

Nesting Habitat Selection and Hatching Success of Whimbrels Near Churchill, Manitoba, Canada

Authors: Ballantyne, Kate, and Nol, Erica

Source: Waterbirds, 34(2) : 151-159

Published By: The Waterbird Society

URL: <https://doi.org/10.1675/063.034.0203>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Nesting Habitat Selection and Hatching Success of Whimbrels Near Churchill, Manitoba, Canada

KATE BALLANTYNE^{1,*} AND ERICA NOL²

¹Environmental & Life Sciences, Trent University, Peterborough, ON, K9J 7B8, Canada

²Biology Department, Trent University, Peterborough, ON, K9J 7B8, Canada

*Corresponding author; E-mail: kate.ballantyne@gmail.com

Abstract.—The Whimbrel (*Numenius phaeopus*) is one of a suite of sub-arctic- and arctic-nesting shorebirds for which encroachment of woody vegetation into previously open habitats may cause a reduction in breeding habitat. Whimbrel nesting habitat selection was studied at two spatial scales near Churchill, Manitoba, Canada, to determine habitat preferences and the degree to which the species avoided woody vegetation. Whimbrels occupied sites at the mesohabitat (territory) scale characterized by either high lichen cover, or high graminoid and standing water cover. No Whimbrels nested in mesohabitat with >17.5% tall shrub cover, and only one pair nested where >38 trees existed within 30 m of the nest. At the microhabitat (nest) scale, Whimbrels nested in two distinct habitats. In lichen-dominated sites, nests had less concealing vegetation than unused sites whereas in graminoid dominated habitats, nests were more concealed than unused sites. Sixty-eight percent of nests were on hummocks or lichen ridges. Hatching success was not predicted by habitat characteristics and was lower than previously reported (2007: 26%; 2008: 14%). Avoidance of woody vegetation by breeding Whimbrels suggests that shrub and tree encroachment would reduce habitat availability in the Churchill region. Received 15 January 2010, accepted 11 March 2011.

Key words.—Habitat selection, hatching success, *Numenius phaeopus*, sub-Arctic, Whimbrel.

Waterbirds 34(2): 151-159, 2011

Whimbrels (*Numenius phaeopus*, Linnaeus 1758) are migratory shorebirds that breed in open boreal, sub-arctic and arctic habitats (Skeel and Mallory 1996). In North America Whimbrels occupy two disjunct geographic breeding regions (Skeel and Mallory 1996). Declining North American populations have garnered this species a status of high conservation concern (Bart *et al.* 2007; Watts and Truitt 2008). Local declines near Churchill, Manitoba, and Wapusk National Park in the western Hudson Bay lowlands may be occurring (Jehl and Lin 2001; Rockwell *et al.* 2009). Although the causes of Whimbrel declines are unknown, alteration of breeding habitat due to climate change (Gough 1998; Caccianiga and Payette 2006; Cornelissen *et al.* 2001; Tape *et al.* 2006), resource extraction (Pirie *et al.* 2009) and increased Snow Goose (*Chen caerulescens*) foraging (Sammler *et al.* 2008) could be contributing factors.

Localized shrub encroachment near Churchill, Manitoba since the 1970s (Ballantyne 2009) and elsewhere within the geographic range of Whimbrels has been documented (Sturm *et al.* 2001; Lloyd *et al.* 2002; Tape *et al.* 2006). Whimbrels in North America have traditionally nested in open, mostly

treeless, habitats (Skeel and Mallory 1996). The degree to which Whimbrels incorporate shrubs and other woody vegetation into their territories, and the consequences for nest success will determine whether Whimbrels can persist in areas with woody vegetation encroachment.

We studied habitat selection of Whimbrels at the vegetation transition zone between boreal forest and coastal tundra. Our objectives were to (1) describe nesting habitat selection of Whimbrels at the mesohabitat (presumed territory) and microhabitat (nest site) scales to determine if there is evidence of selection for areas with less shrub and/or tree cover, and (2) determine whether incorporation of woody vegetation, and other components of habitat selection, adversely affect hatching success. Given the traditionally described open breeding habitat, we predicted that Whimbrels would avoid sites with woody vegetation. If Whimbrels both avoid habitat with woody vegetation and have lower reproductive success in sites near trees and shrubs, then future shrub and tree encroachment may contribute to local population declines.

METHODS

Study Area and Nest Monitoring

Fieldwork was conducted within approximately 79 km² and 58 km² in the vicinity of Churchill, Manitoba (58°44'N, 94°4'W, 28.7 m) during the 2007 and 2008 breeding seasons, respectively. Churchill is on the west coast of Hudson Bay at the mouth of the Churchill River, and characterized by a high sub-arctic climate (Scott 1995). The study area lies between the Hudson Bay coast and the tree line, and within 2 km of road access. The area was comprised of lichen heath, sedge meadow, mixed lichen heath and sedge meadow, hummock bog, fen and sparsely treed habitats.

We located nests through systematic walking surveys, behavioral cues and knowledge of the locations of former territories (Skeel 1976; Lin 1997). When Whimbrels were observed during surveys, we hid and watched adults returning to their nests (Skeel 1976). We recorded nest locations with a Global Positioning System (GPS). Locations of nests and areas surveyed were delineated on 1:50,000 digital National Topographic System (NTS) maps (Natural Resources Canada) within ArcMap 9.2 (ESRI 2006).

Nests were monitored every 1-10 d until eggs showed signs of hatching and subsequently, every 1-3 d until hatch. Nests were observed for <5 s from 1-4 m away to determine whether adults were incubating, but nest checks were avoided when predators were seen in the vicinity. We considered a nest successful if ≥1 egg hatched. We used presence of small eggshell fragments (Mabee 1997), alarm-calling parents, and/or young at or near the nest as signs of success and empty nests early in the incubation period, nest disturbance, and/or destroyed eggs and/or young as signs of nest failure.

Habitat Variable Measurements

Habitat measurements were conducted in 2007 after nests had fledged or failed. We defined mesohabitat (presumed territory) as the area within a 150 m radius circle centered on the nest or a randomly-selected available site. A 150 m radius was chosen because most Whimbrels defended their nests on our approach from this distance, and this approximates the size of a Whimbrel territory (Skeel and Mallory 1996). Hawth's Tools extension (Beyer 2008) for ArcMap 9.2 (ESRI 2006) was used to generate random sites in the area where we searched for nests. We excluded the coast of Hudson Bay and the boreal forest tree line, two habitats not known to be used by nesting Whimbrel (Skeel and Mallory 1996; Peck and Sutherland 2007), and points that fell within water, were >1.5 km from a road and were in known territories. In each 150 m radius mesohabitat scale plot we placed twelve 1 m radius circle plots at 50m, 100m and 150 m from the nest/randomly-selected point in each cardinal direction. For microhabitat analyses we also placed a plot at the nest. We defined the microhabitat (nest site) scale as the area within a 1 m radius of the nest or unused micro-sites at 50m, 100m and 150 m away in the cardinal directions of the nest within occupied mesohabitat only.

In each mesohabitat scale plot we counted the number of trees (≥2 m tall) within 30 m of nests or random points. Within each 1 m radius circle plot percent cover of graminoid (sedge/grass/rush—predominantly sedge), dwarf shrub (≤0.5 m), tall shrub (>0.5 m), tree

(≥2 m), *Dryas* heath (*Dryas integrifolia* and Ericaceae plants), moss, lichen, *Equisetum* spp., herbs (other than above), bare ground, rock, gravel, sand, litter, lake/deep pond and standing water was estimated. We classified soil moisture as dry (1), moist (2), wet (3) or saturated (4) (Pirie 2008). Shallow ponds (<2 m) with and without emergent vegetation or exposed peat were classified as standing water. At the nest site we also recorded distance to nearest water and tree (≥2 m tall), whether nests were located on a hummock or lichen ridge and the presence and compass bearing of protrusions (e.g. moss tussock, clumps of vegetation) rimming the nest cup. Vegetation density was estimated as the percentage of a 21.6 cm × 27.9 cm horizontally placed cover board obscured from 160 cm above the ground at 3 m distance, assessed from each of the four cardinal directions.

Statistical Analysis

Habitat data from the twelve sampling plots within occupied and randomly-selected, available mesohabitat were averaged and compared to assess selection at this scale. At the microhabitat scale, data from nest site sampling plots were compared to the data from the twelve averaged unused micro-sites within the same presumed territory. At both scales, cover classes with mean percent occurrences <5% were removed from analysis [mesohabitat scale: tree (2.5%), *Equisetum* spp. (0%), herbs (1.5%), bare ground (1.5%), gravel (3.5%), rock (0.5%), sand (0.5%) and litter (0.5%); microhabitat scale: tall shrub (1.5%), tree (0.5%), *Equisetum* spp. (0%), herbs (1%), bare ground (1.5%), gravel (0.5%), rock (0.5%), sand (0%) and litter (1%)]. Pearson product-moment correlation analysis showed high correlations ($r \geq 0.40$) between remaining pairs of variables. To avoid multicollinearity (Graham 2003), we used principal component analysis (PCA) based on correlation matrices to reduce variables into a smaller number of principal components (PCs). At the mesohabitat scale PCs 1, 2, 3 and 4 (eigenvalues = 3.77, 1.43, 1.13 and 0.84, respectively) were retained (72% variance explained). At the microhabitat scale PCs 1 and 2 (eigenvalues = 2.51 and 1.56, respectively) were retained (68% variance).

Multiple logistic regression using all linear, additive combinations of retained principal components and a null model were used to build 16 candidate models in which the dependent variable distinguished between occupied and available mesohabitat (Hosmer and Lemeshow 2000). Akaike's Information Criteria (AIC) corrected for small sample size (AICc) and Akaike weights (w_i) were used to assess the relative likelihoods of models, and to calculate importance values to assess the relative importance of predictor variables (Burnham and Anderson 2002). We report parameter estimates and 95% CI for the best-supported model. We assessed the best-supported model reliability by the area under the receiver operating characteristic (ROC) curve (Hosmer and Lemeshow 2000).

Nests were found in two distinct habitats, but this categorization reduced the sample sizes at the microhabitat scale so that logistic regression models did not converge. Thus, we performed paired t-tests to determine if any variables differed significantly between nests and unused micro-sites within the presumed territory. A goodness of fit test (Sokal and Rohlf 1995) was used to determine whether the number of protrusions rimming

the nest to the NE, SE, SW and NW directions deviated from a 1:1:1:1 ratio.

Logistic-exposure models were used to determine which, if any, habitat variables in occupied territories measured in 2007 predicted daily nest survival (DNS) in that year (Shaffer 2004a, b). As above, because of high correlations between habitat features, we used PCA and retained PC 1 (eigenvalue = 4.42, 47% of variance). We used all linear, additive combinations of the following variables to build models: PC1, nest age (using a 5-day laying period and 25-day incubation period (Lin 1997; unpublished data), distance of nest to nearest road, distance of nest to nearest nesting conspecific and the number of trees within 30 m.

We report on nest success from the constant-survival logistic-exposure model (Shaffer 2004a, b). Apparent hatching success (number of nests with ≥ 1 egg hatched/total number of nests), clutch size and the proportion of eggs monitored that hatched is also reported for comparison to previously published data.

Log and Box-Cox transformations were used when data were not normally-distributed. Analyses were conducted using SAS version 9.0 (SAS Institute Inc. 1999), STATISTICA™ version 7 (StatSoft Inc. 2004), and Analyse-it (Analyse-it Software Ltd. 2007). A significance level of 0.05 was used.

RESULTS

In 2007 and 2008 we located 45 (density = 0.57 pairs/km²) and 38 (density = 0.66 pairs/km²) nests respectively, throughout the surveyed area near Churchill. The average distance to a nearest active Whimbrel nest was 481 ± 63 m ($N = 83$ nests), although some Whimbrel pairs nested in areas with no other conspecifics nearby (maximum dis-

tance between pairs: 3.7 km), while other pairs nested in loose aggregations (minimum distance between pairs: 96.3 m).

Mesohabitat Associations

Four PCs accounted for 71.7% of mesohabitat variation at 44 occupied and 47 available sites (Table 1). The first principal component (PC1) described a wet to dry gradient of standing water and graminoids (negative values) to *Dryas* heath (positive values, Table 1). PC2 separated habitat characterized by dwarf shrubs and *Dryas* heath (negative) from habitat characterized by lakes/deep ponds and tall shrubs (positive). PC3 differentiated habitat with high lichen cover (negative) from shrubby habitat with high dwarf and tall shrub cover (positive). PC4 separated habitat with high numbers of trees within 30 m and tall shrub cover (negative) from habitats with moss and lichen cover (positive). The best-supported candidate model to distinguish between Whimbrel occupied and available mesohabitat contained PCs 1, 3 and 4 (Table 2). The area under the ROC curve using the three principal components in the top model was 0.78 (95% CI: 0.69-0.88), indicating useful discrimination (Manel *et al.* 2001). Occupied mesohabitat

Table 1. Eigenvectors, eigenvalues, and variance explained by principal components (PCs) of mesohabitat variables measured at Whimbrel (*Numenius phaeopus*) nests ($N = 44$), and randomly-selected, available sites ($N = 47$) near Churchill, MB, 2007.

	PC			
	1	2	3	4
Mesohabitat variable				
Graminoid	-0.38	-0.20	0.29	-0.11
Dwarf shrub	0.14	-0.34	0.56	0.18
Tall shrub	0.27	0.34	0.38	-0.38
<i>Dryas</i> heath	0.39	-0.30	-0.28	-0.08
Moss	0.28	-0.21	0.20	0.30
Lichen	0.26	-0.01	-0.54	0.10
Lake/deep pond	0.18	0.71	0.07	0.12
Standing water	-0.43	0.12	-0.20	-0.19
Soil moisture	-0.41	-0.24	-0.03	-0.21
# Trees within 30 m	0.29	-0.17	0.01	-0.78
Eigenvalue	3.77	1.43	1.13	0.84
Total variance explained (%)	37.68	14.34	11.34	8.37
Cumulative variance explained (%)	37.68	52.01	63.35	71.72

Table 2. Akaike’s Information Criteria adjusted for small sample size (AICc), ΔAICc, and Akaike weights (w_i) for models composed of all linear, additive combinations of four PCs and a null model from multiple logistic regression analysis to distinguish between Whimbrel (*Numenius phaeopus*) occupied and randomly-selected, available mesohabitat. Parameter importance values (calculated by summing w_i of models containing the parameter of interest), and parameter estimates, standard errors (SE) and 95% confidence intervals (CI) for the best-supported candidate model are presented.

Model	K	AICc	ΔAICc	w_i
PC1, PC3, PC4	4	112.52	0.00	0.75
PC1, PC2, PC3, PC4 (Global)	5	116.24	3.70	0.12
PC1, PC3	3	117.87	5.34	0.05
PC1, PC4	3	118.68	6.14	0.04
PC1, PC2, PC3	4	120.02	7.48	0.02
PC1, PC2, PC4	4	120.87	8.34	0.01
PC1	2	121.87	9.33	0.01
PC3, PC4	3	122.40	9.87	0.01
PC1, PC2	3	123.94	11.40	<0.01
PC2, PC3, PC4	4	124.54	12.00	<0.01
PC3	2	124.57	12.03	<0.01
PC4	2	126.31	13.77	<0.01
PC2, PC3	3	126.64	14.10	<0.01
PC2, PC4	3	128.38	15.85	<0.01
Null	1	128.10	15.56	<0.01
PC2	2	130.12	17.58	<0.01

Parameter	Importance Value	Estimate	SE	95% CI	
				Lower	Upper
Intercept		-0.21	0.25	-0.70	0.29
PC1	0.99	-0.43	0.15	-0.72	-0.14
PC3	0.94	-0.61	0.25	-1.10	-0.13
PC4	0.92	0.76	0.35	0.08	1.44

had more negative PC1 and PC3 scores and more positive PC4 scores than available sites and none of these parameter estimates included zero (Table 2). These results indicate preference for territories with standing water and graminoids (PC1), or lichen cover (PC3) and avoidance of trees and tall shrubs (PC3, PC4). Only one Whimbrel pair nested in an area with >38 trees within 30 m, while no Whimbrels nested in an area with >17.5% tall shrub cover (Fig. 1).

Microhabitat Associations

Two PCs accounted for 68.4% of the variation in microhabitat variables at 44 nests and 44 unused micro-sites (Table 3). PC1 described a dry to wet gradient of *Dryas* heath and lichen (negative) to standing water and graminoids (positive). PC2 separated habitat characterized by dwarf shrubs and moss (negative) from habitat charac-

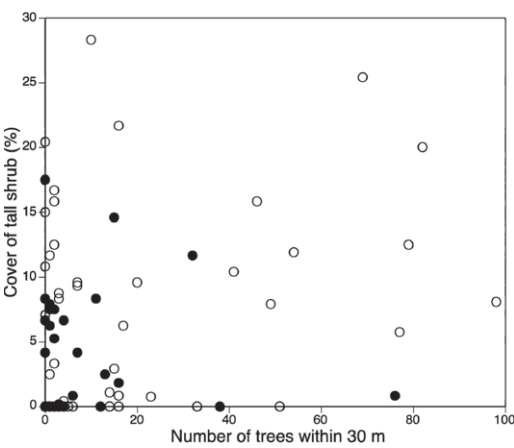


Figure 1. Number of trees within 30 m of nest plotted against percent cover of tall shrub for Whimbrel occupied (●; N = 44), and randomly-selected available (○; N = 47) habitat.

terized by lichen (positive). The plot of PC1 against PC2 showed nesting in two disjunct

Table 3. Eigenvectors, eigenvalues, and variance explained by principal components (PCs) of microhabitat variables measured at Whimbrel (*Numenius phaeopus*) nests (N = 44) and unused micro-sites (N = 44) near Churchill, MB, 2007.

Microhabitat variable	PC	
	1	2
Graminoid	0.45	-0.19
Dwarf shrub	-0.24	-0.66
<i>Dryas</i> heath	-0.50	-0.14
Moss	-0.29	-0.56
Lichen	-0.42	0.45
Standing water	0.48	0.04
Eigenvalue	2.54	1.57
Total variance explained (%)	42.31	26.11
Cumulative variance explained (%)	42.31	68.42

habitat clusters described orthogonally by PC1, reflecting use of both lichen heaths and wetter habitats with high graminoid cover (Fig. 2).

In lichen heath habitat, nest sites had significantly lower PC1 values, corresponding to higher percent lichen and *Dryas* heath cover than unused micro-sites (Table 4). Nest sites also had significantly less concealing vegetative cover than unused micro-sites.

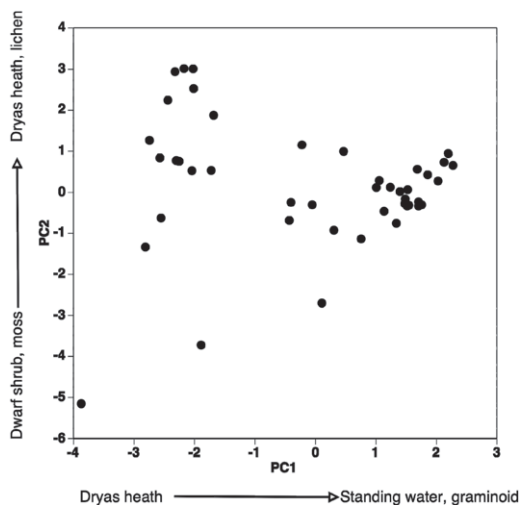


Figure 2. Microhabitat principal components (PC) 1 and 2 scores for nest sites, showing that nests were found in two habitats as described orthogonally by PC1. Axis labels refer to habitat variables with largest eigenvectors. As data were bimodal further microhabitat analyses were conducted separately.

In contrast, in habitats with higher standing water and graminoid cover, nest sites had higher nest concealment values than unused micro-sites (Table 4).

Sixty-eight percent (30/44) of nests were located on a hummock or lichen ridge. Eighty-four percent (37/44) of nests were rimmed by some sort of protrusion, but in no significant pattern of orientation ($G(3) = 5.22$, $P = 0.16$).

Hatching Success

Of the 45 nests located in 2007, 18 (40%) resulted in ≥ 1 hatched young. Constant-survival logistic-exposure modeling resulted in an estimated DSR of 0.947 (95% CI = 0.923-0.964), corresponding to a hatching success of 26% (95% CI = 14-40%). Sixty-nine percent (31/45) of clutches contained four eggs. Of 151 known eggs laid, 58 hatched (38%; five eggs were left in nest unhatched; hatch dates: range = June 30-July 18, mode = July 2, mean = July 5). In 2008, 11 (31%) of the 35 nests monitored resulted in ≥ 1 hatched young. The DSR estimate was 0.926 (95% CI = 0.890-0.950), corresponding to a hatching success of 14% (95% CI = 6-28%). Sixty-eight percent (26/38) of clutches contained four eggs. Of 122 eggs monitored, 45 hatched (37%; hatch dates: range = July 2-July 18, mode = July 4, mean = July 7). Predation was the main cause of nest loss in both years. The only predation events observed were those by Common Ravens (*Corvus corax*). Additionally, a regurgitated owl pellet was found in a depredated nest located 90 m away from a Short-eared Owl (*Asio flammeus*) nest.

The best-supported candidate model to distinguish between nests that hatched successfully and those that failed contained the variable nest age. The parameter estimate for nest age was positive (0.0814, 95% CI: 0.0243-0.1386) indicating that nests further into incubation were more likely to hatch. No models containing habitat variables were well supported, nor had parameter estimates with 95% confidence intervals that did not include zero.

Table 4. Comparison of nest and unused micro-sites (average of 12 measurements) within presumed territory for drier habitats with more lichen (PC1 <-1) and wetter habitats with more graminoids (PC1 >-1).

Microhabitat Variable	Mean ± SE Nest	Mean ± SE Unused	<i>t</i>	<i>P</i>
Lichen-dominated (N = 16)				
PC1	-2.34 ± 0.13	-0.97 ± 0.28	-4.80	<0.01
PC2	0.59 ± 0.59	-0.17 ± 0.33	1.68	0.11
Distance to nearest water (m)	32.04 ± 9.79	20.12 ± 3.97	0.69	0.51
Distance to nearest tree (>2 m) (m)	28.34 ± 5.92	27.82 ± 4.18	-0.25	0.80
Vegetation density (% cover 3 m away)	1.63 ± 0.34	4.43 ± 1.09	-2.09	0.05
Sedge-standing water and graminoid (N = 28)				
PC1	1.17 ± 0.15	0.72 ± 0.18	1.78	0.09
PC2	-0.11 ± 0.15	-0.13 ± 0.08	0.66	0.52
Distance to nearest water (m)	8.51 ± 3.21	6.58 ± 1.55	-1.66	0.11
Distance to nearest tree (>2 m) (m)	37.43 ± 7.11	37.80 ± 4.44	-1.84	0.08
Vegetation density (% cover 3 m away)	5.68 ± 1.24	2.36 ± 0.71	-3.05	<0.01

DISCUSSION

Whimbrels in our study bred in a mix of open habitats, but avoided habitat with high tall shrub and tree cover. Similarly, Whimbrels in the Mackenzie Delta, Northwest Territories nested in a variety of habitats including both upland tundra and low-centered polygon graminoid sites, and were absent in areas with dense shrub and with little to no standing water (Gratto-Trevor 1994; Pirie 2008). By contrast, in eastern Finnish Lapland, Whimbrels nest in a wide range of open habitats including clear-cuts, strip-cuts, bogs, flark fen, mires, alpine and dry heaths, seedling stands and mountain birch forest (Pulliainen and Saari 1993), demonstrating apparently greater flexibility in habitat selection than exhibited by the North American population.

We did not find any habitat variables within the presumed territory that were predictive of hatching success. Few Whimbrels in our study nested near trees or shrubs and neither the number of trees within 30 m of the nest nor percent cover of shrubs predicted nest success. Most shorebirds have evolved to breed in open landscapes, presumably in part to facilitate predator detection (Götmark *et al.* 1995). The function is supported by our and other observations (Jónsson and Gunnarsson 2010) of Whimbrels aggressively defending their nests from mobbing Common Ravens, even while these

predators are several hundred meters away. However, many of our nests were nonetheless presumed lost to ravens as, after Whimbrels had intercepted ravens, these nest predators often returned to fly over the nest area.

In eastern Finnish Lapland, where although a wider range of habitats were occupied, Whimbrel hatching success was higher in the more open alpine heaths than in drier heaths with scattered pines (Pulliainen and Saari 1993). In Scotland, similar to our findings, no habitat variable helped to explain variation in reproductive success (Grant 1991). When preferences displayed during habitat selection are not correlated with nest success then selection for these preferences may be relaxed (Clark and Shutler 1999). Possible incorporation of trees and shrubs into territories as result of the absence of selection against those Whimbrels nesting nearer to trees could aid in adaptation to future environments, if reproduction is sufficient to balance adult mortality and Whimbrels persist in this region.

Preference for shallow ponds in Whimbrel territories may be due to the enhanced foraging opportunities (e.g. amphibians, Didyk and Burt 1999) in these habitats. Whimbrels are associated with sedge pools in Iceland (Gunnarsson *et al.* 2006), and with wet-sedge low-centered polygon habitat in the outer Mackenzie Delta (Pirie 2008). Near Churchill, even the drier, lichen-domi-

nated habitat occupied by Whimbrels contained numerous shallow ponds. The net loss of arctic and sub-arctic ponds due to increased drainage as permafrost warms and increased evapotranspiration due to climate warming (Yoshikawa and Hinzman 2003; Smith *et al.* 2005; Riordan *et al.* 2006), could provide an additional threat to this species' long-term viability above that imposed by shrub and tree encroachment (Chapin *et al.* 1995; Sturm *et al.* 2001).

Within lichen-dominated habitats, nest sites had higher lichen and *Dryas* heath cover than unused micro-sites within the same presumed territory, possibly to enhance egg crypsis (Byrkjedal 1989; Nguyen *et al.* 2007). Nest sites also had lower vegetation density or nest concealment values. By contrast, within habitats with greater standing water and graminoid cover, nest sites were differentiated from unused micro-sites by more dense vegetation. In this wetter habitat type, greater vegetation density may aid in nest concealment, or alternatively, be an artifact of requiring a hummock large and high enough for nest placement. Bimodality in habitat preferences at the nest site scale suggests relative habitat flexibility in that both open wet graminoid and drier lichen heath habitats are available for nesting. Such bimodality contrasts with shorebird species that have strong preferences for only one arctic habitat (e.g. Red-necked Phalaropes, *Phalaropus lobatus*, wet-sedge meadows; Walpole *et al.* 2008) and as a possible consequence, are more restricted in distribution in the Churchill region (Jehl 2004).

Microhabitat selection is probably in part predicted by topographic variables. Upon arrival on breeding grounds, water levels are higher than later in the season and hummocks and ridges offer dry ground, particularly in wet graminoid habitats. Hummocks and ridges may also provide disruptive camouflage and/or a better view of surroundings (Skeel 1976). Placement of the majority of nests on hummocks and/or ridges has been reported by others (Skeel 1983; Grant 1992; Pirie 2008) and appears to be a consistent dominant feature of habitat selection among Whimbrel sub-species.

Whimbrels have lower rates of hatching success than that reported for other species of locally breeding shorebirds (e.g. Semipalmated Plover (*Charadrius semipalmatus*): 70%, Nol *et al.* 1997; Semipalmated Sandpiper (*Calidris pusilla*): 78%, Jehl 2006; Stilt Sandpiper (*C. himantopus*): 83.2%, Jehl 1973; American Golden Plover (*Pluvialis dominica*): 71%, Byrkjedal 1989) although some of these estimates are quite old and are not corrected for exposure days. Whimbrels are also the largest of the locally-breeding shorebirds. Hatching success during our study was low compared to that reported from previous studies on this species conducted near Churchill (49% to 65%, but as high as 86% in hummock bog habitat; Skeel 1976, 1983; Lin 1997; Jehl 2004). Elsewhere, reported estimates of hatching success range from 39% to 78% (Grant 1991; Morozov 1993; Pulliainen and Saari 1993; Pirie 2008). The reason for the comparatively high rate of nest predation in our study is unknown but further investigation, in particular, on the impacts of local raven and other predator populations (Watts *et al.* 1991) is warranted.

Whimbrel predation rates may be even higher during the fledgling stage (Grant 1989; Lin 1997). During the mid-1990s in the Churchill area, only 3/30 (10%) chicks of eight broods survived past two weeks (Lin 1997). A low reproductive rate (four-egg clutch, high nest failure, one brood per year, and delayed age of first breeding) may be countered by high adult survivorship and longevity (89% return rate for *N. p. phaeopus*, Grant 1991; longevity records of 13 years for *N. p. hudsonicus*, Klimkiewicz 2008, 26 years for *N. p. phaeopus*, BTO 2010). Low hatching success of Whimbrels may be the result of climate-mediated changes in predator communities (Post *et al.* 2009). Continued research on Whimbrels near Churchill and elsewhere should focus on obtaining habitat-specific adult and juvenile survival estimates to determine whether this low hatching success is sustainable. Our information, coupled with continued studies on the migration and wintering grounds will further elucidate the conservation status of this species.

ACKNOWLEDGMENTS

Funding was provided by the Natural Sciences and Engineering Research Council of Canada through a Discovery Grant (EN) and a Northern Research Internship (KB), and by Indian and Northern Affairs Canada through the Northern Scientific Training Program. Additional funds were provided by the Northern Research Fund of the Churchill Northern Studies Centre. Previous research near Churchill by M. Skeel, W. Lin and J.R. Jehl Jr. increased understanding of Whimbrels and helped direct our studies. K. Abraham, B. Pond, J. Nocera and L. Manne improved this manuscript. We are grateful to C. Anderson, F. Forsynth, K. Jansen, C. Jardine, A. Rawluk, C. Risley, S. Williams and L. Worrell for their skill in the field. We thank the local community for welcoming researchers on their land.

LITERATURE CITED

- Analyse-it Software Ltd. 2007. Analyse-it Method Evaluation Edition for Microsoft Excel version 2.00. Leeds, U.K.
- Ballantyne, K. 2009. Whimbrel (*Numenius phaeopus*) nesting habitat associations, altered distribution, and habitat change in Churchill, Manitoba, Canada. Unpublished M.Sc. Thesis, Environmental and Life Sciences Graduate Program, Trent University, Peterborough, Ontario.
- Bart, J., S. Brown, B. A. 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.
- Beyer, H. 2008. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools/tool-desc.php>, accessed 1 July 2007.
- British Trust for Ornithology (BTO) 2010. <http://btor-ing.blogspot.com/search?q=whimbrel>, accessed 28 January 2011.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, New York.
- Byrkjedal, I. 1989. Nest habitat and nesting success of Lesser Golden-plovers. *Wilson Bulletin* 101: 93-96.
- Caccianiga, M. and S. Payette. 2006. Recent advance of White Spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). *Journal of Biogeography* 33: 2120-2135.
- Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer and J. A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.
- Clark, R. G. and D. Shutler. 1999. Avian habitat selection: Pattern from process in nest-site use by ducks? *Ecology* 80: 272-287.
- Cornelissen, J. H. C., T. V. Callaghan, J. M. Alatalo, A. Michelsen, E. Graglia, A. E. Hartley, D. S. Hik, S. E. Hobbie, M. C. Press, C. H. Robinson, G. H. R. Henry, G. R. Shaver, G. K. Phoenix, D. G. Jones, S. Jonasson, F. S. Chapin, U. Molau, C. Neill, J. A. Lee, J. M. Melillo, B. Sveinbjornsson and R. Aerts. 2001. Global change and arctic ecosystems: Is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89: 984-994.
- Didyk, A. S. and M. D. B. Burt. 1999. Frogs consumed by Whimbrels, *Numenius phaeopus*, on breeding grounds at Churchill, Manitoba. *Canadian Field-Naturalist* 113: 663-664.
- ESRI. 2006. ArcGIS 9.2. Environmental Systems Research Institute Inc., Redlands, California.
- Götmark, F., D. Blomqvist, O. C. Johansson and J. Bergqvist. 1995. Nest-site selection: A trade-off between concealment and view of the surroundings. *Journal of Avian Biology* 26: 305-312.
- Gough, W. 1998. Projections of sea-level change in Hudson and James Bays, Canada, due to global warming. *Arctic and Alpine Research* 30: 84-88.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809-2815.
- Grant, M. C. 1991. Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel *Numenius phaeopus*. *Ibis* 133: 127-133.
- Grant, M. C. 1992. The effects of re-seeding heathland on breeding Whimbrel *Numenius phaeopus* in Shetland. I. Nest distributions. *Journal of Applied Ecology* 29: 501-508.
- Gratto-Trevor, C. L. 1994. Monitoring shorebird populations in the Arctic. *Bird Trends* 3: 10-12.
- Gunnarsson, T. G., J. A. Gill, G. F. Appleton, H. Gislason, A. Gardarsson, A. R. Watkinson and W. J. Sutherland. 2006. Large-scale habitat associations of birds in lowland Iceland: Implications for conservation. *Biological Conservation* 128: 265-275.
- Hosmer, D. W. and S. Lemeshow. 2000. Applied Logistic Regression, 2nd ed. John Wiley and Sons, Inc., New York, New York.
- Jehl, J. R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. *Wilson Bulletin* 85: 115-147.
- Jehl, J. R., Jr. 2004. Birdlife of the Churchill Region: Status, History, Biology. Trafford Publishing, Victoria, British Columbia.
- Jehl, J. R. Jr. 2006. Coloniality, mate retention and nest site characteristics in the Semipalmated Sandpiper. *Wilson Journal of Ornithology* 118: 478-484.
- Jehl, J. R., Jr. and W. L. Lin. 2001. Population status of shorebirds nesting at Churchill, Manitoba. *Canadian Field-Naturalist* 115: 487-494.
- Jónsson, J. E. and T. G. Gunnarsson. 2010. Predator chases by breeding waders: Interspecific comparison of three species nesting in Iceland. *Wader Study Group Bulletin* 117: 145-149.
- Klimkiewicz, M. K. 2008. Longevity records of North American birds. Version 2008.1. Patuxent Wildlife Research Center. Bird Banding Laboratory. Laurel, Maryland. www.pwrc.usgs.gov/BBL/homepage/longvrec.htm, accessed 7 October 2009.
- Lin, W. L. 1997. Parental behavior and the question of brood division in Whimbrels (*Numenius phaeopus*). Unpublished M.Sc. Thesis, Department of Marine Science, University of San Diego, San Diego, California.
- Lloyd, A. H., T. S. Rupp, C. L. Fastie and A. M. Starfield. 2002. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *Journal of Geophysical Research* 107: 8161.
- Mabee, T. J. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bulletin* 109: 307-313.
- Manel, S., H. C. Williams and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology* 38: 921-931.
- Morozov, V. V. 1993. Zonal peculiarities of the ecology of Whimbrel. *Russian Journal of Ecology* 24: 118-122.

- Nguyen, L., K. Abraham and E. Nol. 2007. Using digital photographs to evaluate the effectiveness of plover egg crypsis. *Journal of Wildlife Management* 71: 2084-2089.
- Nol, E., M. Sullivan Blanken and L. Flynn. 1997. Sources of variation in clutch size, egg size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. *Condor* 99: 389-396.
- Peck, M. and D. A. Sutherland. 2007. Whimbrel. In Cadman, M. D., D. A. Sutherland, G. G. Beck, D. Lepage and A. R. Couturier (Eds.). 2007. *Atlas of the Breeding Birds of Ontario 2001-2005*. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources and Ontario Nature, Toronto, Ontario.
- Pirie, L. 2008. Identifying and modeling Whimbrel *Numenius phaeopus* breeding habitat in the outer Mackenzie Delta, Northwest Territories. Unpublished M.Sc. Thesis, Department of Biology, Carleton University, Ottawa, Ontario.
- Pirie, L. D., C. F. Francis and V. H. Johnston. 2009. Evaluating the potential impact of a gas pipeline on Whimbrel breeding habitat in the outer Mackenzie Delta, Northwest Territories. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 4: 2.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. Martin Schmidt and P. Aastru. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355-1358.
- Pulliamin, E. and L. Saari. 1993. Breeding biology of the Whimbrel *Numenius phaeopus* in eastern Finnish Lapland. *Ornis Fennica* 70: 110-116.
- Riordan, B., D. Verbyla and A. D. McGuire. 2006. Shrinking ponds in subarctic Alaska based on 1950-2002 remotely sensed images. *Journal of Geophysical Research* 111: 1-11.
- Rockwell, R. F., K. F. Abraham, C. R. Witte, P. Matulonis, M. Usai, D. Larsen, F. Cooke, D. Pollak and R. L. Jefferies. 2009. *The Birds of Wapusk National Park*. Wapusk National Park of Canada Occasional Paper 1. Parks Canada, Winnipeg, Manitoba.
- Sammler, J. E., D. E. Andersen and S. K. Skagen. 2008. Population trends of tundra-nesting birds at Cape Churchill, Manitoba, in relation to increasing goose populations. *Condor* 110: 325-334.
- SAS Institute Inc. 1999. SAS version 9.0 for Windows. SAS Institute Inc., Toronto, Ontario.
- Scott, G. A. J. 1995. *Canada's Vegetation: A World Perspective*. McGill-Queen's University Press, Montreal, Québec.
- Shaffer, T. L. 2004a. Logistic-exposure analyses of nest survival (Version 25JUL2006). Prairie Wildlife Research Center, Jamestown, North Dakota. <http://www.npwrc.usgs.gov/resource/birds/nestsurv/index.html>, accessed 1 August 2008.
- Shaffer, T. L. 2004b. A unified approach to analyzing nest success. *Auk* 121: 526-240.
- Skeel, M. A. 1976. Nesting strategies and other aspects of the breeding biology of the Whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. Unpublished M.Sc. Thesis, Department of Zoology, University of Toronto, Toronto, Ontario.
- 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*). No. 219 in *The Birds of North America* online (A. Poole., Ed.). Cornell Lab of Ornithology, Ithaca, New York. <http://bna.birds.cornell.edu/bna/species/219>, accessed 30 January 2009.
- Smith, L. C., Y. Sheng, G. M. MacDonald and L. D. Hinzman. 2005. Disappearing arctic lakes. *Science* 308: 1429.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: The Principles and Practices of Statistics in Biological Research*, 3rd ed. Freeman, New York, New York.
- StatSoft Inc. 2004. STATISTICA Data Analysis Software System version 7 for Windows. StatSoft Inc., Tulsa, Oklahoma.
- Sturm, M., C. Racine and K. Tape. 2001. Climate change—increasing shrub abundance in the Arctic. *Nature* 411: 546-547.
- Tape, K., M. Sturm and C. Racine. 2006. The evidence for shrub expansion in northern Alaska and the pan-Arctic. *Global Change Biology* 12: 686-702.
- Walpole, B., E. Nol and V. Johnston. 2008. Breeding habitat preference and nest success of Red-necked Phalaropes on Niglintgak Island, Northwest Territories. *Canadian Journal of Zoology* 86: 1346-1357.
- Watts, B. and B. Truitt. 2008. Decline in migrant Whimbrel in Virginia. Quarterly News from the Center for Conservation Biology Oct-Dec 2008. http://ccb-wm.org/news/2008_OctDec/whimbrel_decline_VA.htm, accessed 15 November 2008.
- Watts, P. D., B. A. Draper and P. D. Idle. 1991. Environmental influences on roost selection of wintering ravens at Churchill, Manitoba, Canada. *Arctic and Alpine Research* 23: 66-70.
- Yoshikawa, K. and L. D. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. *Permafrost and Periglacial Processes* 14: 151-160.