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RESEARCH ARTICLE

Habitat and social factors influence nest-site selection in Arctic-breeding shorebirds

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ABSTRACT

Habitat selection theory suggests that shorebirds should choose nest sites that maximize survival and fitness. We investigated how habitat, and proximity to conspecific or heterospecific nesting birds, was related to nest-site selection in American Golden-Plovers (*Pluvialis dominica*), Dunlin (*Calidris alpina*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Pectoral Sandpipers (*C. melanotos*), Red Phalaropes (*Phalaropus fulicarius*), and Semipalmated Sandpipers (*C. pusilla*) in Barrow, Alaska, USA, between 2005 and 2012. We used remote-sensing data to link habitat information to used and unused nest sites, and we measured distances from nests to other nearby nesting shorebird neighbors. Results from an information-theoretic approach to identify best-approximating models indicated that all species selected nest sites on the basis of both habitat and social cues. Macroscale tundra moisture level within 50 m of the nest, which was closely associated with vegetation community, was an informative variable for Dunlin, Long-billed Dowitcher, and Red Phalarope, which all selected wetter habitat. Enhanced tundra microrelief increased the probability of nest-site selection for American Golden-Plover, Long-billed Dowitcher, Pectoral Sandpiper, and Semipalmated Sandpiper. American Golden-Plover, Dunlin, Pectoral Sandpiper, and Semipalmated Sandpiper selected sites farther from conspecific nests than predicted by chance. Our results indicate that shorebirds select nest sites on the basis of habitat features, and that some are also influenced by proximity to other nesting shorebirds. These findings indicate that shorebirds select nests that are likely to aid incubation abilities, reduce predator detection of nesting birds, enhance detection of predators, enhance foraging, and reduce competition from conspecifics. The variable needs of the different Arctic-breeding shorebirds indicate that climate change will have both beneficial and harmful consequences. Our habitat models may be useful for predicting areas of high shorebird importance throughout the Arctic Coastal Plain, allowing mitigation of proposed anthropogenic developments.

Keywords: Arctic Coastal Plain, climate change, microhabitat, nest-site selection, shorebird, social interaction, tundra

El hábitat y los factores sociales influyen la selección del sitio de anidación en las aves playeras que crían en el Ártico

RESUMEN

La teoría de selección de hábitat sugiere que las aves playeras deberían elegir sitios de anidación que maximicen la supervivencia y la adecuación biológica. Investigamos como el hábitat y la proximidad a nidos de individuos de la misma o de distintas especies se relacionan con la selección del sitio de anidación en *Pluvialis dominica*, *Calidris alpina*, *Limnodromus scolopaceus*, *Calidris melanotos*, *Phalaropus fulicarius* y *Calidris pusilla* en Barrow, Alaska entre 2005 y 2012. Usamos datos de sensores remotos para vincular la información del hábitat con los sitios de anidación usados y no usados, y medimos la distancia desde los nidos a otras aves playeras vecinas anidando. Los resultados usando un enfoque de la teoría de la información para identificar los modelos de mejor aproximación indicaron que todas las especies seleccionaron sitios de anidación basadas en señales del hábitat y sociales. El nivel de humedad de la tundra a escala macro dentro de los 50 m del nido, que estuvo estrechamente asociado con la comunidad vegetal, fue una variable informativa para *C. alpina*, *L. scolopaceus* y *P. fulicarius*, que seleccionaron hábitats más húmedos. El micro relieve realizado de la tundra aumentó la probabilidad de la selección del sitio de anidación para *P. dominica*, *L. scolopaceus*, *C. melanotos* y *C. pusilla*. *P. dominica*, *C. alpina*, *C. melanotos* y *C. pusilla* seleccionaron sitios más alejados de individuos de la misma especie que lo predicho por azar. Nuestros resultados indican que las aves playeras seleccionan los sitios de anidación basadas en las características del hábitat, y que algunas también están influenciadas por la proximidad a otras aves playeras anidando. Estos resultados indican que las aves playeras seleccionan nidos que probablemente facilitan las tareas de incubación, reducen la detección por parte de los depredadores de las aves

anidando, aumentan la detección de los depredadores, mejoran el forrajeo y reducen la competencia por parte de individuos de la misma especie. Las necesidades variables de las diferentes aves playeras que anidan en el Ártico indican que el cambio climático tendrá tanto consecuencias benéficas como perjudiciales. Nuestros modelos de hábitat pueden ser útiles para predecir las áreas de alta importancia para las aves playeras a través de la planicie costera del Ártico, permitiendo la mitigación de los desarrollos antropogénicos propuestos.

Palabras clave: ave playera, cambio climático, interacción social, micro hábitat, planicie costera del Ártico, selección del sitio de anidación, tundra

INTRODUCTION

Habitat selection theory predicts that nest-site selection in birds is driven by ultimate factors that maximize fitness (Hildén 1965). These factors are evident in selection of locations and microhabitat structures that enable predator avoidance, a favorable nest microclimate, and proximity to food resources for adults and young (Hildén 1965, Martin and Roper 1988, With and Webb 1993, Martin 1998, Clark and Shutler 1999, Smith et al. 2007). Previous work also has demonstrated that space use and nest-site selection in birds can be strongly influenced by conspecific and heterospecific neighbors that can affect resource availability and cue habitat suitability (Hildén 1965, Fretwell and Lucas 1970, Pitelka et al. 1974, Betts et al. 2008).

Habitat characteristics with potential to influence nest-site selection may be easily recognizable in some systems, but features on the tundra landscape of Alaska's Arctic Coastal Plain are ostensibly subtle, and shorebird nests may appear to be randomly distributed. However, the tundra is a mosaic of different habitat types (Brown et al. 1980), which have the potential to affect nest success (Johnson and Walters 2011) and adult survival. Accordingly, we assume that shorebirds place nests in response to habitat types to maximize reproductive fitness, as would be predicted from natural selection theory (Hildén 1965, Clark and Shutler 1999).

Tundra-breeding birds incur higher energetic costs during incubation than other groups (Piersma et al. 2003). Ground-nesting shorebirds may select nest sites with microrelief that reduces exposure to the Arctic cold. Permafrost below the tundra surface acts as a conductive heat sink on ground nests, and cool ambient temperatures and high winds facilitate convective heat loss from exposed eggs and incubating adults (Andreev 1999, Reid et al. 2002, Piersma et al. 2003, Cresswell et al. 2004, Bulla et al. 2015). Although relatively small in height (generally <0.5 m), sloped tundra mounds and ridges may shelter incubating adults or unattended nests from wind, and the slope of the ground also may provide a directional aspect that maximizes solar radiation and heats nests.

Shorebird nest sites also may be selected to reduce predation. Nest sites in areas of greater microrelief may reduce nest detection by terrestrial predators by impeding their line of sight (Tremblay et al. 1997). Alternatively,

some species use early detection to elude and distract predators (Gochfeld 1984). They may prefer flat areas with short or nonexistent vegetation, or position nests on top of tundra mounds and ridges to provide a broad field of view (Johnson et al. 2009, Johnson and Walters 2011). Predator avoidance also may be achieved by nesting in areas surrounded by wet habitat that presents an inconvenient travel route for terrestrial predators (Lecomte et al. 2008). Finally, nest-site selection may be affected by proximity to food resources. Incubating adults may nest close to food resources to retain proximity while feeding, which could be particularly beneficial to uniparental species that take frequent incubation breaks. Additionally, nesting near rich food resources may benefit precocial young that must forage independently shortly after hatch. Preferred invertebrate prey of most shorebird species are more common in wet lowland habitats than in upland areas (Holmes and Pitelka 1968, Holmes 1971, Smith et al. 2007, Tulp and Schekkerman 2008), and a nest located near ponds or wetland areas could facilitate energy intake and increase the survival of young.

Social behaviors such as territoriality and attraction also may influence nest-site selection (Hildén 1965, Fretwell and Lucas 1970). Nesting in conspecific aggregations has been shown to impart reproductive advantages to some species or individuals (Stamps 1988, Blomqvist et al. 2002, Valone and Templeton 2002, Danchin et al. 2004). Nearby birds may aid in predator avoidance by enhancing detection or promoting dilution effects (Stamps 1988, Wrona and Dixon 1991), and the presence of conspecifics may provide the opportunity for extrapair copulations (Wagner 1997, Dale et al. 1999, Blomqvist et al. 2002, Yezerinac et al. 2013). Additionally, young birds or non-site faithful "opportunistic" species without experience-based knowledge about food resources or predation risks within a site may prospect for suitable locations and use public information to select nest sites, based on the presence of breeding conspecifics or heterospecifics (Holmes 1966a, 1971, Pitelka et al. 1974, Reed et al. 1999, Valone and Templeton 2002, Saalfeld and Lanctot 2015). On the contrary, species that exhibit high site fidelity may engage in territorial displays and aggressive behavior to discourage conspecifics and/or heterospecifics from settling nearby (Holmes 1966a, 1971, Recher and Recher 1969, Pitelka et al. 1974, Lanctot et al. 2000,

Johnson and Walters 2011). Avian territoriality on breeding grounds may serve as a paternity assurance mechanism or as a means of protecting limited foraging resources (Birkhead and Møller 1992, Westneat and Sherman 1997).

A limited number of studies have explored how habitat and social features influence nest-site selection in Arctic-breeding shorebirds (Myers and Pitelka 1980, Rodrigues 1994, Smith et al. 2007, Walpole et al. 2008, Johnson and Walters 2011). These studies were relatively short in duration, and only one investigation simultaneously assessed habitat features and the presence of other nesting shorebirds as potential cues (Johnson and Walters 2011). Further, investigators focused only on one or a few species at a time, which limited the ability to detect broad, generalized patterns and heterospecific effects. Saalfeld et al. (2013) developed species-specific, landscape-scale habitat suitability indices for 8 common shorebird species that breed on the Arctic Coastal Plain; although extensive in coverage, that study was based on brief site visits and used presence-only modeling techniques for adults (not nests) that incorporated only habitat variables.

The development of nest-site selection models can help elucidate how climate change may affect the millions of shorebirds that migrate to the Arctic to breed (Johnson and Herter 1989, Bart and Johnston 2012). Accelerated climate change in the Arctic may influence tundra ecology and landscape composition (Walker et al. 2006, Martin et al. 2009, Van Hemert et al. 2015). Climate models predict longer frost-free seasons, increased precipitation, and melting of permafrost, processes that may alter moisture content and vegetative structure of nesting habitat and wetland foraging areas (Martin et al. 2009, Andresen and Lougheed 2015). Additionally, establishing baseline information about nest-site selection could assist the development of models to predict where shorebirds are likely to nest and help inform assessments of the potential impacts of anthropogenic structures that are placed on the tundra.

We used an 8 yr dataset of breeding activities of 6 common shorebird species in Barrow, Alaska, USA, to study nest-site selection. We developed quantitative models composed of habitat and social parameters to infer how habitat and nesting neighbors simultaneously influence nest-site selection. We present information for understanding how predicted climate-induced shifts in habitat could affect shorebird nest-site selection and, ultimately, reproductive success in the Arctic.

METHODS

Study Area

Barrow (71°51'N, 156°39'W) is located at the northernmost tip of Alaska and is bordered by the Chukchi and Beaufort seas. The sun is above the horizon from May 10

to August 2, with mean June temperatures of 1.1–3.1°C (2005–2012; NOAA National Centers for Environmental Information, <http://www.ncdc.noaa.gov/>). The tundra surrounding Barrow is dominated by graminoid, bryophyte, forb, and lichen communities that vary in response to changes in microtopography and drainage (Brown et al. 1980). Landform types are typical of the Arctic Coastal Plain and include high- and low-centered polygons, frost boils, strangmoor, hummocky terrain, and nonpatterned and reticulate-patterned ground; all occur in grouped or mixed formations throughout the Barrow area (Walker et al. 1980). The Barrow region supports a relatively high density of the Arctic's breeding birds, likely because it is a triangular apex of land that concentrates migrants as they travel along the coast (MacLean 1980, Andres et al. 2012). Bird densities also may be enhanced by an Arctic fox (*Vulpes lagopus*) removal program that was implemented to promote nesting success of threatened seaduck species (Saalfeld and Lanctot 2015).

Shorebird Monitoring

We monitored shorebird breeding activities near Barrow from 2005 to 2012, including nests of American Golden-Plover (*Pluvialis dominica*), Dunlin (*Calidris alpina*), Long-billed Dowitcher (*Limnodromus scolopaceus*), Pectoral Sandpiper (*C. melanotos*), Red Phalarope (*Phalaropus fulicarius*), and Semipalmated Sandpiper (*C. pusilla*). These species represented the majority of nesting shorebirds in the area (93% of all nests across 8 yr of study). Other shorebird species occurring in low abundances were not included in the study, including Baird's Sandpiper (*C. bairdii*), Buff-breasted Sandpiper (*C. subruficollis*), Red-necked Phalarope (*P. lobatus*), Western Sandpiper (*C. mauri*), and White-rumped Sandpiper (*C. fuscicollis*). Nests were located between late May and early July on five 600 × 600 m study plots located 3–6 km southeast of Barrow (Figure 1). Landforms and vegetation communities within plots represented regional tundra habitats, and each plot was divided into 144 grid squares of 50 × 50 m, which were delineated with wooden lathes (1 m tall) painted with alphanumeric codes. Each plot was searched daily for nests, using area-search and rope-drag techniques, throughout June and early July (Naves et al. 2008, Saalfeld and Lanctot 2015). Nest location coordinates were recorded with global positioning systems (GPS; Garmin, Olathe, Kansas, USA) with an accuracy of ~3 m on the tundra landscape. We believe most nests were located on our study plots because Arctic foxes, which are one of the primary predators of shorebird nests (Liebezeit and Zack 2008), were removed from the study area each summer (Saalfeld and Lanctot 2015). This predator removal enhanced nest survival (R. B. Lanctot and S. Saalfeld personal observation); this fact, combined with regular

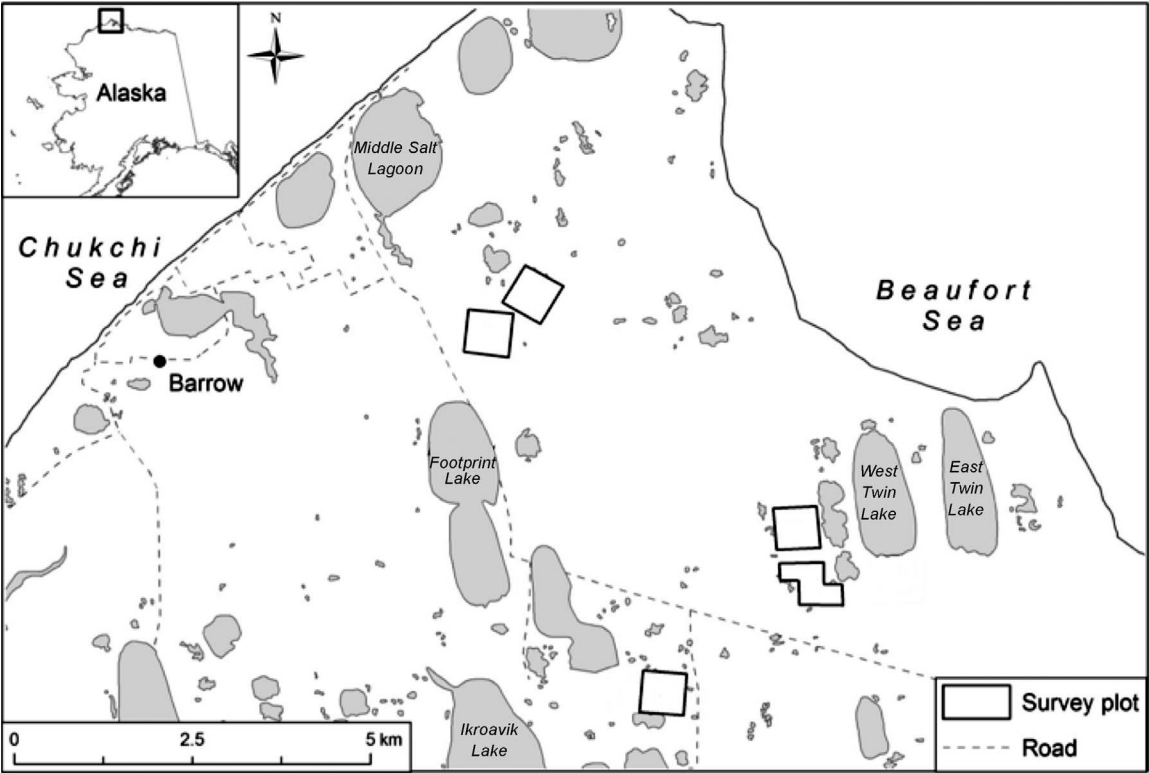


FIGURE 1. Location of Barrow, Alaska, USA, and the 600 × 600 m plots that were surveyed from 2005 to 2012.

visits, has been shown to increase detection rates to >0.85 after only 4 visits to the area (Smith et al. 2009).

Nest Locations

Nest location coordinates were added to a geographic information system database (ArcMap 10; ESRI, Redlands, California, USA). For each nest, we identified 10 random points, within the same plot and during the same year,

where nests did not occur (water bodies were excluded). We assessed a suite of variables representing land cover, microrelief, and proximity to neighbors for each nest and random point. Land-cover data were extracted from a land-cover classification map of the Barrow area (Lin et al. 2012, C. E. Tweedie personal communication; Table 1). Briefly, the map was derived from 0.7 m resolution QuickBird satellite imagery obtained on August 1, 2002,

TABLE 1. Land-cover classifications and soil-moisture definitions presented in an unpublished map, “Land cover classification and change detection near Barrow, Alaska, using QuickBird satellite imagery,” prepared in 2012 by C. E. Tweedie, C. G. Andresen, R. D. Hollister, J. L. May, D. R. Bronson, A. Gaylord, and P. J. Webber.

Moisture level	Tundra type	Study-plot representation	Dominant vascular plant species	Approximate water depth
2	Aquatic graminoid tundra	4%	<i>Carex stans</i> , <i>Eriophorum russeolum</i> , <i>Arctophila fulva</i> , <i>Ranunculus pallasii</i> , <i>Dupontia fisheri</i>	>30 cm
3	Seasonally flooded graminoid tundra	6%	<i>D. fisheri</i> , <i>E. angustifolium</i> , <i>C. stans</i> , <i>Poa arctica</i> , <i>E. russeolum</i>	15–30 cm
4	Wet graminoid tundra	17%	<i>C. stans</i> , <i>P. arctica</i> , <i>D. fisheri</i> , <i>E. angustifolium</i> , <i>E. russeolum</i>	1–15 cm
5	Moist graminoid tundra	28%	<i>C. stans</i> , <i>E. russeolum</i> , <i>D. fisheri</i> , <i>E. angustifolium</i> , <i>P. arctica</i>	0–1 cm
6	Dry-moist dwarf shrub-graminoid tundra	24%	<i>Salix rotundifolia</i> , <i>C. stans</i> , <i>P. arctica</i> , <i>Arctagrostis latifolia</i> , <i>Stellaria laeta</i>	No surface water
7	Dry dwarf shrub-graminoid tundra	18%	<i>Salix rotundifolia</i> , <i>Cassiope tetragona</i> , <i>A. latifolia</i> , <i>Luzula confusa</i> , <i>L. arctica</i>	No surface water
8	Dry dwarf shrub tundra	1%	<i>C. tetragona</i> , <i>S. rotundifolia</i> , <i>L. confusa</i> , <i>A. latifolia</i> , <i>Potentilla hyparctica</i>	No surface water

and represents tundra moisture levels and associated dominant vegetation communities in 8 classifications along a decreasing moisture gradient. Tundra wetness and vegetation growth may experience fluctuations within and among years due to variations in weather, herbivory, and climate change; however, moisture regimes and composition of vegetation communities are unlikely to have changed across the years represented in the present study (Andresen and Lougheed 2015). The map identifies these perennial features and has a ground-proofed accuracy of 74–88% (C. E. Tweedie personal communication; Table 1). Below, we list each variable and provide reasoning for its inclusion in the study.

Microscale tundra moisture level (*qML3*). Tundra vegetation communities vary in response to moisture. Taller, thicker vegetation typically grows in wet areas, whereas shorter, sparser vegetation grows in dry areas (Brown et al. 1980). Vegetation at the nest site composes a microhabitat that may be associated with predator avoidance and thermoregulation (Miller et al. 2014). We generated tundra moisture-level values for each nest and each random point by averaging land-cover classification values within a 3 m radius (Table 1). We chose the 3 m buffer to best reflect shorebird habitat selection at a microscale and because our GPS units had an error of ~3 m on the tundra landscape. We modeled this variable with a quadratic term because it would be impossible or highly unlikely for birds to nest in habitat on either end of the moisture-level spectrum (water or bare ground), and we intended the variable to identify optimum selection of microscale nest-site habitat.

Macroscale tundra moisture level (*ML50*). As above, we generated a tundra moisture level within a 50 m buffer of each nest and each random point to represent habitat selection at a macroscale for generally wetter or drier conditions, which may have implications for predator avoidance. The 50 m buffer represents the greater nest area but is small enough to capture tundra moisture-level diversity across the landscape.

Degree of microrelief (*Microrel*). Microrelief describes variations in tundra topography that result from the mounds, ridges, and troughs of polygon landforms; these features may influence the thermal properties of the nest or the ability to avoid predators. In 2012, a single observer (J.A.C.) walked to the center of each 2,500 m² grid square within each plot and visually assigned a category of microrelief to the four 625 m² quadrants within. Assigned categories were reassessed and confirmed from a second corner of each 25 m² quadrant. Categories of microrelief ranged from 0 to 4, based on the spacing and the degree of height or depth of tundra landforms. A low score indicated flat ground, and increasing scores represented increasing microrelief. A high score was typically recorded for high- or low-centered polygons where the trough to ridge or

center was >0.5 m. Scores were treated as an ordinal variable.

Proportion of water within 50 m (*Wtr50*). Numerous lakes and small ponds occur throughout the study plots. Water can limit how terrestrial predators can approach a nest and may reduce encounter probability (Lecomte et al. 2008); thus, we speculated that shorebirds may prefer to nest in areas of tundra interrupted by water bodies. We used the land-cover classification map to identify water bodies and measured the proportion of water within 50 m of each nest and random point.

Distance to nearest wetland (*Wetland*). Wetlands provide important foraging habitat for newly hatched shorebird broods (Holmes and Pitelka 1968); thus, birds may select nest sites close to wetlands. We measured distances from each nest and each random point to the border of the nearest wetland area. We log transformed distances to normalize their distribution. We restricted “wetlands” to areas that were >50 m², because smaller areas are often ephemeral and difficult to detect.

Distance to nearest conspecific–heterospecific (*Conspecific–Heterospecific*). Distances (log transformed) were measured from nests and random points to each of the nearest conspecific and heterospecific nests. For each focal nest, and for its 10 associated random points, we considered distances only to neighboring nests initiated on the same day or earlier. Heterospecific nests included only our 6 focal shorebird species. Nests that were initiated before other neighboring nests were established on the plot lacked values for nearest-neighbor distances and were thus excluded from analyses. We presume that the earliest-nesting birds select nest sites primarily on the basis of habitat characteristics, and the present study seeks to assess the combined influence of social and habitat cues on nest-site selection.

Models

We developed candidate sets of generalized linear mixed models with the explanatory variables described above and binomial responses representing nest sites or random points. Model sets that contained all possible combinations of variables were compiled for each species. All models for each species included a random effect variable to account for differences among study plots. Year was originally included as a random effect but was dropped because it accounted for no or negligible variation in the data. Thus, we pooled data across years.

Multicollinearity among variables in a model can artificially inflate the standard error of parameter estimates. We assessed variables for correlation (Pearson's $r > 0.6$) and removed *Wtr50* from the analysis because of correlation with other variables.

We fitted models with the package “lme4” in R 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria) and

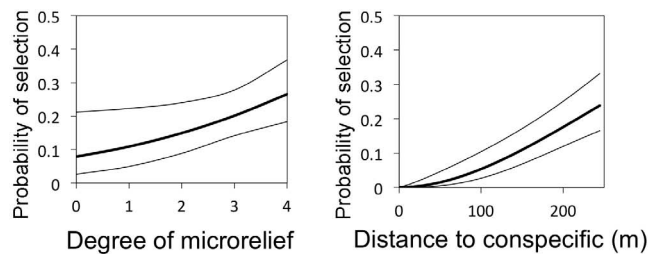
TABLE 2. Model selection results for the presence of shorebird nests in Barrow, Alaska, USA (n = nests/random points). All additive linear combinations of variables were included in our analyses, but (except for the null model) those with AIC_c values >2 are not depicted in tables. Fixed-effect variables include microscale (within 3 m of the nest) tundra moisture level ($qML3$; quadratic term), macroscale (within 50 m of the nest) tundra moisture level (ML50), degree of microrelief (Microrel), distance to nearest wetland (Wetland), distance to nearest conspecific nest (Conspecific), and distance to nearest heterospecific nest (Heterospecific). All models include a random effect for plot. Variables in bold have 95% confidence intervals of parameter estimates that do not overlap zero.

Model	K	AIC_c	ΔAIC_c	w_i
American Golden-Plover ($n = 42/420$)				
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Wetland}$	7	248.8	0.00	0.16
$qML3 + \text{Microrel} + \text{Conspecific} + \text{ML50}$	7	249.3	0.50	0.12
$qML3 + \text{Microrel} + \text{Conspecific}$	6	249.4	0.56	0.12
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific} + \text{Wetland}$	8	250.1	1.28	0.08
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Wetland} + \text{ML50}$	8	250.3	1.54	0.07
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific}$	7	250.5	1.68	0.07
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific} + \text{ML50}$	8	250.5	1.70	0.07
Null	2	285.5	36.71	0.00
Dunlin ($n = 183/1,830$)				
$qML3 + \text{ML50} + \text{Conspecific}$	6	1,084.1	0.00	0.20
$qML3 + \text{ML50} + \text{Conspecific} + \text{Wetland}$	7	1,084.3	0.19	0.18
$qML3 + \text{ML50} + \text{Conspecific} + \text{Wetland} + \text{Microrel}$	8	1,084.7	0.54	0.15
$qML3 + \text{ML50} + \text{Conspecific} + \text{Microrel}$	7	1,084.7	0.55	0.15
$qML3 + \text{ML50} + \text{Conspecific} + \text{Heterospecific} + \text{Wetland} + \text{Microrel}$	9	1,085.8	1.66	0.09
$qML3 + \text{ML50} + \text{Conspecific} + \text{Heterospecific}$	7	1,085.8	1.69	0.08
$qML3 + \text{ML50} + \text{Conspecific} + \text{Heterospecific} + \text{Wetland}$	8	1,086.0	1.82	0.08
$qML3 + \text{ML50} + \text{Conspecific} + \text{Heterospecific} + \text{Microrel}$	8	1,086.0	1.86	0.08
Null	2	1,230.5	146.34	0.00
Long-billed Dowitcher ($n = 146/1,460$)				
$qML3 + \text{ML50} + \text{Microrel} + \text{Wetland} + \text{Heterospecific}$	8	946.9	0.00	0.21
$qML3 + \text{ML50} + \text{Microrel} + \text{Wetland} + \text{Heterospecific} + \text{Conspecific}$	9	948.0	1.07	0.13
$qML3 + \text{ML50} + \text{Microrel} + \text{Wetland}$	7	948.0	1.08	0.13
$qML3 + \text{ML50} + \text{Microrel} + \text{Wetland} + \text{Conspecific}$	8	948.9	1.98	0.08
Null	2	982.5	35.58	0.00
Pectoral Sandpiper ($n = 341/3,410$)				
$qML3 + \text{Microrel} + \text{Conspecific}$	6	2,219.9	0.00	0.12
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific}$	7	2,220.4	0.53	0.10
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Wetland}$	7	2,220.7	0.78	0.08
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific} + \text{Wetland}$	8	2,220.9	1.03	0.07
$qML3 + \text{Microrel} + \text{Conspecific} + \text{ML50}$	7	2,221.5	1.65	0.05
Null	2	2,289.4	69.51	0.00
Red Phalarope ($n = 564/5,640$)				
$qML3 + \text{ML50} + \text{Conspecific}$	6	3,761.3	0.00	0.22
$qML3 + \text{ML50}$	5	3,762.6	1.27	0.12
$qML3 + \text{ML50} + \text{Conspecific} + \text{Microrel}$	7	3,762.7	1.37	0.11
$qML3 + \text{ML50} + \text{Conspecific} + \text{Heterospecific}$	7	3,763.3	1.98	0.08
$qML3 + \text{ML50} + \text{Conspecific} + \text{Wetland}$	7	3,763.3	1.98	0.08
Null	2	3,783.9	22.58	0.00
Semipalmated Sandpiper ($n = 131/1,310$)				
$qML3 + \text{Microrel} + \text{Conspecific} + \text{ML50}$	7	840.1	0.00	0.19
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Wetland}$	7	840.7	0.67	0.14
$qML3 + \text{Microrel} + \text{Conspecific}$	6	840.8	0.70	0.13
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Heterospecific} + \text{ML50}$	8	841.5	1.48	0.09
$qML3 + \text{Microrel} + \text{Conspecific} + \text{Wetland} + \text{ML50}$	8	841.6	1.54	0.09
Null	2	882.0	41.91	0.00

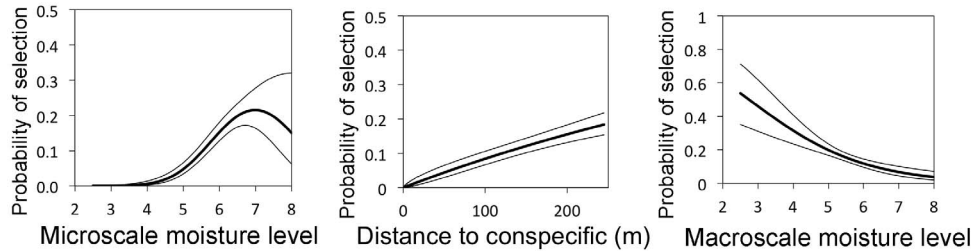
RStudio 0.96.330 (RStudio, Boston, Massachusetts, USA) and used the package “MuMIn” to fit all possible combinations of habitat variables. We ranked models using Akaike’s Information Criterion corrected for sample size (AIC_c ; Burnham and Anderson 2002). We considered variables within the top-ranked model to be informative in nest-site selection if 95% confidence intervals (CI) did not

overlap zero. We further discuss models within 2 AIC_c units of the top-ranked model, because they may compete for best-approximating model (Burnham and Anderson 2002). We evaluated model performance by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) for the top model of each species (Fielding and Bell 1997, Hosmer and Lemeshow 2000,

American Golden-Plover



Dunlin



Long-billed Dowitcher

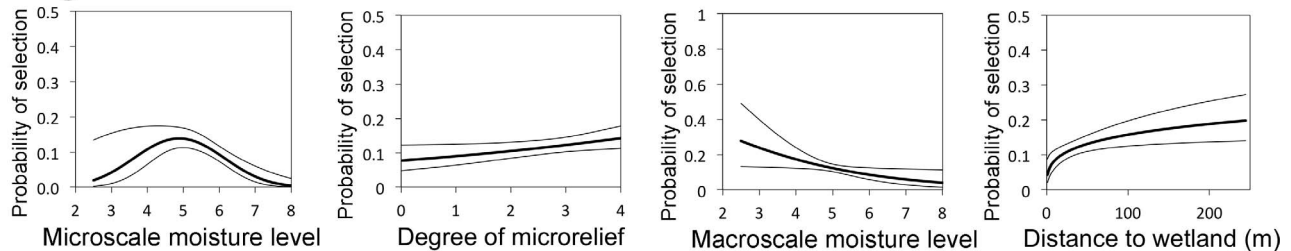


FIGURE 2. Predicted probability of a nest site being present for shorebirds nesting in Barrow, Alaska, USA, between 2005 and 2012, in relation to the value of habitat and social variables from top models (i.e. other covariates in the model were held at their median values). Graphs are displayed only for variables that were considered informative and include 95% confidence intervals. *Figure 2 is continued on the next page.*

Boyce et al. 2002). The AUC evaluates a model's predictive performance by indicating how well it discriminates between locations where nests are present or absent. An AUC value of 1.0 indicates perfect predictability, and a value of 0.5 indicates that the model's predictability is equal to random. We considered values between 0.5 and 0.7 to indicate poor discrimination, values between 0.7 and 0.8 to indicate acceptable discrimination, values between 0.8 and 0.9 to indicate excellent discrimination, and values >0.9 to indicate outstanding discrimination (after Hosmer and Lemeshow 2000).

RESULTS

Between 2005 and 2012 we documented 1,614 nests of the 6 shorebird species, 1,407 of which had neighbors; the latter number included 42 American Golden Plover nests, 183 Dunlin nests, 146 Long-billed Dowitcher nests, 341 Pectoral Sandpiper nests, 564 Red Phalarope nests, and 131 Semipalmated Sandpiper nests. The results of our

analyses indicated that nest-site selection is not random and that habitat and social features influenced where shorebirds nested. The top model ranked well above null models for all species (ΔAIC_c ranged from 23 to 146; Table 2), and the variable $qML3$ was informative for all but one species. Additional informative variables were present for all species, and predicted probability plots demonstrate the strength of the effects of these variables on nest-site selection (Figure 2). Detailed results for each species follow.

American Golden-Plover. Informative variables in the top model were Microrel and Conspecific, and the model also included $qML3$ and Wetland ($w_i = 0.16$; Table 3). All competing models that were within 2 AIC units of the top model included Microrel, Conspecific, and $qML3$, with Microrel and Conspecific being informative in the competing model set, while $qML3$ was informative in only 2 of these models. Various combinations of all remaining variables also appeared in the set, but none were informative. Probability of selection increased with more

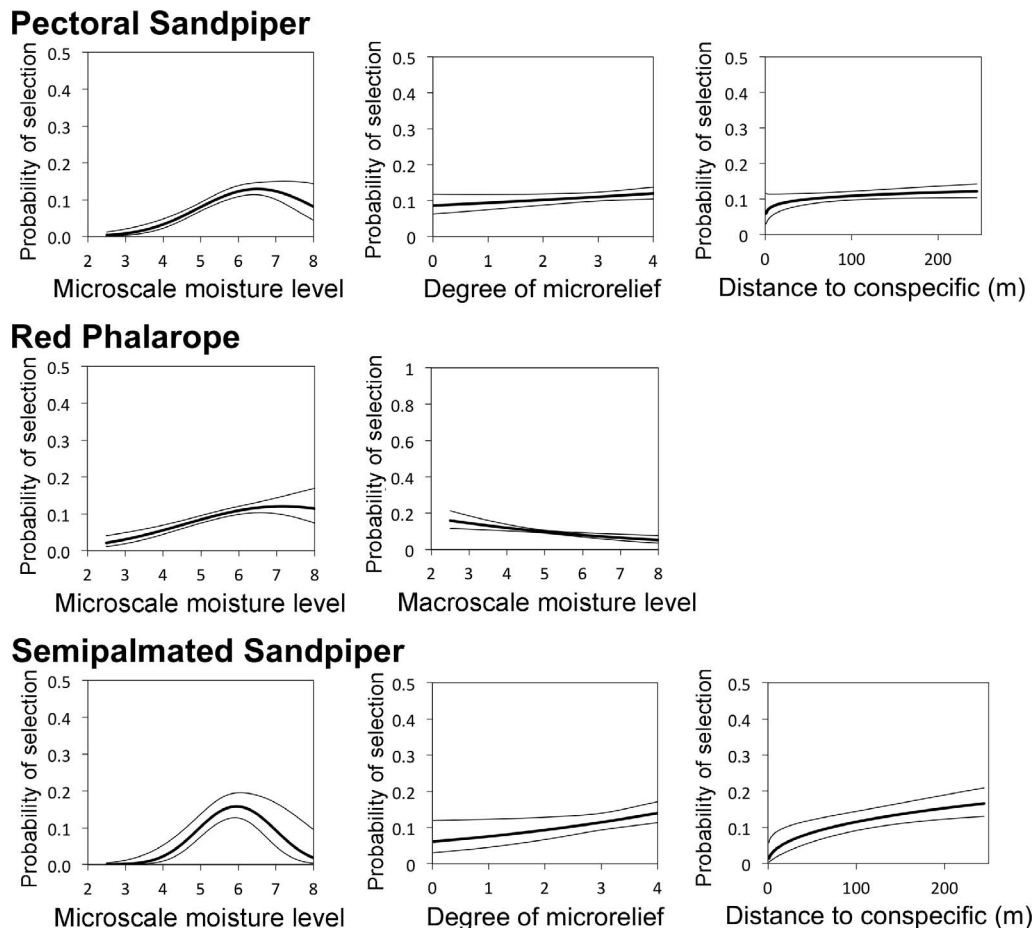


FIGURE 2. Continued.

microrelief and with greater distance from nesting conspecifics (Figure 2). The AUC for the top model was 0.88, indicating that the model performs with excellent discrimination between used and unused sites.

Dunlin. The variables $qML3$, $ML50$, and $Conspecific$ were in the top model, and all were informative ($w_i = 0.20$; Table 3). These informative variables were in all competing models, along with combinations of *Wetland*, *Microrel*, and *Heterospecific*, but the latter 3 were not informative in any model. Microscale moisture-level ($qML3$) selection was optimized on dry-to-moist dwarf shrub–graminoid tundra (moisture level = 6.9; Figure 2), which was drier than that available. Probability of nest-site selection increased with wetter tundra on the macroscale ($ML50$) and with greater distance from conspecifics (Figure 2). AUC for the top model was 0.80, indicating excellent discrimination between used and unused sites.

Long-billed Dowitcher. The top Long-billed Dowitcher model consisted of $qML3$, $ML50$, *Microrel*, *Wetland*, and *Heterospecific* ($w_i = 0.21$; Table 3). The habitat variables

were all informative, but 95% CIs for the *Heterospecific* parameter estimate overlapped zero. Competing models contained all habitat variables, which were informative, along with various combinations of the *Heterospecific* and *Conspecific* social variables, which were not informative. Microscale moisture-level ($qML3$) selection was optimized on wet-to-moist graminoid tundra (moisture level = 4.9; Figure 2), which was wetter than that available. Probability of nest-site selection increased with wetter tundra on the macroscale ($ML50$), more microrelief, and greater distance from wetlands (Figure 2). AUC for the top model was 0.68, indicating poor discrimination between used and unused sites.

Pectoral Sandpiper. All variables in the top model were informative, including $qML3$, *Microrel*, and *Conspecific* ($w_i = 0.12$; Table 3). Other competing models included these informative variables along with combinations of *Heterospecific*, *Wetland*, and $ML50$, which were not informative. Microscale moisture-level ($qML3$) selection was optimized on dry-to-moist dwarf shrub–graminoid tundra (moisture level = 6.5; Figure 2), which was drier

than that available. Probability of nest-site selection increased with more microrelief and greater distance from conspecifics (Figure 2). AUC for the top model was 0.64, indicating poor discrimination between sites where nests are present or absent.

Red Phalarope. There were no informative social variables in the top 3 Red Phalarope models, and *qML3* and *ML50* were the informative habitat variables in the top model ($w_i = 0.22$; Table 3). These informative variables also were in all competing models, along with combinations of Conspecific, Heterospecific, Wetland, and Microrelief, which were not informative. Microscale tundra moisture-level (*qML3*) selection was optimized on dry dwarf shrub–graminoid tundra (moisture level = 7.2; Figure 2), which was drier than that available. Probability of nest-site selection increased with wetter tundra at the macroscale (*ML50*; Figure 2). Area under the ROC curve for the top model was 0.58, indicating poor discrimination between sites where nests are present or absent.

Semipalmated Sandpiper. Informative variables in the top model were *qML3*, Microrel, and Conspecific ($w_i = 0.19$; Table 3). Although the 95% CI for the parameter estimate overlapped zero, *ML50* also appeared in the top-ranked model. All competing models consisted of *qML3*, Microrel, and Conspecific, which were informative, and various combinations of Heterospecific, Wetland, and *ML50*, which were not informative. Microscale tundra moisture level (*qML3*) was optimized on moist graminoid tundra (moisture level = 5.9; Figure 2), which was drier than that available. Probability of nest-site selection increased with more microrelief and greater distance from conspecifics (Figure 2). AUC for the top model was 0.72, indicating acceptable discrimination between used and unused sites.

DISCUSSION

Our results indicate that habitat features influenced nest-site selection in shorebirds, with microscale tundra features affecting most shorebird species. Social features also influenced nest-site selection in species that nested farther from conspecifics than random distributions predicted.

In the extreme Arctic environment, selection of a nest site that reduces the energetic costs of incubation should benefit most shorebirds (With and Webb 1993, Cresswell et al. 2004, Bulla et al. 2015). Our variable for microscale tundra moisture level approximates the type of tundra in the immediate area of the nest (Table 1). As predicted, most shorebird species selected dry-to-moist dwarf shrub–graminoid tundra, which was likely dry enough to ensure proper thermoregulation of the nest cup, but retained moisture sufficient to furnish medium-height vegetation that might conceal the nest and act as a windbreak

(Cresswell et al. 2004). Lower and wetter areas also are last to become free of snow in early to mid-June; the only available habitat to early nesters, such as Dunlin and Semipalmated Sandpipers, may be the more elevated dry-to-moist graminoid tundra that was identified as preferred nesting habitat by the models. Long-billed Dowitchers, by contrast, selected wetter habitat, which was almost certainly available in greater proportions later in the season, when this species typically nests (Saalfeld and Lanctot 2015).

The composition of the vegetation surrounding the nest at a macroscale also was important to some shorebird species. Wet substrate may present an inconvenient route for terrestrial predators, limiting their access to nests (Lecomte et al. 2008), and also provide suitable habitat for invertebrates upon which shorebird species rely for food (Walpole et al. 2008). The macroscale moisture level was important for Dunlin, Long-billed Dowitchers, and Red Phalaropes, all 3 of which were more likely to be present as tundra wetness increased at a macro-level. This result is consistent with previous findings for Long-billed Dowitchers and Red Phalaropes (Rodrigues 1994, Takekawa and Warnock 2000, Latour et al. 2005).

Shorebirds likely reduce costs of thermoregulation by selecting nest sites in areas of pronounced microrelief. Tundra landforms can provide windbreaks that may relieve the stress of maintaining an adequate nest temperature in the Arctic environment. Nesting in areas of high tundra microrelief may further aid in predator avoidance by providing visual obstructions to terrestrial predators. Alternatively, shorebirds may choose to nest atop elevated locations that allow clear views of the surrounding landscape (Ratcliffe 1976). American Golden-Plovers, which are among the largest and most visually conspicuous species of shorebird nesting in Barrow, employ an early-detection and distraction predator-evasion tactic (Byrkjedal 1989). The tactic may be facilitated by areas of high microrelief, where the birds can establish nests atop or on the sides of elevated polygons, hummocks, or ridges. Indeed, our results indicated that degree of microrelief likely increased nesting by American Golden-Plovers. Areas of enhanced microrelief also increased probability of selection for Long-billed Dowitchers, Pectoral Sandpipers, and Semipalmated Sandpipers. Nests of the 2 sandpipers and of Long-billed Dowitchers were often in the troughs near raised mounds and ridges (J. A. Cunningham personal observation), which may have provided relief from the wind for these smaller species with lower surface-to-volume ratios. Such locations also can conceal movement to and from the nest, and they may be especially important in uniparental species such as the Pectoral Sandpiper, which takes frequent incubation breaks to feed (Holmes and Pitelka 1988, Cresswell et al. 2004, Smith et al. 2009).

TABLE 3. Parameter estimates of top models representing probability of nest-site selection by shorebirds in Barrow, Alaska, USA, 2005–2012 ($\hat{\beta}$ = parameter estimate). Fixed-effect variables include microscale (within 3 m of the nest) tundra moisture level ($qML3$; quadratic term), macroscale (within 50 m of the nest) tundra moisture level ($ML50$), degree of microrelief ($Microrel$), distance to nearest wetland ($Wetland$), distance to nearest conspecific nest ($Conspecific$), and distance to nearest heterospecific nest ($Heterospecific$). Variables in bold have unconditional 95% confidence intervals (CI) of parameter estimates that do not overlap zero.

Variable	$\hat{\beta}$	SE	P	95% CI
American Golden-Plover				
$qML3$	−0.60	0.28	0.03	−1.14, −0.05
$qML3^2$	−0.40	0.25	0.11	−0.90, 0.10
$Microrel$	0.36	0.17	0.03	0.04, 0.69
$Wetland$	0.30	0.19	0.11	−0.07, 0.68
$Conspecific$	1.91	0.38	<0.01	1.17, 2.65
Dunlin				
$qML3$	1.27	0.16	<0.01	0.95, 1.59
$qML3^2$	−0.43	0.10	<0.01	−0.63, −0.23
$ML50$	−0.62	0.13	<0.01	−0.87, −0.37
$Conspecific$	1.27	0.16	<0.01	0.71, 1.29
Long-billed Dowitcher				
$qML3$	−0.46	0.16	<0.01	−0.77, −0.16
$qML3^2$	−0.37	0.12	<0.01	−0.61, −0.13
$ML50$	−0.42	0.19	0.03	−0.79, −0.05
$Microrel$	0.19	0.08	0.03	0.02, 0.35
$Wetland$	0.31	0.10	<0.01	0.11, 0.08
$Heterospecific$	−0.68	0.92	0.07	−0.48, 0.02
Pectoral Sandpiper				
$qML3$	−3.23	0.44	<0.01	0.34, 0.64
$qML3^2$	0.49	0.08	<0.01	−0.36, −0.11
$Microrel$	0.13	0.06	0.02	0.02, 0.24
$Conspecific$	−3.23	0.44	0.04	0.01, 0.31
Red Phalarope				
$qML3$	0.28	0.06	<0.01	0.15, 0.40
$qML3^2$	−0.09	0.03	0.01	−0.15, −0.02
$ML50$	−0.22	0.07	<0.01	−0.36, −0.09
$Conspecific$	0.10	0.06	0.07	−0.01, 0.21
Semipalmated Sandpiper				
$qML3$	−3.51	1.16	<0.01	0.13, 0.81
$qML3^2$	0.47	0.17	<0.01	−0.83, −0.27
$ML50$	−0.55	0.14	0.07	−0.61, 0.02
$Microrel$	−0.29	0.16	0.03	0.02, 0.43
$Conspecific$	0.48	0.15	<0.01	0.19, 0.76

We predicted that most shorebirds would prefer nest sites that reduced transit time for newly hatched young to move to wetland foraging areas. Numerous authors have suggested that greater forage is available in wet marshes and along the shores of lakes, rivers, and sloughs (Holmes and Pitelka 1968, Holmes 1971, Smith et al. 2007, Tulp and Schekkerman 2008). However, this variable was informative only for Long-billed Dowitchers, in which, contrary to our prediction, the probability of nest-site selection increased at greater distances from wetlands (Figure 2). This result is puzzling, given that the birds also preferred wetter microscale and macroscale habitat (Figure 2). The

larger wetland areas at our site often were associated with open water and surrounded by relatively flat terrain, and a potential explanation is that dowitchers preferred wet terrain that was interspersed with greater microrelief and away from open water. For the remaining species, it is possible that our measure of distance to the nearest wetland may be too coarse; smaller wetlands that could be beneficial to offspring may have been missed. Alternatively, the proximity to large areas of wetland habitat may not be important because newly hatched shorebird young are capable of moving several hundred meters from the nest within a few days of hatching (Lanctot 1994, Johnson and McCaffery 2004, Ruthrauff and McCaffery 2005, Johnson et al. 2008, Wilson and Colwell 2010, Hill 2012). Certainly, the foraging habits of chicks of each species warrant further investigation to understand how they may affect selection of the nest site.

In addition to habitat features, we predicted that the presence of other nesting birds could influence nest placement, especially for “opportunistic” species that have no prior knowledge of a particular breeding area and might use others to detect favorable food or predator conditions (Holmes 1966b, 1971, Pitelka et al. 1974, Saalfeld and Lanctot 2015). “Conservative” species might be less likely to tolerate other nesting birds to protect important food resources and nesting and brood-rearing sites (Holmes 1966a, 1971, Pitelka et al. 1974, Shields 1984, Saalfeld and Lanctot 2015), to reduce predation (Tinbergen et al. 1967), or to reduce opportunities for extrapair matings (Westneat and Sherman 1997, Yezerinac et al. 2013). As predicted, we found that distance to the nearest conspecific was an informative variable for all conservative species, including American Golden-Plovers, Dunlin, and Semipalmated Sandpipers; all nesting was farther from conspecifics than random nest placement predicted (Table 4 and Figure 2). However, we also found a weak but significant relationship for Pectoral Sandpipers, which is considered an opportunistic species (Pitelka et al. 1974, Saalfeld and Lanctot 2015). It might be that all species prefer to nest away from one another, but in years with extremely high densities of birds (which occurs in the opportunistic species) this may be impossible. Distance to the nearest heterospecific neighbor was not informative for any species, although the variable did appear in the top-ranked model for Long-billed Dowitchers and in the second-ranked model for Pectoral Sandpipers. We therefore hesitate to conclude that heterospecifics do not influence nest-site selection. It is possible that our metric is too coarse to capture the particular dynamics between any 2 species; further study on how heterospecifics interact and influence each other is needed.

Our results indicate that Arctic-breeding shorebirds select nest sites on the basis of characteristics of particular habitat features, and some are influenced by the presence

TABLE 4. Mean values (\pm SD) for habitat and social features of shorebird nests (top) located at Barrow, Alaska, USA, 2005–2012, and of 10 associated random points nest⁻¹ (below).

	Microscale moisture level (qML3)	Macroscale moisture level (ML50)	Degree of microrelief	Distance to wetland (m)	Distance to conspecific (m)	Distance to heterospecific (m)
American Golden-Plover	5.4 \pm 0.72	5.5 \pm 0.66	3.2 \pm 1.16	65 \pm 3.15	251 \pm 1.66	66 \pm 1.75
	5.5 \pm 1.00	5.5 \pm 0.75	2.8 \pm 1.26	50 \pm 3.90	154 \pm 1.88	58 \pm 2.20
Dunlin	5.9 \pm 0.75	5.4 \pm 0.91	2.8 \pm 1.07	48 \pm 2.78	186 \pm 1.76	109 \pm 2.21
	5.4 \pm 1.09	5.3 \pm 0.91	2.6 \pm 1.28	33 \pm 4.18	129 \pm 1.97	97 \pm 2.42
Long-billed Dowitcher	5.0 \pm 0.75	5.0 \pm 0.61	2.9 \pm 1.12	37 \pm 3.12	115 \pm 2.78	44 \pm 2.09
	5.2 \pm 0.99	5.1 \pm 0.82	2.6 \pm 1.30	30 \pm 4.12	134 \pm 2.16	50 \pm 1.96
Pectoral Sandpiper	5.8 \pm 0.83	5.4 \pm 0.81	3.0 \pm 1.07	45 \pm 2.68	107 \pm 2.28	53 \pm 2.18
	5.4 \pm 1.05	5.2 \pm 0.89	2.7 \pm 1.25	33 \pm 4.06	103 \pm 2.15	57 \pm 2.08
Red Phalarope	5.4 \pm 1.03	5.1 \pm 1.02	2.3 \pm 1.21	28 \pm 3.43	88 \pm 2.22	80 \pm 2.06
	5.3 \pm 1.12	5.1 \pm 0.96	2.3 \pm 1.29	26 \pm 4.10	82 \pm 2.23	79 \pm 2.12
Semipalmated Sandpiper	5.6 \pm 0.66	5.3 \pm 0.89	3.3 \pm 0.90	46 \pm 3.05	156 \pm 1.82	85 \pm 2.50
	5.3 \pm 0.97	5.2 \pm 0.84	3.0 \pm 1.13	36 \pm 4.00	131 \pm 2.04	88 \pm 2.38

of other nesting shorebirds. Further study is needed to verify whether our hypothesized reasons for nesting in the various habitat types and at different distances from conspecifics deserve merit. Habitat features, especially landform types that are dependent on the water balance of the landscape, are subject to change with changing climatic conditions. Although some climate-change projections indicate that the Arctic tundra may be wetter in the future (Walker et al. 1999, Martin et al. 2009), increased evaporation due to warmer and longer summers, permafrost degradation, and transpiration from encroaching vegetation might make the tundra drier (Andresen and Loughheed 2015). The latter scenario seems more prevalent in Barrow, where pond surface area and numbers have declined between 1948 and 2013 (Andresen and Loughheed 2015). Given that most of the shorebird species studied here preferred drier habitat than was available, a drier tundra environment could provide more nest habitat for these species. However, the drying of the landscape might be particularly problematic for Long-billed Dowitchers and Red Phalarope, which nested in wetter portions of our study site; and if the landscape becomes too dry, even species that prefer drier areas might find the areas unsuitable.

We anticipate that our models will have utility that extends beyond our Barrow study plots. The landforms, moisture regimes, and vegetation structure at Barrow are representative of much of the tundra habitat throughout Alaska's North Slope where the 6 focal shorebird species in our study are widely distributed (Johnson et al. 2007, Saalfeld et al. 2013). Saalfeld et al. (2013) provided habitat-suitability maps for 8 shorebird species breeding in the North Slope region, which are based on minimum habitat requirements and identify potentially important regions for nesting shorebirds. These maps have utility for informing

large-scale conservation and management deliberations; however, the authors recommend ground surveys to validate use of particular areas by nesting shorebirds. Our relatively fine-scale models can use information acquired from satellite imagery and LiDAR data to identify potential preferred breeding habitat and may be used to focus ground survey efforts and reduce costs. This may be particularly useful to industry and government officials who are proposing and mitigating oil and gas developments within the National Petroleum Reserve–Alaska (Andres et al. 2012). Thus, our results may prove useful for further evaluating the potential effects of anthropogenic development and climate change throughout the region.

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