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Breeding Ecology of Birds at Teshekpuk Lake: A Key Habitat Site on the Arctic Coastal Plain of Alaska

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ABSTRACT. The Teshekpuk Lake Special Area in the National Petroleum Reserve – Alaska (NPR-A) currently has no long-term protection from oil development. In this study, we provide novel information on nest density, productivity, and habitat use at Teshekpuk relative to a developed oilfield site at Prudhoe Bay, Alaska, to assess the importance of Teshekpuk for tundra-nesting birds and to provide recommendations regarding potential oil development. Mean annual nest density of all bird species combined was significantly higher at Teshekpuk than at Prudhoe Bay and was higher than any of five other sites with comparable data on the Alaskan Arctic Coastal Plain. Nest densities were significantly higher at Teshekpuk than at Prudhoe Bay for Lapland longspurs (*Calcarius lapponicus*) and long-billed dowitchers (*Limnodromus scolopaceus*), although those for semipalmated sandpipers (*Calidris pusilla*) were higher at Prudhoe Bay. Total shorebird nest densities at Teshekpuk were among the highest of any sites in the region. At Teshekpuk, shorebirds nested preferentially in wet and emergent habitats, including flooded low-center polygons, non-patterned tundra, and *Carex aquatilis*-dominated habitats. Therefore, we recommend that future oil infrastructure placement in this region avoid these habitats. Using data collected at Teshekpuk and Prudhoe Bay from 2005 to 2008, we modeled nest survivorship for 11 shorebird species and for Lapland longspurs. For longspurs, the best-supported models based on AIC_c values indicated that nest survival was always higher at Teshekpuk, but it was also higher elsewhere in years of high lemming abundance and later in the nesting season. For shorebirds, the best-supported models indicated that nest survivorship was highly variable among years and sites. Uniparental-nesting shorebirds had lower nest survivorship shortly after nest initiation followed by a rapid increase, while biparental survivorship was consistently high throughout the nest lifetime. We recommend that disturbances to nesting habitat be minimized during early June, when vulnerability to nest failure is higher. Because of their high importance to Arctic breeding birds, we recommend that areas within the Teshekpuk Lake Special Area, including our study area and those that are currently under 10-year deferral, be considered for permanent protection.

Key words: Arctic Coastal Plain, Teshekpuk Lake Special Area, National Petroleum Reserve-Alaska, nest diversity, nest density, nest survivorship, shorebirds, Lapland longspur

RÉSUMÉ. La zone spéciale du lac Teshekpuk située dans la réserve nationale de pétrole de l’Alaska (NPR-A) n’est dotée d’aucune protection à long terme en matière de mise en valeur pétrolière. Dans la présente étude, nous fournissons de nouveaux renseignements sur la densité des nids, la productivité et l’utilisation de l’habitat à Teshekpuk à la lumière d’un chantier de mise en valeur pétrolière à la baie Prudhoe, en Alaska et ce, dans le but d’évaluer l’importance de Teshekpuk pour les oiseaux qui nichent dans la toundra ainsi que de fournir des recommandations en matière de mise en valeur pétrolière future. La densité moyenne annuelle des nids de toutes les espèces d’oiseaux prises ensemble était considérablement supérieure à Teshekpuk qu’à la baie Prudhoe et était plus élevée que dans n’importe quel des cinq autres sites aux données comparables sur la plaine côtière arctique de l’Alaska. La densité des nids était considérablement supérieure à Teshekpuk qu’à la baie Prudhoe dans le cas du bruant lapon (*Calcarius lapponicus*) et du bécasseau à long bec (*Limnodromus scolopaceus*), tandis que les densités du bécasseau semipalmé (*Calidris pusilla*) étaient plus élevées à la baie Prudhoe. Les densités totales de nids d’oiseaux de rivage à Teshekpuk comptaient parmi les densités les plus élevées de n’importe quel des sites de la région. À Teshekpuk, les oiseaux de rivage nichaient, de préférence, dans des habitats humides et émergents, ce qui comprend les polygones concaves inondés et la toundra non réticulée de même que les habitats dominés par le *Carex aquatilis*. Nous recommandons donc que l’emplacement d’infrastructures pétrolières futures dans cette région évite ces habitats. À l’aide de données recueillies à Teshekpuk et à la baie Prudhoe de 2005 à 2008, nous avons modélisé la présomption de survie en nid de 11 espèces d’oiseaux de rivage et des bruants lapons. Dans le cas des bruants lapons, les modèles les mieux soutenus d’après les valeurs AIC_c laissent entrevoir que la survie en nid était constamment supérieure à Teshekpuk, mais qu’elle était également plus élevée ailleurs pendant les années de grande abondance de lemmings de même qu’à une période plus tardive de la saison de nidification. Dans le cas des oiseaux de rivage, les modèles les mieux soutenus indiquent que la survie en nid varie beaucoup d’une année à l’autre et d’un emplacement à l’autre. Les oiseaux de rivage en mode de nidification monoparental affichaient un taux de survie en nid

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moins élevé peu après l'initiation du nid, ce qui était suivi d'une augmentation rapide, tandis que le taux de survie des oiseaux en mode de nidification biparental était constamment élevé pendant toute la durée d'existence du nid. Nous recommandons donc que les perturbations à l'habitat de nidification soient réduites au minimum au début de juin car c'est à ce moment-là que la nidification est plus vulnérable. Compte tenu de leur grande importance pour les oiseaux nicheurs de l'Arctique, nous recommandons que les aires faisant partie de la zone spéciale du lac Teshekpuk, ce qui comprend l'aire visée par notre étude et les aires faisant couramment l'objet d'un report de 10 ans, soient considérées à titre de protection permanente.

Mots clés : plaine côtière arctique, zone spéciale du lac Teshekpuk, réserve nationale de pétrole de l'Alaska, diversité des nids, densité des nids, survie au nid, oiseau de rivage, bruant lapon

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INTRODUCTION

The vast (98 200 km^2) Arctic Coastal Plain (ACP) of Alaska supports significant breeding populations of over 90 species of birds, representing millions of individuals (Johnson and Herter, 1989). Significant populations of shorebirds (Pitelka, 1974; Johnson et al., 2007), waterfowl, and other waterbirds breed and stage here (King and Hodges, 1979; Earnst et al., 2005). The 6960 km^2 Teshekpuk Lake Special Area (TLSA), which occurs within the ACP portion of the 95 000 km^2 National Petroleum Reserve – Alaska (NPR-A), has been identified as a region of exceptional importance to wildlife, including nesting and molting birds (Derksen et al., 1979; King and Hodges, 1979). The Bureau of Land Management (BLM) has designated this region as a "Special Area" that is particularly important for wildlife and subsistence hunting (BLM, 1998), one of three Special Areas designated in the NPR-A. Because the TLSA is situated on the eastern border of the NPR-A, adjacent to existing oilfields, and because potentially significant oil reserves exist below Teshekpuk Lake (BLM, 1998), there is increasing interest in the expansion of oil development into this region. Currently, 77% of the TLSA is open to oil development, and more than 607 km^2 have been leased to oil companies for exploration activities since 2002 (www.blm.gov/ak/st/en/html). In 2007, the U.S. District Court for the State of Alaska placed a 10-year moratorium on leasing 1619 km^2 to the north and east of Teshekpuk Lake because of the area's importance to molting brant geese (*Branta bernicla*; King, 1970) and because cumulative environmental impacts of oil development on wildlife and other resources had not been adequately addressed (U.S. District Court, District of Alaska, 2006).

Human disturbance from a variety of sources may have direct or indirect impacts on nesting birds on the ACP. These impacts include loss of nesting habitat due to human-altered hydrology (e.g., impoundments) and road dust, habitat alteration from human-accelerated thermokarst (melting permafrost), disturbance from aircraft noise, and increased predator populations (Troy Ecological Research Associates, 1993; Kertell, 1996; Auerbach et al., 1997; NRC, 2003). Nest predation is a significant cause of nest failure for passerines, waterfowl, and shorebirds at many locations within the Alaskan Arctic (Custer and Pitelka, 1977; Helmers and Gratto-Trevor, 1996) and may be important in regulating populations of some species on the ACP (Troy, 1996). Certain species have lower nest survivorship nearer to oil infrastructure (Liebezeit et al., 2009), and oilfields may be a comparative "sink" for bird populations, with other, more productive regions acting as "sources" (NRC, 2003).

Despite the recognized importance of the TLSA to nesting birds and the likely expansion of oil development and associated human activity in this region, no published studies are available that evaluate the full suite of nesting birds in terms of nest density, nest survivorship, and nesting habitat associations within the TLSA. This information is critical for making informed decisions regarding the impact of development on bird populations in the TLSA. The need for such information is further prompted by the declines documented worldwide of migratory shorebird populations (Brown et al., 2001; Morrison et al., 2006; Bart et al., 2007), which include up to 11 shorebird species that regularly breed on the ACP (U.S. Shorebird Conservation Plan, 2004). Waterfowl that have breeding populations on the ACP, including the Steller's eider (*Polysticta stelleri*) and spectacled eider (*Somateria fischeri*), have also experienced declines in Alaska (Kertell, 1991; Stehn et al., 1993) and are federally listed as threatened species.

Our objectives for this study were 1) to provide baseline information on breeding densities and nest survivorship of birds nesting in different habitat types within the TLSA; 2) to compare breeding densities and nest survivorship of shorebirds and passerines at the Teshekpuk site with those at a nearby site in a human-altered region—the Prudhoe Bay oilfield; and 3) to evaluate the importance of the TLSA as a breeding ground for nesting birds by comparing nest densities there with comparable data from a series of sites across the ACP. On the basis of our findings, we provide recommendations to minimize impacts to nesting birds in the TLSA should development proceed in this region.

METHODS

Study Sites and Study Plot Selection

During June and July of 2005–08, we collected data at a site approximately 10 km south of the SE shoreline of

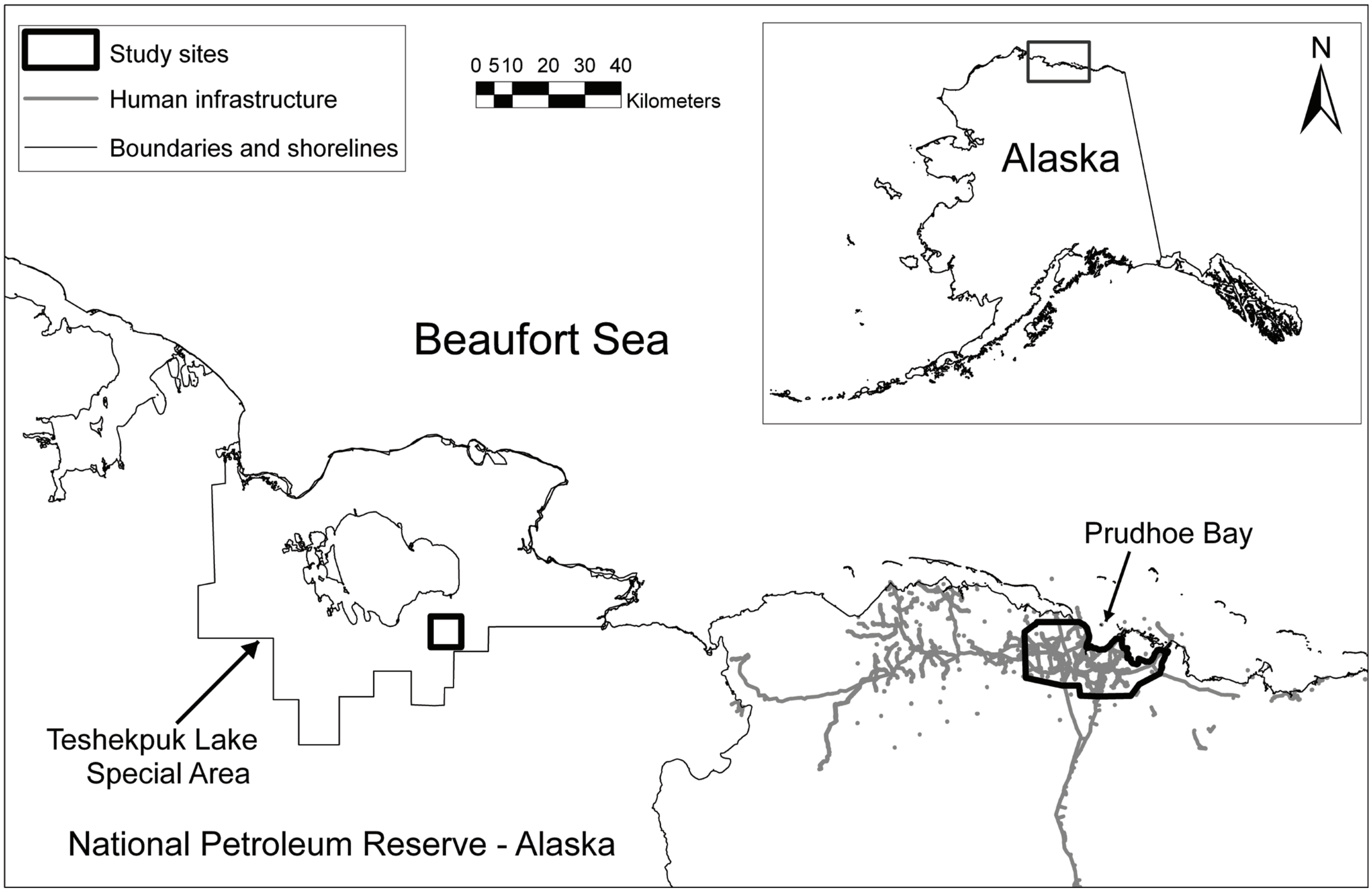

FIG. 1. The Teshekpuk and Prudhoe Bay study sites sampled from 2005 to 2008 on the Arctic Coastal Plain of Alaska, USA.

Teshekpuk Lake (70˚25′ N, 153˚07′ W) and another site within the Prudhoe Bay oilfield (70˚17′ N, 148˚32′ W), 160 km due east of Teshekpuk Lake (Fig. 1). The Teshekpuk study site covered an area of ~50 km^2 and was located in a remote area with minimal human disturbance (more than 75 km from the nearest road and human settlement). The Prudhoe Bay site covered an area of ~500 km^2 within the network of oilfield infrastructure, which includes gravel roads, airstrips, pipelines, oil production pads and processing facilities, power stations and lines, gravel mines, and living quarters.

Habitat at both sites was characterized by a mosaic of dry or moist upland tundra, often with high densities of cottongrass tussocks (*Eriophorum* spp.), moist or wet meadows of graminoids, low shrubs, aquatic marshes dominated by sedges (*Carex* spp.), pendant grass (*Arctophila fulva*), and lakes and ponds. The topography was generally flat, with elevations typically below 50 m. Micro-topographic features included high- and low-centered polygons, strangmoor or disjunct polygon ridges, hummocks, tussocks, and frost boils, with occasional pingos (Walker et al., 1980). Mean daily temperature during the study (average of daily minimums and maximums for June and July, as recorded at the Deadhorse Airport in Prudhoe Bay) was 6.3˚C (Weather Underground, Inc., 2009).

After selecting a random starting point at each site, we systematically established 18 plots at the Teshekpuk site and 12 at Prudhoe Bay. Distance between plots ranged from under 50 m to 8 km at Teshekpuk and from 60 m to 28 km apart at Prudhoe Bay. All plots were 100 × 1000 m (10 ha) and were subdivided into 40 subplots (each 50 × 50 m), which were marked at 50 m intervals along centerline axes using 1.2 m wooden survey stakes. Each subplot was further divided into 25 × 25 m quadrats. We used random compass bearings to select the orientation of each plot so that open water covered no more than 20% of the plot. At Prudhoe Bay, plots were located over 100 m from roads and oilfield infrastructure to reduce potential effects of disturbance and habitat modification from road dust accumulation (Troy, 2000).

Field Methods

On each plot, we conducted four nest searches per year between 9 June and 3 July. We used both rope-drag and behavioral nest search techniques, following methods adapted from Troy Ecological Research Associates (1993). Nest locations for all species were recorded with a global positioning system (GPS) and marked by a wooden tongue depressor placed within 5 m of the nest. Searches were conducted from approximately 0730 to 2000 Alaska Daylight Time. We monitored active nests every 3 to 6 days until their fate was determined.

For nest fate, we recorded four outcomes: success, predation, non-predation failure, or unknown. We defined a nest as successful if at least one chick hatched (precocial species) or fledged (altricial species). We assigned nest fate as "successful" or "depredated" on the basis of previously established criteria (Mabee, 1997; Martin et al., 1997). Causes of nest failure other than predation included abandonment, trampling by caribou (*Rangifer tarandus*) or muskox (*Ovibos moschatus*), and human disturbance. Nest fate was classified as "unknown" if we had no clear evidence (or contradictory evidence) about the cause of nest failure, or if we discontinued monitoring nests because the field season ended. To reduce potential researcher effects on nest predation, we used a number of methods; these included conducting nest checks from a distance with binoculars, avoiding the creation of dead-end paths when checking nests, and not approaching or searching for nests when predators were nearby (Martin and Geupel, 1993).

To obtain an index of abundance of potential nest predators, we conducted three surveys on each plot annually. Each survey consisted of three 10-minute point counts along the plot centerline using a method similar to that of Ralph et al. (1993; see also Liebezeit et al., 2009). Point counts were separated by at least 200 m and conducted at least 10 minutes apart. We counted all visual and aural detections of documented or suspected potential nest predators (Poole et al., 2003; Liebezeit and Zack, 2008) within an area 300 m beyond the plot boundary. We avoided re-counting individual predators by noting differences in plumage (e.g., light morph versus dark morph jaegers) and pelage (arctic fox) and by tracking active predator nests and fox den activity on or near study plots.

We classified the dominant landform of each 25 × 25 m quadrat according to Walker et al. (1980). These landforms are large-scale, geophysical features that may contain a variety of vegetation types. We condensed the landform categories from Walker et al. (1980) into four groups: "Upland" (high-centered polygons, hummocky terrain and vegetated dunes), "Mixed" (mixed high- and low-centered polygons), "Low" (low-centered polygons), and "Marsh" (non-patterned ground, strangmoor, and disjunct polygon rims). We used an ocular technique (James and Shugart, 1970) to estimate the proportion of each nest concealed by vegetative cover overhead. Because availability of lemmings (*Lemmus trimucronatus*, *Dicrostonyx groenlandicus*) as alternative prey may strongly influence nest predation rates (Summers, 1986; Bêty et al., 2001), we estimated gross lemming abundance each year from incidental observations of individuals on study plots (number observed each day) as low (up to 3), medium (4 to 7), or high (8 or more). On all study plots, we estimated snow cover within each subplot to the nearest 10% several times during the first weeks of each season.

Statistical Analysis

We compared nest density and predator activity at Teshekpuk and Prudhoe Bay by species groups and by individual species for which we had adequate sample sizes, using a two-way ANOVA with year, site, and the interaction term (Zar, 1999). Our dependent variables for each of these estimates were nest density (nests/km^2) and average predator detections (per 30-min count) per plot. We used one-way ANOVA to test for differences in nest density across vegetation classes at Teshekpuk.

We examined nesting habitat preference at the Teshekpuk site by conducting a use vs. availability analysis using the Bureau of Land Management/Ducks Unlimited National Petroleum Reserve Alaska (NPR-A) earth-cover classification (referred to hereafter as the "BLM/DU map"), a 30 × 30 m resolution raster layer of 17 major earth/vegetation classes (Ducks Unlimited Inc., 1998). We used ArcGIS (version 9.2; Environmental Systems Research Institute, Redlands, California) to determine the area of each earth-cover class within all study plots and the Hawths analysis tool to determine the corresponding earth-cover class for each nest at the 30 × 30 m scale. We collapsed 11 of the earth classes into four categories (dry, moist, wet, emergent) based on tundra wetness. The "Dry" category includes tussock tundra, dwarf shrub, sparsely vegetated ground, and barren ground; "Moist" includes sedge grass meadow and moss/lichen; "Wet" includes wet tundra; and "Emergent" includes turbid water, *Carex aquatilis*, and flooded tundra with low-center polygons or non-patterned ground. We used the log-likelihood alternative to the chi-square goodness-of-fit test (Manly et al., 2002) to determine whether nesting habitat class use differed from that expected on the basis of availability and compared Bonferroni-adjusted confidence intervals to evaluate preference or avoidance of particular habitat classes. We did not perform this same analysis for the Prudhoe Bay site because the BLM/DU map did not cover this region and the landform classes were not completely analogous to the BLM/DU map classes. We used log-linear regressions to estimate the snowmelt completion date from our snow cover data. All analyses were conducted using NCSS (version 2004; Number Cruncher Statistical System, Kaysville, Utah) unless otherwise stated. Results were reported as mean ± SE, and were considered significant if $p < 0.05$.

Each nest has an "age" or "nest lifetime," defined as the period from its initiation date (when the first egg was laid) to its termination date (when the nest succeeded, failed, or its fate became unknown). We back-calculated nest initiation dates from nest age estimates obtained by (1) assuming one day for each egg laid when nests were discovered during the laying stage, (2) using published nesting stage lengths (Poole et al., 2003) if hatch date was known, (3) judging the stage of nestling development (passerines only; Hussell and Montgomerie, 2002), or (4) using egg flotation (Liebezeit et al., 2007). If the fate of a nest was observed, the date of this observation was considered the termination date. If the day of hatch/fledge occurred between nest visits, we used the estimated hatch/fledge date as the termination date. For failed nests, Program MARK (White and Burnham, 1999) incorporates probabilities of failure for each day between the last observed active date and first observed inactive date; thus, no final exposure day is estimated (Dinsmore et al., 2002). If nest fate was not known, the termination date was assigned as the last day the nest was known to be active (Manolis et al., 2000).

We examined competing, biologically relevant models of nest daily survival rate using the program MARK nest survivorship model (White and Burnham, 1999; Dinsmore et al., 2002). For each covariate, we developed a set of a priori predictions. We included year and site in our analysis since we expected high variation between sites and years in nest survivorship, as found in previous studies from this region (Summers and Underhill, 1987; Troy, 2000; Liebezeit et al., 2009). Because of major differences in nesting biology, we conducted separate analyses for shorebirds and passerines (precocial vs. altricial nesters). Within the shorebird analysis, we treated uniparental and biparental nesters as separate groups (included in analysis as "behavior") because previous researchers have found differences in nest survivorship between these shorebird groups (Norton, 1972; Cartar and Montgomerie, 1985; Smith, 2009). In our analysis, uniparental shorebird species included pectoral sandpiper (*Calidris melanotos*), buff-breasted sandpiper (*Tryngites subruficollis*), and the phalarope species (*Phalaropus* spp.). For these species one adult takes sole responsibility in incubating eggs, whereas in biparental species both adults share this duty (Oring, 1982). We were unable to run models for other bird groups (e.g., waterfowl) because of limited sample sizes. We also considered other variables found to affect nest survivorship, including nest age (Grant et al., 2005), day of season (Zimmerman, 1984; Winter, 1999), nest stage (passerines only: incubation versus nestling stage; Grant et al., 2005), vegetative concealment (Martin, 1993), predator abundance (Cain et al., 2006), lemming abundance (Summers, 1986), snowmelt (Summers and Underhill, 1987), and habitat type (i.e., landform). In the analysis, we removed nests that failed for other reasons, since we were most interested in the impact of nest predation on survivorship.

Daily survival rate (DSR) was estimated for a 51-day period (2 June to 23 July) for both shorebirds and passerines. We considered 20 models for passerines and 171 models for shorebirds, with various combinations of the variables and interactions considered. We did not perform a goodness-of-fit test because this test is unavailable for the nest survival models in program MARK. The logit function was used to constrain survival to the interval 0–1, and model selection was conducted with AIC_c (Burnham and Anderson, 2002). In contrast to using a modeling strategy that limits the number of models (Burnham and Anderson, 2002), because of the complexity of predictions of interest, and the numerous potential interactive effects, we decided on an approach that uses all combinations (Doherty et al., 2010). This method of variable selection (i.e., cumulative AIC_c weights) may perform better than more traditional ad hoc strategies (Doherty et al., 2010) because all variables are equally represented in the set of models. We used a model-averaging approach (Burnham and Anderson, 2002) and computed the relative importance of predictor variables by summing Akaike weights across all models in the model set examined.

The snowmelt variable could be a surrogate for year. To evaluate the variability of snowmelt as a replacement for year in the shorebird analysis, we used an analysis of deviance procedure (Skalski et al., 1993). The most general model that explains all of the deviance explainable by year included site, behavior, site*behavior, and year, and the baseline model with no year-to-year variation included site, behavior, and site*behavior. An alternative model used the covariate snowmelt instead of year: site, behavior, site*behavior, and snowmelt. The percentage of deviance explained by the covariate model was computed, and an F test constructed to compute a probability level.

RESULTS

Descriptive Analyses

From 2005 to 2008, we discovered and monitored 1074 nests of 26 species within study plots at the Teshekpuk and Prudhoe Bay study sites. These included 592 nests of 11 shorebird species, 359 nests of one passerine, 98 nests of seven waterfowl species, and 25 nests of seven species representing other bird groups (Table 1). At both sites, the most common species were Lapland longspur (*Calcarius lapponicus*; $n = 359$), semipalmated sandpiper (*Calidris pusilla*; $n = 168$), and pectoral sandpiper ($n = 138$), which together made up 62% of the total nests found. Lapland longspurs were the only passerine species for which we found nests at both sites (hereafter we refer to the passerine category as "longspurs").

Overall mean annual nest density was significantly higher at Teshekpuk (mean = 100.97 ± 6.36) than at Prudhoe Bay (mean = 76.67 ± 7.73; Table 1). Most of the variation was explained by site ($F_{112} = 16.93$, $p < 0.001$), although year was also a significant explanatory variable ($F_{112} = 6.41$, $p = 0.001$). Shorebird and waterfowl nest densities were similar at both sites (Table 1), but shorebird densities varied significantly between years at both sites ($F_{112} = 5.08$, $p = 0.003$). Among individual species, nest densities (nests/km^2) were higher at Teshekpuk than at Prudhoe Bay (Table 1) for both Lapland longspurs (Teshekpuk: mean = 39.17 ± 2.72; Prudhoe Bay: mean = 17.08 ± 2.93; $F_{112} = 60.9$, $p < 0.001$) and long-billed dowitchers (*Limnodromus scolopaceus*; Teshekpuk: mean = 6.11 ± 1.25; Prudhoe Bay: mean = 1.04 ± 0.65; $F_{112} = 12.91$, $p < 0.001$), whereas nest densities of semipalmated sandpipers were higher at Prudhoe Bay (mean = 21.46 ± 5.09; $F_{112} = 16.65$, $p < 0.001$) than at Teshekpuk (mean = 8.75 ± 1.66).

TABLE 1. Species and average nest densities (nests/km^2 from 2005 to 2008 ± SE) found at the Teshekpuk and Prudhoe Bay sites. Densities per vegetation class are shown for the Teshekpuk site only. Sample unit = number of plots (Teshekpuk, $n = 18$; Prudhoe Bay, $n = 12$).

			Teshekpuk Vegetation Class			
Species	Teshekpuk	Prudhoe Bay	Dry	Moist	Wet	Emergent
Shorebirds:						
American golden-plover (*Pluvialis dominica*)	1.67 ± 0.61	0.42 ± 0.28	3.69 ± 1.63	0.94 ± 0.55	0	1.67 ± 1.16
Black-bellied plover (*Pluvialis squatarola*)	1.99 ± 0.57	0.42 ± 0.28	0.51 ± 0.51	1.98 ± 0.87	3.88 ± 2.71	2.20 ± 1.14
Buff-breasted sandpiper (*Tryngites subruficollis*)	0	0.83 ± 0.36	0	0	0	0
Dunlin (*Calidris alpina*)	3.52 ± 0.83	1.46 ± 0.57	3.30 ± 1.47	4.74 ± 1.61	3.25 ± 3.25	1.02 ± 0.71
Long-billed dowitcher (*Limnodromus scolopaceus*)	6.11 ± 1.25	1.04 ± 0.65	6.67 ± 2.76	5.55 ± 1.96	2.93 ± 2.14	6.16 ± 3.31
Pectoral sandpiper (*Calidris melanotos*)	12.78 ± 1.46	11.04 ± 1.93	6.45 ± 2.10	15.88 ± 2.19	17.70 ± 5.33	14.56 ± 5.21
Red phalarope (*Phalaropus fulicarius*)	6.99 ± 1.60	3.54 ± 1.43	4.65 ± 2.06	5.13 ± 1.89	14.16 ± 5.50	9.71 ± 3.85
Red-necked phalarope (*Phalaropus lobatus*)	5.09 ± 0.91	7.92 ± 3.24	2.19 ± 1.29	2.54 ± 0.95	13.52 ± 9.83	14.51 ± 6.74
Ruddy turnstone (*Arenaria interpres*)	0	0.21 ± 0.21	0	0	0	0
Semipalmated sandpiper (*Calidris pusilla*)	8.75 ± 1.66	21.46 ± 5.09	8.22 ± 2.57	7.23 ± 1.86	12.73 ± 7.12	5.42 ± 2.22
Stilt sandpiper (*Calidris himantopus*)	2.36 ± 0.68	3.13 ± 0.98	2.62 ± 1.14	0.99 ± 0.55	1.02 ± 0.70	3.23 ± 1.43
Passerines:						
Lapland longspur (*Calcarius lapponicus*)	39.17 ± 2.72	17.08 ± 2.93	35.94 ± 4.46	42.19 ± 3.89	53.65 ± 10.86	41.90 ± 11.22
Waterfowl:						
Cackling goose (*Branta hutchinsii*)	0	0.42 ± 0.42	0	0	0	0
Greater scaup (*Aythya marila)*	0.14 ± 0.14	0	0	0	0	1.26 ± 1.26
Greater white-fronted goose (*Anser albifron*s)	3.61 ± 0.99	5.63 ± 1.57	5.94 ± 3.45	4.63 ± 2.24	5.94 ± 3.01	6.17 ± 3.36
King eider (*Somateria spectabilis*)	3.10 ± 0.66	1.25 ± 0.49	1.99 ± 0.93	1.53 ± 0.71	2.65 ± 1.71	4.05 ± 1.80
Long-tailed duck (*Clangula hyemalis*)	0.56 ± 0.32	0	0.25 ± 0.25	0	0.54 ± 0.54	0.69 ± 0.69
Northern pintail (*Anas acuta*)	0.93 ± 0.32	0.42 ± 0.28	1.98 ± 1.07	0.24 ± 0.24	0.54 ± 0.54	0
Tundra swan (*Cygnus columbianus*)	0.14 ± 0.14	0.21 ± 0.21	0	0	0	0.48 ± 0.48
Other:						
Arctic tern (*Sterna paradisaea*)	0.69 ± 0.39	0	0	0	2.17 ± 2.17	0.34 ± 0.34
Pacific loon (*Gavia pacifica*)	0.28 ± 0.28	0	0	0.42 ± 0.42	0	0.34 ± 0.34
Pomarine jaeger (*Stercorarius pomarinus*)	0.14 ± 0.14	0	0.33 ± 0.33	0	0	0
Rock ptarmigan (*Lagopus mutus*)	0	0.21 ± 0.21	0	0	0	0
Sabine’s gull (*Xema sabini*)	0.14 ± 0.14	0	0	0	0	0.48 ± 0.48
Short-eared owl (*Asio flammeus*)	0.56 ± 0.56	0	2.12 ± 2.12	0	0	0
Willow ptarmigan (*Lagopus lagopus*)	2.27 ± 0.70	0	2.78 ± 1.42	3.12 ± 1.74	0	0.34 ± 0.34
Shorebirds	49.26 ± 4.55	51.46 ± 5.83	38.29 ± 7.50	44.98 ± 4.95	69.19 ± 16.10	58.48 ± 13.05
Waterfowl	8.47 ± 1.65	7.92 ± 1.56	10.16 ± 3.55	6.39 ± 2.23	9.67 ± 4.19	12.65 ± 4.39
Other	4.07 ± 0.90	0.21 ± 0.21	5.23 ± 2.39	3.54 ± 1.75	2.17 ± 2.17	1.51 ± 1.11
All species	100.97 ± 6.36	76.67 ± 7.73	89.62 ± 10.48	95.52 ± 7.62	134.67 ± 18.08	114.54 ± 17.76

At Teshekpuk, the distribution of the shorebird nests found among the four habitat classes differed significantly from that expected from the abundance of the habitats ($\chi^2_3 = 8.30$, $p = 0.04$; Fig. 2). Densities of shorebirds tended to be lower than expected in dry and moist habitat and higher than expected in wet and emergent habitat; however, no single habitat explained a significant degree of variation.

Nest Predation, Predators, and Alternative Prey

Across years at both Teshekpuk and Prudhoe Bay, 617 of 1074 monitored nests (57.4%) hatched or fledged successfully, 336 nests (31.3%) failed, and 121 nests (11.3%) had unknown fates. Nest predation was the most important cause of nest failure (304 nests; 90.4% of failures). Other sources of nest failure included abandonment for unknown reasons ($n = 18$; 5.4%), human disturbance ($n = 10$; 3%), and caribou or muskox trampling ($n = 4$; 1.2%).

We detected 15 species of potential predators during predator surveys (Fig. 3). Glaucous gulls (*Larus hyperboreus*) and the three jaeger species (*Stercorarius pomarinus*, *S. parasiticus*, *S. longicaudus*) were the most common predators observed, together representing 89% of total detections. Counts of total potential predators were highly variable, and the average number detected per 30-minute survey at Prudhoe Bay (mean = 2.65 ± 0.75; $n = 36$) did not differ from that at Teshekpuk (mean = 2.25 ± 0.64; $n = 48$; $F_{112} = 0.03$; $p = 0.87$), although yearly differences were significant ($F_{112} = 8.04$; $p < 0.001$). However, glaucous gulls were detected more often at Prudhoe Bay (mean = 1.46 ± 0.36) than at Teshekpuk (mean = 0.61 ± 0.24; $F_{112} = 13.66$; $p < 0.001$), with little interannual variation ($F_{112} = 0.91$; $p = 0.44$).

Lemming numbers were low (average of < 0.8 individuals observed per day) at both sites in all years except 2006, when we observed moderate numbers of individuals at Prudhoe Bay (4.5 per day) and high numbers at Teshekpuk (10 per day). From 2005 to 2008, we observed progressively earlier snowmelt at each site. In 2005, the mean snowmelt completion date at both sites was 16 June, whereas in 2008 snowmelt had already occurred before our arrival on 6 June.

Modeling Analyses

The three top longspur nest survivorship models were highly competitive ($\Delta AIC_c < 2$) and included a combination

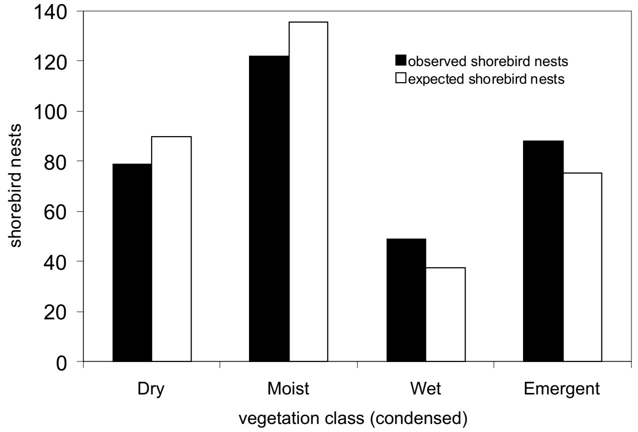

FIG. 2. Observed versus expected numbers of shorebird nests in four vegetation classes (collapsed from 11 BLM/DU earth cover classes) at the Teshekpuk study site, Alaska, in 2005–08.

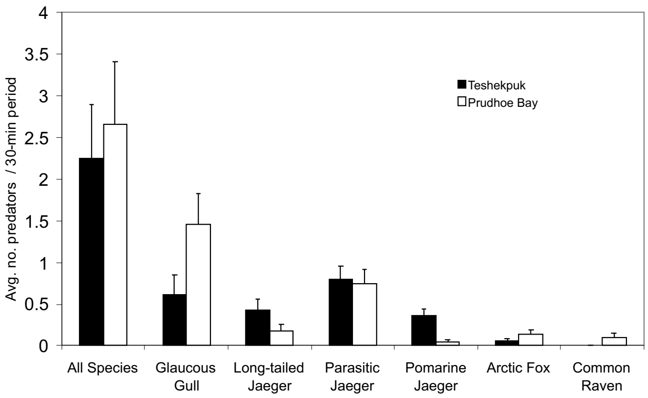

FIG. 3. Average number of potential nest predators observed per 30-minute survey within 300 m of the observer on the Teshekpuk and Prudhoe Bay study sites, Alaska, in 2005–08. The most abundant species are shown separately. The remaining species observed were arctic ground-squirrel (*Spermophilus parryii*), golden eagle (*Aquila chrysaetos*), lemmings, northern harrier (*Circus cyaneus*), peregrine falcon (*Falco peregrinus*), red fox (*Vulpes vulpes*), short-eared owl (*Asio flammeus*), snowy owl (*Bubo scandiaca*), and short-tailed weasel (*Mustela erminea*).

of site, lemming, and day of season (Table 2). The variable importance weights summed across all models suggested that site (variable weight = 0.99) was the key variable explaining most of the variation in the candidate model set (Table 2). Parameters derived from model averaging of the top models indicated that longspur nest survivorship was higher at Teshekpuk than at Prudhoe Bay, was higher in years of higher lemming abundance, and increased in a linear trend on the logit scale as the nesting season progressed (Fig. 4). The top models did not contain the nest stage variable, indicating that differences in survivorship between incubation and nestling stages were not detectable (variable weight = 0.02). The best longspur models also did not include concealment (0.03) or age of nest (0.07).

Model uncertainty for shorebird nest survivorship was high, with no single model out-competing the others (Table 3). Variable importance values suggest the most important covariates included site (1.0), year (0.99), behavior (0.98), site*behavior (0.98), behavior*age (0.70), nest age (0.70), and concealment (0.44). For uniparental shorebirds, model averaging indicated lower survivorship for nests shortly after initiation, followed by a rapid increase in survivorship; this pattern was particularly evident at Prudhoe Bay (Fig. 5A). Biparental nesting shorebirds also showed a trend of higher survivorship later in the season (Fig. 5B); however, the slope of this trend was much less steep than the one for uniparental shorebirds, and the range of survivorship was much narrower (Fig. 5B). In general, model averaging of parameters suggested high variability in survivorship between years and sites, lower survivorship of uniparental nesting shorebirds early in the nest lifetime, and higher survivorship with increasing vegetative nest concealment.

In both the shorebird and the passerine analyses, snowmelt completion date (our surrogate climate variable) and habitat type (landform) were not included in the top models. Snowmelt completion date failed to act as a replacement for year-specific survival (Analysis of deviance test; p = 0.20). Correlations between year-specific survival and snowmelt were not particularly high (Teshekpuk = 0.72; Prudhoe Bay = 0.79).

DISCUSSION

Overall nest densities at the Teshekpuk Lake site far exceeded those found at six other sites on the Arctic Coastal Plain, including the Prudhoe Bay oilfield site, for which data collection was comparable (Table 4; Rodrigues, 2002; Burgess et al., 2003; Johnson et al., 2004, 2005; S. Kendall pers. comm., 2009; Liebezeit et al., 2009). A large part of this discrepancy was due to the high Lapland longspur nest density at Teshekpuk. Very high densities of longspur nests have been documented in western Arctic Alaska near Barrow, although yearly fluctuations were significant (Custer and Pitelka, 1977). It is possible that habitat differences were responsible for the consistently higher longspur densities detected at Teshekpuk versus most of the other sites. Supporting this assertion are the similar high densities of longspur nests at the Fish Creek site, located closest to the Teshekpuk site (Table 4; Liebezeit et al., 2009). Moreover, the fact that tussocks were more prevalent in the drier upland tundra habitat at Teshekpuk compared to Prudhoe Bay (J. Liebezeit, pers. obs.) may help explain the higher nest densities for this species, since longspurs typically nest in concealed sites provided by tussocks and ridges (Rodrigues, 1994).

The high nest densities of shorebirds at Teshekpuk were similar to those at the Canning River and Prudhoe Bay sites, both of which were close to the coast and centered on major river deltas (the Canning and Sagavanirktok River deltas, respectively). Wetland and coastal habitats typically support higher densities of shorebirds (Brown et al., 2007), and shorebird nest density is generally thought to be lower farther inland on the ACP (Johnson and Herter, 1989; Cotter and Andres, 2000; but see Brown et al., 2007). The relatively high shorebird densities at the more inland Teshekpuk site may have been due to the fact that wetland habitats in the western Alaskan ACP extend farther inland

TABLE 2. The top 10 a priori models of daily survival rate (DSR) of passerine (Lapland longspur) nests found at Teshekpuk and Prudhoe Bay, Alaska, in 2005–08, with respect to key covariates.

Model	*K*[1]	AIC_c	ΔAIC_c	*w*[2]	Deviance
Site, Lemming, Day of Season	4	730.77	0	0.24	722.76
Site, Lemming	3	731.89	1.11	0.14	725.88
Site, Day of Season	3	731.95	1.18	0.14	725.94
Site, Predator, Lemming	4	732.82	2.05	0.09	724.81
Site	2	733.45	2.68	0.06	729.44
Site*Lemming	4	733.72	2.95	0.06	725.71
Site*Day of Season	4	733.81	3.04	0.05	725.80
Site, Year	5	734.63	3.85	0.03	724.61
Site, Predator*Lemming	5	734.69	3.92	0.03	724.68
Site, Age	3	734.98	4.21	0.03	728.97

[1] Number of parameters in model.

[2] Akaike weight.

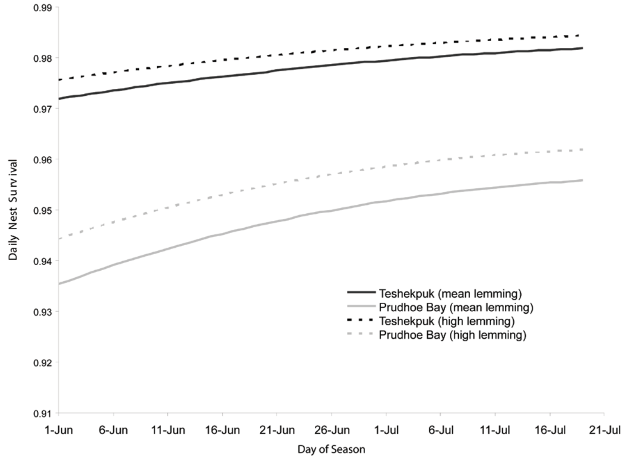

FIG. 4. Graphical representation, using model averaging, of the daily nest survival rate for the most competitive AIC_c passerine models.

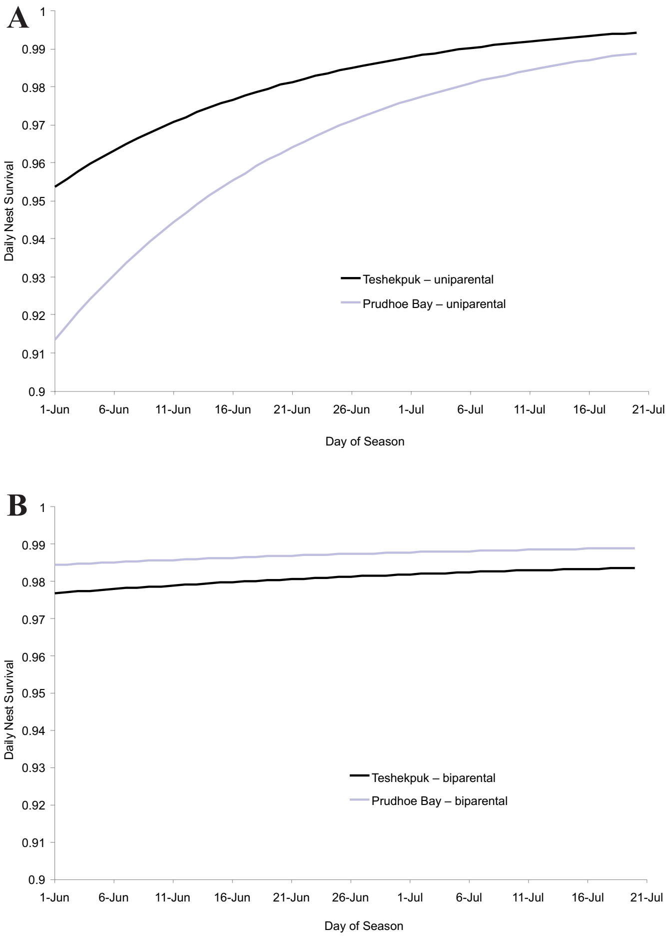

FIG. 5. Graphical representation of the most competitive shorebird nest survivorship models depicting uniparental (A) and biparental (B) nesting shorebirds using model averaging. Model averaging necessitated using "day of season" rather than "age" on the x-axis because these variables are partially confounded (age is contained within day of season).

than those at sites farther east. Although studies at other sites have examined nest densities on the ACP (Myers et al., 1980; Garner and Reynolds, 1986; Cotter and Andres, 2000; ongoing studies by the U.S. Fish and Wildlife Service at Barrow, Alaska), the different design (e.g., non-random plot choice) and data collection (e.g., nest searching effort) used in these studies make it difficult to compare their findings to the present results.

Our finding of higher long-billed dowitcher densities at Teshekpuk than at Prudhoe Bay is consistent with other studies, which found that dowitchers are not a common breeder at Prudhoe Bay (Hohenberger et al., 1994) but were more common in the western strata of the coastal plain (Johnson et al., 2007). Elsewhere, dowitchers have been found to nest most commonly in wet tundra (Takekawa and Warnock, 2000); however, they did not show a preference for wetter over drier habitats at the Teshekpuk site (see Table 1), at least at the 30 × 30 m scale of measurement used in our habitat analysis. Our finding of higher semipalmated sandpiper densities at Prudhoe Bay contradicts other studies that reported this species more frequently in the western coastal plain than farther east (Johnson and Herter, 1989; Gratto-Trevor, 1992; Johnson et al., 2007). It is possible that this difference was simply due to inherent habitat differences between the two sites.

Also consistent with previous studies is our finding at Teshekpuk that wetter nesting habitats (BLM/DU categories of wet tundra, *Carex aquatilis*, low-center polygons, and

TABLE 3. The most competitive a priori models of daily survival rate (DSR) of shorebird nests found at Teshekpuk and Prudhoe Bay, Alaska, in 2005–08, with respect to key covariates.

Model	K[1]	AIC_c	ΔAIC_c	w[2]	Deviance
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Conceal	10	1027.36	0.00	0.07	1007.33
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age	9	1027.43	0.07	0.06	1009.40
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Lemming, Predator, Predator*Lemming	12	1027.95	0.59	0.05	1003.91
Site, Behavior, Site*Behavior, Year, Day of Season, Age, Behavior*Age	10	1027.97	0.61	0.05	1007.94
Site, Behavior, Site*Behavior, Year, Day of Season, Age, Behavior*Age, Conceal	11	1028.15	0.79	0.04	1006.11
Site, Behavior, Site*Behavior, Year, Day of Season	8	1028.31	0.95	0.04	1012.29
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Lemming, Predator, Predator*Lemming, Conceal	13	1028.45	1.09	0.04	1002.40
Site, Behavior, Site*Behavior, Year, Day of Season, Age, Behavior*Age, Lemming, Predator, Predator*Lemming	13	1028.55	1.20	0.04	1002.50
Site, Behavior, Site*Behavior, Year, Day of Season, Conceal	9	1028.79	1.43	0.03	1010.77
Site, Behavior, Site*Behavior, Year, Day of Season, Lemming, Predator, Predator*Lemming	11	1028.88	1.52	0.03	1006.84
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Predator	10	1029.19	1.84	0.03	1009.17
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Predator, Conceal	11	1029.20	1.84	0.03	1007.16
Site, Behavior, Site*Behavior, Year, Day of Season, Age, Behavior*Age, Lemming, Predator, Predator*Lemming, Conceal	14	1029.27	1.92	0.02	1001.21
Site, Behavior, Site*Behavior, Year, Age, Behavior*Age, Lemming, Conceal	11	1029.36	2.01	0.02	1007.33

[1] Number of parameters in model.

[2] Akaike weight.

TABLE 4. Average annual nest densities (nests/km^2) for all birds (overall) and by species group at Teshekpuk Lake and Prudhoe Bay oilfield compared with those at five other sites on the Arctic Coastal Plain sampled under a standardized protocol as part of a previous study (Liebezeit et al., 2009).[1] Sites are listed from west to east (from top to bottom). Distance (km) from site to coastline is also shown.

			Nest density (nests/km^2)				
Study Site[2]	Data from years	Distance from coastline (km)	Overall	Shorebird	Passerine	Waterfowl	Other[3]
Teshekpuk	2005–08	34	101.1	49.3	39.2	8.5	4.1
Fish Creek	2002–04	18	81.1	42.4	32.1	4.7	1.9
Kuparuk	2002–04	23	58.9	33.4	18.8	6.2	0.5
Prudhoe	2005–08	5	76.7	51.5	17.1	7.9	0.2
Thomson	2002–03	3	59.9	32.6	25.4	1.7	0.2
Canning	2002–06	4	78.8	51.8	23.1	2.2	1.7
Jago	2004	30	23.2	21.4	0.9	0.9	0

[1] See Liebezeit et al. (2009) for detailed description of study sites, including plot site selection, locations, years sampled, and number of plots sampled per year at each site.

[2] The Teshekpuk and Prudhoe Bay sites include data reported in this study (see Table 1). The data for all other sites were collected from personal communications and unpublished reports (See Discussion).

[3] "Other" category includes ptarmigans, loons, jaegers, gulls, raptors, owls, and Arctic terns.

non-patterned flooded tundra) supported higher densities of breeding shorebirds than drier nesting habitats (BLM/DU tussock tundra, dwarf shrub, barren ground, sedge grass meadow, and moss/lichen). Cotter and Andres (2000) found that drained lake basin habitat (similar to our wet and emergent categories) supported the highest densities of shorebirds at an inland site in the NPR-A. Likewise, Derksen et al. (1981) reported that breeding birds at a number of sites in the NPR-A were especially dependent on wetlands with emergent hydrophytes. Brown et al. (2007) found that shorebird species richness and density were highest in riparian and wetland habitats along the coast in the Arctic National Wildlife Refuge. Like Cotter and Andres (2000), we found wet habitats to be particularly important for nesting phalaropes, while American golden-plovers (*Pluvialis dominica*) and dunlin (*Calidris alpina*) nested more frequently in drier habitats. However, in contrast to that study, we found that the two most common shorebirds, semipalmated and pectoral sandpipers, did not show a preference for nesting in wetter habitats and nested in similar densities across the habitat types at the Teshekpuk site.

Our modeling results for longspurs indicated higher survivorship at Teshekpuk than at Prudhoe Bay. While we cannot say with certainty that this finding is related to negative impacts from oilfield development, it does agree with findings from Liebezeit et al. (2009) that documented lower longspur survivorship closer to oilfield infrastructure. In addition, at least one potential nest predator, the glaucous gull, was more numerous at Prudhoe Bay, although most evidence suggests that the arctic fox was the more important predator at this site (Liebezeit and Zack, 2008). Lemming abundance was included as a variable in the top models, with years of higher lemming numbers corresponding to lower predation rates. This pattern generally agrees with the prey-switching hypothesis (Summers, 1986; Summers and Underhill, 1987; Bêty et al., 2001), which states that in years of high lemming abundance, predators will prey less frequently on nest contents. In 2006, we detected a noticeable increase in lemming numbers at both sites and observed, for the only time during the study, more pomarine jaegers active throughout the breeding season, which included successful breeding attempts (J. Liebezeit, pers. obs.). Pomarine jaegers are a lemming obligate predator (Wiley and Lee, 2000); thus, these observations suggest a real shift in the response of predators to lemming abundance. Increasing longspur survivorship as the breeding season progressed was another important variable in the top models, particularly at Prudhoe Bay, but there are no other comparable studies of passerines in Arctic North America. In the Great Plains, in contrast to our findings, Grant et al. (2005) documented decreasing survival during the season for clay-colored sparrows (*Spizella pallida*) and vesper sparrows (*Pooecetes gramineus*) in North Dakota; Winter (1999) found no relationship between date and nest success for dickcissel (*Spiza americana*) and Henslow's sparrow (*Ammodramus henslowii*) in Missouri; and Zimmerman (1984) found predation highest in the middle of the season for dickcissel in Kansas. We may have observed higher predation rates for longspurs at the start of the breeding season because predators were more abundant at both sites between 1 and 20 June (J. Liebezeit, unpubl. data), exerting greater predation pressure. Early season nests were also less well hidden (because of either poor placement or immature vegetation) and thus were more susceptible to predation. We were surprised that vegetative concealment had relatively low explanatory power in our models of longspur nest survivorship, which contradicted findings of Liebezeit et al. (2009) from other sites in the ACP. However, higher predation rates on earlier, poorly concealed nests in our study may have been explained better by day of season, and concealment may have been relatively unimportant for nests later on.

The high variability between both years and sites that we documented for shorebird nest survivorship is consistent with other studies in the Arctic (Summers and Underhill, 1987), including those on the Alaskan ACP (Troy, 2000; Liebezeit et al., 2009). The dissimilarity between uniparental and biparental shorebird nesters in survivorship trends, particularly with respect to nest age, was not surprising. Nest attendance is typically lower at uniparental nests (Norton, 1972; Cartar and Montgomerie, 1985), and lower nest attendance, especially during early incubation, can lead to higher rates of nest predation in uniparental shorebirds (Smith, 2009). However, it is the adult activity associated with nest attendance that may be the real source of predation risk (Cresswell et al., 2003). In support of this theory, Smith (2009) documented a significant positive relationship between more numerous incubation recesses, restless movements of nesting uniparental shorebirds, and increased nest failure. Unlike Smith (2009), however, we did not find increased biparental survivorship as nest age increased. The frequency of nest attendance bouts, particularly for uniparental shorebirds, may be highly influenced by temperature and other environmental factors (Tulp and Schekkerman, 2006), but we did not examine such effects in this study.

Interestingly, we documented lower nest survivorship for uniparental nesters at Prudhoe Bay than at Teshekpuk in three of four years. It is possible that the predators reportedly attracted to human infrastructure (Ballard et al., 2000; NRC, 2003) increase predation rates on this group of shorebirds. In support of this idea, Liebezeit et al. (2009) found evidence that phalaropes (a uniparental nester) suffered greater predation near human infrastructure in the Prudhoe Bay region, although pectoral sandpipers, another uniparental shorebird, showed no effect. Although predators were included in some of the top shorebird models, the variable importance weight was rather low (0.46), suggesting that predator abundance was not a very important influence on nest survivorship; thus, the assumption that predators attracted to infrastructure increase pressure on uniparental nesters is at best speculative. We did detect high interannual variation in overall predator numbers, which may be another reason why predators did not have higher variable importance. Our finding that shorebird nests with more overhead vegetation concealment were less likely to be depredated makes biological sense although other shorebird studies have not always documented this trend (Colwell, 1992; Liebezeit et al., 2009).

Our nest density and survivorship results should be considered potentially interactive (Wilson et al., 2007). Specifically, as rates of nest failure increase, the probability that a researcher will find a given nest decreases, and thus predation rate and nest density may be inversely correlated. The higher survivorship and apparent nest density of longspurs at Teshekpuk could be related. In contrast, the lower nest survivorship of shorebirds at Prudhoe Bay in some years may have led to an underestimation of nest density. However, we believe that our intensity of nest searching and our standardization of methods across sites minimized this potential source of bias.

Our study provides additional evidence that the Teshekpuk region is an important area for nesting birds on the ACP. Because of its importance as a molting area for waterfowl (King and Hodges, 1979) and as a calving ground for the Teshekpuk Lake caribou herd (Carroll et al., 2005), we recommend that the region of our study and the region of 10-year development deferral be granted permanent protection. If future energy development expands into the Teshekpuk region, we recommend that wetter tundra habitats be avoided for placement of infrastructure because of their importance as nesting habitat for shorebirds. However, shorebird protection should be assessed at the species level, and particular management actions may override this general recommendation. Because many nesting birds (particularly longspurs and uniparental shorebirds) are prone to nest predation during the early nesting period in this region, we also suggest that future management efforts limit human disturbance to these species during this phase of the nesting season. Because of planned energy extraction activities, we recommend more intensive studies on the factors influencing nest survivorship and its variability throughout the NPR-A. As a first step, studies similar to this one are needed in the eastern planning area of the NPR-A so that a broader assessment for the entire region can be made.

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