NEST SITE SELECTION IN ARCTIC-BREEDING SHOREBIRDS: EFFECTS OF

HABITAT, SOCIAL FACTORS, AND EXPERIENCE

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NEST SITE SELECTION IN ARCTIC-BREEDING SHOREBIRDS: EFFECTS OF

HABITAT, SOCIAL FACTORS, AND EXPERIENCE

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and hereby certify that, in their opinion, it is worthy of acceptance.

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ABSTRACT

Nest site selection in birds is driven by proximate and ultimate factors that maximize fitness, including a location and structure that offers safety from predators, a favorable nest microclimate, proximity to food resources for adults and young, and social organizations with neighboring con- and heterospecifics. Furthermore, individual birds can learn from experience and modify nest site selection over their lifetimes. We investigated how habitat features, social organizations, and experience influenced nest site selection in six shorebird species that breed on the Arctic tundra around Barrow, Alaska. First, we developed sets of generalized linear mixed models to examine nest site selection patterns as they relate to habitat and social variables for each species, and used an information theoretic approach to identify best-fitting models. In a second analysis, we developed generalized linear mixed models with explanatory variables relating to breeding dispersal in male and female Dunlin (*Calidris alpina*). Variables were representative of mate fidelity (divorced/faithful), years of site experience, previous hatching success, nest initiation date, and population density of other nesting shorebirds. Next, we compared hatching success between Dunlin that were faithful or not to their mate or territory of the previous year. Results indicated that shorebird nest site selection

is not random, and all species studied selected nest sites on the basis of both habitat and social cues. We also found that divorce influenced breeding dispersal in female Dunlin, and divorced females moved farther than faithful females, faithful males, and divorced males. Results indicated that there were no strong correlates of breeding dispersal for male Dunlin, but territory-faithful males experienced greater hatching success than those that changed territories. We provide habitat models that may be used to predict probability of nest site selection in other locations of the Arctic Coastal Plain of Alaska, and offer insights of how shorebirds may be affected by a changing Arctic landscape.

THESIS FORMAT

The chapters of this thesis were written as independent manuscripts prepared for submission to peer-reviewed journals. As a result, the chapters contain some redundant material and are followed by a separate literature cited sections. Additionally, I use the plural noun "we" rather than "I".

CHAPTER 1
INTRODUCTION

Shorebirds are a diverse and widespread group, and most species accomplish remarkable feats of migration each spring. Many species travel to the northern limits of the earth to breed, settling throughout the circumpolar reaches of Arctic tundra where they take advantage of widespread foraging and nesting habitat, ample invertebrate prey, and 24 hour daylight (Johnson and Herter 1989, Schekkerman et al. 2003). By late spring, the tundra pulses with life as shorebirds sing, court, and populate their nesting territories. These diminutive birds select and nestle into scrapes amid a mosaic carpet of mosses, lichens, grasses, and forbs. They then lay and warm clutches of cryptically mottled eggs against the cold Arctic air. The nest site is presumably chosen to provide a favorable environment for the survival of eggs, young, and adults alike. However, the habitat, social, behavioral, and ecological features influencing this selection are poorly understood.

Nest site selection in birds is driven by proximate and ultimate factors that maximize fitness (Hilden 1965), including a location and structure that offers safety from predators, a favorable nest microclimate, and proximity to food resources for adults and young (Martin and Roper 1988, With and Webb 1993, Smith et al. 2007). Previous work has demonstrated that space use and nest site selection in birds also can be influenced by social conditions. For example, con- and heterospecific neighbors may affect resource availability and cue habitat suitability (Hilden 1965, Fretwell and Lucas 1970, Pitelka et al. 1974, Betts et al. 2008). Furthermore, experience such as reproductive outcome in the

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previous year may influence site fidelity or breeding dispersal of individuals, and thus modify nest site selection (Clark and Shutler 1999).

The Arctic is experiencing a rate of climate change nearly twice the global average, and the average annual temperature of Alaska's North Slope region is projected to rise 1.6°C by 2051-2060 (Martin et al. 2009). Rising temperatures could inflict considerable change on the Arctic's climate-mediated ecology and landscape composition, and will likely affect the millions of shorebirds that migrate to the region to breed each summer (Johnson and Herter 1989). For example, warmer temperatures and longer growing seasons are likely to influence patterns of availability of invertebrate prey, challenging birds to adjust migration and breeding schedules in order to fully capitalize on food resources (Meltofte et al. 2007, Martin et al 2009). Possible landscape changes include altered vegetation communities, encroachment of shrubs, degradation of microtopographic relief, and increased surface water, and may limit habitat suitable for shorebird nests (Shur et al. 2003, Arctic Climate Impact Assessment 2004, Martin et al. 2009). Challenges to shorebirds are further compounded by increasing habitat loss at wintering grounds and migratory stopover areas (Brown et al. 2001), and population declines have been observed in North America and elsewhere (Thomas et al. 2006, Bart et al. 2007). Understanding current nest site selection by shorebirds at their breeding grounds may help us anticipate how shorebirds will react to a changing Arctic landscape, and enable focused management efforts at their Arctic breeding grounds.

This thesis addresses nest site selection by a suite of common shorebird species that breed on the tundra around Barrow, Alaska, and throughout Alaska's North Slope region. In Chapter 2, I developed fine-scale predictive nest site selection models that

incorporate both habitat and social features as explanatory variables. I used satellite-derived land cover imagery, ground survey data, and nearest neighbor measurements to attribute information to nest sites, and compared these with information in available sites. I identified models that best explained nest site selection for American Golden-Plover (*Pluvialis dominica*), Dunlin (*Calidris alpina*), Long-billed Dowitcher (*Limnodromus scolopaceus*), Pectoral Sandpiper (*Calidris melanotos*), Red Phalarope (*Phalaropus fulicarius*), and Semipalmated Sandpiper (*Calidris pusilla*). These models can identify habitat features important to shorebirds that may be influenced by changing climactic conditions, and also account for how social features influence nest placement. They may have further utility in predicting the probability of fine-scale nest site selection in any given area of the North Slope region, and could assist focus of ground survey efforts in areas slated for development.

Chapter 3 addresses a behavioral component of nest site selection and explores the possible effects of experience (for example, reproductive outcome in the previous year) and other factors on breeding dispersal by a site-faithful species, the Dunlin. A bird's site tenacity may be relevant to its ability to respond to unfavorable breeding conditions and move to a better situation, or remain constant to a sub-optimal habitat. Thus, this investigation may clarify the Dunlin's resilience to the potential effects of climate change.

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CHAPTER 2
HABITAT AND SOCIAL FACTORS INFLUENCE NEST SITE SELECTION IN ARCTIC-BREEDING SHOREBIRDS

ABSTRACT

Habitat selection theory suggests shorebirds should choose nest sites that maximize their survival and fitness. Factors of importance in nest site selection include a location and structure that offers safety from predators, a favorable nest microclimate, and proximity to food resources for adults and young, as well proximities to con- or heterospecific nesting birds that are shaped by social conditions. We investigated how habitat features and social features, including proximity of con- or heterospecific nesting birds, related to nest site selection in six shorebird species in Barrow, Alaska between 2005 and 2012. We located nests on long-term study plots, and used satellite-derived land cover data to link habitat information to nest sites and to random locations on the plots. We classified tundra moisture level at two spatial scales (3 m and 50 m), and measured degree of tundra microrelief, proportion of water in the greater nest area (within 50 m), and distances to wetland habitat. We also measured distances from nests to other nearby nesting shorebird neighbors to assess whether inter-nest distance affected nest site selection. Based on these measures, we developed sets of candidate generalized linear mixed models to examine nest site selection patterns in each of six shorebird species. We used an information theoretic approach to identify best-fitting models, and performed model averaging on top models. These analyses indicated nest site selection was not random for any species; all species selected nest sites on the basis of both habitat and social cues. Micro-scale tundra moisture level within 3 m of the nest, which was closely associated with vegetation community, was included in highly-ranked models for all species,

including American Golden-Plovers (*Pluvialis dominica*), Dunlin (*Calidris alpina*),

Long-billed Dowitchers (*Limnodromus scolopaceus*), Pectoral Sandpipers (*Calidris melanotos*), Red Phalaropes (*Phalaropus fulicarius*) and Semipalmated Sandpipers

(*Calidris pusilla*). Macro-scale tundra moisture level within 50 m of the nest was an

informative variable for American Golden-Plovers, Dunlin, Long-billed Dowitchers, and

Red Phalaropes, with selection for drier habitat in plovers and for wetter habitat in the

other species. Elevated tundra microrelief increased probability of nest site selection for

American Golden-Plovers, Long-billed Dowitchers, Pectoral Sandpipers, and

Semipalmated Sandpipers. Proximity to conspecifics affected nest site selection for all

species, with all nesting farther from conspecifics than chance predicted. Also, Long-

billed Dowitchers selected nest sites that were closer to heterospecific shorebirds. Our

results indicate that shorebirds select nest sites based on habitat features and proximity to

other nesting shorebirds. We provide habitat models that may be used to predict

probability of nest site selection in other locations on Alaska's Arctic Coastal Plain, and

offer insights of how shorebirds may be affected by a changing Arctic landscape.

INTRODUCTION

Habitat selection theory predicts that nest site selection in birds is driven by proximate

and ultimate factors that maximize fitness (Hilden 1965). These factors may include

selection of a location and microhabitat structure that enables avoidance of predators, a

favorable nest microclimate, and proximity to food resources for adults and young

(Hilden 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 con- and heterospecific

neighbors that can affect resource availability and cue habitat suitability (Hilden 1965,

Fretwell and Lucas 1970, Pitelka et al. 1974, Betts et al. 2008).

Habitat features with potential to influence nest site selection may be easily

recognizable in some systems, but on the ostensibly invariable landscape of the Arctic

tundra of Alaska's Arctic Coastal Plain, 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

survival. We hypothesized that shorebirds place nests in response to habitat types to

maximize reproductive fitness as would be predicted from natural selection theory

(Hilden 1965, Clark and Shutler 1999).

Ground nesting shorebirds may select nest sites with microrelief that reduces

exposure to the Arctic cold. Tundra-breeding birds incur higher energetic costs during

incubation than other groups (Piersma et al. 2003). 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 (Andreev 1999, Reid et al. 2002,

Piersma et al. 2003, Cresswell et al. 2004). Although relatively small in height (often < 1

m), sloped tundra mounds and ridges may provide incubating adults or unattended nests

shelter from wind, and a slope may also provide a directional aspect that maximizes solar

radiation and heats nests. Shorebird nest sites also may be selected to reduce predation or

to maximize access to food resources. Predation is a threat to survival of shorebird nests

and incubating adults, and shorebirds may select nest sites in areas of greater microrelief

to reduce nest detection by terrestrial predators (Tremblay et al. 1997). Alternatively,

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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 may also 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 the nest's

proximity to rich food resources. Incubating adults may nest close to food resources to

retain proximity while feeding, or to shorten distance to foraging sites for precocial

young. Preferred invertebrate prey of most shorebird species are more common in wet

lowland habitats than in upland areas (Holmes and Pitelka 1968, Smith et al. 2007, Tulp

and Schekkerman 2008), and a nest located near ponds or wetland areas could increase

the survival of young.

Social behaviors such as territoriality and attraction may also influence nest site

selection (Hilden 1965, Fretwell and Lucas 1970). Nesting in conspecific aggregations

has been shown to impart reproductive advantages to some species (Stamps 1988,

Blomqvist et al. 2002, Valone and Templeton 2002, Danchin 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 increases the potential

for extra-pair copulations (Wagner 1997, Blomqvist et al. 2002, Dale et al. 1999).

Additionally, young birds or non-site faithful 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

con- or heterospecifics (Valone and Templeton 2002). On the contrary, some species

engage in territorial displays and aggressive behavior to discourage con- and/or heterospecifics from settling nearby (Recher and Recher 1969, 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 thus may have been affected by annual variability, 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. A recent study by Saalfeld and colleagues (2013) developed species-specific landscape-scale habitat suitability indices for eight common shorebird species breeding on the Arctic Coastal Plain. Although extensive in coverage, this study was based on quick site visits and used presence-only modeling techniques that incorporated only habitat variables.

The development of nest-site selection models could help us assess how climate change affects 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). 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). Additionally, establishing baseline information on nest site selection could assist the development of models to predict where shorebirds are likely to nest and help inform evaluations of the potential impacts of anthropogenic structures that are placed on the tundra.

We used an eight-year dataset of breeding activities of six common shorebird species in Barrow, Alaska 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. Finally, we present information that may be helpful 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 10 May to 2 August, with mean June temperatures ranging between 1.1 and 3.1°C (2005 to 2012; National Climatic Data Center 2013). 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 include high- and low- centered polygons, frost boils, strangmoor, hummocky terrain, and non-patterned and reticulate-patterned ground; all occur in grouped or mixed formations throughout the Barrow area (Walker et al. 1980). These landforms and vegetation communities are also present throughout the much of the Arctic Coastal Plain of Alaska (Walker et al. 1980). The Barrow region supports a relatively high density of the Arctic's breeding birds, likely

because the area is a triangular apex of land that may concentrate migrants as they travel North (MacLean 1980, Andres et al. 2012). Bird densities also may be enhanced by an arctic fox (*Vulpes lagopus*) removal program that was implemented by the United States Fish and Wildlife Service (USFWS) to promote nesting success of vulnerable species (Saalfeld et al. 2013).

Shorebird monitoring

The USFWS 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 (*Calidris melanotos*), Red Phalarope (*Phalaropus fulicarius*), and Semipalmated Sandpiper (*Calidris pusilla*). These species represented the majority of nesting shorebirds in the area (93% of all nests across 8 years of study). Other shorebird species occurring in low abundances were not included in the study, including Baird's Sandpiper (*Calidris bairdii*), Buff-breasted Sandpiper (*Calidris subruficollis*), Red-necked Phalarope (*Phalaropus lobatus*), Western Sandpiper (*Calidris mauri*), and White-rumped Sandpiper (*Calidris 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 2.1). Landforms and vegetation communities within plots represented regional tundra habitats, and each was divided into 144 50×50 m grid squares that were delineated with 1 m tall wood lathes painted with alphanumeric codes. Each plot was searched daily for nests using area search and rope drag techniques (Naves et al. 2008, Saalfeld and Lanctot, in review). Nest location coordinates were recorded with global positioning systems that have an accuracy of approximately 3 m on the tundra landscape. Fox removal in the area

reduced nest predation (Liebezeit and Zack 2008, Smith et al. 2009, R. B. Lanctot et al. unpubl. data) and we believe very few nests on study plots were depredated before being located.

Data

Nest location coordinates were added to a geographic information system database (GIS; ArcMap 10, ESRI, Redlands, CA). Ten random points were generated for each nest and were based on the plot and year of the corresponding nest. Random points were restricted to 'available' habitat within plots, and did not overlap water bodies. We developed a suite of variables that included landcover, microrelief, and social factors, and we assessed these variables for each nest and random point. Land cover data were extracted from a 'land cover classification' map of the Barrow area (C. E Tweedie et al. unpubl. data, Lin et al. 2012). Briefly, the map is derived from 0.7 m resolution QuickBird satellite imagery obtained on 1 August 2002 (Figure 2.2), and represents tundra moisture levels and associated dominant vegetation communities in eight classifications along a decreasing moisture gradient. Tundra wetness and vegetation growth may experience fluctuations within and among years due to variations in weather or herbivory, however moisture regimes and composition of vegetation communities exist in response to relatively stable tundra micro topography, and thus change little across years (Brown et al. 1980). The map identifies these perennial features and has a ground-proofed accuracy of 74 to 88% (C. E. Tweedie et al. unpubl. data; Table 2.1). Information on other nesting shorebirds was also incorporated into our models based on the presence of nests detected during the study. Below we list the variables extracted

from this map and provide a justification for why each was considered important (see also Table 2.2).

Micro-scale tundra moisture level (qML3).– Tundra vegetation communities vary in response to moisture, with taller, thicker vegetation typically growing in wet areas, and shorter, sparser vegetation growing in dry areas (Brown et al. 1980). Vegetation at the nest site composes a microhabitat that may be associated with predator avoidance and thermoregulation. We generated tundra moisture level values for each point by averaging land cover classification values within a 3 m radius of the nest or random point (Table 2.1). We chose the 3 m buffer to best reflect shorebird habitat selection at a micro-scale, and because our GPS units had an error of approximately 3 m on the tundra landscape. We modeled this variable as 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 micro-scale nest site habitat.

Macro-scale tundra moisture level (ML50).– Tundra moisture level within a 50 m buffer represented general habitat selection at a macro-scale, 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. This variable was calculated similarly to *qML3*, but it was not included in models as a quadratic form because it was intended to approximate preference for generally wetter or drier habitat surrounding the larger nest area.

Degree of microrelief (Microrel).– Microrelief describes variations in tundra topography that result from the mounds, ridges, and troughs of polygon landforms; these

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features may influence the thermal properties of the nest or ability to avoid predators as discussed above. In 2012, a single observer (JC) walked to the center of each 50m^2 grid square within each plot and visually assigned a category of microrelief to the four 25m^2 quadrants within. Assigned categories were re-assessed and confirmed from a second corner of each 25m^2 quadrant. Categories of microrelief ranged from 0 to 4, based on the spacing and 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 (Water).– Numerous lakes and small ponds occur throughout the study plots. Water can limit direction of approach by terrestrial predators (Lecomte et al. 2008), and we speculated that shorebirds may prefer to nest in areas of tundra interrupted by water bodies. Thus, 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), and birds may thus select nest sites close to wetlands. We measured distances from each nest and random point to the border of the nearest wetland area. We log transformed distances to normalize their distribution. We restricted wetlands to those areas that were > 50 m^2, as smaller areas may be ephemeral and present limited utility to foraging broods.

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 initiated on the same day or earlier. It is possible that nest placement for some species may be influenced by territorial displays of neighbors before the neighbors initiated nests (Lanctot et al. 2000, Johnson and Walters 2011), and only measuring to nests that have already been established may not account for the influence of displaying neighbors. However, we intended this variable to be generally applicable to all species, and to address the question of whether the presence of established nests attracts or repels others from nesting nearby. Heterospecific nests included only our six focal shorebird species. Some nests were initiated before neighboring nests were established on the plot, and thus lack values for nearest neighbor distances. In these cases, we assigned a value representing the greatest possible distance between two nests in a study plot, plus one meter. This allowed us to avoid the potential bias of excluding the habitat choices of early nesters from our analysis.

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 errors of parameter estimates. We assessed variables for correlation (Pearson's $r > 0.6$), and removed Water from the analysis because of correlation with other variables.

We fit models with the package 'lme4' in program R Studio (R version 2.15.1, The R Foundation for Statistical Computing, 2012, and R Studio version 0.96.330, RStudio, Inc., 2009-2011), and used the 'MuMIn' package 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 models within 2 AIC_c units of the top-ranked model to compete for best approximating, and calculated model-averaged parameter estimates (Burnham and Anderson 2002). We considered variables within top-ranked models to be informative in nest site selection if *P*-values of model averaged parameter estimates were less than 0.05 and 95% unconditional confidence intervals did not include zero. We evaluated model performance by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) for the averaged model of each species (Fielding and Bell 1997, Hosmer and Lemeshow 2000, Boyce et al. 2002). The area under the curve (AUC) evaluates a model's predictive performance by indicating how well it discriminates between locations where nests are present and absent. An AUC value of 1.0 indicates perfect predictability, and a value of 0.5 indicates the model's predictability is equal to random. We used Hosmer and Lemeshow's (2000) guidelines for interpreting AUC values to assess model performance. 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 over 0.9 to indicate outstanding discrimination.

RESULTS

Between 2005 and 2012 we documented 1,614 nests of the six shorebird species (Table

2.3). Results indicated that nest-site selection is not random, and the habitat and social

features we examined influenced where shorebirds nest. Top models ranked well above

null models for all species (ΔAIC$_c$ was between 43 and 222; Table 2.4), and the variables

qML3 and Conspecific were informative for all species. Informative variables differed

among species, and predicted probability plots demonstrate the strength of the effects of

these variables on nest site selection (Figure 2.3). Detailed results for each species

follow.

 American Golden-Plover.– There were two competing models for American

Golden-Plover (total w_i = 0.66; Table 2.4). Informative variables included qML3, ML50,

Microrel, and Conspecific (Parameter estimate *P*-value $\leq$ 0.01; Table 2.5). Micro-scale

moisture level (qML3) selection was optimized on moist graminoid tundra (moisture

level = 5.0; Table 2.1; Figure 2.3), which was slightly wetter than available. However,

probability of selection increased with decreasing tundra wetness at the macro scale

(ML50). Selection also increased with increasing degree of microrelief, and increasing

distance from other nesting plovers (Table 2.5; Figure 2.3). The AUC for the averaged

model was 0.91, indicating the model performs with outstanding discrimination between

used and unused sites.

 Dunlin.– There were six competitive models in the Dunlin candidate set (total w_i =

0.88; Table 2.4). Informative variables included qML3, ML50, and Conspecific (*P* <

0.01; Table 2.5). Micro-scale moisture level (qML3) selection was optimized on dry to

moist dwarf-shrub graminoid tundra (moisture level = 6.9; Table 2.1; Figure 2.3), which

was drier than available. Probability of nest site selection increased with increasing

tundra wetness on the macro-scale (ML50) and increasing distance from conspecifics

(Table 2.5; Figure 2.3). AUC for the averaged model was 0.85, indicating the model

performs with excellent discrimination between used and unused sites.

   Long-billed Dowitcher.– The global model was the sole competitive model for the

Long-billed Dowitcher (w_i = 0.50; Table 2.4). All variables were informative, including

qML3, ML50, Microrel, Wetland, Conspecific ($P \leq 0.01$), and Heterospecific ($P = 0.03$;

Table 2.5). Micro-scale moisture level (qML3) selection was optimized on wet to moist

graminoid tundra (moisture level = 4.8; Table 2.1; Figure 2.3), which was wetter than

available. Probability of nest site selection increased with increasing tundra wetness on

the macro-scale (ML50), increasing degree of microrelief, and increasing distance from

wetlands (Table 2.5; Figure 2.3). Selection also increased with increasing distance from

conspecifics, and with decreasing distance to heterospecifics (Table 2.5; Figure 2.3).

AUC for the model was 0.79, indicating acceptable discrimination between used and

unused sites.

   Pectoral Sandpiper.– There were 5 competing top models in the Pectoral

Sandpiper set (total w_i = 0.77; Table 2.4). Informative variables included qML3,

Microrel, and Conspecific ($P < 0.01$; Table 2.5). Micro-scale moisture level (qML3)

selection was optimized on dry to moist dwarf shrub graminoid tundra (moisture level =

6.5; Table 2.1; Figure 2.3), which was drier than available. Probability of nest site

selection increased with increasing degree of microrelief and increasing distance from

conspecifics (Table 2.5; Figure 2.3). AUC for the averaged model was 0.77, indicating

acceptable discrimination between sites where nests are present or absent.

Red Phalarope.– There were four competitive models in the habitat set (total w_i = 0.77; Table 2.4). Informative variables included qML3, ML50, and Conspecific ($P \le$ 0.01; Table 2.5). Micro-scale tundra moisture level (qML3) selection was optimized on dry dwarf shrub graminoid tundra (moisture level = 7.2; Table 2.1; Figure 2.3), which was drier than available. Probability of nest site selection increased with increasing tundra wetness at the macro-scale (ML50), and increasing distance from conspecifics (Table 2.5; Figure 2.3). Area under the ROC curve for the averaged model was 0.81, indicating excellent discrimination between sites where nests are present or absent.

Semipalmated Sandpiper.– There were five competing models in the Semipalmated Sandpiper set (total w_i = 0.81; Table 2.4). Informative variables included qML3, Microrel, and Conspecific ($P < 0.01$; Table 2.5). Micro-scale tundra moisture level (qML3) was optimized on moist graminoid tundra (moisture level = 5.9; Table 2.1; Figure 2.3), which was drier than that available. Probability of nest site selection increased with increasing degree of microrelief and increasing distance from conspecifics (Table 2.5; Figure 2.3). AUC for the averaged model was 0.81, indicating the model performs with excellent discrimination between used and unused sites.

DISCUSSION

Our results indicate that habitat features influenced nest site selection in shorebirds, with various macro- and micro-scale tundra features influential for the six shorebird species. Social features also influenced nest site selection, and all species nested farther from conspecifics than predicted by random distributions.

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 2004). Our variable for micro-scale tundra moisture level approximates the type of tundra in the immediate area of the nest (Table 2.1). In general, wetter tundra grows higher vegetation, which may aid in predator avoidance or shelter from wind. However the 'active layer' of soil is slower to thaw in these areas, and the frozen ground beneath nests may tax thermodynamic abilities of birds to maintain eggs at adequate incubation temperatures. In contrast, dry areas grow short or sparse vegetation, but these sites may provide better ground insulation because of a lack of moisture and ice. Most birds selected dry to moist graminoid dwarf shrub tundra, which was likely dry enough to ensure proper thermoregulation of the nest cup, but retained moisture sufficient to furnish medium-height vegetation that assists in concealment of the nest and could act as a wind break (Cresswell 2004). Lower and wetter areas also are last to become free of snow in early- to mid-June, and the only available habitat to early nesters may be the more elevated dry to moist graminoid tundra that was identified as preferred nesting habitat by the models. Indeed, Long-billed Dowitchers selected wetter habitat, which was almost certainly available in greater proportions because they typically begin nesting later in the season (mean nest initiation on 21 June, unpubl. data) than the other shorebird species (mean nest initiation on 15 June, unpubl. data). In contrast to other published results (Johnson and Connors 2010), our results indicated American Golden-Plovers selected wetter habitat (Figure 2.3); this finding may relate to the scale at which we measured this variable. American Golden-Plovers typically nest in areas with a high degree of microrelief, and on the dry tops of elevated mounds (Johnson and Connors 2010). We speculate that our micro-scale moisture level measurement might not capture this species' actual nest site habitat, because dry mound tops are surrounded by lower, wetter slopes

and wet or watery troughs. Three meter buffers of the micro-scale measure that included

these nearby wet patches likely resulted in an overall wetter value.

Composition of the landscape surrounding the nest may be important for predator

avoidance. Areas of wet substrate may present an inconvenient route for terrestrial

predators, limiting their directions of approach (Lecomte et al. 2008). The macro-scale

moisture level measurement was informative for Dunlin, Long-billed Dowitchers, and

Red Phalaropes, with selection by these three species increasing with increasing tundra

wetness. This result is consistent with previous findings for Long-billed Dowitchers and

Red Phalaropes (Rodrigues 1994, Takekawa and Warnock 2000, Walpole et al. 2008),

and Phalaropes may use wet habitat in the vicinity of the nest for foraging (Walpole et al.

2008). The macro-scale moisture level variable was also informative for American

Golden-Plovers, and their probability of nest site selection increased with generally drier

habitat in the greater nest area. This result better corresponds with prior findings

(Johnson and Connors 2010) and our own observations of American Golden-Plovers (JC)

than the micro-scale result, and reinforces our impression that our micro-scale

measurement misrepresented habitat selection for plovers.

Costs of thermoregulation may be reduced 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 small mounds. Indeed,

our results indicate that degree of microrelief was influential in selection for American

Golden-Plovers. Areas of enhanced microrelief also increased probability of selection for

Long-billed Dowitchers, Pectoral Sandpipers and Semipalmated Sandpipers. The latter

two species are markedly smaller than the American Golden-Plover (75g and 43g vs

160g, respectively, unpubl. data), and are thus presented with greater surface to volume

ratio challenges that may preclude nesting in exposed locations atop mounds. Nests of

the two sandpipers and of Long-billed Dowitchers were often beneath raised mounds and

ridges (JC, pers. obs.), which may have provided relief from the wind. Such locations

can also 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 (Cresswell 2004, Smith 2009).

We predicted that shorebirds would prefer nest sites that reduced transit time for

newly hatched young to wetland foraging areas. Distance to nearest wetland was

informative only for Long-billed Dowitchers. We speculate that the variable would have

been more apparent in top-ranked models of the six species if proximity to food were

generally important to shorebirds. It is possible that this variable is not indicative of nest-

site preferences related to brood foraging opportunities. Shorebird broods are capable of

moving several hundred meters from the nest within a few days of hatching (Johnson and

McCaffery 2004, Ruthrauff and McCaffery 2005, Johnson et al. 2008, Wilson and

Colwell 2010, Hill 2012), so nesting in close proximity to a wetland may not necessarily

enhance brood survival. For Long-billed Dowitchers, probability of nest site selection

increased at greater distances from wetlands (Figure 2.3). This result is puzzling, given

that our results suggest Dowitchers also preferred wetter micro- and macro-scale habitat

(Figure 2.3). A possible explanation for this is that Long-billed Dowitchers also

preferred to nest in areas of enhanced microrelief (Figure 2.3), and some of the larger

wetland areas at our study site were often surrounded by flatter terrain. Dowitchers may

have been nesting in or near smaller patches of wetland habitat that were broken by the

ridges and mounds they are attracted to, and were thus too small to be included in

distance to wetland measurements.

In addition to habitat features, we anticipated that the presence of other nesting

birds could influence nest placement. "Conservative" species might be less likely to

tolerate other nesting birds because they tend to exhibit high site fidelity, and exclude

conspecifics from important food resources and safe nesting and brood-rearing sites

(Holmes 1966b, 1971, Pitelka et al. 1974, Shields 1984). Alternatively, nomadic or

"opportunistic" species display low site fidelity and may settle in response to favorable

food or predator conditions (Pitelka et al. 1974, Saalfeld and Lanctot, in review). These

birds may have no prior knowledge of the breeding grounds, and may thus be attracted to

other nesting individuals as signals of habitat suitability (Holmes 1966b, 1971, Pitelka et

al. 1974). In Barrow, Dunlin and Semipalmated Sandpipers were site faithful and often

returned to nest on or near previously used territories in consecutive years (R. Lanctot,

unpubl. data). Monogamy also characterizes mating systems in these species, and greater

inter-nest distances may be related to the prevention of extrapair matings (Westneat and

Sherman 1997, Yezerinac et al. 2013). In our study, distance to nearest conspecific was

an informative variable for all six species, and all nested farther from conspecifics than

random nest placement predicted (Table 2.6; Figure 2.3). However, this relationship was

not particularly strong for Pectoral Sandpipers, Long-billed Dowitchers, or Red

Phalaropes, which are considered opportunistic species (Pitelka et al. 1974, Saalfeld and

Lanctot, in review). Long-billed Dowitchers were the only species for which

heterospecific distance was informative, with the birds nesting closer to heterospecifics

than predicted, even after accounting for habitat. Dowitchers have not been observed to

engage in territorial disputes with other shorebirds except in the immediate vicinity of the

nest, and are gregarious enough that they sometimes forage with conspecifics from

neighboring nests (Johnsgard 1981, Takekawa and Warnock 2000). Dowitchers may be

drawn to heterospecifics that signal suitable habitat, but avoid nesting near conspecifics

because they are relatively large birds that can attract predator attention moving to and

from nests (Table 2.6; Figure 2.3).

Our results indicate that Arctic-breeding shorebirds select nest-sites based on

characteristics of particular habitat features, and the birds also are influenced by the

presence of other nesting shorebirds. Habitat features, especially landform types that are

based on freeze and thaw cycles in the Arctic, are subject to change with changing

climactic conditions. Some climate change projections predict a wetter tundra

environment in the future, which could change the vegetative composition of the tundra

landscape (Martin et al. 2009, Walker et al. 1999). A warmer, wetter environment may

also result in sinking of raised tundra polygons and increase the area of ponded surface

water (Martin et al. 2009). Given that most of our shorebird species preferred drier

habitat than available, a wetter tundra environment could limit preferred nest habitat for

these species. This might be particularly problematic for conservative species that exhibit high site fidelity and territoriality. For example, Dunlin nest site selection is optimized on dry dwarf-shrub graminoid tundra, which composes approximately 18% of the area of our study plots (Table 2.1). Should future climactic conditions result in one 'moisture level' increase in wetness, this habitat will be reduced to approximately 1% of our study plots. Territorial Dunlin will exclude conspecifics from the limited suitable habitat, and while some birds may continue to use sub-optimal habitat, climate-induced changes in habitat conditions may reduce breeding densities below current levels. In contrast, opportunistic species such as Pectoral Sandpipers, Red Phalaropes, and Long-billed Dowitchers appear to have a greater tolerance for smaller inter-nest distances (Table 2.6), and thus are better equipped to settle in limited habitat. In addition, opportunistic species may have more latitude to find suitable habitat elsewhere. These results suggest that each shorebird species must be assessed individually when determining the likely impacts of future climate change, and that continued monitoring of nesting shorebirds will be essential to understanding how they will react to changing climactic, ecological, and habitat conditions.

Our results should be validated in other locations, but we anticipate that the 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 six 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 eight 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 informing large-scale conservation and management deliberations, however the authors recommend ground surveys to validate use of an area 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 further 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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FIGURES
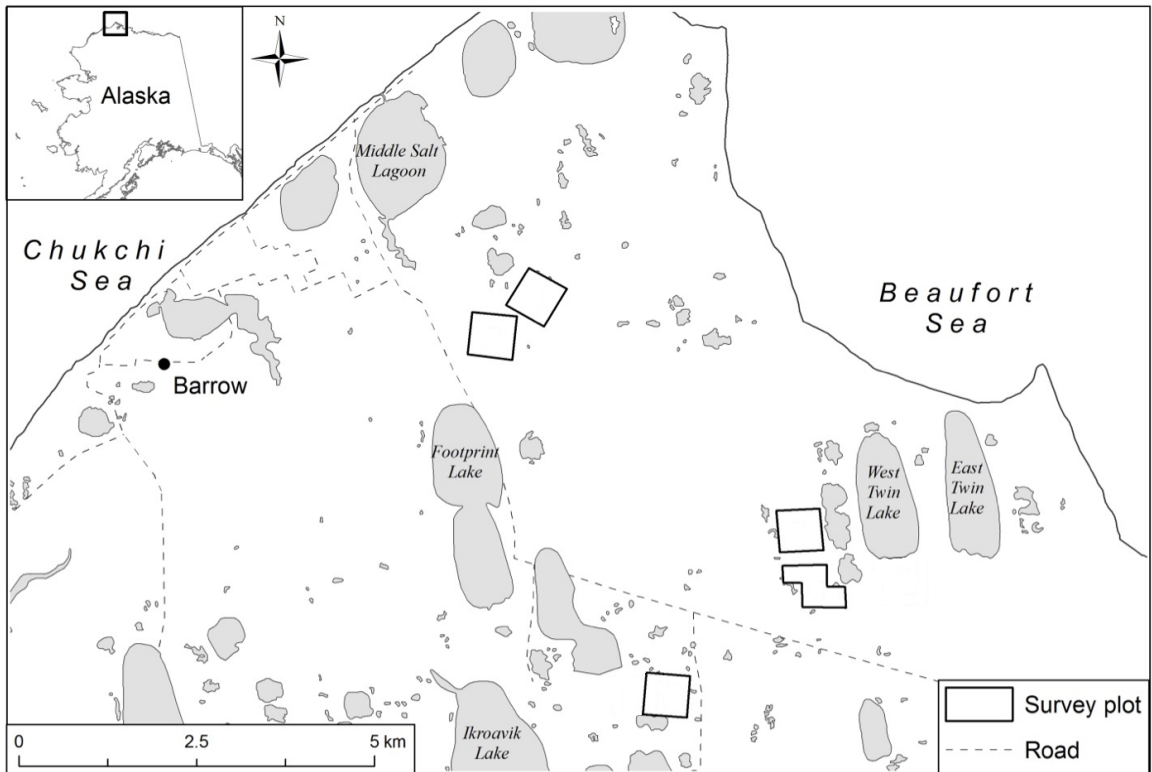
Figure 2.1. Study area map showing locations of Barrow and 600 x 600 m plots that were surveyed from 2005 – 2012.
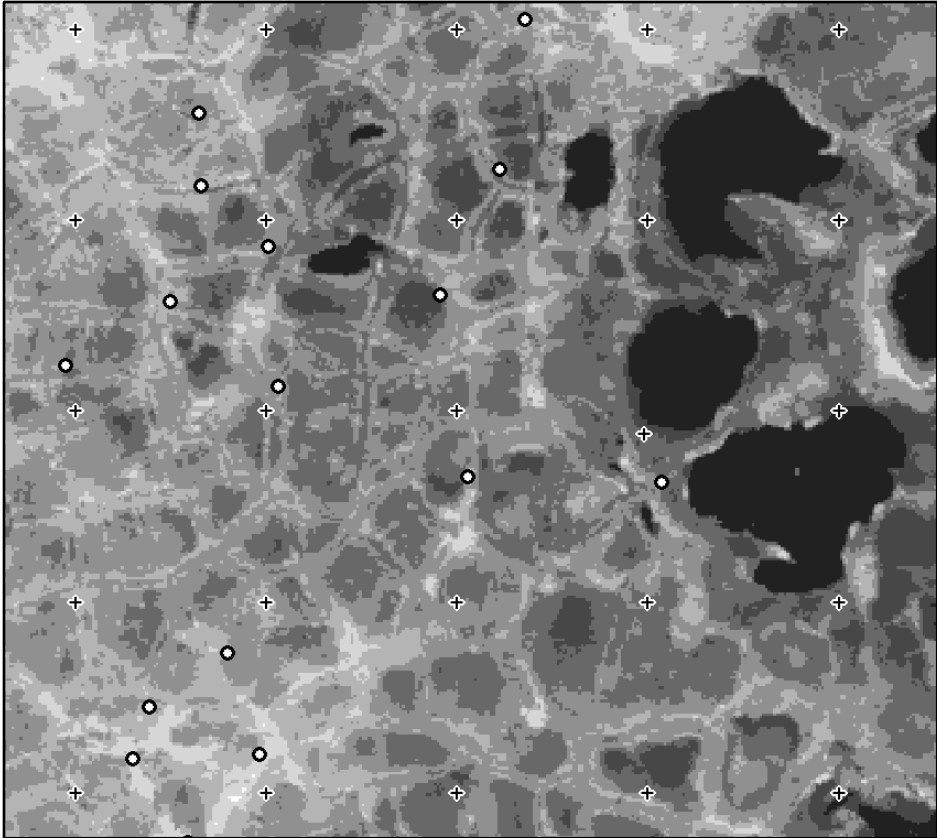
Figure 2.2. Clip of the Land cover Classification map from Tweedie et al. (unpublished data), with grid-stakes (crosses) and nest sites (circles) reflecting various species on one of the study plots in Barrow, AK, in 2012. Distance between grid-stakes is 50 m. Darker shades indicate wetter tundra, and water bodies are black.

American Golden-Plover
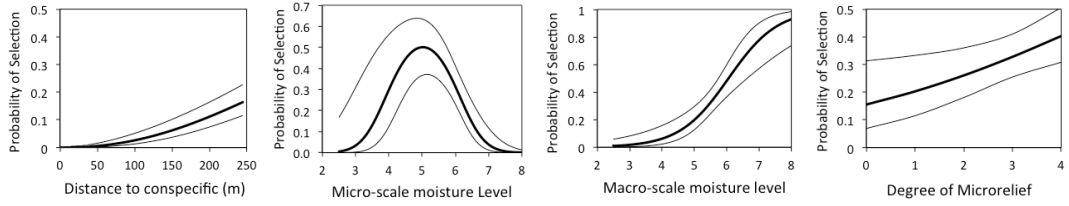
Dunlin
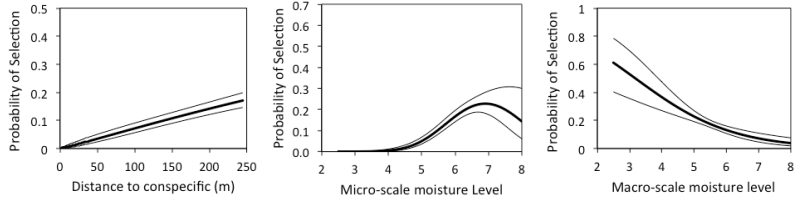
Long-billed Dowitcher
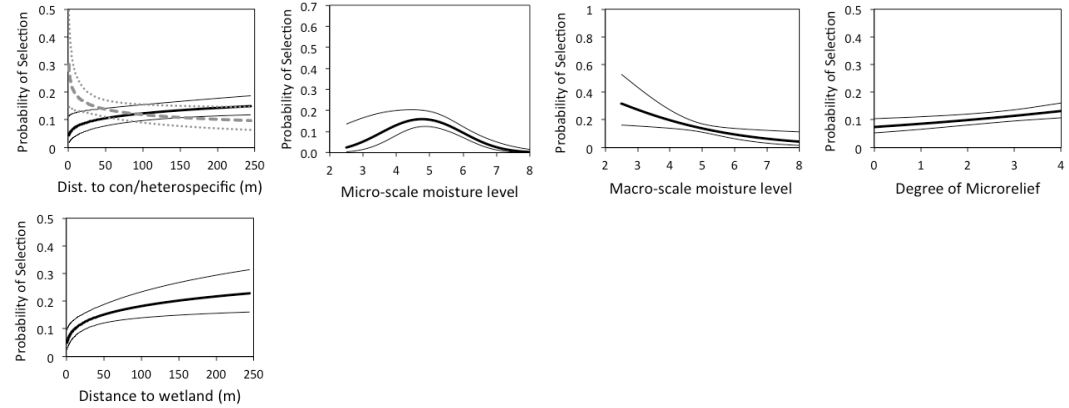
Pectoral Sandpiper
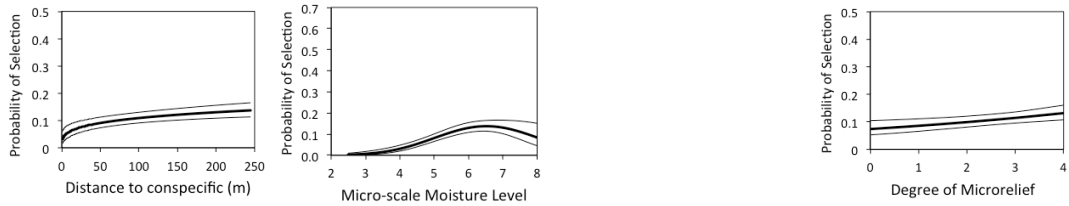
Red Phalarope
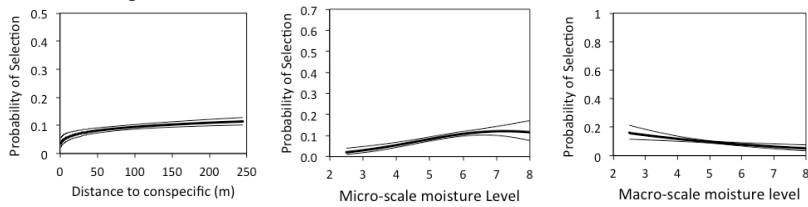
Semipalmated Sandpiper
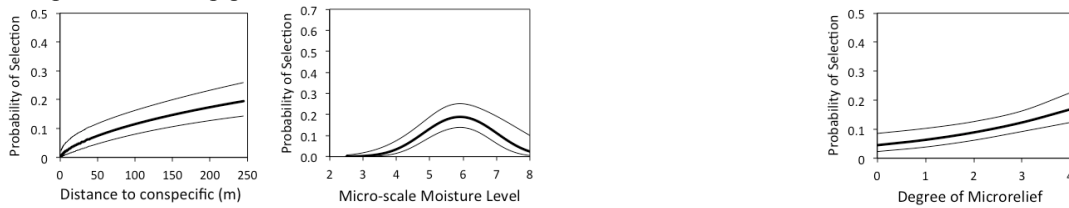
Figure 2.3. Predicted probability of a nest site being present for shorebird species in relation to the value of variables from averaged models (i.e., other covariates in the model were held at their median values). Graphs are only displayed for variables that were considered informative and include 95% confidence intervals. For the Long-billed Dowitcher, distance to conspecific and heterospecific nests are represented by dark and gray dashed lines, respectively. Graphs represent shorebirds that nested in Barrow, AK, 2005 – 2012.

TABLES

Table 2.1. Land cover classifications and soil moisture definitions presented by C. E.

Tweedie et al. (unpubl. data).

Tundra Moisture Level	Tundra type and representation on study plots	Dominant vascular plant species	Soil moisture definitions
2	Aquatic graminoid tundra 4%	*Carex stans, Eriophorum russeolum, Arctophila fulva, Ranunculus pallasii, Dupontia fisheri*	Aquatic – Water deeper than middle of shin
3	Seasonally flooded graminoid tundra 6%	*Dupontia fisheri, Eriophorum angustifolium, Carex stans, Poa arctica, Eriophorum russeolum*	Seasonally flooded (Wet) – Water ankle to shin deep
4	Wet graminoid tundra 17%	*Carex stans, Poa arctica, Dupontia fisheri, Eriophorum angustifolium, Eriophorum russeolum*	Moist – Water between toe and ankle deep
5	Moist graminoid tundra 28%	*Carex stans, Eriophorum russeolum, Dupontia fisheri, Eriophorum angustifolium, Poa arctica*	Moist – Some water appears around sole of boot
6	Dry-moist dwarf shrub graminoid tundra 24%	*Salix rotundifolia, Carex stans, Poa arctica, Arctagrostis latifolia, Stellaria laeta*	Dry – No indication of surface water

| 7 | Dry dwarf shrub-graminoid tundra 18% | *Salix rotundifolia, Cassiope tetragona, Arctagrostis latifolia, Luzula confuse, Luzula arctica* | Dry – No indication of surface water |
| 8 | Dry dwarf shrub tundra 1% | *Cassiope tetragona, Salix rotundifolia, Luzula confuse, Arctagrostis latifolia, Potentilla hyparctica* | Dry – No indication of surface water |

Table 2.2. Variables investigated in explaining nest-site selection in six shorebird species at Barrow, Alaska between 2005 and 2012. Influential variables were those where P-values of model averaged parameter estimates < 0.05, and 95% confidence intervals did not include zero. (+) and (-) signs indicate whether variable had a positive or negative effect on nest site selection for each species. See text for explanation and citations related to hypotheses.

Fixed effect: Habitat	Hypotheses	Influential variable for:
Micro-scale tundra moisture level (qML3)	Preference for nest site vegetation community and tundra moisture level, which may influence nest microclimate and crypsis. + infers preference for drier than available.	American Golden-Plover (-), Dunlin (+), Long-billed Dowitcher (-), Pectoral Sandpiper (+), Red Phalarope (+), Semipalmated Sandpiper (+)
Macro-scale tundra moisture level (ML50)	General preference for nest area vegetation communities and tundra moisture level, possible association with predator avoidance. + infers preference for drier areas.	American Golden-Plover (+), Dunlin (-), Long-billed Dowitcher (-), Red Phalarope (-)
Degree of microrelief (Microrel)	Tundra microrelief may offer shelter from wind, enhanced view of surroundings, or concealment. + infers preference for areas with greater microrelief.	American Golden-Plover (+), Long-billed Dowitcher (+), Pectoral Sandpiper (+), Semipalmated Sandpiper (+)
Distance to nearest wetland (Wetland)	Proximity to preferred chick foraging habitat could reduce risky transit after hatch. + infers preference for areas away from wetlands	Long-billed Dowitcher (+)
Fixed effect: Social		
Distance to nearest conspecific nest (Conspecific)	Exclusion by territorial conspecifics to ensure resource security or prevent extrapair matings. Attraction to	American Golden-Plover (+), Long-billed Dowitcher (+), Dunlin (+), Pectoral Sandpiper (+), Red Phalarope

	conspecifics as signals of habitat suitability, or formation of 'hidden leks'. + infers preference to nest away from conspecifics	(+), Semipalmated Sandpiper (+)
Distance to nearest heterospecific nest (Heterospecific)	Attraction to other shorebirds that may signal suitable nesting habitat or offer safety from predators. + infers presence to nest away from heterospecifics.	Long-billed Dowitcher (-)

Table 2.3. Summary of shorebird nests located on long-term study plots in Barrow, AK, 2005 – 2012.

Species	Total
American Golden-Plover	76
Dunlin	226
Long-billed Dowitcher	173
Pectoral Sandpiper	371
Red Phalarope	607
Semipalmated Sandpiper	161
Total	1,614

Table 2.4. Model selection results for predicting the presence of shorebird nests in Barrow, AK. Tables include models within 2 AIC_c units of the top model, and a null model. All models include a random effect for Plot. (n = nests/random points)

American Golden-Plover (n = 76/760)

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + ML50 + Microrel + Conspecific	7	364.1	0.00	0.45
qML3 + ML50 + Microrel + Conspecific + Heterospecific	8	365.7	1.58	0.21
Null	2	513.4	149.26	0.00

Dunlin (n = 226/2260)

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + ML50 + Conspecific + Microrel	7	1295.8	0.00	0.21
qML3 + ML50 + Conspecific	6	1295.8	0.09	0.20
qML3 + ML50 + Conspecific + Wetland	7	1296.3	0.56	0.16
qML3 + ML50 + Conspecific + Microrel + Wetland	8	1296.3	0.58	0.16
qML3 + ML50 + Conspecific + Heterospecific	7	1297.5	1.70	0.09
qML3 + ML50 + Conspecific + Microrel + Heterospecific	8	1297.7	1.91	0.08
Null	2	1518.7	222.90	0.00

Long-billed Dowitcher (n = 173/1730)

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + ML50 + Microrel + Wetland + Conspecific + Heterospecific	9	1108.9	0.00	0.50
Null	2	1163.5	54.55	0.00

Pectoral Sandpiper (n=371/3710)

Model	K	AIC_c	ΔAIC_c	w_i

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + Microrel + Conspecific	6	2399.7	0.00	0.24
qML3 + Microrel + Conspecific + Wetland	7	2400.3	0.58	0.28
qML3 + Microrel + Conspecific + Heterospecific	7	2400.6	0.94	0.15
qML3 + Microrel + Conspecific + Wetland + Heterospecific	8	2401.1	1.36	0.12
qML3 + Microrel + Conspecific + ML50	7	2401.6	1.92	0.09
Null	2	2490.4	90.74	0.00

Red Phalarope (n=607/6070)

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + ML50 + Conspecific	6	4029.3	0.00	0.30
qML3 + ML50 + Conspecific + Microrel	7	4030.7	1.36	0.15
qML3 + ML50 + Conspecific + Wetland	7	4031.2	1.86	0.12
qML3 + ML50 + Conspecific + Heterospecific	7	4031.3	1.99	0.11
Null	2	4072.1	42.79	0.00

Semipalmated Sandpiper (n=161/1610)

Model	K	AIC_c	ΔAIC_c	w_i
qML3 + Microrel + Conspecific + Heterospecific	7	1004.9	0.00	0.24
qML3 + Microrel + Conspecific + Heterospecific + ML50	8	1005.5	0.61	0.18
qML3 + Microrel + Conspecific	6	1005.9	0.96	0.15
qML3 + Microrel + Conspecific + Heterospecific + Wetland	8	1006.2	1.23	0.13
qML3 + Microrel + Conspecific + ML50	7	1006.6	1.64	0.11
Null	2	1083.0	78.08	0.00

Table 2.5. Parameter estimates of averaged models describing probability of nest site selection by shorebirds in Barrow, AK 2005 – 2012. $\hat{\beta}$ = parameter estimate, SE = standard error, P = P-value, 95% CI = unconditional 95% confidence interval.

Variable	$\hat{\beta}$	SE	P	95% CI
American Golden-Plover				
ML3	-0.82	0.27	<0.01	-1.35, -0.29
ML3^2	-0.82	0.21	<0.01	-1.24, -0.40
ML50	1.32	0.31	<0.01	0.71, 1.93
Microrel	0.32	0.13	0.01	0.06, 0.59
Wetland	-	-	-	-
Conspecific	2.22	0.26	<0.01	1.71, 2.74
Heterospecific	-0.09	0.13	0.50	-0.34, 0.16
Dunlin				
ML3	1.31	0.15	<0.01	1.01, 1.61
ML3^2	-0.47	0.10	<0.01	-0.67, -0.27
ML50	-0.67	0.14	<0.01	-0.95, -0.39
Microrel	0.10	0.07	0.15	-0.03, 0.23
Wetland	0.13	0.10	0.20	-0.07, 0.33
Conspecific	1.10	0.12	<0.01	0.86, 1.34
Heterospecific	-0.04	0.07	0.63	-0.18, 0.10
Long-billed Dowitcher				
ML3	-0.59	0.15	<0.01	-0.88, -0.30
ML3^2	-0.39	0.11	<0.01	-0.61, -0.17
ML50	-0.43	0.17	0.01	-0.77, -0.09
Microrel	0.25	0.08	<0.01	0.09, 0.41
Wetland	0.32	0.10	<0.01	0.13, 0.08
Conspecific	0.25	0.10	0.01	0.0.05, 0.45

Heterospecific	-0.25	0.12	0.03	-0.48, -0.02

Pectoral Sandpiper

ML3	0.51	0.08	<0.01	0.34, 0.67
ML3^2	-0.25	0.06	<0.01	-0.38, -0.13
ML50	-0.03	0.11	0.77	-0.24, 0.18
Microrel	0.16	0.06	<0.01	0.05, 0.27
Wetland	-0.08	0.06	0.19	-0.21, 0.04
Conspecific	0.29	0.07	<0.01	0.15, 0.43
Heterospecific	-0.08	0.07	0.28	-0.23, 0.07

Red Phalarope

ML3	0.29	0.06	<0.01	0.16, 0.41
ML3^2	-0.08	0.03	0.01	-0.15, -0.02
ML50	-0.23	0.07	<0.01	-0.37, -0.09
Microrel	-0.03	0.04	0.42	-0.10, 0.04
Wetland	-0.02	0.05	0.70	-0.12, 0.08
Conspecific	0.23	0.05	<0.01	0.13, 0.34
Heterospecific	0.01	0.05	0.90	-0.10, 0.11

Semipalmated Sandpiper

ML3	0.39	0.15	<0.01	0.10, 0.69
ML3^2	-0.51	0.13	<0.01	-0.76, -0.26
ML50	-0.20	0.16	0.23	-0.52, 0.12
Microrel	0.37	0.10	<0.01	0.17, 0.56
Wetland	-0.09	0.10	0.33	-0.29, 0.10
Conspecific	0.69	0.13	<0.01	0.44, 0.94
Heterospecific	-0.16	0.09	0.08	-0.34, 0.02

Table 2.6. Mean values with standard deviations for habitat and social features of nests and random points. Values (mean ± SE) for nests are on top, with random point values below. Shorebird nests were recorded in Barrow, AK, 2005 – 2012.

	Micro-scale moisture level (qML3)	Macro-scale moisture level (ML50)	Degree of Microrelief	Distance to Wetland (m)	Distance to Conspecific (m)	Distance to Heterospecific (m)
American	5.4±0.66	5.6±0.60	3.3±1.10	63±1.03	423±0.72	88±1.03
Golden-Plover	5.4±1.06	5.4±0.84	2.7±1.28	41±1.45	196±0.68	77±1.05
Dunlin	5.9±0.73	5.4±0.89	2.7±1.11	47±1.06	233±0.73	146±1.00
	5.4±1.11	5.3±0.92	2.5±1.30	32±1.44	145±0.71	125±1.05
Long-billed	5.0±0.76	5.0±0.61	2.8±1.13	34±1.16	157±1.19	45±0.76
Dowitcher	5.2±1.02	5.1±0.83	2.6±1.31	30±1.43	147±0.80	51±0.68
Pectoral	5.7±0.83	5.4±0.80	3.0±1.07	45±0.99	126±0.97	57±0.83
Sandpiper	5.4±1.06	5.2±0.89	2.7±1.26	33±1.41	111±0.81	59±0.76
Red Phalarope	5.4±1.03	5.1±1.02	2.3±1.21	28±1.25	103±0.96	88±0.82
	5.3±1.11	5.1±0.95	2.3±1.30	26±1.41	87±0.83	84±0.81
Semipalmated	5.6±0.69	5.3±0.87	3.3±0.89	45±1.10	207±0.84	45±1.05
Sandpiper	5.3±0.99	5.2±0.85	2.9±1.19	34±1.41	153±0.77	34±0.95

CHAPTER 3
DIVORCE INFLUENCES BREEDING DISPERSAL BY DUNLIN (*CALIDRIS ALPINA*) IN BARROW, ALASKA

ABSTRACT

Nest site selection in birds is influenced by habitat features, experience, and the social

and spatial organizations of neighboring con- and heterospecifics. Prior reproductive

success, and experience at a site or with a mate may inform subsequent nest site selection

at a site or prompt breeding dispersal. We identified factors apparently influencing

breeding dispersal in a population of Dunlin (*Calidris alpina*) in Barrow, Alaska. We

marked Dunlin with unique color combinations and monitored nesting activity over

eleven breeding seasons to estimate breeding dispersal (distance moved between nest

sites in two consecutive years). We developed generalized linear mixed models with

single fixed effects to explain variation in breeding dispersal for males and females

separately. Fixed effects were representative of mate fidelity years of site experience,

previous hatching success, nest initiation date, and population density of other nesting

shorebirds. We also compared hatching success between Dunlin that nested with their

mate from the previous year (faithful) or nested with a new mate (divorced), and Dunlin

that had changed territories or were territory-faithful. Results indicated that 37% of the

nests monitored were tended by faithful pairs. Mate fidelity influenced breeding

dispersal in female Dunlin, with divorced females moving farther than faithful females.

We did not find strong correlation between male breeding dispersal and the parameters

we quantified, but territory-faithful males experienced greater hatching success than

those that changed territories. We did not find strong evidence that experience influences

breeding dispersal by Dunlin in Barrow, AK, and we conclude that divorce was likely the

result of usurpation of one pair member by an earlier-arriving competitor, resulting in breeding dispersal.

INTRODUCTION

Nest site selection in birds involves preferences for habitat features that offer a favorable microclimate and enable predator avoidance and access to food resources, all of which can ultimately exert a positive influence on reproductive success (Martin 1998, Clark and Shutler 1999, Forstmeier and Weiss 2004). Such preferences are presumed to be partly innate (Klopfer 1963, Hilden 1965), but research indicates that the nest-site selection strategy of an individual can further be shaped by experience. Reproductive success increases with age or breeding experience (Nol and Smith 1987, Reid 1988, Pyle et al. 2001), and it is evident that some individuals may use prior experience to inform selection of subsequent nesting locations (Beletsky and Orians 1991, Citta 2007, Kim et al. 2007). Returning to or dispersing from a breeding territory may be such a facultative response. Reproductive outcome has been investigated as a potential influence on site tenacity in various groups of birds (Gratto et al. 1985, Beletsky and Orians 1991, Haas 1998, Serrano et al. 2001, Citta 2007, Johnson and Walters 2008), typically with the presumption that breeding dispersal is more likely among unsuccessful than successful breeders (Dubois and Cezilly 2002). Whether breeding dispersal is a facultative strategy that maximizes fitness should depend on species' life histories and breeding habitats (Dhondt and Adriaensen 1994, Choudhury 1995).

In migratory species, the ability to evaluate alternative site options can be impeded by time constraints (Choudhury 1995). Birds with multiple years of experience

nesting in a particular territory may be less likely to move and forfeit the benefit of familiarity (Hilden 1965, Pyle et al. 2001, Serrano et al. 2001, Johnson and Walters 2008, Johnson et al. 2010). Site fidelity can save time and energy needed to search for a new location, and familiarity with an area's resources might further enhance reproductive success (Shields 1984). Alternatively, if there is heightened variation in habitat patch quality within a breeding area, breeding dispersal may be a viable option for improving nesting habitat and the associated reproductive success (Choudhury 1995, Valcu and Kempenaers 2008). Circumstantial factors unrelated to individual experience, such as changing conditions at the breeding ground, may also be a factor influencing breeding dispersal (Saalfeld and Lanctot, in review). Higher rates of breeding dispersal have been recorded in species that breed in habitats that experience regular disturbance (Haig and Oring 1988, Cezilly et al. 2000). Similarly, annual fluctuations in the density of nesting con- and heterospecifics could prompt breeding dispersal when territorial pressure from neighbors excludes an individual from a previously used site, or if lower nest density allows a bird opportunity to move to a more favorable territory (Fretwell and Lucas 1969, Johnson and Walters 2011).

Breeding dispersal in species that show some degree of site tenacity can be associated with mate loss, or divorce, of prior pair members (Thorup 1999). In these cases it is difficult to discern whether breeding dispersal is caused by divorce, or vice versa (Cezilly 2000, Valcu and Kempenaers 2008, Bai and Severinghaus 2012). As with site fidelity, mate fidelity may be beneficial when familiarity among pair members improves breeding coordination, reduces time associated with pairing, and reduces the need for energetically costly courtship behavior and competition for mates (Slagsvold

and Dale 1991, Rees et al. 1996, Black 1996, Lanctot et al. 2000). However, mate

fidelity in a migratory species may also be largely influenced by survival rates and timing

of migration. An individual that waits too long for a familiar mate to arrive at the

breeding ground may risk delayed nest initiation, or could miss the opportunity to breed

if its former mate is deceased (McNamara and Forslund 1996). Thus, immediate pairing

to avoid delays in nest initiation will inevitably result in displacing later-arriving familiar

mates (McNamara and Forslund 1996).

The needs of male and female birds differ at the onset of breeding (Trivers 1972),

and breeding dispersal decisions may largely depend on an individual's sex if pair

members seek to maximize their own fitness. In species where males secure and defend a

breeding territory, it may be advantageous for them to return to a familiar territory where

relationships with competing neighbors are settled and they can allocate energy to mate

attraction (Krebs 1982, Oring and Lank 1984, Desrochers and Magrath 1996). Females

may be less concerned with the energy expenditure of defending a territory, and thus

have more freedom to disperse, explore, and select a preferred habitat or mate

(Desrochers and Magrath 1996).

We investigated factors that may influence breeding dispersal in Dunlin (*Calidris

alpina*) breeding near Barrow, Alaska. The Dunlin is a shorebird species with a

circumpolar breeding distribution in Arctic and temperate regions, and the subspecies *C.

a. arcticola* breeds on the Arctic coastal tundra along the north coast of Alaska. Dunlin

are monogamous and exhibit biparental care. In Barrow, Alaska, Dunlin show

considerable breeding site fidelity (Hill 2012, Saalfeld and Lanctot, in review), providing

an opportunity to follow mate and site choices of individuals over consecutive years.

Expecting that Dunlin benefit from familiarity with a mate or site, we also examined how divorce and site changes affected reproductive output.

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 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). The Barrow region supports a relatively high density of the Arctic's breeding birds, likely because the area is a triangular apex of land that may concentrate migrants as they travel North (MacLean 1980, Andres et al. 2012). Bird densities in Barrow also may be enhanced by an arctic fox (*Vulpes lagopus*) removal program that was implemented by the United States Fish and Wildlife Service (USFWS) to promote breeding success of vulnerable species (Saalfeld et al. 2013).

Shorebird monitoring

We monitored breeding activities for a suite of shorebird species near Barrow from 2003 to 2013. We located nests between late May and early July on four to six 600×600 m study plots located 3 - 6 km southeast of Barrow. We searched each plot daily for nests using area search and rope drag techniques (Naves et al. 2008). Nests were marked discretely, and nest location coordinates recorded with a global positioning system (Garmin ltd., Olathe Kansas).

We monitored nests at five-day intervals, and then every other day prior to expected hatch. We determined nest initiation date by backdating incomplete clutches (assuming 1 egg laid per day), backdating from hatch date using previously determined species-specific incubation lengths (The Birds of North America Online), or by floating eggs (Liebezeit et al. 2007). We determined hatch by presence of chicks in or near the nest cup, or evidence at the nest that suggested hatch, such as disappearance of eggs shortly after they were seen pipped or starred and presence of small shell bits in the nest cup. Dunlin chicks typically left the nest within one day of hatching and were highly mobile and cryptic, and it was not possible to follow broods to fledging. Chicks found in or near nest cups were given a USGS metal band. We trapped adults on nests during incubation or shortly after hatch using bow nets, and determined sex using combinations of morphometric measures, behavior, pairing with a mate of known sex, and molecular analyses (Gates et al. 2013). All captured birds were given a unique plastic (Darvic) color band combination and a USGS metal band. Returning banded adults were recorded in following years by re-sighting and by recapturing adults on nests found on and in the vicinity of the study plots.

Analyses

Correlates of breeding dispersal

We compiled records of all individually banded Dunlin that nested in two consecutive years (years i and $i-1$) for which we were able to confirm the identity of the mate, if the mate was banded, or if the mate was unbanded in both years. Individuals that nested in the study area for multiple years contributed multiple records to the dataset. Nest location coordinates were added to a geographic information system database (GIS;

ArcMap 10, ESRI, Redlands, CA), and distances between an individuals' nest sites in years i and $i – 1$ were measured in meters. We then used Dunlin nesting records to examine the influence of the following factors on breeding dispersal in Dunlin.

Status (faithful or divorced). – Breeding dispersal may occur when birds seek out a new mate, either because the prior mate did not return, was not favored, or it paired with another bird. Status (binomial) was assigned to individuals each year, depending on whether or not they reunited with their mate of the previous year. In accordance with previously presented lexicon (e.g. Black 1996), reunited pairs were considered 'faithful,' and birds that paired with a new mate were considered 'divorced.'

Site experience (years observed on study plots). – Increasing age and site experience have previously been associated with greater site tenacity (Hilden 1965, Pyle et al. 2001, Serrano et al. 2001, Johnson et al 2010). We predicted less site-experienced or younger birds would disperse greater distances than older birds. We were not able to determine actual age for individuals because of minimal natal philopatry to our study plots by banded chicks, and variable accuracy of ageing techniques on captured adults. However, site experience may approximate a 'minimum age' (Oring and Lank 1984) for males because returning males are unlikely to disperse far from their previously used territory (Soikkeli 1967, Thorup 1999, Flodin and Blomqvist 2012), and unbanded birds encountered are likely new breeders.

Previous hatch (n chicks in year i – *1).* – Prior reproductive outcome has been associated with breeding dispersal and divorce in various groups of birds (Gratto et al. 1985, Beletsky and Orians 1991, Haas 1998, Citta 2007, Serrano et al. 2001), although previous studies of Dunlin and other Arctic-breeding shorebirds have shown mixed

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results (Sokkeli 1967, Thorup 1999, Sandercock et al. 2000, Johnson and Walters 2008, Flodin and Blomqvist 2012). Male and female Dunlin typically share incubation of 4-egg clutches, and both or one parent (usually the male) tends chicks that leave the nest within a day of hatching (Holmes 1966, Warnock and Gill 1996). Our variable for previous hatch indicates the number of chicks hatched in year i - 1 (0-4 chicks). We favored number of chicks hatched over a dichotomous hatch/fail measure because it may approximate the likelihood of extended pre-fledging chick survival and coincident brood attendance by one or both parents.

Initiation rank (nest initiation date). – Timing of arrival at the breeding grounds is likely an important correlate of mate and site fidelity if mis-matched arrival times of previous mates result in 'forced' divorce (Soikkeli 1967, Dhondt and Adriaensen 1994). Timing of arrival and laying are correlated in Dunlin (Jönsson 1987), so we used nest initiation as an index of arrival timing. Initiation rank is the ordinal date a nest was initiated minus the ordinal date of the first Dunlin nest initiated in that year, plus one.

Density (nest density within study plot). – We suspected that shorebird (con- and heterospecific) nest density might affect breeding dispersal by either pushing individuals from previously used territories (high densities), or opening up new areas for individuals to disperse (low densities). We created a variable for density (nests per km^2) of all shorebird nests within the same study plot and year. Other shorebird species included American Golden-Plover (*Pluvialis dominica*), Long-billed Dowitcher (*Limnodromus scolopaceus*), Pectoral Sandpiper (*Calidris melanotos*), Red Phalarope (*Phalaropus fulicarius*), and Semipalmated Sandpiper (*Calidris pusilla*).

We used an information theoretic approach (Burnham and Anderson 2002) and generalized linear mixed models to identify correlates of breeding dispersal. Breeding dispersal distance was included as a response in models, each composed of a single fixed effect explanatory variable (presented above; Table 3.1). Random effects were included for individual, plot, and year, but likelihood ratio tests showed that plot and year did not improve model fit in any model set, and these latter two variables were thereafter excluded. We tested a global model for correlation of fixed effects and found none.

We analyzed males and females separately. Models used a Gamma error distribution and log link. We ranked models by Akaike's Information Criterion for small sample size (AIC_c), and considered models competitive if AIC_c scores were within 2 units of the top ranked model (Burnham and Anderson 2002). We used model averaging and multi-model inference (Burnham and Anderson 2002) to evaluate multiple models in the competing set, and we evaluated the effects of explanatory variables therein. We considered variables to be informative if the 95% confidence intervals for parameter estimates did not overlap zero. We used program R Studio for all statistical analyses (R version 3.0.3, The R Foundation for Statistical Computing, 2014, and R Studio version 0.98.501, RStudio, Inc., 2009-2013).

Effects of mate and site fidelity

We also examined whether mate-faithfulness and site fidelity were associated with enhanced reproductive output in Dunlin. We grouped Dunlin according to sex and status (faithful or divorced), and sex and site fidelity (territory-changed or territory-faithful). We considered Dunlin territory-faithful if they remained within 192 m of their previous nest site, and that they changed territories if they moved beyond 192 m in a subsequent

nesting attempt (Sedgwick 2004). The 192 m figure was selected because it represents the median nearest neighbor distances for Dunlin at our Barrow study area (unpublished data). We used non-parametric Wilcoxon rank sum tests to compare the number of chicks hatched among divorced and faithful groups, and then among changed-territory and territory-faithful groups. These analyses were restricted to individuals in their second year recorded at the study site to avoid confounding by potential site experience and age effects, and to avoid pseudoreplication of individuals.

Effects of hatching success on greater breeding area fidelity

Our analyses require records of individuals that appeared at the study site in at least two years, and could not include those that dispersed greater distances than we were able to detect. If poor hatching success indeed prompts greater breeding dispersal distances, our analyses may not account for this influence. 'Single year' birds may have suffered mortality during the non-breeding season, or returned to the breeding grounds but dispersed far beyond our study area. To ascertain whether our analyses are biased towards more successful breeders (and thus returners), we used a Wilcoxon rank sum test to compare the 'first year' hatching success of males that made a single appearance and males that returned more than once. This analysis was restricted to males with site experience of 1 year, and did not include records from before 2005 to better approximate site experience.

RESULTS

We recorded between 43 and 64 Dunlin nests annually on or near the study plots, with a total of 461 nests. Sixty-six percent of the adults associated with these nests were given

USGS metal bands and color combinations throughout the study period (n = 510). In

each of the breeding seasons between 2005 and 2013, an average of 24% and 40% of

nesting females and males, respectively, had been banded in a previous year. Hatching

success was generally high, and between 75% and 96% of Dunlin nests hatched at least

one chick most years ($n = 342$, $\bar{x}$ = 3.1 chicks per nest, $s^2 = 2.0$). Hatching success was

lower in 2009 and 2010 because of increased predation, with 33% ($n = 63$) and 52% ($n = 42$) of nests hatching at least one chick, respectively.

Correlates of breeding dispersal

We identified 150 records of Dunlin that nested in two consecutive years (years i and $i -$

1) and had banded mates identified in both years (Table 3.2). These were comprised of

103 individuals that were recorded on the study site in repeated years (site experience

between 2 and 9 years; Table 3.3) at 101 nests. We found that 37% of nests were

attended by faithful pairs. Faithful pairs (males and females) moved a median distance of

87 m (range: 1 - 219, $n = 37$), divorced males moved a median distance of 106 m (range:

0 - 834, $n = 53$), and divorced females moved a median distance of 205 m (range: 34 -

852, $n = 23$).

In our analyses that explored factors that influence the distance females dispersed,

the *status* model ranked highest ($w_i = 0.94$) and there were no other competing models

($\Delta AIC_c \leq 2$)(Table 3.4). The *status* parameter ($\beta = 0.791$, 95% CI = 0.444, 1.138)

indicates that faithful females moved 90 m (95% CI = 71 m, 113 m) from their previous

nest site, and divorced females moved 197 m (95% CI = 146 m, 265 m)(Figure 3.1).

For the model set exploring male breeding dispersal, the *previous hatch* model

ranked highest ($w_i = 0.35$), followed by three competing models, which include *density*

($w_i = 0.18$), the *null* model ($w_i = 0.15$), and *status* ($w_i = 0.13$)(Table 3.4). The model

averaged parameter estimates and 95% confidence intervals for *previous hatch* ($\beta = -$

0.140, 95% CI = -0.247, -0.033) and *density* ($\beta = 0.003$, 95% CI = 0.000, 0.005) did not

overlap zero and these variables were considered informative. The *previous hatch*

parameter indicated that males move greater distances from their previous nest site after

hatching fewer chicks the previous year (Figure 3.2). For example, parameter estimates

for *previous hatch* indicated that males that did not hatch any chicks in the prior year

moved 134 m (95% CI = 78 m, 228 m), and those that hatched four chicks moved 105 m

(95% CI = 83 m, 133 m)(Figure 3.1). The *density* model suggests that males moved

farther with increasing population densities of other nesting shorebirds. At the lowest

recorded nest density of 36 nests per km^2, males moved 100 m (95% CI = 75 m, 137 m),

and at the highest nest density of 270 nests per km^2, they moved 115 m (95% CI = 76 m,

174 m)(Figure 3.2). Finally, the male *status* model ranked below the null model and

accounts for no more variation in the data than random, and had 95% confidence

intervals of the parameter estimate that overlapped zero ($\beta = 0.260$, 95% CI = -0.035,

0.556). Parameter estimates and confidence intervals for variables in competitive models

are listed in Table 3.5.

Effects of mate and site fidelity

Site fidelity appeared to be beneficial to males, as territory-faithful males ($n = 24$)

hatched more chicks (mean 3.8 ± 0.5 SD) than changed-territory males ($n = 10$, 2.6 ± 1.6

SD; Wilcoxon rank sum: $W = 65$, $p = 0.01$; Table 3.6). There was no difference in

number of chicks hatched between changed-territory and territory-faithful females ($W =$

117, $p = 0.46$; Table 3.6). Mate fidelity did not affect hatching success for males ($W = 94$, $p = 0.07$; Table 3.6) or females ($W = 115.5$, $p = 0.11$; Table 3.6).

Effects of hatching success on greater breeding ground fidelity

Eighty of 163 male Dunlin returned to the study area in years following banding, and 83 were not detected again (Table 3.2). There was no difference in number of chicks hatched between single-year birds (mean $\pm$ SD: 3.1 ± 1.4) and returners (3.2 ± 1.4, Wilcoxon rank sum test: $W = 2660$, $p = 0.43$).

DISCUSSION

Female-biased dispersal is common in avian species that employ a monogamous mating system with resource defense by males (Greenwood 1980, Clarke et al. 1997), and Dunlin likewise exhibited this breeding dispersal behavior at Barrow, AK. Previous studies showed that divorced birds move farther than faithful birds, with divorced females in particular moving great distances from nest sites of the previous year (Soikkeli 1967, Thorup 1999, Sandercock et al. 2000, Flodin and Blomqvist 2012, Gates 2013). Our results support assertions that mate fidelity is an important determinant of breeding dispersal by females. However, divorced and faithful males did not differ in dispersal distances. In contrast, prior hatching success and current density of shorebird nests at the breeding ground had some influence on male movement.

Divorced females dispersed farther from a prior year's nest site location than those that re-paired with their mates in subsequent years. Male Dunlin typically arrive and settle in their territories at the breeding grounds earlier than females (Holmes 1966, Jönsson 1987), allowing later-arriving females the opportunity to settle with a quality mate or breeding habitat of their choosing (Oring and Lank 1984). Our analyses

comparing hatching success of divorced vs. faithful and changed-territory vs. territory-faithful female Dunlin revealed no difference between groups, suggesting that breeding dispersal may be a low-risk behavior for females that allows for enhanced reproductive success associated with superior mate and territory options (Table 3.6). However, mate quality may be more important than territory quality for female Dunlin in Barrow for several reasons. First, suitable nesting habitat is widely available (Cunningham 2014, Cunningham et al., in prep.), which results in low variation of habitat quality and potentially minimal margins for improvement (Valcu and Kempenaers 2008, Choudhury 1995). Additionally, adult Dunlin and other sandpipers typically forage outside of their nesting territories (Holmes 1966, Lanctot et al. 2000), and broods are led away from the territory shortly after hatching (Holmes 1966, Hill 2012), further minimizing the necessity for habitat of any special quality. Jönsson (1987) offered support for the theory that sexual selection promotes size dimorphism among male and female Dunlin (smaller males and larger females), suggesting competition among males and females for quality mates (see also Blomqvist et al 1997, and Jönsson and Alerstam 1990).

Alternatively, some suggest that familiarity with a previous mate can be beneficial if it reduces time and energy of courtship behaviors or enhances coordination of shared incubation duties (Lanctot et al. 2000, Reneerkens et al. 2014). If this holds true, breeding dispersal may not serve to seek out better options, but is caused by displacement when a female arrives at the breeding ground after her prior mate has already paired with another bird. Our initiation rank model was not informative of breeding dispersal, but we lack sufficient data on exact arrival times of individuals to fully discount this possible influence.

Soikkeli (1967) found that divorce in the *C. a. schinzii* Dunlin subspecies in
Finland was a result of mismatched arrival times. Our model predicts that divorced
female Dunlin will move approximately 200 m from their previous nest site, which is just
beyond the median nearest neighbor distance for Dunlin at our study site (192 m),
suggesting that female Dunlin may show some degree of tenacity to familiar sites and
then pair with available, suitable nearby males. We surmise that mate faithfulness may
not necessarily be deliberate in *C. a. arcticola*, but a fortunate situation arising from
opportune combinations of synchronous arrival and site tenacity, facilitated by familiarity
of both members of a previous pair. However, we also acknowledge that an unknown
number of divorced female Dunlin may have dispersed far beyond our study area where
we were unable to detect them, potentially biasing our results towards those that did not
disperse so far.

Territory-faithful male Dunlin experienced greater hatching success than those
that divorced or changed territories, and mate fidelity also appeared to moderately
enhance hatching success for males (Table 3.6). Accordingly, we propose that familiarity
with a territory and to a lesser degree, a mate, are important for males. Site fidelity likely
has a positive influence on reproductive success and overall fitness for males because it
enhances knowledge of local resources, predation risk, and competing conspecific
neighbors (Oring and Lank 1984). Site fidelity also removes the need to search for a new
breeding site, which may be particularly important for male Dunlin. Available Dunlin
territories are limited by competing males (Holmes 1966), and those that quickly return to
a familiar territory may have an advantage in securing their place at the breeding ground.
Also, male Dunlin arrive when much of the available tundra habitat may be partially

obscured by remaining winter snowpack. The inability to immediately assess habitat underlines the potential importance of experience and familiarity with a prior breeding site for these birds.

During our study, we recorded relatively few instances of males changing territories (16 out of 90, including males with any number of years of site experience). Most males remained faithful to their territories and made relatively small movements within these territories between years. Thus, the number of chicks hatched in the previous year and shorebird population density, the variables we identified to be associated breeding dispersal in males, were not particularly strong (Figure 3.2). Males that did not hatch any chicks in the previous year moved 29 m farther than those that hatched a full clutch of four. Males may be responsive to chick production because they care for the brood through fledging, whereas females typically depart within a few days of hatching (Holmes 1966, Warnock and Gill 1996). Increasing population density of other nesting shorebirds also prompted males to move slightly farther. Over the study period, the population of breeding shorebirds in Barrow has fluctuated among plots and years. In particular, Pectoral Sandpipers and Red Phalaropes experience substantial population fluctuations (Cunningham 2014, Cunningham et al. *in prep*), which may exert pressure on Dunlin territories and cause them to adjust their nest location.

We did not find a difference in hatching success between 'first-year' males (site experience = 1) that bred at the study site in one year only, and those that returned in following years. Approximately 52% of first-year males returned in one or more following years during the study period. This approximates the Barrow male Dunlin apparent survival rate of 0.60 described by Hill (2012). It is likely that the majority of

non-returners suffered mortality during the non-breeding season rather than dispersing beyond our detection, and our comparison of hatching success elucidates that non-returners are not necessarily failed or poorer-quality breeders.

Divorce and breeding dispersal have been investigated in different breeding populations of *C. a. schinzii* subspecies in Scandinavia (Soikkeli 1967, Soikkeli 1970, Thorup 1999, Flodin and Blomqvist 2012). However, with differing return rates, breeding habitat composition, nesting densities, and variations of other life history traits in these populations, we considered *C. a. arcticola* may experience different rates and causes of breeding dispersal than those found in studies of *C. a. schinzii*. In general, the *C. a. schinzii* populations studied occurred in areas where the topography of the breeding grounds 'contained' the population, better enabling observers to track breeding dispersal movements of individuals (Soikkeli 1967, 1970, Thorup 1999). Tundra breeding habitat in Barrow is relatively expansive, and we were not able to track individuals that dispersed far beyond our fixed 600×600 m plots. Incidentally, *C. a. schinzii* also show a higher return rate to their breeding grounds than the Barrow *C. a. arcticola* population (62-94% vs. 49.5%; Thorup 1999, Hill 2012, respectively). Nonetheless, breeding dispersal distances by faithful pairs, divorced males, and divorce females of *C. a. schinzii* were roughly similar to our Barrow *C. a. arcticola* population (Soikkeli 1967, 1970, Thorup 1999). *C. a. schinzii* also show mate fidelity rates of 72%, 67%, and 75% (Soikkeli 1967, Thorup 1999, Flodin and Blomqvist 2012, respectively), which are higher than what we found in Barrow (37%). However, the *C. a. schinzii* mate fidelity rates were calculated from records where both mates from year i-1 were recorded in year i. We did not record sufficient cases of both returning pair members to calculate mate fidelity rates in this

manner, likely because of the lower return rates in Barrow. Thorup (1999) reported that prior hatching success influenced breeding dispersal in both males and females in Denmark, although hatching success did not influence dispersal in Sweden (Flodin and Blomqvist 2012). Flodin and Blomqvist (2012) also reported that divorced and re-paired females improved their hatching success, suggesting that female divorce and breeding dispersal serve to secure a 'better option' of mate or site.

We did not find strong evidence that breeding dispersal by Dunlin in Barrow, AK results from past experience. Rather, divorce prompted female breeding dispersal. Our results suggest that mate fidelity could moderately enhance hatching success for males, but we did not detect a reproductive advantage or disadvantage for faithful or divorcing females. Hill (2012) presented an apparent survival rate of 0.41 for female Dunlin at Barrow, and while a male may benefit from mate familiarity, the tenable probability that his prior mate may not return may be reason enough to opportunistically pair with a new mate.

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FIGURES

Figure 3.1. Predictions of female and male Dunlin breeding dispersal by status.

Whiskers are 95% confidence intervals. Dunlin nested in Barrow, AK, from 2005 to
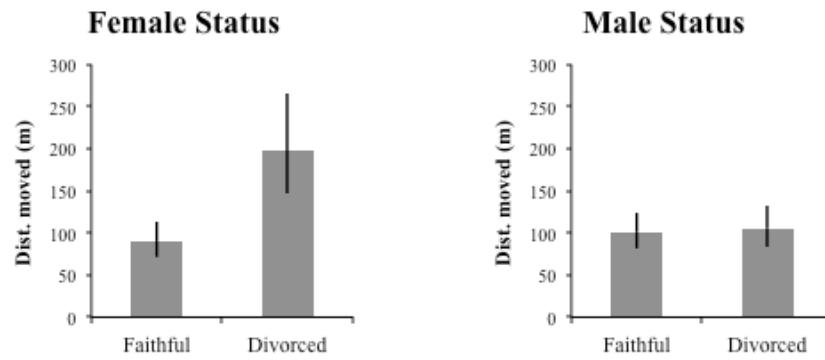
2013.

Figure 3.2. Predictions of male Dunlin breeding dispersal by shorebird population

density, and by the number of chicks hatched during the previous season. Dashed lines

are 95% confidence intervals. Dunlin nested in Barrow, AK, from 2005 to 2013.
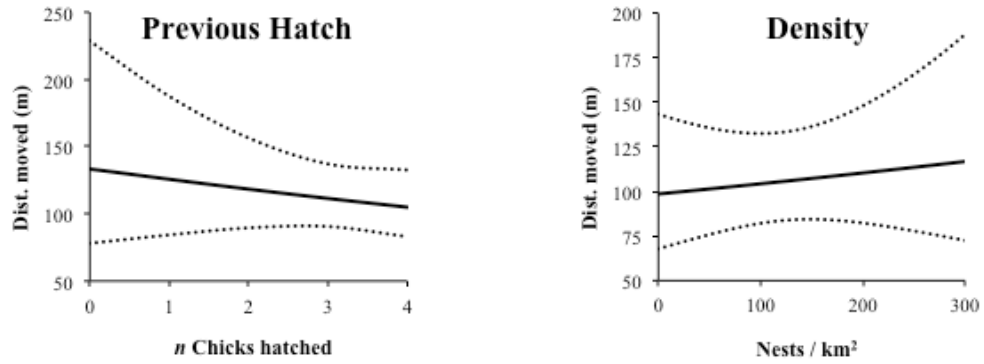
TABLES

Table 3.1. Models used to predict breeding dispersal in Dunlin at Barrow, AK, from 2005 to 2013.

Model	Description
Status	Faithful to or divorced from mate of previous year
Previous hatch	Number of chicks hatched in previous year
Site experience	Number of years since year of first banding
Initiation rank	Date of nest initiation minus date of first Dunlin nest
Density	Density of all shorebird nests on study plot (nests/km^2)
Null	
Global model	

Table 3.2. Records of banded Dunlin that nested in Barrow, AK between 2005 and 2013. Divorced and faithful male and female observations were used to identify correlates of breeding dispersal and effects of mate and site fidelity. Records of single-year and returned males are individuals of 'site experience = 1', and were used to infer effects of hatching success on greater breeding site fidelity.

Condition	Males	Females
Divorced	53	23
Faithful	37	37
Total	90	60
Single-year	83	
Returned	80	
Total	163	

Table 3.3. Counts of records of male and female Dunlin by site experience. These records were used for analyses of correlates of breeding dispersal, and include multiple records of individuals that occurred in multiple years. Dunlin were recorded in Barrow, AK from 2003 to 2013.

Site experience	Males	Females
2	37	38
3	18	14
4	19	8
5	10	2
6	4	1
7	3	-
8	1	-
9	1	-

Table 3.4. AIC$_c$ tables of models explaining breeding dispersal by male and female Dunlin in Barrow, AK, from 2005 to 2013.

Model	K	logLik	ΔAIC$_c$	w_i
Males				
Previous hatch	4	-571.88	0.00	0.35
Density	4	-518.53	1.30	0.18
Null	3	-519.81	1.68	0.15
Status	4	-518.88	2.00	0.13
Site experience	4	-519.11	2.46	0.10
Initiation rank	4	-519.80	3.84	0.05
Global	8	-515.30	4.14	0.04
Females				
Status	4	-348.74	0.00	0.94
Global	8	-347.43	7.48	0.02
Null	3	-354.47	9.17	0.01
Site Experience	4	-353.50	9.53	0.01
Initiation rank	4	-353.79	10.10	0.01
Density	4	-353.96	10.43	0.01
Previous hatch	4	-354.15	10.83	0.00

Table 3.5. Parameter estimates and confidence intervals for competitive models explaining breeding dispersal by Dunlin in Barrow, AK, from 2005 to 2013.

Variable	β	95% C.I.
Males		
Previous hatch	-0.140	-0.247, -0.033
Density	0.003	0.000, 0.005
Females		
Status	0.791	0.444, 1.138

Table 3.6. Wilcoxon rank sum tests comparing number of chicks hatched between divorced and faithful Dunlin, and Dunlin that changed territories or remained territory-faithful. This analysis only included Dunlin with two years site experience. Dunlin nested around Barrow, AK between 2005 and 2013.

Group	Mean # hatched ± SD	*n*	*W*	*P*
Males				
Divorced	3.2 ± 1.3	22	94	0.07
Faithful	3.9 ± 0.4	15		
Changed-territory	2.6 ± 1.6	10	65	0.01
Territory-faithful	3.8 ± 0.5	24		
Females				
Divorced	3.4 ± 1.2	15	115.5	0.11
Faithful	3.8 ± 0.9	22		
Changed-territory	3.4 ± 1.3	11	117	0.46
Territory-faithful	3.7 ± 0.9	24		

CHAPTER 4
SUMMARY

Shorebirds are challenged by the loss of critical habitat at wintering and migratory

stopover areas (Brown et al. 2001). They also face the impending reality of climate

change, which has the potential to impact shorebirds throughout their annual ranges, but

may be particularly disruptive to the landscape and ecology of their Arctic breeding

grounds (Martin et al. 2009). The intention of this study was to develop a better

understanding of the habitat, social, and behavioral factors influencing nest site selection

in a variety of shorebird species that are representative of those breeding throughout

Alaska's North Slope region (Johnson et al. 2007, Saalfeld et al. 2013), which will enable

better-focused management and conservation efforts in the face of these challenges. I

identified different habitat features salient to nest site selection by six species, and

indicated the influence of con- and heterospecifics on nest placement. I also clarified the

potential influences of breeding dispersal in a site-faithful species, the Dunlin (*Calidris

alpina*).

In Chapter 2, I focused on six species of shorebird breeding on the Arctic tundra

around Barrow, Alaska. These species had different migratory routes, mating systems,

degrees of site fidelity, and variations of other life history traits. I demonstrated that

there are combinations of habitat and social factors that these shorebirds respond to when

selecting nest sites, and that the influential factors differ among species. Physical

variation of the tundra landscape is subtle, but its patchy mosaic of ponds, wetlands,

moist meadows, and dry upland areas with varying degrees of microrelief present

multiple nest site options for shorebirds, and the six species studied appear to consider

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these options differently. A unifying salient habitat feature was tundra moisture level within three meters of the nest site. Most species selected slightly drier tundra for their immediate nest area than that available, however Long-billed Dowitchers (*Limnodromus scolopaceus*) selected habitat that was slightly wetter. I also showed that nest placement for all six species is influenced by distance to the nearest conspecific, with birds nesting farther from conspecifics than predicted by random distributions. As expected, this variable was particularly strong in species known to be moderately site-faithful and territorial, including American Golden Plovers (*Pluvialis dominica*), Dunlin (*Calidris alpina*), and Semipalmated Sandpipers (*Calidris pusilla*).

These results may indicate that shorebirds will be sensitive to changing habitat conditions associated with climate change. Climate models predict a 1.6°C increase in summer temperatures and a 12% increase in summer precipitation by 2051-2060 (Martin et al. 2009). The tundra permafrost, which shapes the tundra's microtopography, hydrological regimes, and vegetation communities, may degrade under warmer temperatures, and vegetative structure and composition may change with a lengthened growing season (Shur et al. 2003, Arctic Climate Impact Assessment 2004). These changes may limit suitable nest site habitat for some species, and could have a considerable impact on territorial species such as American Golden Plovers, Dunlin, and Semipalmated Sandpipers (Saalfeld and Lanctot, in review), which may exclude conspecifics from the limited suitable habitat. Alternatively, Long-billed Dowitchers, Pectoral Sandpipers (*Calidris melanotos*), and Red Phalaropes (*Phalaropus fulicarius*) will likely tolerate smaller inter-nest distances (Saalfeld and Lanctot, in review), and may be better-equipped to settle in limited habitat.

In Chapter 3, I investigated potential causes of breeding dispersal in both sexes of Dunlin. Experience did not appear to strongly influence breeding dispersal in male or female Dunlin, however divorce prompted breeding dispersal by females. Additionally, site-fidelity, and to a lesser degree mate-fidelity appeared to enhance hatching success of male Dunlin, but these had no effect on females. This study does not provide direct evidence of whether breeding dispersal causes divorce (i.e. female initiated divorce), or breeding dispersal is a result of divorce. However, given my observations of breeding-dispersal by female Dunlin, I concluded that dispersing females did not initiate divorce to prospect for a superior mate or habitat, but were usurped from their prior mate or habitat by an earlier-arriving or higher-quality female. Dunlin appear to be site-faithful by default, and males in particular benefit from this situation. However, relatively low survival rates in the population render mate-fidelity an unrealistic but occasionally fortuitous event.

This study has improved our understanding of the habitat, social, and behavioral features influential in nest site selection by Arctic-breeding shorebirds. Habitat features that are influential in nest site selection for shorebirds include tundra wetness and microtopographic relief, which are shaped by the Arctic's climactic regime and are subject to change with a warming climate (Shur et al. 2003, Arctic Climate Impact Assessment 2004). However, it is not known how resilient shorebirds will be to these changes, and continued study of these birds can enhance our understanding of how they will be affected by the changing Arctic landscape. For example, additional study of how habitat choices influence hatching success can inform how well the birds might tolerate nesting in sub-optimal habitat. Also, climate change will likely modify abundance and

schedules of invertebrate prey for shorebird adults and young, and also modify the

abundance of important egg and chick predators such as Arctic fox (*Vulpes lagopus*),

Glaucous Gulls (*Larus hyperboreus*), Common Ravens (*Corvus corax*), and Jaegers

(*Sterocorarius sp.*) (Martin et al. 2009). Continued monitoring of nest and chick survival

can help discern any changes in breeding productivity under these altered food schedules

and predation risks. Finally, further study of the breeding dispersal movements of site-

faithful and nomadic shorebird species will enhance understanding of birds' reactions to

habitat conditions and elucidate their ability to seek out suitable nest habitat.

This study also provided quantitative models that may be useful in predicting

habitat that shorebirds will select for their nest sites. The models first require validation

at locations outside the study plots surveyed, but could eventually be used to focus

ground survey efforts for nesting shorebirds and inform human development projects on

tundra habitat in the Arctic Coastal Plain region.

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