons (fall migration, winter, spring migration, and breeding) to be independent. Seasons when transmitters were deployed were considered to be left-censored on the day of deployment.

Seasons when transmitters failed or that were survived by birds were considered to be right-censored on the day of transmitter failure or at the end of the season, respectively. We estimated the dates of mortality (or presumed mortality) to be the midpoint between the last date the bird was assumed to be alive and the first date assumed dead. We considered all seasons that individuals were tracked to be independent samples for analytical purposes. We used the Andersen-Gill (A-G) version of the Cox proportional hazards model (Andersen and Gill 1982) to test for differences in survival relative to the 2 main populations of origin (Mackenzie River, Hudson Bay), transmitter size (9.5 g, 5.0 g), and season (fall, winter, spring, breeding). We also examined and compared combined migratory (spring, fall) and stationary (winter, breeding) periods. The primary assumption when comparing survival functions with A-G Cox is that the hazards are proportional over time (Andersen and Gill 1982, Winterstein et al. 2001). We compared plots of the logarithms of the estimated cumulative hazard functions and Schoenfeld residuals to test for violations of the proportional hazards assumption (Schoenfeld 1982, Cleves et al. 2016). If logarithm plots with curves of groups are not parallel or plots of Schoenfeld residuals indicate a nonzero slope, the proportional hazards assumption is violated. We used a chi-square goodness of fit test on the Schoenfeld residuals to test for a nonzero slope.

To estimate monthly survival, we used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958) with a staggered entry design (Winterstein et al. 2001) in Stata 15.0

(Stata, College Station, Texas, USA). Months when transmitters were deployed were considered to be left-censored on the date of deployment. Months when transmitters failed or that were survived by birds were considered to be right-censored on the date of transmitter failure or at the end of the month, respectively. We estimated the dates of mortality (or presumed mortality) to be the midpoint between the last date the bird was assumed to be alive and the first date assumed dead. We considered all months that individuals were tracked to be independent samples for analytical purposes. It is possible that carry-over effects between seasons or months may have influenced mortality and if so this assumption would underestimate the influence of specific periods on mortality patterns. We estimated annual survival as the product of monthly survival estimates. We estimated the SE of annual survival using a bootstrap technique in Stata (Cleves et al. 2016). To examine spatial patterns in confirmed and probable mortality events, we mapped locations based on the last transmitter signals received.

RESULTS

The annual cycle was subdivided for each individual and year into 4 seasons by departure from and arrival to wintering and breeding grounds (Figure 2, Table 2). Mean transition dates for winter were August 29 ± 2.0 days (mean ± SE) and April 12 ± 1.8 days for arrival and departure, respectively. Mean transition dates for breeding were June 2 ± 1.5 days and July 13 ± 2.0 days for arrival and

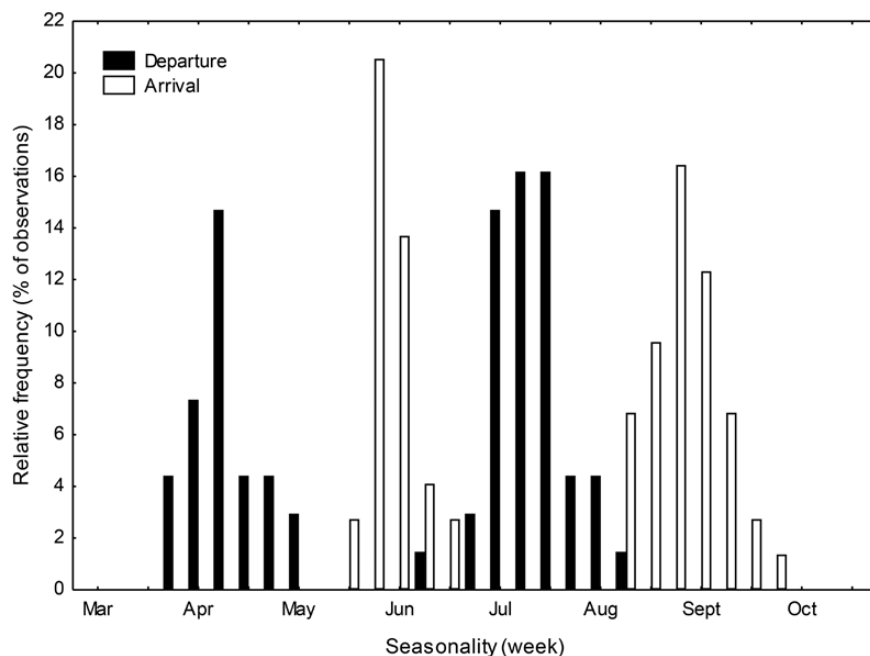


FIGURE 2. Relative weekly frequency of arrival and departure dates on wintering and breeding grounds for Whimbrels ($n = 33$) tracked with satellite transmitters throughout the Western Atlantic Flyway (2008–2017). Dates represent transitions between seasons (winter, spring migration, breeding, fall migration) throughout the annual cycle.

TABLE 2. Length (days) of seasons for individual Whimbrels and associated hazard rates as determined by satellite tracking between 2008 and 2017. Daily hazard rates (and 95% confidence intervals, CI) were estimated using the Cox Proportional Hazard model. Sample sizes represent number of individuals (total number of seasons) for which length of season could be determined.

| Season | <i>n</i> (seasons) | Mean \pm SE | Range | Hazard rate | 95% CI |
|------------------|--------------------|-----------------|---------|-------------|----------------|
| Fall migration | 33 (53) | 45.3 \pm 2.2 | 29–88 | 0.0044 | 0.0024–0.0082 |
| Winter | 29 (43) | 222.5 \pm 2.3 | 200–249 | 0.0012 | 0.0006–0.0023 |
| Spring migration | 22 (42) | 47.1 \pm 2.2 | 22–70 | 0.0053 | 0.0027–0.0106 |
| Breeding | 33 (44) | 41.6 \pm 2.6 | 8–83 | 0.0001 | 0.00009–0.0045 |

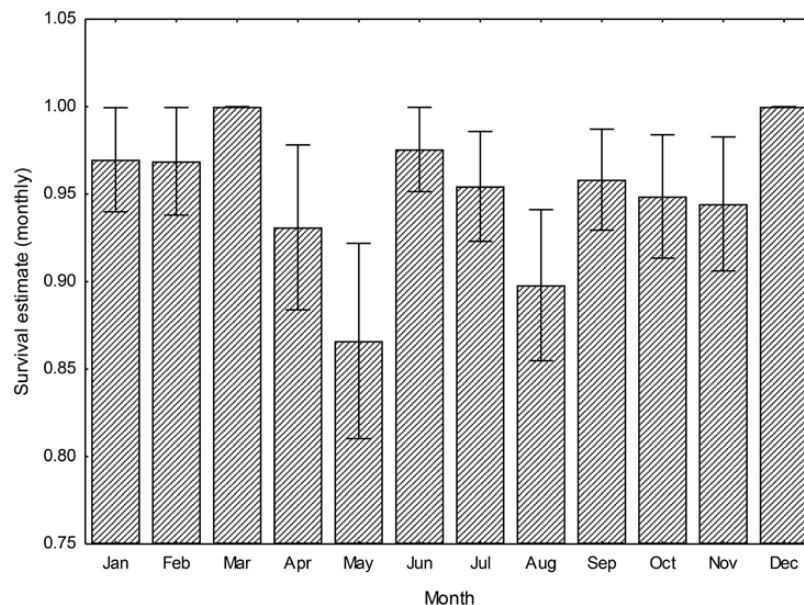


FIGURE 3. Monthly Kaplan-Meier survival estimates (\pm SE) for Whimbrels ($n = 33$) tracked with satellite transmitters throughout the Western Atlantic Flyway (2008–2017). No birds were lost during March and December (survival = 1). All birds survived all days of the period leaving no variance.

departure, respectively. The mean length of seasons was similar for fall migration, spring migration, and breeding, with each period averaging approximately 1.5 mo (Table 2). One individual was resident on the breeding ground for only 8 days, possibly reflecting an aborted breeding season or early failure. Winter dominated the annual cycle, averaging nearly 7.5 mo or 62% of the year.

Survival Estimates

We recorded 5 confirmed mortalities and 16 probable mortalities among our sample of 33 adults monitored by satellite tracking during a total time of 12,802 bird-days. We found no evidence that daily hazard rates differed between breeding populations at Mackenzie River and Hudson Bay ($df = 1$, $\chi^2 = 1.0$, $P = 0.33$) or between birds carrying transmitters of different sizes ($df = 1$, $\chi^2 = 1.2$, $P = 0.28$). However, daily hazard rates varied significantly ($df = 3$, $\chi^2 = 14.3$, $P < 0.01$) with season (Table 2) and were more than 5 times higher on average during the migration periods compared to the stationary periods (0.0049 ± 0.0022 and 0.00092 ± 0.00042 for migration and stationary peri-

ods, respectively). We tested the assumption of the Cox model that hazards were proportional over time within seasons by evaluating Schoenfeld residuals. During both the winter and breeding periods, tests of nonzero slopes of Schoenfeld residuals were nonsignificant ($\chi^2 < 0.5$, $P > 0.1$), suggesting no change in hazard risk with time. During both spring and fall migration, tests of nonzero slopes were significant ($\chi^2 > 7.5$, $P < 0.01$), suggesting a possible shift in proportional hazards during the period. Monthly survival estimates varied from a low of 0.87 in May to 1.0 in March and December (Figure 3) with an overall mean of 0.95 ± 0.01 . Estimated annualized survivorship was 0.54 ± 0.21 . As indicated by the seasonal hazard rates, there appear to be 2 bottlenecks during the year when survival is reduced—August through November and April through May. More than half (57%) of the total mortality recorded during the study occurred between late July and early November during fall migration (48%) or shortly after birds arrived on the wintering grounds (10%). One-third (33%) of mortality recorded occurred during the later stages (April through May) of spring migration.

Confirmed or probable mortality events were widely distributed throughout the geographic areas where birds were tracked (Figure 1). However, the greatest concentration of events was along the northern coast of South America from Guyana to Brazil. Contact with these birds was lost as they moved west to east along the shoreline toward Brazil or just after arriving on winter territories in Brazil. A second cluster of fall events was located on islands within the Caribbean Basin. Mortality events during spring migration were scattered. Most events occurred within terminal spring staging areas ($n = 2$) or during final flights to breeding grounds ($n = 5$).

Mortality

Most mortality events were categorized as “probable death of a bird” and the underlying cause was undetermined. However, some of the causes of mortality were confirmed or could be inferred by circumstances. Two birds were shot by hunters on Point Allegre and Port Louis Swamp on Guadeloupe during fall migration. One of the transmitters was turned in by a hunter and the second was recovered in the swamp. A third bird was presumably taken by a predator and the transmitter was left on the roof of a bank in San Mateo, Puerto Rico. Two birds were lost over the open ocean as they were approaching land. One of these birds was lost in a fallout over the Atlantic within 600 km of Brazil following a 6,290-km flight from the Gulf of St. Lawrence, Canada. The second bird was lost in the spring over the Gulf of Mexico within 120 km of land following a 6,260-km flight from Brazil. One of the birds classified as “probable mortality” was lost 5 days after being photographed in poor condition while staging during the fall along the lower Delmarva Peninsula in Virginia.

DISCUSSION

The annualized survival rate estimated from the cohort of tracked adults was 0.54 ± 0.21 . The “break-even” survival rates for this population are believed to fall between 0.8 and 0.9 (see Methods section). Previous estimates of adult survival for North American Whimbrels have been derived from the return rates of marked adults to nesting territories (Skeel 1983, Perz 2014, Johnson et al. 2016). Recent return rates reported from the Churchill study area include 0.64 (2011–2013) and 0.65 (2012–2013) (Perz 2014, Johnson et al. 2016). The former return rate resulted in an apparent survival rate of 0.73 ± 0.06 (Perz 2014). The collective population of Whimbrels using the Atlantic Flyway is believed to have declined by 50% between the early 1990s and the mid-2000s, or an average annual rate of decline of 4% per year (Watts and Truitt 2011, Morrison et al. 2012). Among 37 shorebird populations evaluated within the Western Atlantic Flyway, the Whimbrel was the fifth-most sensitive to increases in adult mortality (Watts et al.

2015b). The mean survival rate reported here is well below the range estimated for population maintenance, suggesting that low adult survival may be contributing to population declines. However, the variance of the survival estimate is high, such that the 95% CI includes the full range of sustainable values, placing some uncertainty on the role that survivorship has played in documented declines.

One of the drawbacks of using tracking devices to estimate survival is the potential confounding influence of the device on mortality. Over the past 30 yr, the use of tracking devices to investigate bird movement has grown dramatically and concerns of impacts on behavior and survival have followed (Vandenabeele et al. 2012, Enstipp et al. 2015, Weiser et al. 2016, Schacter and Jones 2017). One primary concern is load and the impact that added mass may have on flight range. Weiser et al. (2016), working across a wide range of shorebird species, reported that the impact of tracking devices on return rates to the breeding grounds was higher for small-bodied species compared to larger species, and was higher when the load was greater than 3% of body mass. However, Wong and Sandercock (2007) demonstrated that transmitters attached with leg loop harnesses reduced breeding return rates for Upland Sandpipers (*Bartramia longicauda*) compared to controls. Johnson et al. (2016) showed that the return rate of Whimbrels to the Churchill study area was not influenced by attachment of 0.65-g geolocators. We found no effect of transmitter size (9.5 vs. 5.0 g) on daily hazard rates. The 9.5-g and 5.0-g transmitters represent a load of 2% and 1%, respectively, for lean-mass birds arriving in Virginia from South America (F. M. Smith et al. personal observation). During spring stopover, birds put on 200 g of fat such that the transmitter adds an additional $\leq 5\%$ (9.5 g) to this fat load or a load of 2% and 1% for fat-mass birds. The influence of this load on the power and total energy consumption required to complete a long flight is expected to be very small (Hedenstrom 2010). However, increased load is only one type of impact associated with the use of transmitters to track migrating birds. Pennycuik et al. (2012) demonstrated that square-fronted transmitters may increase the drag coefficient by 50%, increasing energy expenditure and reducing flight range or energy reserves available upon arrival.

We recorded >100 flights longer than 2,000 km, >40 flights longer than 4,000 km, and 25 flights longer than 5,000 km (B. D. Watts et al. personal observation). All of these flights were completed except for 2, including a bird that was lost during fall migration over the Atlantic within 600 km of Brazil following a 6,290-km flight from the Gulf of St. Lawrence, Canada, and a bird that was lost during spring migration over the Gulf of Mexico within 120 km of land following a 6,260-km flight from Brazil. Transmitters may have reduced flight range for these 2 birds resulting in their inability to complete transoceanic flights. It is also

possible that transmitters may have contributed to the loss of birds during their final movements to breeding grounds. However, it seems unlikely that transmitters contributed in a substantive way to the clusters of mortality along the northern coast of South America or on Caribbean islands. All birds along the coast were lost after a week or more from the time they made landfall and so would likely have recovered from their transoceanic flights. Birds lost on the islands were put down by storms. Two of these birds were confirmed to have been shot.

We recorded mortality during all seasons. The general structure of the annual cycle as determined directly by satellite tracking is similar to that reported elsewhere derived from geolocators (Johnson et al. 2016) and from observations of arrival and departure dates (Skeel and Mallory 1996, Wilke and Johnston-Gonzalez 2009). More than 60% of the annual cycle is dominated by the winter period, so birds are exposed to hazards within the winter range for an extended time. By comparison, birds are exposed to hazards on the breeding grounds for only 11% of the year and during spring and fall migration each for only about 13% of the year. However, during migration birds are likely exposed to a greater diversity of hazards as they navigate a series of stopover locations and flights with extreme energetic demands. Daily hazard rates were more than 5 times higher during migration compared to the stationary periods.

Fall migration accounts for nearly half (47%) of all confirmed or probable mortality events recorded, and thus appears to be the most significant bottleneck in survivorship for Whimbrels using the Western Atlantic Flyway. An additional 10% of the total mortality events were recorded shortly after birds arrived on the wintering grounds. A large portion of the fall and winter mortality (>60%) occurred where both legal and illegal hunting activity is currently concentrated and during the peak time of hunting season (Watts and Turrin 2016).

Large shorebird species such as the Whimbrel, yellowlegs (*Tringa* spp.), and godwits (*Limosa* spp.) are prized by hunters and face a disproportionate amount of the harvest pressure (Hutt 1991, Ottema and Ramcharan 2009, Wege et al. 2014, Andres 2017). The estimated sustainable mortality limit is 1,200 for Whimbrels using the Western Atlantic Flyway (Watts et al. 2015b). The annual harvest on a portion of Barbados alone ranges from 100 to 160 individuals (Wege et al. 2014). Whimbrel harvest levels within the French West Indies are poorly documented, but the take of more than 100 individuals from a single swamp was documented in 2013 (A. Levesque personal communication). Annual harvest of Whimbrel within Saint Pierre and Miquelon is estimated to be in the range of 50–80 individuals (J. Paquet personal observation). Given these estimated takes for such a small portion of the areas where they may be legally taken, it is possible that the legal har-

vest alone may exceed the estimated sustainable mortality limit. Of particular concern is hunting within the coastal countries of northern South America. Whimbrels that make landfall along the western coast of northern South America (e.g., Venezuela, Guyana) and slowly move east toward winter territories in Brazil have high exposure to hunters along this route. All winter mortality or probable mortality events occurred as birds were just arriving on winter territories, a period that overlaps the peak hunting season. Both legal and illegal take continue to be a concern throughout the primary wintering area along the northern coast of South America (northern Brazil, French Guiana, Suriname, and Guyana), although harvest levels in that region are poorly understood (Ottema and Spaans 2008, Morrison et al. 2012, Andres 2017, Atlantic Flyway Shorebird Initiative Harvest Working Group 2017).

Many confirmed or probable mortality events occurred during spring migration within terminal staging sites or during final movements to breeding grounds. Staging areas used to fuel final flights to the breeding grounds have been suggested to be particularly consequential to the success of the annual cycle for some shorebird species (Piersma et al. 2005, Morrison et al. 2007, Aharon-Rotman et al. 2016). These sites often support concentrated food resources that allow birds to acquire and store enough energy to make final flights to breeding grounds and arrive in a condition adequate to withstand unpredictable weather conditions and prepare for breeding (e.g., Tulp et al. 2009, Vezina et al. 2012, Hua et al. 2013), often under tight schedules (e.g., Sandercock 1998, Atkinson et al. 2007, Smith et al. 2010). Departure from terminal staging areas and arrival on breeding grounds is highly synchronous in Whimbrels (Johnson et al. 2016, Watts et al. 2017). Whimbrels appear to have high mate fidelity (Skeel 1983) and the interval between arrival and egg laying is often short (Skeel and Mallory 1996), suggesting an advantage to highly synchronous arrival. Despite the possible importance of linkages between terminal staging areas and breeding success, relationships to adult mortality have not been investigated. Given the significance of this bottleneck, identifying the underlying causes of mortality during this period should be a research priority. As indicated above, there is a possibility that survival of spring migration may have been impacted by the use of transmitters.

With the exception of when they are engaged in long flights, Whimbrels must contend with increasing predation pressure throughout their entire annual cycle. In particular, there has been a dramatic recovery of Peregrine Falcons (*Falco peregrinus*) from historic lows in the 1980s caused by the widespread use of dichlorodiphenyltrichloroethane (DDT) (Anderson et al. 1995). Throughout much of their annual cycle, Peregrine Falcons specialize on shorebirds (e.g., Dekker 1995, Steidl et al. 1997, Long 2009), and their recovery has increased predation

pressure several-fold within wintering areas (Risebrough et al. 1990, Ottema and Spaans 2008) and stopover sites (Ross et al. 2012, Watts et al. 2015a) since the 1980s. Changes in predation pressure related to Peregrine Falcon recovery have been suggested to influence selection of stopover sites (Ydenberg et al. 2002), foraging tactics (Ydenberg et al. 2004), and migration timing and pathways (Lank et al. 2002) for small sandpipers. Peregrine Falcons and other predators play a role in survival patterns in Whimbrel and at least one of the mortality events recorded here was likely caused by a Peregrine Falcon (transmitter was stationary and transmitting from the roof of a building in Puerto Rico and was recovered with the leg-loop harness intact). The increase in Peregrine Falcon density within significant winter areas almost certainly plays a role in winter mortality. In addition to the bird that was taken in Puerto Rico, birds that were lost before dispersing from the capture site in the Mackenzie River may have been lost to the resident pair of Gyrfalcons.

We were not able to independently verify that our classifications of losses of transmitter contact were accurate. Only 24% of classifications were confirmed and “probable death” was the largest category, representing 55% of contact losses. If some of the losses assigned to this category were actually due to transmitter failure we would have underestimated the annual survival rate. However, there is no reason to suspect that transmitter failures would exhibit a seasonal pattern. More than 80% of events occurred during the later stages of spring and fall migration, periods that represent only 10% of the annual cycle. Therefore, while there may be errors of attribution for some birds, we are confident in the seasonal patterns detected.

Conclusions

Annual survival of adult Whimbrels using the Western Atlantic Flyway appears to be on the lower end of that required for population maintenance, suggesting that adult mortality may be a contributing factor to ongoing declines. We identified 2 bottlenecks in mortality, including (1) the latter half of spring migration and (2) the latter half of fall migration extending into early winter. Causes of mortality within stopover areas or during long flights are unclear but may be due in part to the use of transmitters. The recovery of Peregrine Falcons may have increased mortality within stopover areas and on winter grounds. Mortalities during the later stages of fall migration and soon after arrival on the winter grounds represent nearly 60% of the annual total and were documented during the fall hunting season and within the last remaining area throughout the Western Hemisphere where significant legal and illegal hunting occurs.

Although hunting continues to occur within a relatively small geographic region, the area included is very significant to shorebirds within the Western Atlantic Flyway.

Since an initial symposium was held in the fall of 2011, hunting has been identified as a potential population-level constraint for some shorebird species (Andres 2017). Hunting has been included in the recent Atlantic Flyway Shorebird Initiative (National Fish and Wildlife Foundation 2015) and an international coalition has been focused on strategic tasks including quantifying sustainable harvest levels, assessing current policies, estimating current harvest levels within key geographic areas, and strengthening enforcement of existing laws (Atlantic Flyway Shorebird Initiative Harvest Working Group 2017). However, a continuing impediment to effective management has been our inability to achieve an adequate assessment of current harvest levels. Investments in efforts to clarify factors contributing to reduced adult survival throughout the Flyway and discussions about how to improve policies to ensure sustainable populations should be priorities.

ACKNOWLEDGMENTS

We owe a great debt of gratitude to the technicians involved in assisting of trapping Whimbrels, especially Avery Nagy-MacArthur, Beth MacDonald, David Curtis, Jethro Runco, Shannon Ehlers, Julie Kelso, Alex Lamoreaux, Anna Fasoli, Angus Smith, Kristina Beckmann, Joanna Panipak, Alvan Buckley, Lisa Bachellier, Gennyne McCune, Tyler Kydd, Christine Anderson, Andy Day, Chris Depkin, Caitlyn Robert, Jessie McIntyre, Jessica Hawkes, and Patrick Champagne. Alex Wilke of The Nature Conservancy and Julie Guillemot of the University of Moncton Shippagan Campus provided logistical and technical support. We thank Brad Andres for supporting the project. We thank Lane, Roy, and Maureen Stewart for providing logistical support and access to their blueberry fields on the Acadian Peninsula. We thank the pilots of Aklak Air, Canadian Helicopters, Chesapeake Aviation, and FD Air Tours for safely delivering us to and from field sites. We also thank Erica Lawler, Jane Lopez, Cindy Corbet, and Michael Cole from the College of William & Mary Sponsored Programs office for fiscal and administrative assistance. We thank an Associate Editor and 2 anonymous reviewers for instructive comments on an earlier draft of this manuscript.

Funding Statement: This study and publication were completed with logistical support and/or funding provided by the U.S. Fish and Wildlife Service, Environment and Climate Change Canada, the National Fish and Wildlife Foundation's Atlantic Flyway Shorebird Initiative, The Nature Conservancy, The Georgia Department of Natural Resources Non-game Section, Manomet Inc., The Environmental Resources Network (TERN), a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant, the New Brunswick Wildlife Trust Fund, the Polar Continental Shelf Program, and the Virginia Coastal Zone Management Program at the Department of Environmental Quality. No funders had any influence on the content of the submitted or published manuscript. No funders required approval of the final manuscript to be published.

Ethics Statement: All birds were captured and handled under the Institutional Animal Care and Use Committee protocol IACUC-2017-04-18-12065 of The College of William and Mary, Environment Canada Animal Care Committee protocols EC-PN-12-006, EC-PN-13-006, EC-PN-14-006, Mount Allison University Animal Care Committee protocol 15-14, and the Government of the Northwest Territories Wildlife Care Committee protocol NWTWCC2014-007.

Author Contributions: B.D.W. formulated the questions, B.D.W., F.M.S., D.J.H., T.K., J.P., L.P.-D., J.R., B.W., and P.W. conducted the research, B.D.W. wrote the paper and analyzed the data, and F.M.S., D.J. H., J.P., and J.R. edited the paper.

Data Deposits: Our data are deposited within Movebank, a free online animal tracking database hosted by Max Planck Institute for Ornithology at <https://www.movebank.org/>.

LITERATURE CITED

- Aharon-Rotman, Y., S. Bauer, and M. Klaassen (2016). A chain is as strong as its weakest link: Assessing the consequences of habitat loss and degradation in a long-distance migratory shorebird. *Emu-Austral Ornithology* 116:199–207.
- Andersen, P. K., and R. D. Gill (1982). Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100–1120.
- Andres, B. A. (2017). Changes in shorebird harvest policy and management actions for the Western Atlantic Flyway, 2012–2017. Unpublished report, U.S. Fish and Wildlife Service, Falls Church, VA, USA. <https://www.shorebirdplan.org/wp-content/uploads/2018/08/Andres-Shorebird-Hunting-Policy-Changes-2017.pdf>
- Atkinson, P. W., A. J. Baker, K. A. Bennett, N. A. Clark, J. A. Clark, K. B. Cole, A. Dekinga, A. Dey, S. Gillings, P. M. Gonzalez, et al. (2007). Rates of mass gain and energy deposition in Red Knot on their final spring staging site is both time- and condition-dependent. *Journal of Applied Ecology* 44:885–895.
- Atlantic Flyway Shorebird Initiative Harvest Working Group (2017). Achieving a sustainable shorebird harvest in the Caribbean and northern South America—progress report, 2011–2017. Unpublished report, U.S. Fish and Wildlife Service, Migratory Bird Program, Falls Church, VA, USA. <https://www.shorebirdplan.org/wp-content/uploads/2018/08/AFSI-Shorebird-Hunting-Progress-Report-Sep-2017.pdf>
- Bainbridge, I. P., and C. D. T. Minton (1978). The migration and mortality of the Curlew in Britain and Ireland. *Bird Study* 25:39–50.
- Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de L. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts (2004). Rapid population decline in Red Knots: fitness consequences of decreased refueling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London, Series B* 271:875–882.
- Ballantyne, K. (2009). Whimbrel (*Numenius phaeopus*) nesting habitat associations, altered distribution, and habitat change in Churchill, Manitoba, Canada. M.S. thesis, Trent University, Peterborough, ON, Canada.
- Ballantyne, K., and E. Nol (2015). Localized habitat change near Churchill, Manitoba and the decline of nesting Whimbrels (*Numenius phaeopus*). *Polar Biology* 38:529–537.
- Bart, J., S. Brown, B. Harrington, and R. I. G. Morrison (2007). Survey trends of North American shorebirds: Population declines or shifting distributions? *Journal of Avian Biology* 38:73–82.
- Brown, S., C. Hickey, B. Harrington, and R. Gill (Editors) (2001). United States Shorebird Conservation Plan, 2nd edition. Manomet Center for Conservation Sciences, Manomet, MA, USA. <https://www.shorebirdplan.org/wp-content/uploads/2013/01/USShorebirdPlan2Ed.pdf>
- Burger, J. (1986). The effect of human activities on shorebirds in two coastal bays in the northeastern United States. *Environmental Conservation* 13:123–130.
- Butler, R. W., and M. J. F. Lemon (2001). Trends in abundance of Western and Least sandpipers migrating through southern British Columbia. *Bird Trends* 8:36–39.
- Cleves, M. A., W. E. Gould, and Y. V. Marchenko (2016). An Introduction to Survival Analysis Using Stata. Stata Press, College Station, TX, USA.
- Cramp, S., and K. E. L. Simmons (Editors) (1983). The Birds of the Western Palearctic, Volume 3. Oxford University Press, Oxford, UK.
- Dekker, D. (1995). Prey capture by Peregrine Falcons wintering on southern Vancouver Island, British Columbia. *Journal of Raptor Research* 29:26–29.
- Donaldson, G., C. Hyslop, R. I. G. Morrison, L. Dickson, and I. Davidson (Editors) (2000). Canadian shorebird conservation plan. Canadian Wildlife Service, Ottawa, ON, Canada. <https://waterbirds.org/wp-content/uploads/CW69-15-5-2000-eng.pdf>
- Anderson, J. H., W. Heinrich, L. Kiff, and C. M. White (1995). Population changes in North American Peregrines. *Transactions of the North American Wildlife and Natural Resources Conference* 60:142–161.
- Enstipp, M. R., J. Frost, T. E. Hollmen, R. D. Andrews, and C. Frost (2015). Two methods of radio transmitter attachment and their effects on the behavior and energetics of captive Long-tailed Ducks (*Clangula hyemalis*) during winter. *Animal Biotelemetry* 3:36–49.
- Escudero, G., J. G. Navedo, T. Piersma, P. de Goeij, and P. Edelaar (2012). Foraging conditions “at the end of the world” in the context of long-distance migration and population declines in Red Knots. *Austral Ecology* 37: 355–364.
- Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. I. Regelin (1988). Satellite telemetry: A new tool for wildlife research and management. United States Fish and Wildlife Service Resource Publication 172, Washington, D.C, USA.
- Foster, C. R., A. F. Amos, and L. A. Fuiman (2009). Trends in abundance of coastal birds and human activity on a Texas barrier island over three decades. *Estuaries and Coasts* 32:1079–1089.
- Galbraith, H., R. Jones, P. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page (2002). Global climate change and sea level rise: Potential losses of intertidal habitat for shorebirds. *Waterbirds* 25:173–183.
- Grant, M. C. (1991). Nesting densities, productivity and survival of breeding Whimbrel *Numenius phaeopus* in Shetland. *Bird Study* 38:160–169.
- Gratto-Trevor, C. L., V. H. Johnston, and S.T. Pepper (2001). Evidence for declines in Arctic populations of shorebirds. *Bird Trends* 8:27–29.

- Hedenstrom, A. (2010). Extreme endurance migration: What is the limit of non-stop flight? *PLoS Biology* 8:e1000362.
- Howe, M. A., P. H. Geissler, and B. A. Harrington (1989). Population trends of North American shorebirds based on the International Shorebird Survey. *Biological Conservation* 49:185–199.
- Hua, N., T. Piersma, and Z. Ma (2013). Three-phase fuel deposition in a long-distance migrant, the Red Knot (*Calidris canutus piersma*), before the flight to High Arctic breeding grounds. *PLOS One* 8:e62551.
- Hupp, J. W., J. A. Schmutz, and C. R. Ely (2008). Seasonal survival of radio-marked Emperor Geese in western Alaska. *Journal of Wildlife Management* 72:1584–1595.
- Hutt, M. B. (1991). Shooting of migrating shorebirds in Barbados. In *Conserving Migratory Birds* (T. Salathé, Editor). ICBP Technical Publication No. 12, International Council for Bird Preservation, Cambridge, UK. pp. 77–91.
- 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.
- Jehl, J. R., Jr. (1971). Patterns in hatching success in subarctic birds. *Ecology* 52:169–173.
- Jehl, J. R., Jr. (2007). Disappearance of breeding Semipalmated Sandpipers from Churchill, Manitoba: More than a local phenomenon. *The Condor* 109:351–360.
- Jehl, J. R., Jr., and W. Lin (2001). Population status of shorebirds nesting at Churchill, Manitoba. *Canadian Field-Naturalist* 115:487–494.
- Johnson, A. S., J. Perz, E. Nol, and N. R. Senner (2016). Dichotomous strategies? The migration of Whimbrels breeding in the eastern Canadian sub-Arctic. *Journal of Field Ornithology* 87:371–383.
- Kaplan, E. L., and P. Meier (1958). Nonparametric estimation from incomplete observations. *Journal of American Statistical Association* 53:457–481.
- Klaassen, R. H. G., M. Hake, R. Standberg, B. J. Koks, C. Treirweiler, K.-M. Exo, F. Bairlein, and T. Alerstam (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology* 83:176–184.
- Klima, J., K. Ballantyne, J. Perz, A. S. Johnson, J. A. Jackson, J. Lamarre, and L. McKinnon (2013). North American longevity records for American Golden-Plover *Pluvialis dominica* and Whimbrel *Numenius phaeopus* from Churchill, Manitoba, Canada. *Wader Study Group Bulletin* 120:134–135.
- Lank, D. B., and R. C. Ydenberg (2003). Death and danger in migratory stopovers: Problems with “predation risk.” *Journal of Avian Biology* 34:225–228.
- Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg (2002). Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303–319.
- Long, E. C. (2009). Prey utilization and energy demand of a breeding Peregrine Falcon (*Falco peregrinus*) population. M.A. thesis. College of William and Mary, Williamsburg, VA, USA.
- Maclean, G. L. (1972). Clutch size and evolution in the Charadrii. *Auk* 89:299–324.
- McCaffery, B. J. (1996). The status of Alaska’s large shorebirds: a review and an example. *International Wader Studies* 8:28–32.
- Meltofte, H., T. Piersma, H. Boyd, B. J. McCaffery, B. Ganter, V. V. Golovnyuk, K. Graham, C. L. Gratto-Trevor, R. I. G. Morrison, E. Nol, H.–U. Rosner, et al. (2007). Effects of climate variation on the breeding ecology of Arctic shorebirds. *Bioscience* 59:1–48.
- Mendez, V., J. A. Alves, J. A. Gill, and T. G. Gunnarsson (2018). Patterns and processes in shorebird survival rates: A global review. *Ibis* 160:1–19.
- Morrison, R. I. G., and R. K. Ross (1989). *Atlas of Nearctic shorebirds on the coast of South America*. Canadian Wildlife Service Special Publication, Ottawa, ON, Canada.
- Morrison, R. I. G., R. K. Ross, and L. J. Niles (2004). Declines in wintering populations of Red Knots in southern South America. *The Condor* 106:60–70.
- Morrison, R. I. G., N. C. Davidson, and J. R. Wilson (2007). Survival of the fittest: Body stores on migration and survival in Red Knots *Calidris canutus islandica*. *Journal of Avian Biology* 38:479–487.
- Morrison, R. I. G., D. S. Mizrahi, R. K. Ross, O. H. Ottema, N. Pracontal, and A. Narine (2012). Dramatic declines of Semipalmated Sandpipers on their major wintering areas in the Guianas, northern South America. *Waterbirds* 35:120–134.
- National Fish and Wildlife Foundation (2015). *Atlantic Flyway shorebird initiative: a business plan*. National Fish and Wildlife Foundation, Washington, DC, USA. <http://www.nfwf.org/amoy/Documents/afsi-business-plan-17-0523.pdf>
- Nebel, S., J. L. Porter, and R. T. Kingsford (2008). Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation* 141:971–980.
- Ottema, O. H., and S. Ramcharan (2009). Declining numbers of Lesser Yellowlegs *Tringa flavipes* in Suriname. *Wader Study Group Bulletin* 116:87–88.
- Ottema, O. H., and A. L. Spaans (2008). Challenges and advances in shorebird conservation in the Guianas, with a focus on Suriname. *Ornitologia Neotropical* 19:339–346.
- Pattie, E. L. (1990). A 16-year record of summer birds on Truelove Lowland, Devon Island, Northwest Territories, Canada. *Arctic* 43:275–283.
- Peach, W. J., P. S. Thompson, and J. C. Coulson (1994). Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. *Journal of Animal Ecology* 63:60–70.
- Pennycuik, C. J., P. L. F. Fast, N. Ballerstadt, and N. Rattenborg (2012). The effect of an external transmitter on the drag coefficient of a bird’s body, and hence on migration range, and energy reserves after migration. *Journal of Ornithology* 153:633–644.
- Perz, J. (2014). Demography of a breeding population of Whimbrel (*Numenius phaeopus*) near Churchill, Manitoba, Canada. M.S. thesis. Trent University, Peterborough, ON, Canada.
- Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology* 148:45–59.
- Piersma, T., D. I. Rogers, P. M. González, L. Zwarts, L. J. Niles, I. de Lima Donascimento, C. D. T. Minton, and A. J. Baker (2005). Fuel storage rates before northward flights in Red Knots world-wide: Facing the severest constraint in tropical intertidal environments? In *Birds of Two Worlds* (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 262–273.
- Pirie, L. D. (2008). Identifying and modeling Whimbrel (*Numenius phaeopus*) breeding habitat in the outer Mackenzie Delta, Northwest Territories. M.S. thesis. Carleton University, Ottawa, ON, Canada.
- Prater, A. J., J. H. Marchant, and J. Vuorinen (1977). *Guide to the Identification and Ageing of Holarctic Waders*. BTO Guide 17. British Trust for Ornithology, Tring, UK.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* 132:652–661.

- Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Risebrough, R. W., A. M. Springer, S. A. Temple, C. M. White, J. L. B. Albuquerque, P. H. Bloom, R. W. Fyfe, M. N. Kirven, B. A. Luscombe, D. G. Roseaneau, et al. (1990). Observaciones del Halcon Peregrino, *Falco peregrinus* subspp. *Revista Brasileira de Biologia* 50:563–574.
- Ross, R. K., P. A. Smith, B. Campbell, C. A. Friis, and R. I. G. Morrison (2012). Population trends of shorebirds in southern Ontario, 1974–2009. *Waterbirds* 35:15–24.
- Russell, R. W. (1999). Comparative demography and life history tactics of seabirds: Implications for conservation and marine monitoring. In *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals* (J. A. Musick, Editor). American Fisheries Society, Bethesda, MD, USA. pp. 51–69.
- Sandercock, B. K. (1998). Chronology of nesting events in Western and Semipalmated sandpipers near the Arctic Circle. *Journal of Field Ornithology* 69:235–243.
- Sandercock, B. K. (2003). Estimation of survival rates for wader populations: A review of mark-recapture methods. *Wader Study Group Bulletin* 100:163–174.
- Sanzenbacher, P. M., S. M. Haig, and L. W. Oring (2000). Application of a modified harness design for attachment of radio transmitters to shorebirds. *Wader Study Group Bulletin* 91:16–20.
- Schacter, C. R., and I. L. Jones (2017). Effects of geolocation tracking devices on behavior, reproductive success, and return rate of *Aethia* auklets: An evaluation of tag mass guidelines. *Wilson Journal of Ornithology* 129:459–468.
- Schoenfeld, D. (1982). Partial residuals for the proportional hazards regression model. *Biometrika* 69:239–241.
- Skeel, M. A. (1983). Nesting success, density, philopatry and nest-site selection of the Whimbrel (*Numenius phaeopus*) in different habitats. *Canadian Journal of Zoology* 61:218–225.
- Skeel, M. A., and E. P. Mallory (1996). Whimbrel (*Numenius phaeopus*). In *The Birds of North America* (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/219>
- Smith, P. A., H. G. Gilchrist, M. R. Forbes, J. L. Martin, and K. Allard (2010). Inter-annual variation in the breeding chronology of Arctic shorebirds: Effects of weather, snow melt and predators. *Journal of Avian Biology* 41:292–304.
- Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Steidl, R. J., C. R. Griffin, T. P. Augspurger, D. W. Sparks, and L. J. Niles (1997). Prey of Peregrine Falcons from the New Jersey coast and associated contaminant levels. *Northern Wildlife* 52:11–19.
- Tulp, I., H. Schekkerman, R. H. G. Klaassen, B. J. Ens, and G. H. Visser (2009). Body condition of shorebirds upon arrival at their Siberian breeding grounds. *Polar Biology* 32:481–491.
- Vandenabeele, S. P., E. L. Chepard, A. Grogan, and R. P. Wilson (2012). When three percent may not be three percent: Device-equipped seabirds experience variable flight constraints. *Marine Biology* 159:1–14.
- Vezina, F., T. D. Williams, T. Piersma, and R. I. G. Morrison (2012). Phenotypic compromises in a long-distance migrant during the transition from migration to reproduction in the High Arctic. *Functional Ecology* 26:500–512.
- Vickery, P. D., M. L. Hunter, Jr., and J. V. Wells (1999). Effects of fire and herbicide treatment on habitat selection in grassland birds in southern Maine. In *Ecology and Conservation of Grassland Birds of the Western Hemisphere* (P. D. Vickery and J. R. Herkert, Editors). *Studies in Avian Biology* 19:149–159.
- Watts, B. D., and B. R. Truitt (2011). Decline of Whimbrels within a mid-Atlantic staging area (1994–2009). *Waterbirds* 34:347–351.
- Watts, B. D., and C. Turrin (2016). Assessing hunting policies for migratory shorebirds throughout the Western Hemisphere. *Wader Study* 123:6–15.
- Watts, B. D., B. R. Truitt, F. M. Smith, E. K. Mojica, B. J. Paxton, A. L. Wilke, and A. E. Duerr (2008). Whimbrel tracked with satellite transmitter on migratory flight across North America. *Wader Study Group Bulletin* 115:119–121.
- Watts, B. D., K. E. Clark, C. A. Koppie, G. D. Therres, M. A. Byrd, and K. A. Bennett (2015a). Establishment and growth of the Peregrine Falcon breeding population within the mid-Atlantic Coastal Plain. *Journal of Raptor Research* 49:359–366.
- Watts, B. D., E. T. Reed, and C. Turrin (2015b). Estimating sustainable mortality limits for shorebirds using the Western Atlantic Flyway. *Wader Study* 122:37–53.
- Watts, B. D., F. M. Smith, and B. R. Truitt (2017). Departure patterns of Whimbrels using a terminal spring staging area. *Wader Study* 124:141–146.
- Wege, D. C., W. Burke, and E. T. Reed (2014). Migratory shorebirds in Barbados: Hunting, management and conservation. Unpublished report by Birdlife International (in collaboration with the Barbados Wildfowling Association and Canadian Wildlife Service). <https://www.shorebirdplan.org/wp-content/uploads/2018/08/Shorebird-hunting-Barbados-Wege-2014.pdf>
- Weiser, E. L., R. B. Lancot, S. C. Brown, J. A. Alves, P. F. Battley, R. Bentzen, J. Bety, M. A. Bishop, M. Boldenow, L. Bollache, et al. (2016). Effects of geolocators on hatching success, return rates, breeding movements, and change in body mass in 16 species of Arctic-breeding shorebirds. *Movement Ecology* 4:12.
- Wetlands International (2006). *Waterbird Population Estimates*. 4th edition. Wetlands International, Wageningen, The Netherlands.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46(Supplement):120–139.
- Wilke, A. L., and R. Johnston-Gonzalez (2009). Conservation Plan for the Whimbrel (*Numenius phaeopus*), Version 1.0. Manomet Center for Conservation Sciences, Manomet, MA, USA. <https://docplayer.net/44585585-Conservation-plan-for-the-whimbrel-numenius-phaeopus.html>
- Winterstein, S. R., K. H. Pollock, and C. M. Bunck (2001). Analysis of survival data from radiotelemetry studies. In *Radio Tracking and Animal Populations* (J. J. Millsbaugh and J. M. Marzluff, Editors). Academic Press, San Diego, CA, USA. pp. 351–380.
- Wong, T. W., and B. K. Sandercock (2007). Optimizing radio retention and minimizing radio impacts in a field study of Upland Sandpipers. *Journal of Wildlife Management* 71:971–980.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf (2002). Trade-offs, condition dependence and stopover site selection in migrating sandpipers. *Journal of Avian Biology* 33:47–55.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith, and J. Ireland (2004). Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. *Proceedings of the Royal Society of London, Series B* 271:1263–1269.