

Breeding habitat preference and nest success of Red-necked Phalaropes on Niglintgak Island, Northwest Territories

Bree Walpole, Erica Nol, and Vicky Johnston

Abstract: Red-necked Phalaropes (*Phalaropus lobatus* (L., 1758)) breed throughout arctic and subarctic wetlands. These wetlands provide Red-necked Phalaropes dense graminoid habitat that shelters and conceals nests, and freshwater ponds where phalaropes engage in social interactions and feed on small aquatic invertebrates. We studied breeding habitat preference of Red-necked Phalaropes at multiple scales and determined which, if any, nest-site characteristics influenced hatching success. Red-necked Phalaropes avoided habitat at the meso (home range) scale containing large areas of mud and shrub cover, and selected sites with greater cover of graminoids, aquatic emergents, and open water than that available in the environment. At the micro (nest) scale, phalaropes chose sites dominated by graminoids and water. In 2005, concealed nests experienced higher daily nest survival than exposed nests. In 2006, 40% of nests were destroyed during a summer storm surge and we detected no differences in habitat characteristics between the remaining successful and unsuccessful nests. We suggest that annual differences in the adaptive value of nest-site selection depend on the relative abundance of mammalian and avian predators. A habitat model using data at the meso scale correctly identified phalarope habitat and has the potential to be used broadly across the western Arctic.

Résumé : Les phalaropes à bec étroit (*Phalaropus lobatus* (L., 1758)) se reproduisent dans l'ensemble des terres humides des régions arctique et subarctique. Ces terres humides procurent aux phalaropes à bec étroit un habitat de graminoides denses qui protège et dissimule les nids et des étangs d'eau douce dans lesquels les phalaropes mènent leurs interactions sociales et se nourrissent de petits invertébrés aquatiques. Nous étudions les préférences d'habitat de reproduction des phalaropes à bec étroit à plusieurs échelles et déterminons, lorsqu'il y a lieu, les caractéristiques des sites de nidification qui influencent le succès de l'éclosion. À l'échelle moyenne (du domaine vital), les phalaropes à bec étroit évitent les habitats contenant de grandes étendues de boue et une couverture de buissons et choisissent des sites avec une couverture plus importante de graminoides, de plantes aquatiques émergentes et d'eau libre que les sites généralement disponibles dans le milieu. À l'échelle fine (du nid), les phalaropes sélectionnent les sites dominés par les graminoides et l'eau. En 2005, les nids cachés ont connu une survie journalière des petits au nid plus élevée que les nids exposés. En 2006, 40 % des nids ont été détruits durant une vague de tempêtes estivales et nous ne détectons aucune différence de caractéristiques entre les nids restants qu'ils aient eu ou non du succès. Nous croyons que les différences annuelles de valeur adaptative du choix du site de nidification dépendent de l'abondance des mammifères et des oiseaux prédateurs. Un modèle d'habitat basé sur des données à l'échelle moyenne identifie correctement l'habitat des phalaropes et peut potentiellement servir de façon plus large dans tout l'ouest de l'Arctique.

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Introduction

Bird species distribute themselves among habitats nonrandomly (Cody 1985; Scott et al. 2002). These distribution patterns usually coincide with the spatial distribution of resources required for survival and reproduction (Hall et al. 1997). If natural selection is the driving force for habitat preference, then individuals inhabiting preferred (higher

quality) sites should experience higher fitness (Cody 1985; Clark and Shutler 1999). This match between fitness and high-quality habitat may be obscured if (i) there is sufficient high-quality habitat to sustain all individuals in a population or (ii) there is a lag in habitat preferences in a rapidly changing environment (Pribil and Picman 1997; Pribil 1998). The lack of an apparent advantage for habitat preferences may also be explained if variables were measured at an inappropriate scale, lacked biological relevance, and (or) failed to capture the study species' essential needs for survival. Under some conditions, individuals disperse among different habitats in proportion to the availability of resources. This strategy, termed the ideal free distribution (Fretwell and Lucas 1969), would also lend itself to equal fitness among individuals.

Red-necked Phalaropes (*Phalaropus lobatus* (L., 1758)) have undergone drastic population declines in North America since the mid-1980s (Duncan 1996; Donaldson et al. 2000; Brown et al. 2005). These declines have been re-

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flected on their breeding grounds in northern Manitoba (Gratto-Trevor 1994; Jehl and Lin 2001; Sammler et al. 2008), and Barrow, Alaska (D.M. Tracy, personal communication). Although the cause(s) of these declines is(are) currently unknown, habitat alterations on their breeding grounds owing to increasing goose populations, anthropogenic development, and temperature increases could be contributing factors. Three threats specifically related to higher continental temperatures have the potential to negatively impact breeding phalarope populations: (1) encroachment of shrub vegetation into previous wetland habitats (Beck et al. 2005; Sturm et al. 2005; Tape et al. 2006), (2) premature drying and (or) disappearance of freshwater ponds (Smith et al. 2005) critical for raising young, and (3) loss of synchrony between nest timing and insect emergence (Visser et al. 1998; Pearce-Higgins et al. 2005). The construction of a breeding habitat model for this species should depict the range of habitat conditions that Red-necked Phalaropes can tolerate and describe habitats that result in the highest rates of reproductive success. These habitats would be the focus of conservation efforts for the species.

Red-necked Phalaropes do not defend a nesting territory (Rubega et al. 2000), but instead occupy a relatively small home range. We tested the hypothesis that Red-necked Phalaropes exhibit habitat preferences at two spatial scales (home range and nest site); we provide a habitat model for the home-range scale and test whether nest-site habitat preference at this study area is adaptive. As predation is the most important cause of nest failure for this (Höhn 1968; Reynolds 1987) and most other bird species (Ricklefs 1969; Colwell 1992; Jehl and Lin 2001) and because Red-necked Phalarope males (the incubating sex) use cryptic behavior and coloration to avoid detection by predators (Rubega et al. 2000), we predicted that highly concealed nests would experience improved reproductive success. Arctic-nesting shorebirds experience elevated energetic costs during incubation (Piersma et al. 2003). As permafrost can act as a heat sink for unlined nests of ground-nesting shorebirds, uniparental male Red-necked Phalaropes have costly energetic commitments to reheat eggs after feeding breaks or predator-induced disturbances. Thus, we also predicted that nests would be located in areas with relatively high and stable temperatures compared with that in their surroundings and tested whether the simple Red-necked Phalarope nest design (scrape) enhanced temperatures compared with sites immediately outside of the nest.

Materials and methods

Fieldwork was conducted in a 6 km² study site located in the Kendall Island Migratory Bird Sanctuary on Niglintgak Island (roughly 60 km²; 69.045°N, 135.048°W), Northwest Territories, during the summers of 2005 and 2006. Niglintgak Island sits in the mouth of the Mackenzie River Delta, Northwest Territories, where it is susceptible to tidal flooding, particularly at ice breakup and during heavy summer rain (Gratto-Trevor 1996). The island and region are slated for massive increases in gas exploration and development (Mackenzie Gas Project, Inuvik, Northwest Territories, 2004). The habitat consists primarily of arctic sedge wetland dominated by the genera *Carex* L. and *Salix* L., with tempo-

rary and permanent shallow ponds scattered throughout. This research was limited to Niglintgak Island because of logistical difficulties and expenses associated with working at this remote location. Previous investigations of the island indicated that the island supported numerous breeding Red-necked Phalaropes and that nests would be accessible to researchers by foot (C. Gratto-Trevor 1994; C. Gratto-Trevor, personal communication). Study sites in 2005 and 2006 were adjacent but nonoverlapping, although contained within one contiguous wetland.

Nests were found by walking the study site and observing behavioral cues of nesting pairs (mate guarding, investigating nest sites, flushing), or by dragging through the study site a heavy nylon rope hung every metre with plastic streamers (6 cm wide and 60 cm long). Nest locations were recorded with a global positioning system (GPS) unit and marked discretely with a 15 cm × 2 cm wooden tongue depressor of the same colour as the surrounding dead grasses, 2 m north of the nest. Males were caught during the incubation stage with a ground trap placed over their nest, and banded with unique plastic color band combinations and with a standard Canadian Wildlife Service stainless steel band. Nests were monitored every 1–3 days until nest fate could be determined. We limited trampling in the nest vicinity by observing nests for flushed males from a distance (about 5–15 m) and by limiting time spent at the nest site. Vegetation measurements were taken following nest completion to minimize human-induced disturbance to active nests. Nests that hatched at least one chick were considered “successful”, whereas depredated nests (determined by noting disturbed nest, predator tracks, large eggshell fragments (Mabee 1997), and (or) loss of entire clutch before the predetermined hatch date, calculated assuming 4 days for laying and 20 days for incubation (Rubega et al. 2000)) were considered to have “failed”. Successful nests were verified by the presence of Red-necked Phalarope chicks within the home range, parental behavior (reluctance to leave home range, communication with chicks), and (or) by the presence of small, clean eggshell remnants (Mabee 1997) in the base of the nest cup.

Vegetation measures were completed at two different scales (mesohabitat and microhabitat; Fig. 1). We defined nest mesohabitat as the habitat contained within a circle of 40 m radius centered on the nest, an area approximating that of Red-necked Phalarope home ranges (Rubega et al. 2000). We did not attempt to quantify Red-necked Phalarope home-range size, but 36 of 41 (90%) color-banded males were observed only within 40 m of their nests.

Habitat features contained within 1 m of nests or nonuse sites were defined as microhabitat. Microhabitat measures were taken in three locations: (1) nest sites; (2) random locations within 40 m of nest sites, henceforth referred to as nonuse within the home range; and (3) nonuse sites located beyond 40 m of nests, henceforth referred to as nonuse outside the home range, with the caveat that the 40 m radius may not encompass home ranges in their entirety. Nonuse sites within the home range were located in a random direction and distance (up to 40 m) from the nest site.

Mesohabitat measures were completed at all nest sites and presumed nonuse sites, defined as those sites that did not overlap with active Red-necked Phalarope home ranges.

Nonuse sites were monitored regularly throughout the breeding season to ensure an absence of breeding Red-necked Phalaropes. Dominant terrestrial features were quantified in 1 m increments along 40 m transects in each cardinal direction from the center of the nest or nonuse site (Fig. 1). Cover of graminoid (grasses and sedges), mud, aquatic emergents, shrub (woody plants between 30 and 100 cm high, primarily *Salix* spp.), moss, open water, dwarf shrub (*Salix* spp., genus *Betula* L., ≤ 30 cm high), and herb were estimated by dividing the number of 1.0 m increments from each habitat-cover class by the total number of increments.

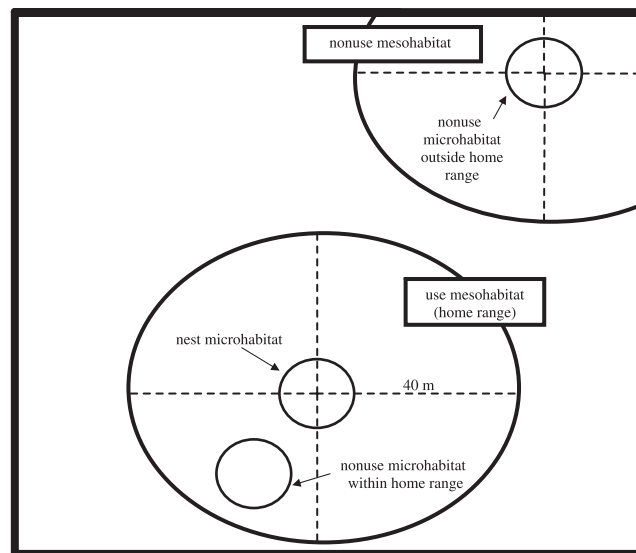
Microhabitat characteristics included measuring maximum vegetation height directly above nests and at a distance of 1 m in each cardinal direction. Percent ground cover (graminoid, mud, aquatic emergents, shrub, moss, open water, dwarf shrub, and herb) was estimated within each quarter of the nest circle. Distances between nests and open water (ponds >1 m²) were also measured with 50 m long tapes. All sites were categorized as low, medium, or high surface roughness, where low sites were almost flat, high sites contained very uneven ground (including hummocks), and medium sites were intermediate in roughness. Temperature was monitored after hatch within empty nests and in a random direction directly beside the nest cups every 10 min for a minimum of 22 h with Thermistor probes attached to Hobo-Temp-XT data loggers (Onset Instrument Corporation, Pocasset, Massachusetts, USA) or iBCod miniature temperature data loggers (Alpha Mach Incorporated, Mont Saint-Hilaire, Quebec, Canada). Microhabitat measurements were also recorded at presumed nonuse sites within and outside home ranges. Temperature recorders were calibrated before use.

Data analyses

Analyses at both scales examined year and site effects to determine whether preferences changed as a result of slight differences in the available habitat features of the two sections of the study area used in the 2 years. Pearson correlation analysis was used to determine the relationship between habitat variables measured at the microhabitat and mesohabitat scales. Significant ($P < 0.05$) and moderate to strong positive relationships were found between percent cover of habitat types at the microhabitat and mesohabitat scales for all variables common to each analysis including graminoid ($r = 0.58$), mud ($r = 0.70$), shrub ($r = 0.81$), and open water ($r = 0.56$).

Mesohabitat features with overall mean occurrences $<5\%$ (dwarf shrub (3%), moss (3%), and herb (1%)) were removed from further analyses. To avoid multicollinearity (Pearson product correlation, $r \geq 0.4$), the remaining variables that include percentage of graminoid, mud, aquatic emergents, shrub, and open water were summarized with a principal components analysis (PCA). We used unconditional, multiple logistic regression to test 16 candidate models in which the dependent variable distinguished between occupied mesohabitat and presumed nonuse sites (Hosmer and Lemeshow 2000). The three principal components and year and site were identified as predictor variables. Candidate models included all possible additive combinations of predictor variables and a constant model. Akaike's informa-

Fig. 1. Schematic drawing of the habitat sampling design. Microhabitat was collected within a 1 m radius of Red-necked Phalarope (*Phalaropus lobatus*) nest sites, nonuse sites located within the home range, and nonuse sites outside of the home range. Mesohabitat approximated home ranges with a radius of 40 m and was measured surrounding nest sites and at presumed nonuse sites.



tion criterion corrected for small sample size (AIC_c) and Akaike weights (w_i) were used to determine the most parsimonious of the 16 candidate models (Hurvich and Tsai 1989; Burnham and Anderson 2001). Models with ΔAIC_c values ≤ 2 were identified as the best subset. Importance values were calculated for each parameter by summing the w_i values for all models in which the parameter of interest was included within the confidence set. The confidence set of candidate models included those with w_i values within 10% of the top model (Burnham and Anderson 2001). Model averaging was used to compute all parameter estimates. We evaluated model performance by calculating the area under the curve (AUC) for each variable from receiver operator characteristic (ROC) curves (Hosmer and Lemeshow 2000; Manel et al. 2001). Performance can range between models with no discrimination (AUC values of 0.5) and models with perfect predictability (AUC values of 1.0) (Manel et al. 2001; Boyce et al. 2002).

At the microhabitat scale, we excluded aquatic emergents (1%), dwarf shrub (2%), herb (1%), and moss (3%), which had mean occurrence values $<5\%$, from further analyses. High ($r \geq 0.40$) correlations were evident among some microhabitat variables: percent cover of graminoid, mud, and shrub, as well as mean vegetation height. Thus, we used PCA to describe covariation among percent cover of graminoid, mud, shrub, open water, and mean vegetation height. Additive combinations of predictor variables (year and site, distance to water, surface roughness, and PC1 and PC2 scores) and a constant model resulted in 33 candidate models.

We had anticipated determining whether Red-necked Phalaropes select their nest sites nonrandomly from available habitats in the landscape by distinguishing between microhabitat at nest sites and nonuse sites outside home

Table 1. Mean and 95% confidence interval (CI) of mesohabitat measured at Red-necked Phalarope (*Phalaropus lobatus*) nest sites and nonuse sites on Niglingak Island, Northwest Territories, 2005 and 2006.

	2005				2006			
	Use (n = 33)		Nonuse (n = 33)		Use (n = 63)		Nonuse (n = 50)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Percent cover								
Graminoid	46	39–53	33	25–40	52	47–58	36	30–42
Mud	32	25–38	27	18–37	3	1–5	25	18–32
Aquatic emergents	4	2–6	5	0–9	17	12–21	4	2–6
Shrub	4	0–8	29	21–36	1	0–1	20	15–26
Moss	0	0–1	2	1–3	3	1–6	3	1–5
Open water	13	8–18	1	0–1	19	14–24	3	1–4
Dwarf shrub	0	0–0	0	0–0	3	1–5	5	2–8
Herb	0	0–0	0	0–2	0	0–0	3	2–5
PC1 score	0.10	–0.17 to 0.37	1.15	0.76 to 1.55	–1.31	–1.48 to –1.13	0.82	0.57 to 1.08
PC2 score	0.45	0.07 to 0.82	–0.37	–0.73 to –0.01	0.13	–0.16 to 0.41	–0.21	–0.47 to 0.06
PC3 score	0.66	0.43 to 0.89	–0.32	–0.72 to 0.08	–0.15	–0.41 to 0.10	–0.03	–0.37 to 0.30

Note: Dominant terrestrial cover type was estimated in 1 m increments along 40 m transects running from the center of nests and nonuse sites in each cardinal direction. PC, principal component.

ranges. As much of the variation in microhabitat was accounted for in the mesohabitat measurements, this analysis would have been redundant so it was not conducted.

Microhabitat characteristics of nest sites and nonuse sites within presumed home ranges were compared using conditional (paired) multiple logistic regression (Hosmer and Lemeshow 2000). This method was used because nest and nonuse sites located within the home range lacked independence. We modeled the differences between nest sites and nonuse sites within the home range in relation to four variables (distance to water, surface roughness, and PC1 and PC2 scores). Models were compared as with mesohabitat characteristics. Model performance was not tested for microhabitat variables owing to the paired nature of nest sites and nonuse sites within the home range.

Mean temperature measurements were normally distributed with homogenous variances. We used two-way analysis of variance, with nest site treated as the within-subject effect, to compare temperature means within the nest cup, directly beside the nest cup, and at nonuse sites within the home range because these sites may lack independence (Quinn and Keough 2002). Means of temperatures at nonuse sites within and outside the home range were compared with two-tailed, independent *t* tests.

Nesting success

We fit a multiple logistic exposure model of daily nest survival, including PC1 and PC2 scores and distance to water as continuous variables and surface roughness and year and site as categorical variables (Shaffer 2004). The logistic exposure method accounts for differences in exposure days between nests (Shaffer 2004). Models were compared as with meso- and micro-habitats.

We used SAS version 8.02 (SAS Institute Inc. 1999), STATISTICA™ version 7 (StatSoft Inc. 2004), or ROC plotting and AUC calculation transferability test version 1.3-7 (Schröder 2004) for all analyses. Results of inferential statistics were considered significant at an α of 0.05.

Table 2. Eigenvectors, eigenvalues, and variance explained by principal components (PCs) analysis of mesohabitat variables measured within a 40 m radius circle centered on Red-necked Phalarope (*Phalaropus lobatus*) nests (use mesohabitat, *n* = 96) and at nonuse mesohabitat sites (*n* = 83) of equal size in 2005 and 2006.

Habitat variable	PC		
	1	2	3
Graminoid	–0.46	–0.50	0.51
Mud	0.51	0.44	0.38
Aquatic emergents	–0.41	0.06	–0.51
Shrub	0.46	–0.42	–0.53
Open water	–0.39	0.62	–0.18
Eigenvalue	1.77	1.16	1.15
Total variance explained (%)	35.39	23.22	22.94
Cumulative variance explained (%)	35.39	58.61	81.56

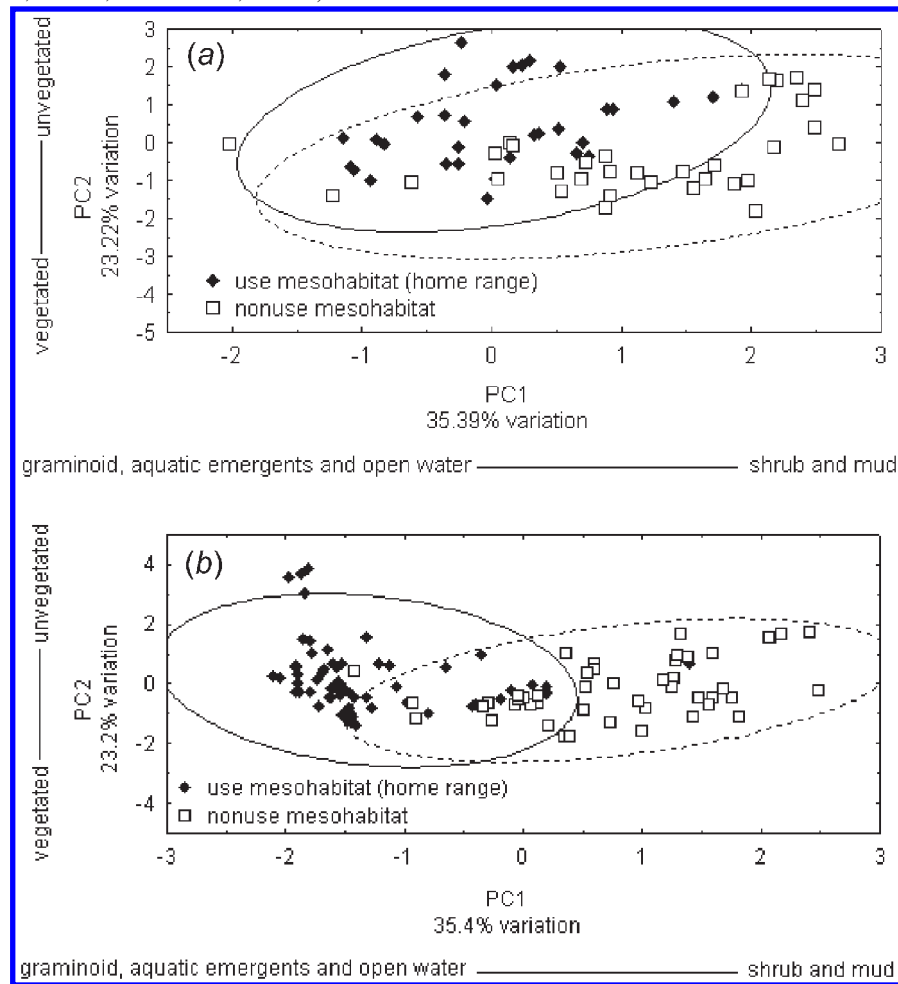
Results

Mesohabitat preference

Percent cover by graminoid, aquatic emergents, mud, shrub, and open water were quantified at 96 use sites (home ranges) and 83 nonuse sites over the two study years (Table 1). Three principal components (PCs) accounted for 81.6% of the variation, with PC1, PC2, and PC3 scores responsible for 35.4%, 23.2%, and 22.9% of the total variation, respectively (Table 2, Fig. 2). PC1 separated graminoid wetland habitats that contain high cover of graminoid, aquatic emergents, and open water (negative values) from habitats containing high shrub and mud cover (positive values). PC2 represented a gradient from vegetated (negative values) to unvegetated (positive values) sites. Habitats dominated by mud and graminoid were associated with positive PC3 values. By contrast, habitats with high aquatic emergents, shrub, and open water cover had negative PC3 values.

The candidate models containing PC1, PC2, and year and

Fig. 2. Principal components (PCs) analysis with 95% prediction ellipses of dominant mesohabitat measurements from a circle of 40 m radius surrounding Red-necked Phalarope (*Phalaropus lobatus*) nests in (a) 2005 (use mesohabitat, $n = 33$; nonuse sites, $n = 33$) and (b) 2006 (use mesohabitat, $n = 63$; nonuse sites, $n = 50$).



site, as well as PC1, PC2, PC3, and year and site, were within the best subset ($\Delta AIC_c \leq 2$). The remaining candidate models were weakly competitive with the best subset and had w_i values < 0.03 . As year and site appeared within the top two candidate models, analyses were rerun to determine variability in mesohabitat use between 2005 (use and nonuse sites, both $n = 33$) and 2006 (use sites, $n = 63$; non-use sites, $n = 50$). In 2005, two candidate models were contained within the best subset in which the top model included all variables (PC1, PC2, and PC3) and was followed by the model containing PC1 and PC2 scores (Table 3a). PC1 score was included in 4 of the 5 top models and both PC1 and PC2 had high importance values. Model averaged parameter estimates for PC1, PC2, and PC3 scores were -1.58 , 1.29 , and 0.30 , respectively (Fig. 2). Model performance (using AUC calculations) ranged from moderate to good for all variables. These results imply that Red-necked Phalaropes are using graminoid wetland habitat that contains water (unvegetated) while avoiding mesohabitats dominated by shrub.

In 2006, three models were within the best subset and one additional model was included within the subset of most parsimonious models ($\Delta AIC_c \leq 4$; Table 3b). Although all variables were represented in this subset, PC1 score was the

only variable present in every model within this ranking. The contribution of PC1 score was also indicated by an importance value of 1.00 and excellent model predictability (Table 3b). The model averaged parameter estimates of PC1, PC2, and PC3 scores were -2.70 , 0.75 , and 0.28 , highlighting the importance of graminoid with little to no shrub intrusion for breeding Red-necked Phalaropes (Fig. 2).

Microhabitat preference

Five microhabitat variables (mean height, percentage of graminoid, mud, shrub, and open water) were measured at 96 nest sites, 96 nonuse sites within the home range, and 83 nonuse sites outside the home range (Table 4). Two PCs accounted for 40% and 29% of microhabitat variation, respectively (Table 5, Fig. 3). As with the mesohabitat analyses, PC1 contrasted graminoid vs. shrubby habitats and PC2 contrasted vegetated vs. unvegetated sites (Table 5).

Eight of the 33 candidate models were supported in the best subset of models for discriminating between nest sites and nonuse sites within the home range, and these 8 models contained combinations of all variables except year and site (Table 6). PC1 score was the sole variable present in all models within the subset of parsimonious models. Although no single model stands alone within our subset, the high im-

Table 3. Log likelihood ($-2 \cdot \ln L$), number of parameters (k), Akaike's information criterion (AIC), AIC adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_i) are provided for the subset of most parsimonious models ($\Delta AIC_c \leq 4$) deduced from multiple, unconditional logistic regression analysis to predict Red-necked Phalarope (*Phalaropus lobatus*) mesohabitat (home range) occupancy in (a) 2005 (use mesohabitat, $n = 33$; nonuse sites, $n = 33$) and (b) 2006 (use mesohabitat, $n = 63$; nonuse sites, $n = 50$).

	k	$-2 \cdot \ln L$	AIC	AIC_c	ΔAIC_c	w_i	Importance value	AUC
(a) 2005								
Model								
PC1, PC2, PC3	4	51.65	59.65	60.31	0	0.64		
PC1, PC2	3	55.17	61.17	61.55	1.24	0.34		
Constant	1	91.50	93.50	93.55	33.25	<0.001		
Parameter								
PC1							0.99	0.80
PC2							0.99	0.73
PC3							0.64	0.75
(b) 2006								
Model								
PC1, PC2	3	55.29	61.29	61.51	0	0.41		
PC1, PC2, PC3	4	53.87	61.87	62.24	0.73	0.29		
PC1, PC3	3	57.21	63.21	63.43	1.91	0.16		
PC1	2	59.50	63.50	63.60	2.10	0.14		
Constant	1	155.15	157.15	157.18	95.68	<0.001		
Parameter								
PC1							1.00	0.96
PC2							0.70	0.59
PC3							0.44	0.55

Note: Models are ranked by suitability and performance was evaluated by calculating the area under the curve (AUC) for each variable from receiver operator characteristic curves. PC, principal component.

portance value calculated for PC1 indicated that Red-necked Phalarope nests were located nonrandomly within the mesohabitat (home range) surrounding nests. PC1 score resulted in a model averaged parameter estimate of -1.17 , implying that nests were typically surrounded by more graminoid and water and less mud and shrub compared with nonuse sites within the home range (Fig. 3).

Nonuse sites outside the home range contained the most variability, suggesting that these sites were the most diverse and represent the widely available microhabitats present within the study site (Fig. 3). The majority of nonuse sites outside the home range were excluded from the nest site 95% prediction ellipse. By contrast, most nonuse sites within the home range were contained in the nest site 95% prediction ellipse, demonstrating a similarity in habitat, with the exception that nonuse sites within the home range were less consistent and some were located in dryer areas with less graminoid than nest sites.

Air temperature was measured at 22 nest sites (mean = 8.18°C , 95% CI = 7.14 – 9.22°C), directly beside 24 nest sites (mean = 8.27°C , 95% CI = 7.44 – 9.10°C), at 19 nonuse sites within the home range (mean = 8.88°C , 95% CI = 7.83 – 9.93°C), and at 22 nonuse sites outside the home range (mean = 8.45°C , 95% CI = 7.54 – 9.35°C). There was no significant variation among locations within the home range ($F_{[2,34]} = 0.51$, $P = 0.61$) or between nonuse sites within and outside the home range ($t_{[1,39]} = 0.65$, $P = 0.52$).

Nesting success

Mean vegetation height and percent cover were quantified

at all nests with known fate (Table 7). In 2005, 16 of 27 (59%) nests hatched successfully with the remainder lost to predation. In 2006, 9 of 65 (14%) nests hatched with 30 (46%) depredated and 26 (40%) destroyed by a storm that covered the entire study site with 20–100 cm of water. For many nests the flood occurred during or immediately before hatch, so these nests were excluded from further analysis. Daily nest survival in 2005 (mean = 0.950 , 95% CI = 0.920 – 0.979) was significantly higher than in 2006 (mean = 0.909 , 95% CI = 0.904 – 0.913 ; $t_{[1,66]} = 3.30$, $P < 0.01$). Because year and site was included in 16 of the top 20 models and had the highest importance value, we analyzed factors influencing nest success for 2005 and 2006 separately.

In 2005, 3 of 16 models were included in the best subset to predict nesting success (Table 8). PC2 score was included in all of these models, as well as in all models within the confidence set, and had an importance value over 3 times that of competing variables. The model averaged PC2 parameter estimate was -1.52 , indicating that in 2005 successful nests were surrounded by more vegetation than unsuccessful nests. Sixty-four percent (9 of 14) of nests with PC2 scores >0.5 were depredated, whereas only 15% (2 of 13) of nests with PC2 scores <0.5 were depredated (Fig. 4). The constant model was included in the best subset of models for multiple logistic exposure analyses on 2006 nest data with a ΔAIC_c value of 0.39 and a w_i value of 0.19. Thus, no models were able to predict daily nest survival in 2006 (Fig. 4).

Discussion

Red-necked Phalaropes were attracted to mesohabitat do-

Table 4. Mean and 95% confidence interval (CI) of microhabitat measured at Red-necked Phalarope (*Phalaropus lobatus*) nest sites and nonuse sites in 2005 and 2006.

	2005						2006					
	Nest site (n = 33)			Nonuse within home range (n = 33)			Nest site (n = 63)			Nonuse within home range (n = 63)		
	Mean	95% CI		Mean	95% CI		Mean	95% CI		Mean	95% CI	
Percent cover												
Graminoid	69	62–75	54	43–65	27–44	36	75	70–81	73	68–79	41	34–48
Mud	26	20–31	39	29–50	29–50	40	5	4–7	8	5–12	34	26–41
Aquatic emergents	0	0–0	1	0–2	0–3	1	2	0–4	1	0–2	1	0–2
Shrub	2	0–4	4	1–7	9–21	15	1	0–1	1	0–1	13	9–18
Moss	2	1–4	1	0–2	1–4	3	2	1–4	4	2–6	2	1–4
Open water	0	0–1	1	0–3	0–0	0	11	8–15	7	4–9	1	0–2
Dwarf shrub	0	0–0	0	0–0	0–2	1	2	1–4	4	2–6	5	2–7
Herbaceous vegetation	0	0–1	0	0–0	0–2	1	0	0–1	1	0–1	4	2–5
Mean vegetation height (cm)	26	23–28	25	21–29	28–45	37	29	28–31	30	28–32	35	28–42
Distance to water (m)	13	8–19	8	5–12	24–64	44	5	3–7	5	3–7	24	18–30
PC1 score	–0.16	–0.44 to 0.12	0.48	0.05 to 0.91	1.12 to 2.03	1.57	–1.09	–1.20 to –0.99	–0.84	–1.04 to –0.65	1.2	0.78 to 1.62
PC2 score	0.41	0.17 to 0.66	0.72	0.24 to 1.21	–0.95 to 0.45	–0.25	–0.16	–0.25 to –0.07	–0.12	–0.26 to 0.02	–0.21	–0.70 to 0.26

Note: Nonuse sites within the home range were located within 40 m of nests, whereas nonuse sites outside the home range were located beyond 40 m of nests. Dominant terrestrial cover type was estimated within a circle of 1 m radius centered on nest or nonuse sites. PC, principal component.

Table 5. Eigenvectors, eigenvalues, and variance explained by principal components (PCs) analysis of microhabitat variables measured at 96 Red-necked Phalarope (*Phalaropus lobatus*) nest sites, 96 nonuse sites located within 40 m of nests (nonuse sites within the home range), and 83 nonuse sites located beyond 40 m of nests (nonuse sites outside the home range) in 2005 and 2006.

Habitat variable	PC	
	1	2
Mean vegetation height	0.17	–0.73
Graminoid	–0.59	–0.20
Shrub	0.49	–0.49
Mud	0.54	0.42
Open water	–0.27	–0.06
Eigenvalue	2.02	1.44
Total variance explained (%)	40.43	28.87
Cumulative variance explained (%)	40.43	69.30

minated (>40% cover) by graminoid wetlands in both 2005 and 2006 and avoided habitats with >8% shrub cover. As predicted, phalaropes preferred mesohabitat with ponds. Ponds provided important feeding sites (Rubega et al. 2000) and a stage where prebreeding social interactions took place (Höhn 1971; Rodrigues 1994; Walpole et al. 2008). Although we occasionally observed adult Red-necked Phalaropes seizing invertebrates from stalks of graminoid vegetation, the air, or damp and exposed mud, they typically spent the majority of their time feeding on surface invertebrates in freshwater ponds (Rubega et al. 2000). Although our model was tested using internal data and hence is not externally validated, we suggest that the high predictability of our models using PC1 in both years of study would bode well for predicting Red-necked Phalarope nesting habitat throughout, at least, the western Arctic breeding range.

Year and site was identified as a contributing factor in distinguishing between used and unused mesohabitat by Red-necked Phalaropes. This may be an artifact of using nonoverlapping study sites between 2005 and 2006. The study site in 2005 contained more shrub habitat than the 2006 site. As a result, 2005 nonuse sites outside the home range were randomly located in habitats dominated by shrubs, whereas this was not the case in 2006. We also expected habitat variability between 2005 and 2006 as a result of very different weather during the breeding seasons. The wet weather in 2006 (flood) was contrasted with a comparatively dry 2005 breeding season. Some areas recorded as mud in 2005 represent temporary ponds that dried throughout the breeding season. Annual variability was captured in our habitat measurements because habitat variables were recorded at the end of the nesting season to reduce the potential impacts that observers might have had on nest success.

Along with mesohabitat preference within the landscape, Red-necked Phalaropes also preferred specific nesting microhabitats within their home range. Nest sites and nonuse sites within the home ranges were distinguished, as at the mesoscale, by the relative proportions of graminoid and open water, with nest sites containing less mud and shrub than nonuse sites. This result is in agreement with our pre-

Fig. 3. Principal components (PCs) analysis with 95% prediction ellipses of microhabitat vegetation measurements from Red-necked Phalarope (*Phalaropus lobatus*) nest sites ($n = 96$), nonuse sites within 40 m of nests (nonuse sites within the home range; $n = 96$), and nonuse sites beyond 40 m of nests (nonuse site outside the home range; $n = 83$) in 2005 and 2006.

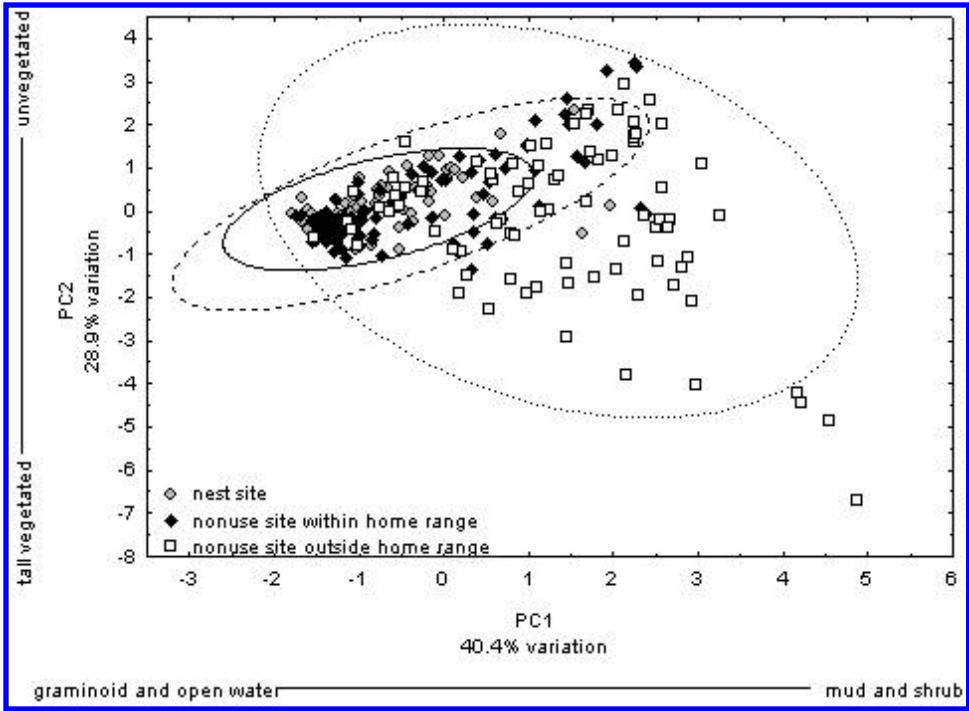


Table 6. Log likelihood ($-2 \cdot \ln L$), number of parameters (k), Akaike's information criterion (AIC), AIC adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_i) are provided for the subset of most parsimonious models ($\Delta AIC_c \leq 4$; 16 of 33) deduced from multiple, conditional logistic regression to differentiate between Red-necked Phalarope (*Phalaropus lobatus*) nest sites ($n = 96$) and nonuse sites located within 40 m of nests (nonuse sites within the home range; $n = 96$) in 2005 and 2006.

	<i>k</i>	$-2 \cdot \ln L$	AIC	AIC_c	ΔAIC_c	w_i	Importance value
Model							
Distance to water, PC1, PC2	4	109.21	115.21	115.67	0.00	0.13	
PC1, PC2	3	111.48	115.48	115.75	0.09	0.13	
Distance to water, PC1	3	111.54	115.54	115.81	0.14	0.12	
PC1	2	113.72	115.72	115.85	0.19	0.12	
PC1, surface roughness	4	112.65	116.65	117.11	1.44	0.06	
PC1, PC2, surface roughness	5	110.44	116.44	117.13	1.47	0.06	
Distance to water, PC1, PC2, surface roughness	6	108.21	116.21	117.19	1.52	0.06	
Distance to water, PC1, surface roughness	5	110.56	116.56	117.25	1.58	0.06	
Distance to water, PC1, PC2, year and site	5	109.21	117.21	117.90	2.24	0.04	
PC1, PC2, year and site	4	111.54	117.48	117.94	2.27	0.04	
PC1, year and site	3	113.72	117.72	117.99	2.32	0.04	
Distance to water, PC1, year and site	4	111.54	117.54	118.00	2.33	0.04	
PC1, year and site, surface roughness	5	110.56	118.65	119.34	3.68	0.02	
PC1, PC2, year and site, surface roughness	6	110.44	118.44	119.42	3.75	0.02	
Distance to water, PC1, PC2, year and site, surface roughness	7	108.22	118.21	119.53	3.86	0.02	
Distance to water, PC1, year and site, surface roughness	6	110.56	118.56	119.54	3.87	0.02	
Constant	1	126.93	128.92	129.38	13.71	<0.001	
Parameter							
PC1							1.00
PC2							0.51
Distance to water							0.50
Surface roughness							0.33
Year and site							0.25

Note: Models are ranked by suitability. PC, principal component.

Table 7. Mean and 95% confidence interval (CI) of microhabitat measured at successful and depredated Red-necked Phalarope (*Phalaropus lobatus*) nests in 2005 and 2006.

	2005 (<i>n</i> = 27)				2006 (<i>n</i> = 39)			
	Successful (<i>n</i> = 16)		Depredated (<i>n</i> = 11)		Successful (<i>n</i> = 9)		Depredated (<i>n</i> = 30)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Percent cover								
Graminoid	74	64–83	62	51–73	69	48–90	73	65–82
Mud	21	15–27	36	25–48	5	0–12	5	3–8
Aquatic emergents	0	0–0	0	0–0	0	0–0	2	0–5
Shrub	3	0–7	1	0–2	4	0–8	0	0–1
Moss	2	0–3	1	0–2	5	0–10	2	1–4
Open water	0	0–0	0	0–0	7	1–13	13	7–18
Dwarf shrub	0	0–1	0	0–0	6	0–13	3	0–5
Herb	1	0–2	0	0–0	1	0–2	1	0–1
Mean vegetation height (cm)	28	24–32	21	16–26	28	22–34	30	27–33
Distance to water (m)	18	8–27	12	6–18	3	1–6	7	3–11
PC1 score	–0.31	–0.78 to 0.17	0.10	–0.36 to 0.56	–0.74	–1.25 to –0.23	–1.11	–1.24 to –0.98
PC2 score	0.16	–0.11 to 0.42	0.95	0.46 to 1.45	–0.17	–0.42 to 0.08	–0.17	–0.33 to –0.02

Note: Nests were monitored regularly throughout the breeding season to determine fate. Dominant terrestrial cover type was estimated within a circle of 1 m radius centered on nest or nonuse sites. PC, principal component.

Table 8. Log likelihood ($-2 \ln L$), number of parameters (k), Akaike’s information criterion (AIC), AIC adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_i) are provided for the subset of most parsimonious models ($\Delta AIC_c \leq 4$; 5 of 16) deduced from logistic exposure analysis to predict daily nest survival of 17 successful and 10 unsuccessful Red-necked Phalarope (*Phalaropus lobatus*) nest sites in 2005.

	<i>k</i>	$-2 \ln L$	AIC	AIC_c	ΔAIC_c	w_i	Importance value
Model							
PC2	2	68.60	72.60	72.61	0.00	0.39	
PC1, PC2	3	68.12	74.12	74.16	1.54	0.18	
Distance to water, PC2	3	68.40	74.40	74.44	1.82	0.16	
PC2, surface roughness	4	67.69	75.69	75.77	3.15	0.08	
Distance to water, PC1, PC2	4	67.82	75.82	75.90	3.28	0.08	
Constant	1	78.96	80.96	80.96	8.34	0.006	
Parameter							
PC2							0.92
PC1							0.30
Distance to water							0.23
Surface roughness							0.12

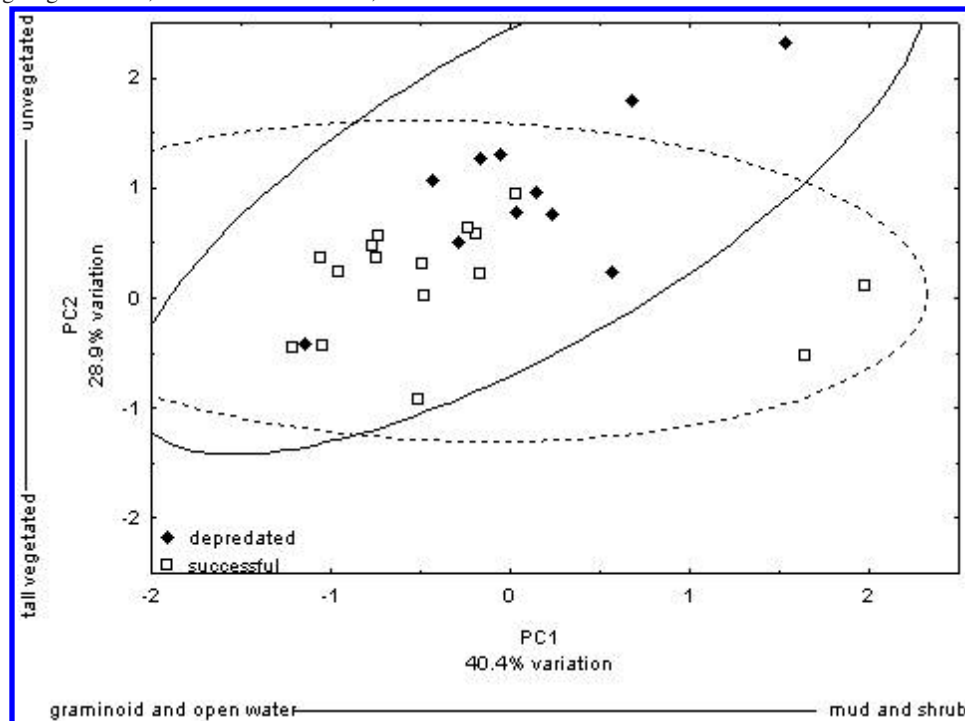
Note: Models are ranked by suitability. PC, principal component.

diction and is also a probable adaptive response to nest predation pressures. As well as providing concealment from predators, dense graminoids presumably act as wind blocks, decreasing heat loss through convection. These results are consistent with those of Rodrigues (1994) and in the closely related Red Phalarope (*Phalaropus fulicarius* (L., 1758)) in which nests were associated with graminoid cover in sedge meadow and marsh habitat (Latour et al. 2005; Smith et al. 2007a, 2007b). Similarly, Colwell and Oring (1990) found that Wilson’s Phalaropes (*Phalaropus tricolor* (Vieillot, 1819)) typically nested in homogeneous, graminoid habitat that was taller and denser than random sites. Thus, the genus *Phalaropus* appears to exhibit relatively conservative nest-site habitat preference (but see Smith et al. 2007b). Contrary to our mesohabitat results, microhabitat preference was consistent regardless of annual variability and (or) inconsisten-

cies in our study area, suggesting a lack of flexibility in nest microhabitat characteristics.

The large prediction ellipse for nonuse sites outside the home range implies that the level of variability between microhabitats increased with distance from nests. The prediction ellipse of nonuse microhabitat sites within home ranges fully overlapped the prediction ellipse containing microhabitat at nest sites. Although we presume that nonuse sites excluded from the nest-site confidence ellipse represent unsuitable nesting habitat within the study area, it is possible that nonuse sites contained within the nest-site confidence ellipse were also unsuitable because they were not surrounded by appropriate mesohabitat features. This would be the case if habitat preference is a hierarchical decision based first on the selection of home range followed by the selection of a specific nest site. Otherwise, these nonuse sites

Fig. 4. Principal components (PCs) analysis with 95% prediction ellipses of microhabitat vegetation measurements (mean vegetation height, proportions of graminoid, open water, mud, and shrub) from successful ($n = 16$) and depredated ($n = 11$) Red-necked Phalarope (*Phalaropus lobatus*) nests on Niglintgak Island, Northwest Territories, in 2005.



could indicate that potential nest sites were available but unoccupied.

Our prediction that Red-necked Phalarope nests would be located nonrandomly with respect to temperature regime was not supported. There was no difference in mean temperature between nest sites, sites immediately adjacent to nests, nonuse sites within the home range, and nonuse sites outside the home range. We also found that nest-cup structure did not influence mean nest temperature. We presume that these predictions were not supported because our study site lacked variation in temperature, possibly because of the low variability in microhabitat relief. Red-necked Phalaropes probably use a combination of strategies to optimize the thermal properties of their nests, including the use of dense vegetation as shelter from extreme climatic elements, direction of nest entrance away from prevailing winds to decrease wind penetration, and an adjusted frequency of recesses and length of incubation periods in response to external temperatures (Tulp and Schekkerman 2006).

In 2005, the presence and height of vegetation, representing nest concealment and shelter, were the strongest predictors of daily nest survival. This result complements the cryptic response of Red-necked Phalaropes to predators. As adult males do not actively defend their nests when approached by predators, nest concealment strategies are necessary and were expected. Potential avian nest predators such as Long-tailed Jaegers (*Stercorarius longicaudus* Vieillot, 1819), Glaucous Gulls (*Larus hyperboreus* Gunnerus, 1767), and Sandhill Cranes (*Grus canadensis* (L., 1758)) were observed frequently in 2005, and all depredated nests were intact and lacked tracks, suggesting that mammals were not responsible for nest losses. In contrast, 2006 observations included the aforementioned avian predators, as well

as red foxes (*Vulpes vulpes* (L., 1758)). Although a lack of mammalian signs in 2005 does not imply a complete absence of mammals, we suggest that the frequent sightings of red foxes in 2006 explain why nests surrounded by more vegetation and thus highly concealed did not experience increased daily nest survival. Nest concealment was beneficial for nests when visual predators were dominant in 2005 but did not influence daily nest survival in 2006 when a predator employing olfactory cues was present. Our 2006 results agree with that of Colwell (1992) who found the nest success of Wilson's Phalaropes was not influenced by concealment. By contrast, Smith et al. (2007a) found that microhabitat variability, particularly measures of nest concealment, could best predict the nest success of Red Phalaropes.

Nest failure resulting from periodic catastrophic events, such as the flood in 2006, may also impose an important selective force on the breeding habitat selection of Red-necked Phalaropes. Over time, such pressures may encourage nesting on higher and drier upland graminoid sites, although it is unknown what counter factors might negatively impact the survival of such nests. If current nest preference reflects these selective forces, then one can presume that the preference for wet graminoid meadows has proven to be advantageous over the long term, despite irregular flooding events. Storm surges that result from onshore winds are not uncommon in late summer in the Mackenzie Delta (Blasco 1991 in Gratto-Trevor 1996). The variable site fidelity of this species (Rubega et al. 2000) might be in response to the ephemeral nature of some breeding habitats.

This study confirms the reliance of Red-necked Phalaropes on graminoid meadows and arctic ponds, two habitat features at risk in the north. Along with efforts to slow climate

change, conservation strategies for this species should focus on preserving graminoid wetlands in the Arctic that currently host successful, breeding populations of Red-necked Phalaropes and are distant from sites slated for development. Although flooding had a profoundly negative influence on annual reproductive success in our study area, the flushing of water in coastal environments of the Arctic can also act to counter shrub encroachment (Gratto-Trevor 1996; Toyra and Pietroniro 2005). The presence of shrub emerged repeatedly in our models as a feature avoided by Red-necked Phalaropes, and thus, wetlands that experience periodic flooding will probably continue to be preferred. Given that encroachment of shrub has been occurring in the western Arctic in response to climate warming (Sturm et al. 2005; Tape et al. 2006), we can also predict widespread loss of suitable habitat with climate warming.

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