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Author(s): J. R. Liebezeit, S. J. Kendall, S. Brown, C. B. Johnson, P. Martin, T. L. McDonald, D. C. Payer, C. L. Rea, A. Streever, A. M. Wildman and S. Zack

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Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska

J. R. LIEBEZEIT,^{1,9} S. J. KENDALL,² S. BROWN,³ C. B. JOHNSON,⁴ P. MARTIN,⁵ T. L. McDONALD,⁶ D. C. PAYER,² C. L. REA,⁷ B. STREEVER,⁸ A. M. WILDMAN,⁴ AND S. ZACK¹

¹Wildlife Conservation Society, Pacific West Office, 718 SW Alder St., Suite 210, Portland, Oregon 97205 USA

²U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge, 101 12th Ave, Rm. 236, Fairbanks, Alaska 99701 USA

³Manomet Center for Conservation Sciences, P.O. Box 1770, Manomet, Massachusetts 02345 USA

⁴ABR, Inc., Environmental Research and Services, P.O. Box 80410, Fairbanks, Alaska 99708 USA

⁵U.S. Fish and Wildlife Service, Field Office, 101 12th Ave., Rm. 110, Fairbanks, Alaska 99701 USA

⁶West, Inc., 2003 Central Avenue, Cheyenne, Wyoming 82001 USA

⁷ConocoPhillips Alaska, Inc., P.O. Box 100360, ATO 1902, Anchorage, Alaska 99510 USA

⁸BP Exploration (Alaska), Inc., P.O. Box 196612, Anchorage, Alaska 99519 USA

Abstract. Nest predation may influence population dynamics of birds on the Arctic Coastal Plain (ACP) of Alaska, USA. Anthropogenic development on the ACP is increasing, which may attract nest predators by providing artificial sources of food, perches, den sites, and nest sites. Enhanced populations or concentrations of human-subsidized predators may reduce nest survival for tundra-nesting birds. In this study, we tested the hypothesis that nest survival decreases in proximity to human infrastructure. We monitored 1257 nests of 13 shorebird species and 619 nests of four passerine species at seven sites on the ACP from 2002 to 2005. Study sites were chosen to represent a range of distances to infrastructure from 100 m to 80 km. We used Cox proportional hazards regression models to evaluate the effects of background (i.e., natural) factors and infrastructure on nest survival. We documented high spatial and temporal variability in nest survival, and site and year were both included in the best background model. We did not detect an effect of human infrastructure on nest survival for shorebirds as a group. In contrast, we found evidence that risk of predation for passerine nests increased within 5 km of infrastructure. This finding provides quantitative evidence of a relationship between infrastructure and nest survival for breeding passerines on the ACP. A posteriori finer-scale analyses (within oil field sites and individual species) suggested that Red and Red-necked Phalaropes combined (*Phalaropus fulicarius*, *P. lobatus*) had lower productivity closer to infrastructure and in areas with higher abundance of subsidized predators. However, we did not detect such a relationship between infrastructure and nest survival for Semipalmated and Pectoral Sandpipers (*Calidris pusilla*, *C. melanotos*), the two most abundant shorebirds. High variability in environmental conditions, nest survival, and predator numbers between sites and years may have contributed to these inconsistent results. We recommend targeted management actions to minimize anthropogenic effects and suggest new research needed on this issue as expanding development is planned for the ACP of Alaska. In particular, we recommend research on demography of key predators and their importance with respect to nest survival, and experimental studies that better address challenges posed by high natural variability.

Key words: Alaska, USA; Arctic Coastal Plain; Cox proportional hazards model; development; infrastructure; nest predator; nest survival; passerines; shorebirds; subsidized predators.

INTRODUCTION

Predation can regulate prey populations and influence species composition (Crooks and Soulé 1999). Nest predation, the consumption of eggs or young at active nests, can be the primary factor regulating population growth for some species (George 1987). Anthropogenic development may attract or augment certain nest predators, increasing local nest predation (Haskell et

al. 2001, Marzluff 2001). These “subsidized predators” (Soulé et al. 1988) are increasing in our urbanizing world (Marzluff 2001) and, most recently, these increases are occurring in once-remote places including the Arctic (Restani et al. 2001, NAS 2003).

The avifauna of the Arctic Coastal Plain (ACP) is dominated by shorebirds, in respect to both diversity of breeding species and aggregate abundance (Pitelka 1974, U.S. Fish and Wildlife 2005). In addition to shorebirds, the ACP is an important breeding area for waterfowl (Derksen et al. 1981, Johnson 2000), other waterbird species, and passerines. Although millions of shorebirds breed on the ACP, many populations are in decline

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⁹ E-mail: jliebezeit@wcs.org

(Howe et al. 1989, Morrison et al. 2006, Bart et al. 2007). Although declines have been attributed to habitat loss and degradation in wintering and stopover areas to the south (Lancot and Laredo 1994), nest predation is also believed to be a key factor influencing population growth for some species on the ACP (Troy 2000, NAS 2003).

Much of the 98 200-km² ACP of Alaska is still undeveloped, although the demand for oil and natural gas will likely spur more development. Currently, relative to the entire ACP, the physical footprint of oil infrastructure is small (as of 2001, 70.23 km²; NAS 2003) even when land fragmented by the network of infrastructure is included (~2600 km²; NAS 2003). Direct effects of habitat loss and fragmentation, therefore, may not be major factors affecting bird populations in this region. However, human activity can create disturbances to wildlife, including birds, beyond the physical footprint of infrastructure (Murphy and Anderson 1993, Monda et al. 1994, Johnson et al. 2003). In particular, the influence of subsidized nest predators may extend well beyond infrastructure because the key predators involved are highly mobile (Eberhardt et al. 1982, Poole et al. 2003). If predator distribution and abundance is sufficiently altered by human activity, productivity of tundra birds could be affected at a regional scale.

Human development can lead to increases in subsidized predator populations by altering predator distribution, productivity, and survival (Marzluff et al. 2001, Kristan and Boarman 2007). On the ACP, predators are attracted to areas of human activity by the availability of anthropogenic food (e.g., at landfills and dumpsters) and increased availability of artificial breeding and perch sites (e.g., buildings, bridges, and culverts; Day 1998). In particular, arctic foxes (*Vulpes lagopus*; see Plate 1), Common Ravens (*Corvus corax*), and Glaucous Gulls (*Larus hyperboreus*) can benefit from human presence, and high densities of these species may adversely influence the productivity of prey species. Burgess and Banyas (1993) reported a higher density of fox dens in the Prudhoe Bay region compared to adjacent areas outside of the oil fields, although baseline data on fox populations prior to development are lacking. Eberhardt et al. (1982) found that arctic foxes in areas with oil development were more sedentary than foxes in undeveloped areas and foraged primarily in areas of high human activity. Raven breeding range has expanded into human-altered regions of the ACP, probably due to increased availability of nest sites (Day 1998). In addition, Glaucous Gulls are attracted to human food wastes on the ACP (Murphy et al. 1987), although Noel et al. (2006) found no evidence that Glaucous Gull numbers in Beaufort Sea lagoons were influenced by the presence of humans. In recent years, improved waste management practices within ACP oil fields and villages have reduced the availability of artificial food. However, access to artificial food persists, albeit at lower levels, and artificial breeding and perching sites remain in place.

Despite evidence indicating increased nest predator concentrations in areas of human development on the ACP, few studies have attempted to evaluate effects on the nesting success of prey species. Studying anthropogenic effects on nest success is challenging because the relationship may be influenced by spatial and temporal variation in weather conditions, natural predator-prey population cycles, habitat differences, and other environmental factors.

We measured spatial and temporal patterns of nest survival to evaluate effects of human development on nest predation for tundra-nesting birds. Our objectives were to evaluate nest survival at a regional scale, at sites across the ACP exposed to different levels of infrastructure, and at a local scale (i.e., within the oil fields) where human development is most intensive. We hypothesized that nest survival of tundra birds is inversely related to distance to infrastructure. Finally, we have recommended management actions and new research that will further our knowledge of this issue and help to reduce the impacts of nest predators on nesting birds in areas of human activity on the ACP of Alaska.

METHODS

Study sites and plot delineation

We collected data during June and July 2002–2005 at seven sites spanning 390 km on the Arctic Coastal Plain (ACP) of Alaska (Fig. 1). Not all sites were sampled in all years (Table 1). Study sites ranged in size from ~766 km² (Prudhoe Bay) to 24 km² (Jago). The Prudhoe Bay and Kuparuk study sites were located within oil fields, and all plots at these sites were <5 km from human infrastructure (referred to as “infrastructure” hereafter). Satellite oil fields including Alpine, Northstar, and Endicott lie between study sites. Oil field infrastructure includes gravel roads, airstrips, pipelines, oil production and processing facilities, power stations and lines, gravel mines, and living quarters. Landfills operated by the North Slope Borough are located in the Prudhoe Bay oil field and in the villages of Nuiqsut and Kaktovik. The industrial town of Deadhorse borders the Prudhoe Bay oil field. Infrastructure is typically built on a ~1.5-m gravel layer to prevent thawing of the underlying permafrost. The Prudhoe Bay and Kuparuk sites contain gravel footprints covering 27.9 and 7.5 km², respectively. As of 2001, this includes 808 km of roads in Prudhoe Bay and 221 km of roads in Kuparuk (NAS 2003). The nearest Native villages to the study area (Nuiqsut and Kaktovik) also contain substantial amounts of infrastructure, but lie outside the boundaries of the individual study sites (Fig. 1).

All other study sites, with the exception of Prudhoe Bay and Kuparuk, were in remote areas with either no infrastructure (i.e., Teshekpuk, Canning, Jago, Fish Creek) or minimal infrastructure (i.e., Thomson had three abandoned gravel pads). Median distance of nests to infrastructure classified as having a high value for nesting or perching sites was 1.0 km for Kuparuk, 1.3

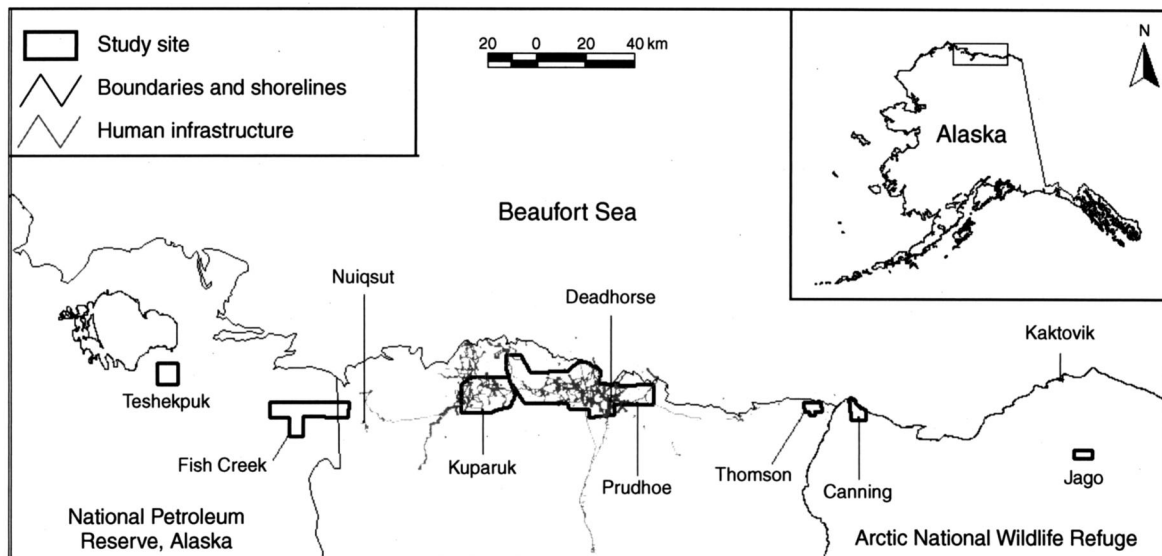


FIG. 1. Study sites sampled from 2002 to 2005 on the Arctic Coastal Plain of Alaska, USA.

km for Prudhoe Bay, 22.7 km for Thomson, 25.6 km for Fish Creek, 29.9 km for Jago, 40.5 km for Canning, and 80.8 km for Teshekpuk.

Habitat at each site 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 or low shrubs, aquatic marshes dominated by sedges (*Carex* spp.) or pendant grass (*Arctophila fulva*), and lakes and ponds. The topography was generally flat, with elevations typically <50 m. Microtopographic features included high- and low-

centered polygons, strangmoor/disjunct polygon ridges, hummocks, tussocks, and frost boils (Walker et al. 1980). [A strangmoor (or "string bog") is a bog consisting of slightly elevated ridges and islands with woody or herbaceous plants, alternating with flat, wet sedge mat areas. String bogs occur on slightly sloping surfaces, with ridges at right angles to the direction of water flow.] Mean temperature for June and July during the study was 5.5°C at the Deadhorse Airport (Weather Underground 2008).

We randomly or systematically established 5–24 plots in each study site (Table 1). Most plots were 100 × 1000

TABLE 1. Number of plots and years sampled at each study site and number of shorebird and passerine nests monitored at study sites on the Arctic Coastal Plain, Alaska, 2002–2005.

Study area	No. plots sampled†	Number of nests, by year				Total no. nests
		2002	2003	2004	2005	
Shorebirds						
Teshekpuk	16	67	67
Fish Creek	24	115	91	91	...	297
Kuparuk	24	80	70	78	...	228
Prudhoe	12	...	52	83	63	198
Thomson	24	55	53	108
Canning	20	49	94	93	102	338
Jago	5	21	...	21
Total	...	299	360	366	232	1257
Passerines						
Teshekpuk	16	51	51
Fish Creek	24	53	78	65	...	196
Kuparuk	24	46	52	32	...	130
Prudhoe	12	...	12	19	14	45
Thomson	24	43	41	84
Canning	20	9	34	36	33	112
Jago	5	1	...	1
Total	...	151	217	153	98	619

Notes: Study areas are Fish and Judy creeks, Kuparuk River, Prudhoe Bay, Canning River Delta, Point Thomson, Teshekpuk, and Jago River. Ellipses indicate that no data were available.

† There were 24 plots sampled at Prudhoe in 2004, 20 plots sampled at Thomson in 2003, and nine plots sampled at Canning in 2002.

m or 200×500 m (10 ha), although plots at Jago and four at Canning in 2003 were 400×400 m (16 ha). Plots were subdivided into $40 \times 50 \times 50$ m subplots. Each subplot was further divided into 25×25 m quadrats. At the oil field sites, plots were located >100 m from roads and pads to reduce potential effects of disturbance and habitat modification (Troy 2000).

Field methods

We conducted four nest searches on each plot per year during 6 June to 8 July, following methodology adapted from Troy (1993). Nest locations for all species were recorded with a global positioning system (GPS) and were marked by a wooden tongue depressor placed within 5 m of the nest. Searches were conducted from approximately 07:30 to 20:00 hours Alaska Daylight Time. We monitored active nests every 3–7 days until their fate was determined.

We recorded four outcomes for nest fate: success, predation, non-predation failure, or unknown. We estimated nest fate as “successful” or “predated” based on previously established criteria (Troy 1993, Mabee 1997, Martin et al. 1997). A nest was considered successful if at least one chick hatched (in the case of precocial nesters) or fledged (in the case of altricial nesters). Causes of nest failure, other than predation, included inclement weather, abandonment, trampling by caribou or musk ox, and human disturbance. These events were infrequent (1.6%; 30 of 1876 nests), so we combined them in a “non-predation failure” category. Nest fate was classified as “unknown” if we had no clear evidence or had contradictory evidence at the nest site.

Each nest had a “nest lifetime,” defined as the period from initiation date (when the first egg was laid) until the 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 nestling development (passerines only; Hussell and Montgomerie 2002); or (4) egg flotation (Mabee et al. 2006, Liebezeit et al. 2007). If the fate of a nest was observed, this was considered the termination date. If a nest terminated between two final visits, termination date was assigned as the midpoint between these visits. If nest fate was not known, termination date was assigned as the last day the nest was known active (Manolis et al. 2000). We reduced researcher effects on nest predation by using methods described by Martin and Geupel (1993).

We conducted at least three predator surveys on each plot annually. Each survey consisted of three 10-min point counts separated by ≥ 200 m on the plot centerline (Ralph et al. 1993). We recorded all visual and aural detections of 20 documented or suspected potential nest predators (Table 2; see Poole et al. 2003). Predators observed both within and outside plots (≤ 300 m from

the plot edge) were tallied. We classified nest predators as potentially subsidized (referred to as “subsidized” hereafter) or nonsubsidized, depending on whether the species is known to benefit from human food, waste, or structures (Table 2; see NAS 2003).

We measured a set of “natural” environmental covariates to use in models of background failure rates. “Natural” covariates that we considered most likely to affect nest survival included dominant landform, nest concealment, lemming abundance, and snow cover (Table 2). Dominant landform was recorded for each quadrat using the classification of Walker et al. (1980). We used an ocular estimate of vegetative cover at each nest to estimate overhead concealment (James and Shugart 1970). We indexed lemming abundance because availability of this alternate prey may strongly influence nest predation rates (Summers and Underhill 1987). Lemming abundance was estimated from incidental observations of individuals on study plots per unit time. Sites were classified each year as having “low,” “medium,” or “high” lemmings (i.e., ≤ 0.1 , >0.1 and <0.25 , or ≥ 0.25 individuals observed per 30 min). We estimated snow cover to the nearest 10% within each subplot at the start of each season.

Analysis

We classified infrastructure into five categories based on potential to provide nest predators with food or sites for perching, nesting, or denning (Table 3): distance to sites with low, medium, and high potential for food availability, and distance to infrastructure with low and high potential to provide den, nest, or perch sites to predators (a combination of vertical height and structural complexity, hereafter termed low- or high-value structures; Table 3). Correlation among infrastructure covariates was accounted for in model fitting. Some types of infrastructure (e.g., active drill rigs) were not stationary. When infrastructure was moved, affected covariates were recalculated.

We measured a second class of infrastructure covariates by calculating the density of the underlying gravel footprint within circular buffers centered on each nest. We used 3-km (TOE3) and 16-km (TOE16) radii for buffers, because these approximated mean home range sizes and movement distances of subsidized predators (Eberhardt et al. 1982, Poole et al. 2003). We used ArcView (version 3.3; Environmental Systems Research Institute, Redlands, California, USA) to measure the proximity of nests to village or oil field structures, and to calculate the density of infrastructure within the defined buffers (Table 2).

We used program CONTRAST (Sauer and Williams 1989) to compare incubation vs. nestling-stage daily survival rates of Lapland Longspurs for all site-year comparisons. We used a one-way analysis of variance with a Bonferroni correction (Krebs 1999) to adjust α levels for a posteriori comparisons of our index of predator activity between sites and years. All descriptive

TABLE 2. Covariates considered during survival model estimation.

Covariate†	Covariate level	Description (number of factor levels)
Natural covariates		
YEAR	site	continuous year effect
YR.FACTOR	site	discrete year effect (5)
SITE	site	study sites (7)
LAND.FORM‡	nest	land form types at each nest (7)
CONCEALMENT	nest	vegetative concealment above each nest
PLOVER	nest	plover nest or non-plover nest
SITE.YEAR	site	combined study site by year (17)
PRED.NON.SUBSIDIZED§	plot	average no. predators that do not use human infrastructure
LN.PRED.NON.SUBSIDIZED¶	plot	LN (PRED.NONSUBSIDIZED + C2)
SNOW COVER	plot	percentage snow cover at start of breeding season
LEMMING ABUNDANCE	site	lemming abundance (3): low, medium, high
Human infrastructure covariates		
HIGHFOOD, MEDFOOD, LOWFOOD	nest	distance (km) of nests to nearest human food source, measured to each of three levels (see Table 3)
LN.HIGHFOOD, LN.MEDFOOD, LN.LOWFOOD	nest	LN HIGHFOOD, LN MEDFOOD, LN LOWFOOD
LOWSTRUCT, HIGHSTRUCT	nest	distance (km) of nests to nearest structural feature, measured to each of two levels of structure (see Table 3)
LN.LOWSTRUCT, LN.HIGHSTRUCT	nest	LN LOWSTRUCT, LN HIGHSTRUCT
TOE3, TOE16	plot	gravel footprint area (ha) within 3 km and 16 km of plots, respectively (see Table 3)
LN.TOE3, LN.TOE16¶	plot	LN (TOE3 + C1), LN (TOE 16 + C1)
Subsidized nest predator covariates#		
PRED.SUBSIDIZED	plot	average number of predators that potentially use or are associated with human development
LN.PRED. SUBSIDIZED	plot	LN (PRED.SUBSIDIZED + C2)

† SNOW COVER and LEMMING ABUNDANCE were not included in the modeling analyses (see *Results*).

‡ UNIT0, non-patterned ground; UNIT1, high-centered polygons, center-trough relief > 0.5 m; UNIT2, high-centered polygons, center-trough relief < 0.5 m; UNIT3, low-centered polygons, rim-center relief > 0.5 m; UNIT4, low-centered polygons, rim-center relief < 0.5 m; UNIT5, mixed high- and low-centered polygons; UNIT7, strangmoor and/or disjunct polygon rims; OTHER, frost-boil tundra + vegetated dune + hummocky terrain + open water + upland bluff + reticulate-patterned ground.

§ The most common nonsubsidized predators include Parasitic Jaeger (*Stercorarius parasiticus*), Long-tailed Jaeger (*Stercorarius longicaudus*), Arctic Tern (*Sterna paradisaea*), Sabine's Gull (*Xema sabini*), Snowy Owl (*Nyctea scandiaca*), arctic ground squirrel (*Spermophilus parryii*), and short-tailed weasel (*Mustela erminea*).

¶ C1 and C2 indicate that the smallest positive covariate/2 was added to all values to ensure valid logarithms (C1 = 1.813814, C2 = 0.03267974).

Subsidized predators include Glaucous Gull (*Larus hyperboreus*), Common Raven (*Corvus corax*), arctic fox (*Vulpes lagopus*), red fox (*Vulpes vulpes*), and brown bear (*Ursus arctos*).

analyses were conducted using SYSTAT (version 11.0; Systat Software, Richmond, California, USA). Results were reported as mean \pm SE, and were considered significant if $P < 0.05$.

We used a two-step model selection procedure to address two basic questions: (1) "How much of the variation observed is due to natural or background variability?" and (2) "When background variability is controlled, is proximity to infrastructure and (or) index of subsidized nest predators related to nest survival?" During step 1, we fitted a priori background survival models that contained natural covariates only (Table 2). Models were sorted by the P value associated with each model's overall score test, and the best background model was selected as the model with the smallest score P value. We could not use Akaike's information criterion (AIC; Burnham and Anderson 2002) to rank models because of differences in sample size between models. However, for models with the same sample size, AIC resulted in the same ordering as sorting by the score P value. During step 2, we added infrastructure and subsidized predator covariates (Table 2) individually to

the best background model to evaluate whether they explained additional variation in survival. In all analyses, we only included nests with known initiation dates found within plot boundaries during scheduled nest searches.

We used a staggered-entry Cox proportional hazards model to evaluate time to predation as a function of our covariates (Cox 1972, Cox and Oakes 1984, Nur et al. 2004). The model potentially contained frailty effects (Clayton and Cuzick 1985, Klein and Moeschberger 1997), time-varying covariate effects, and adjustments for autocorrelation. Events of interest were nest predations. Nest fates other than predation (i.e., success, unknown, or non-predation failure) were considered "censor" events. The proportional hazards model allowed time-varying covariates and staggered entry by using the counting process formulation (Andersen and Gill 1982) of a standard proportional hazards model. The Cox proportional hazards model accommodated time-varying covariates by subdividing nest lifetimes into intervals during which covariates were constant and relating length of the interval to values of covariates

TABLE 3. Human infrastructure types on the Arctic Coastal Plain of Alaska categorized by their potential to provide food and structures that may benefit nest predators.

Infrastructure type	Food potential			Structural value†	
	Low	Med	High	Low	High
Group I					
Production (oil well) pads with drill rig camps			X		X
Alyeska Pump stations #1 and #2			X		X
Operations camp facilities			X		X
Villages (Kaktovik, Nuiqsut, and Deadhorse)			X		X
North Slope Borough Landfill			X	X	
Group II					
Processing facilities, gathering centers, and flow stations		X			X
Warehouse facilities with daily use but no residency		X			X
Group III					
Production (oil well) pads w/o drill rig camps, injection pads	X				X
Active Roads, pullouts, caribou crossings (joined with roads)	X			X	
Docks (West Dock)	X				X
Docks (East Dock)	X			X	
Airport runways				X	
Support pads (power stations, staging areas, warehouses)		X			X
Active gravel mines with elevated piles	X			X	
Bridges	X				X
Group IV					
Inactive Distant Early Warning (DEW) line site					X
Abandoned pads and roads				X	
Inactive gravel mines with elevated piles				X	
Group V					
Pipelines				X	
Power poles, light poles, posts, dish antennae, stacks				X	
Towers					X
Exposed well heads				X	
Unused drill rigs					X
Group VI: Buffer covariates					
3 km, the total area of human-placed gravel within a 3 km radius of the plot center					
16 km, the total area of human-placed gravel within a 16 km radius of the plot center					

Notes: Group I: sites with high availability of food and nesting structures, including residences, dining halls or food services, and tall buildings (>20 ft) or towers that have been used by nesting ravens; they have the highest numbers and activity level of people and traffic, are occupied 24 hours a day, and are used daily for food waste. Group II: sites with moderate levels of food availability, moderate to high levels of human activity, and high availability of nesting structures; they are used 24 hours a day by multiple people and vehicles but have no food service or residences. Group III: sites that may be used daily or less, are not occupied 24 hours a day, lack food service or dumpsters used for food waste, and usually have ≤ 1 vehicle parked on a daily basis; the only food source would be that transported in vehicles. Group IV: Unused or abandoned pads with no human activity, but with structural components that may be used as den, nest, or perch sites. Group V: structures that generally are not on gravel pads but may be used for perching or, in some cases, nesting; rated high if nests occur annually, low if used for perching but rarely for nesting. Group VI: human-placed gravel on the North Slope acts as a surrogate for all human infrastructure since the footprint of human-placed gravel is directly correlated with infrastructure; almost all facilities are built on a 1–2 m base of gravel to prevent permafrost melt; unlike the distance covariates, these buffer covariates take into account density of human disturbance.

† Rated “high” if infrastructure type is known to be used for nesting or denning; rated “low” if known use is only for perching.

during the interval. Observed data were subdivided into interval-event triplets $(a_{ijk}, b_{ijk}, \delta_{ijk})$, where a_{ijk} and b_{ijk} were the beginning and ending dates of interval k for nest j on study site i , and δ_{ijk} was an indicator function that equaled 1 if the nest was predated during interval k or 0 if the nest either survived or was censored during interval k . Interval start and end dates were computed relative to the earliest observed nest initiation each year.

Frailty effects included in the model were random effects associated with all nests on a plot, and allowed random fluctuations in the baseline hazard for each plot.

The frailty effect associated with plot p_i was assumed to be an independent random deviate from a Gamma distribution with mean 1 and unknown variance σ^2 .

Cox proportional hazard coefficients and random effect variance (σ^2) were estimated by the method of maximum penalized likelihood (Gray 1992, Therneau et al. 2003) using the R statistical package (version 2.4.1) and its *coxph* and *frailty* functions (*available online*).¹⁰ The Efron approximation was used for tied survival

¹⁰ (<http://www.r-project.org>)

times. The utility of including frailty effects was assessed by both a Wald chi-square test and by inspecting results when frailties were removed from the model. If the Wald chi-square test indicated nonsignificance and coefficients of the fixed effects changed little when frailty effects were removed, we reverted to a regular proportional hazards model by excluding the frailty effects. In addition to testing for the presence of plot frailties, we tested for the presence of subplot frailties in the same way by adding a random effect due to subplot membership. If either frailty effect was significant, the most significant effect was included in the model.

In part, inclusion of frailty effects in the Cox model would have mitigated natural spatial dependencies in nest lifetimes had such dependencies been present. We acknowledge, however, that complicated spatial and temporal dependencies potentially manifesting themselves in other ways may have been present. For this reason we chose to compute final coefficient standard errors and confidence intervals using block bootstrapping (Lahiri 2003), whereby whole plots were randomly resampled with replacement. We considered 95% block bootstrap confidence intervals for infrastructure coefficients that did not contain 0 to be significant predictors of survival, over and above the best set of natural predictors.

The proportional hazards assumption inherent in the Cox model was tested following methods of Grambsch and Therneau (1994) by calculating correlation between scaled Schoenfeld residuals and survival time in models that contained significant infrastructure covariates.

Following the a priori analyses, we conducted a posteriori exploratory analyses using the same modeling approach. We conducted these additional analyses because we hypothesized that pooling species into two groups (i.e., shorebirds and passerines) may have obscured relationships operating at the species level. Therefore, we explored the potential infrastructure and predator effects for the most abundant shorebird species (Semipalmated Sandpiper (*Calidris pusilla*), Pectoral Sandpiper (*C. melanotos*), and phalaropes [Red-necked (*Phalaropus lobatus*) and Red Phalarope (*P. fulicarius*) combined]). We also hypothesized that if effects were expressed only at a fine scale in close proximity to infrastructure, analyzing data at a broad scale across all study sites might mask important relationships. Therefore, we modeled the effect of infrastructure and subsidized predators on species groups separately at each oil field site.

RESULTS

Descriptive analysis results

We monitored 1941 nests, of which 1257 nests representing 13 shorebird species and 619 nests of four passerine species were included in analyses (Tables 1 and 4). The remaining nests were excluded because they were outside plots, were discovered incidentally, belonged to species or groups with inadequate sample sizes, or initiation date could not be estimated. At all sites, the

majority of shorebird nests belonged to Pectoral Sandpipers, Semipalmated Sandpipers, and phalaropes. Nearly all of the passerine nests belonged to Lapland Longspurs (*Calcarius lapponicus*; Table 4). There was pronounced spatial and interannual variation in shorebird species composition, most notably in Pectoral Sandpiper and Red Phalarope nest density. Prominent among-site differences included an absence of plover (*Pluvialis* spp.) nests on plots at Canning, few Red-necked Phalarope nests at Thomson, relatively high numbers of Semipalmated Sandpiper nests at Prudhoe Bay in 2005, and high numbers of Red Phalarope nests at Canning in 2002.

Across years and sites, 1035 of 1876 monitored nests (55%) hatched or fledged successfully. Fates were unknown for 371 nests (20%). Nest predation was the most common cause of nest failure ($n = 439$ of 1876 nests; 23%). Other sources of failure included nest abandonment ($n = 21$; 1%), weather ($n = 2$; 0.1%), caribou trampling ($n = 3$; 0.2%), and human disturbance ($n = 4$; 0.2%). For Lapland Longspurs, daily nest survival was significantly higher during the incubation stage than the nestling stage for only one of 16 unique combinations of site and year (Canning 2003; $\chi^2_1 = 11.98$, $P < 0.01$).

The number of predators observed during surveys varied spatially and temporally, although at the two oil field sites we consistently detected more subsidized than nonsubsidized predators. Nonsubsidized predators predominated at Fish Creek and Thomson (Fig. 2). Jaegers (*Stercorarius* spp.) comprised >80% of nonsubsidized predators at all sites in all years, and accounted for 32–77% of total predators. The most common jaeger species was the Parasitic Jaeger (*S. parasiticus*). Frequency of nonsubsidized predators was higher at Thomson than at Fish Creek, Kuparuk, and Prudhoe Bay ($F = 4.406$, $df = 6, 319$, $P \leq 0.01$). Most sites, except Fish Creek, had at least one year when subsidized predators were detected more often than at the other sites (Fig. 2). Frequency of subsidized predators across years was lower at Fish Creek than at Canning, Kuparuk, and Prudhoe Bay ($F = 3.831$, $df = 6, 319$, $P \leq 0.05$). At all sites Glaucous Gulls were the most common subsidized predator, comprising $\geq 75\%$ of all subsidized predators. Common Ravens and arctic foxes accounted for $\leq 16\%$ and $\leq 9\%$ of subsidized predators, respectively.

Mean nest concealment varied considerably, with the highest value for passerine nests ($57.3\% \pm 1.1\%$, mean \pm SE) and the lowest for plover nests ($0.2\% \pm 0.1\%$). Nest concealment for shorebirds other than plovers was $21.4\% \pm 0.6\%$. Because of differences in timing in collection of snow cover data among study sites, we were unable to include these data in our background models. However, there were some common patterns observed in the chronology of the spring thaw among sites. Earliest snow melt at all sites occurred in 2002, while 2004 and 2005 had the latest snowmelt.

TABLE 4. Species and total number of nests monitored on the Arctic Coastal Plain, Alaska, 2002–2005.

Species	Species group	No. nests
Greater White-fronted Goose (<i>Anser albifrons</i>)	waterfowl	27
Cackling Goose (<i>Branta hutchinsii</i>)	waterfowl	1
Northern Pintail (<i>Anas acuta</i>)	waterfowl	4
Greater Scaup (<i>Aythya marila</i>)	waterfowl	1
King Eider (<i>Somateria spectabilis</i>)	waterfowl	16
Long-tailed Duck (<i>Clangula hyemalis</i>)	waterfowl	1
Willow Ptarmigan (<i>Lagopus lagopus</i>)	other	5
Rock Ptarmigan (<i>L. mutus</i>)	other	1
Red-throated Loon (<i>Gavia stellata</i>)	other	3
Pacific Loon (<i>G. pacifica</i>)	other	3
Black-bellied Plover (<i>Pluvialis squatarola</i>)	shorebird	15
American Golden Plover (<i>P. dominica</i>)	shorebird	28
Unidentified plover (<i>P. spp.</i>)	shorebird	1
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	shorebird	1
Bar-tailed Godwit (<i>Limosa lapponica</i>)	shorebird	3
Ruddy Turnstone (<i>Arenaria interpres</i>)	shorebird	1
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	shorebird	359
Pectoral Sandpiper (<i>C. melanotos</i>)	shorebird	396
Dunlin (<i>C. alpina</i>)	shorebird	71
Stilt Sandpiper (<i>C. himantopus</i>)	shorebird	56
Buff-breasted Sandpiper (<i>Tryngites subruficollis</i>)	shorebird	10
Long-billed Dowitcher (<i>Limodromus scolopaceus</i>)	shorebird	79
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	shorebird	113
Red Phalarope (<i>P. fulicarius</i>)	shorebird	124
Arctic Tern (<i>Sterna paradisaea</i>)	other	2
Parasitic Jaeger (<i>Stercorarius parasiticus</i>)	other	1
Eastern Yellow Wagtail (<i>Motacilla tschutschensis</i>)	passerine	2
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	passerine	12
Lapland Longspur (<i>Calcarius lapponicus</i>)	passerine	598
Common Redpoll (<i>Carduelis flammea</i>)	passerine	7
Total		1941

Note: Only passerines and shorebirds were included in the survival analysis; other species/groups were not included due to low sample sizes.

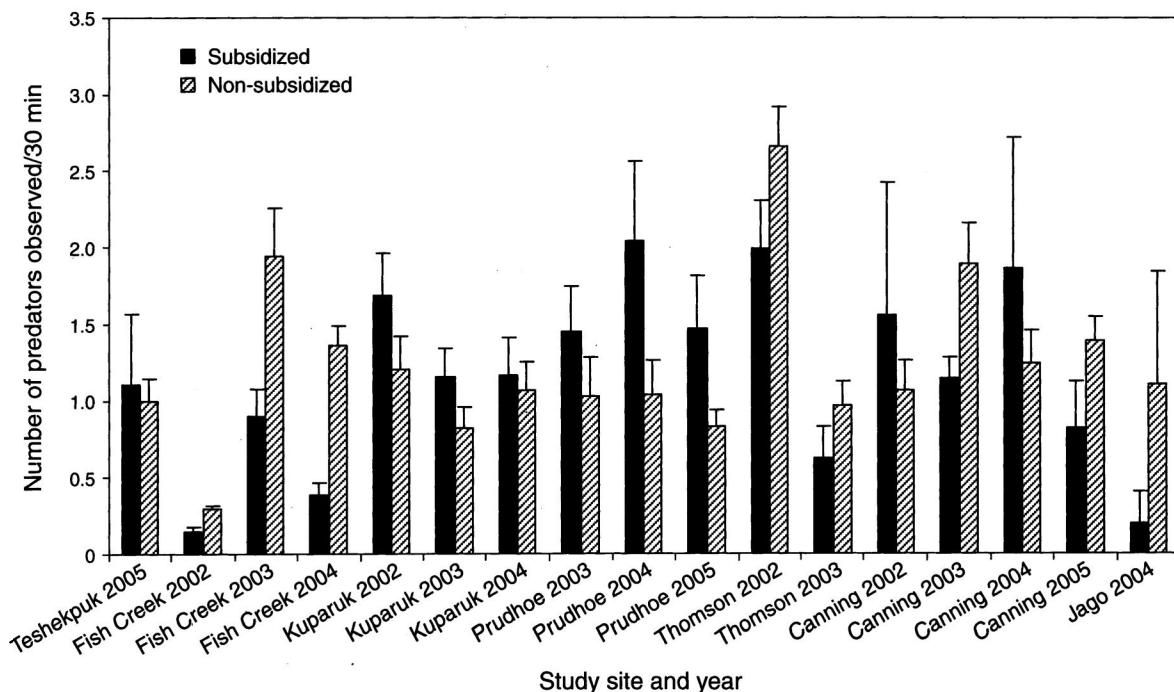


FIG. 2. Number of detections (mean + SE) of subsidized and nonsubsidized predators observed in 30-min visual scans at seven study sites on the Arctic Coastal Plain, Alaska, 2002–2005.

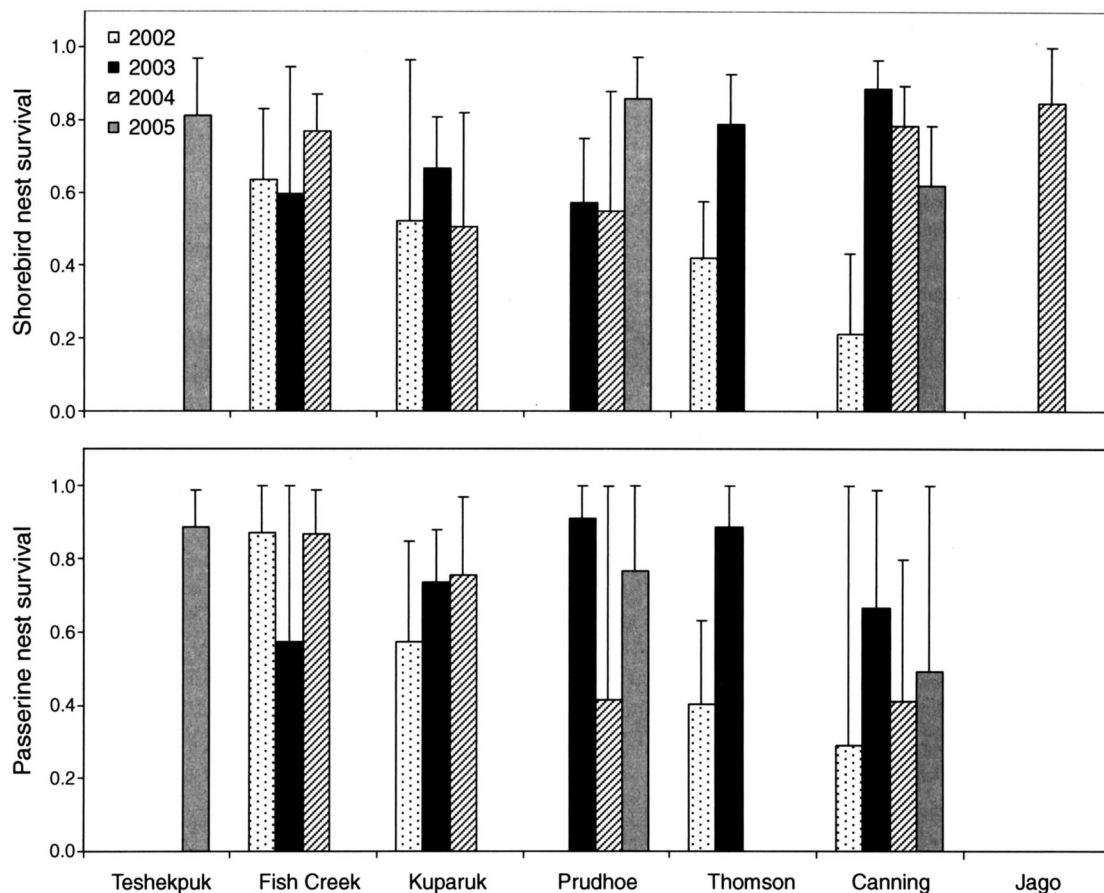


FIG. 3. Mean nest survivorship for the shorebird and passerine groups at each study site and year, calculated from the terminus of respective Kaplan-Meier curves (error bars indicate half-width 95% confidence intervals).

At the three sites where lemming abundance was indexed (Prudhoe Bay, Kuparuk, and Teshekpuk), lemming numbers were low (<0.1 individual observed per 30 min) in all years. Observations at the other study sites indicate that lemmings were also scarce in all years. Since there were no apparent spatial or temporal differences in lemming abundance, these data were not included in our background models.

Modeling results

We did not detect random plot or subplot effects in the background models (plot level: $P = 0.08$ – 0.28 for shorebirds and 0.27 – 0.92 for passerines; subplot level: $P = 0.13$ – 0.29 for shorebirds and 0.92 for passerines). Therefore, we concluded that nest fates were not spatially correlated and we removed random plot and subplot effects from subsequent models.

Overall nest survival fluctuated considerably among years and study sites (Fig. 3). The best-fitting background model for shorebird nests contained SITE.YEAR (Table 5). Overall nest survival for shorebirds ranged from 0.21 at Canning in 2002 to 0.89 at the same study site in the following year. Both Canning and Thomson in 2002 had lower daily survival rates than Fish Creek in

2003 (the reference), whereas Canning in 2003 had higher daily survival rates than Fish Creek in 2003 (Table 6). Daily nest survival for other SITE.YEAR combinations did not differ from that of Fish Creek in 2003.

The best background model for passerine nests contained SITE and CONCEALMENT (Table 5). Overall nest survival for passerines ranged from 0.29 at Canning in 2002 to 0.91 at Prudhoe Bay in 2003 (Fig. 3). The Kuparuk, Canning, and Jago sites had lower survival rates than Fish Creek (the reference; Table 6); however, the Jago River site had only one passerine nest and that nest failed. Survival rates at other study sites (Teshekpuk, Prudhoe Bay, and Thompson) were not significantly different from Fish Creek. The background model for passerines suggested that a 10% increase in CONCEALMENT decreased the instantaneous probability of predation by 7.4%.

Addition of infrastructure covariates to the best background shorebird model did not improve model fit (i.e., 95% confidence intervals for all infrastructure covariates contained 0; Table 7). However, addition of three of 15 infrastructure covariates in the best background passerine model did improve fit for that model (i.e., 95% confidence intervals around the

TABLE 5. Background models fit to nest survival data for the shorebird and passerine groups, sorted by the score test *P* value.

Model terms	No. parameters	<i>P</i>
Shorebirds		
SITE.YEAR	16	<0.001
SITE + CONCEALMENT + SITE:CONCEALMENT	13	<0.001
PLOVERS + CONCEALMENT + PLOVERS:CONCEALMENT	3	<0.001
PLOVERS + CONCEALMENT	2	<0.001
SITE + CONCEALMENT	7	<0.001
YR.FACTOR	3	<0.001
YEAR	1	<0.001
PLOVERS	1	<0.001
SITE + YEAR	7	0.001
PREDNONHUM	1	0.004
SITE	6	0.005
SITE + LAND.FORM	13	0.009
CONCEALMENT	1	0.009
CONCEALMENT + LAND.FORM	8	0.032
LN.PRED.NONSUBSIDIZED	1	0.068
LAND.FORM	7	0.132
Passerines		
SITE + CONCEALMENT	7	0.001
SITE + CONCEALMENT + STUDY,SITE:CONCEALMENT	12	0.003
SITE	6	0.004
SITE.YEAR	16	0.006
SITE + YEAR	7	0.007
CONCEALMENT	1	0.015
SITE + LAND.FORM	13	0.026
CONCEALMENT + LAND.FORM	8	0.161
PRED.NONSUBSIDIZED	1	0.192
LAND.FORM	7	0.425
YEAR	1	0.516
YR.FACTOR	3	0.686
LN.PRED.NONSUBSIDIZED	1	0.804

Note: PREDNONHUM is non-human predators.

coefficients of LN.HIGHSTRUCT, TOE16, and LN.TOE3 did not contain 0; Table 7). Grambsch and Therneau (1994) global tests of proportional hazards were not significant (*P* values ranged from 0.10 to 0.25) for these three passerine models, indicating that the proportional hazards assumptions were met.

Nonsubsidized predator abundance did not enter into the best shorebird or passerine background models (Table 5). Likewise, subsidized predator abundance did not explain any remaining variation after accounting for background effects (Table 7). The best-fitting passerine model containing LN.HIGHSTRUCT indicated that a nest's instantaneous probability of survival decreased rapidly within ~1 km of high-value structures, with evidence of decreased survival out to 5 km. For example, if all other factors are held constant, a nest located 2 km from a high-structure feature had a 34% ($1 - [\exp(-0.61349(\log(2)))/\exp(-0.61349(\log(1)))]$) lower hazard than a nest located 1 km from a high-value structure. The hazard decreased 13% between a nest located 4 km and a nest located 5 km from a high-value structure. Thus, the model suggests that in the oil field sites (Prudhoe Bay and Kuparuk) nest survival was lowest (~25–30%) near high-value structures, but increased to $\geq 50\%$ when distance to infrastructure approached 5 km (Fig. 4).

To illustrate the effect of distance to infrastructure on model predictions, we held concealment constant at 70% for a passerine nest at Prudhoe Bay. The model predicts that such a nest would have a ~32% chance of surviving to fledging during a 50-day breeding season if it was located 300 m from a high-structure feature (Fig. 4). A nest located 1 km from the nearest high-value structure would have ~48% chance of survival, whereas a nest located 5.8 km from the nearest high-value structure would have ~83% chance of survival.

To estimate a typical passerine survival curve for each study site, we computed the median distance to high-structural features at each study site and assumed that a nest was 70% concealed. We estimated one survival curve for each study site and censored the Jago site because it contained only one passerine nest. Nest survival was highest at Fish Creek and lowest at Canning (Fig. 5). Paired sites with similar nest survival values in descending order were Fish Creek and Teshekpuk, Prudhoe Bay and Thomson, and Kuparuk and Canning (Fig. 5).

A posteriori test results

The disparate modeling results for relationships of passerine and shorebird nests to infrastructure led us to explore whether pooling species or the scale of the

TABLE 6. Coefficients of the best-fitting background proportional hazards models; negative coefficients for an effect in either model (shorebird or passerine) imply that survival was higher (i.e., hazard was lower); positive coefficients imply the opposite.

Effect	Coefficient	Exp (coefficient)	Uncorrected		
			SE (coefficient)	Wald Z	Wald P†
Shorebirds					
Canning 2003	−0.883	0.414	0.422	−2.094	0.036
Prudhoe 2005	−0.788	0.455	0.468	−1.682	<i>0.093</i>
Teshekpuk 2005	−0.695	0.499	0.422	−1.648	<i>0.099</i>
Jago 2004	−0.335	0.716	0.622	−0.538	<i>0.590</i>
Thomson 2003	−0.213	0.808	0.405	−0.526	<i>0.600</i>
Canning 2004	−0.193	0.825	0.346	−0.557	<i>0.580</i>
Fish Creek 2002	−0.057	0.945	0.305	−0.186	<i>0.850</i>
Fish Creek 2004	0.021	1.022	0.329	0.065	<i>0.950</i>
Kuparuk 2002	0.024	1.024	0.330	0.072	<i>0.940</i>
Prudhoe 2004	0.275	1.317	0.317	0.869	<i>0.380</i>
Canning 2005	0.362	1.436	0.300	1.205	<i>0.230</i>
Kuparuk 2003	0.404	1.498	0.325	1.245	<i>0.210</i>
Kuparuk 2004	0.425	1.530	0.310	1.371	<i>0.170</i>
Prudhoe 2003	0.605	1.831	0.334	1.809	<i>0.070</i>
Thomson 2002	1.108	3.028	0.292	3.799	<0.001
Canning 2002	1.202	3.327	0.299	4.018	<0.001
Passerines					
Teshekpuk	−0.121	0.886	0.499	−0.243	<i>0.810</i>
CONCEALMENT	−0.008	0.992	0.003	−2.318	0.020
Prudhoe	0.445	1.561	0.413	1.078	<i>0.280</i>
Thomson	0.523	1.687	0.307	1.704	<i>0.088</i>
Kuparuk	0.806	2.239	0.287	2.807	0.005
Canning	0.821	2.273	0.286	2.872	0.004
Jago	2.588	13.308	1.027	2.522	0.012

Notes: The reference level for the shorebird model was Fish Creek 2003; the reference level for the passerine model was Fish Creek. SE (coefficient), Wald Z, and Wald P are uncorrected for spatial autocorrelation in the data. Wald P > 0.05 would remain so if corrected; these values are italicized in the table.

† No spatial dependency in time to predation was found (frailty effects tests), and the background model was not corrected for spatial dependencies. If undetected spatial dependencies existed, the correction would increase P values; thus, boldface P values (those <0.05) could conceivably increase to values >0.05 if corrected for spatial correlation.

original analysis was obscuring responses for individual species or finer spatial scales. We ran similar models for each oil field site and found that TOE16, LN.MED-FOOD, and LN.PRED.SUBSIDIZED at the Kuparuk site explained significant remaining variation when added to the shorebird background model. The significance of these covariates suggests that shorebird nest survival is lower when there is more infrastructure within 16 km of nests, medium-level food sources are nearer, or more subsidized predators are within 300 m of plots. Addition of these same covariates did not improve the best background models for shorebirds at Prudhoe Bay or for passerines at Kuparuk. Insufficient data were available to run similar models for passerines in Prudhoe Bay.

For phalaropes across all sites, LN.HIGHSTRUCT, LN.PRED.SUBSIDIZED, and LN.LOWFOOD significantly improved model fit, suggesting that nests closer to infrastructure and in areas of numerous subsidized predators were less likely to survive. LOWFOOD and LN.LOWFOOD improved model fit for Semipalmated Sandpipers at Kuparuk, although this result suggests that nest survival was actually higher closer to low-food infrastructure, the opposite of what we predicted.

Inclusion of infrastructure and subsidized predator covariates did not improve the best background models for all other comparisons ($n = 5$) or there were insufficient data to perform the tests ($n = 2$).

DISCUSSION

Human infrastructure had a negative effect on nest survival for passerines, the second most abundant group of birds nesting on the ACP. Passerine nest survival declined within 5 km of oil field infrastructure that provided nesting, perching, or denning sites for nest predators but increased with the percentage of vegetative cover over a nest. Contrary to our original hypothesis, however, we detected no overall effect of infrastructure (or any other measured covariate) on shorebird (all species pooled) nest survival, the most abundant guild of nesting birds on the ACP.

We considered that differing nesting behavior of passerines and shorebirds might explain the responses that we observed in nest survival. Lapland Longspurs raise altricial young that remain in the nest for 9–11 days after hatch (Hussell and Montgomerie 2002), whereas shorebird young are precocial and typically leave the nest within 24 h of hatching. Begging noise by young

TABLE 7. Coefficients and 95% confidence intervals for infrastructure and subsidized predator effects when added to the best background model. Confidence intervals were computed by bootstrap resampled plots with replacement. Confidence intervals not containing 0 are considered significant predictors of decreased survival.

Development effect	Coefficient	95% bootstrap CI		Contains zero?
		Lower limit	Upper limit	
Shorebirds				
HIGHFOOD	-0.013	-0.040	0.015	yes
LN.HIGHSTRUCT	0.009	-0.237	0.248	yes
TOE3	0.001	-0.003	0.004	yes
LN.TOE3	0.100	-0.180	0.413	yes
TOE16	-0.0001	-0.001	0.001	yes
LN.TOE16	0.024	-0.159	0.137	yes
LN.HIGHFOOD	-0.008	-0.221	0.173	yes
PRED.SUBSIDIZED	0.028	-0.033	0.121	yes
LN.PRED.SUBSIDIZED	0.060	-0.001	0.129	yes
LOWFOOD	-0.011	-0.042	0.019	yes
LN.LOWFOOD	-0.017	-0.300	0.307	yes
MEDFOOD	-0.011	-0.037	0.014	yes
LN.MEDFOOD	-0.248	-0.478	0.198	yes
LOWSTRUCT	-0.010	-0.042	0.021	yes
LN.LOWSTRUCT	-0.199	-0.413	0.016	yes
HIGHSTRUCT	-0.008	-0.036	0.020	yes
Passerines				
HIGHFOOD	-0.036	-0.079	0.003	yes
LN.HIGHSTRUCT	-0.613	-1.031	-0.246	no
TOE3	0.004	-0.0002	0.012	yes
LN.TOE3	0.441	0.025	1.071	no
TOE16	0.001	0.0004	0.003	no
LN.TOE16	0.103	-0.145	0.479	yes
LN.HIGHFOOD	-0.323	-0.617	0.065	yes
PRED.SUBSIDIZED	0.096	-0.025	0.195	yes
LN.PRED.SUBSIDIZED	0.096	-0.022	0.241	yes
LOWFOOD	-0.021	-0.060	0.023	yes
LN.LOWFOOD	-0.280	-0.784	0.422	yes
MEDFOOD	-0.026	-0.056	0.003	yes
LN.MEDFOOD	-0.414	-1.024	0.065	yes
LOWSTRUCT	-0.017	-0.055	0.032	yes
LN.LOWSTRUCT	-0.307	-0.630	0.066	yes
HIGHSTRUCT	-0.026	-0.068	0.010	yes

(Leech and Leonard 1997, Haskell 1999) and increased parental activity at the nest (Martin et al. 2000), during the nestling phase might increase detection and predation at passerine nests. For most site-year comparisons in our study, however, daily survival rate did not differ between incubation-stage and nestling-stage Lapland Longspurs.

The inconsistency of modeling results between the two major groups of nesting birds led us to investigate whether pooling all shorebird species may have obscured significant species-specific effects. The result for phalaropes supported the concept that proximity to infrastructure negatively influenced nest survival for some shorebird species, but neither Pectoral Sandpipers nor Semipalmated Sandpipers showed a similar response. Noting that the infrastructure response for passerines appeared to have a threshold within a few kilometers of infrastructure, we also investigated whether effects were restricted to within the oil field sites. At this finer scale, subsidized predator and infrastructure covariates did enter the shorebird model as significant predictors of lower nest survival for Kuparuk, but not for Prudhoe Bay. Overall, our a posteriori analyses for shorebirds

that evaluated species-specific and guild-specific effects of spatial scale did not consistently support (and in one case, contradicted) the findings of the passerine models. Inconsistencies in these results may reflect fundamental differences in how species respond to infrastructure, or may be related to differences in habitat or infrastructure between oil field sites.

We determined that predation was the primary cause of nest failure in our study, and therefore, it follows that nest survival should have been highly correlated with predator activity. Contrary to expectations, our a priori models suggested that neither subsidized nor nonsubsidized predator abundance was related to nest survival. Several explanations are possible: (1) our counts did not adequately measure predator abundance or provide an unbiased estimate of predation risk; (2) predation was confounded by other variables in our modeling approach; and (or) (3) high temporal and spatial variation in predator numbers may have obscured subtle effects.

Our predator counts were probably biased against arctic foxes because they are less active diurnally (Eberhardt et al. 1982), during the period we conducted surveys, and because airborne predators are more

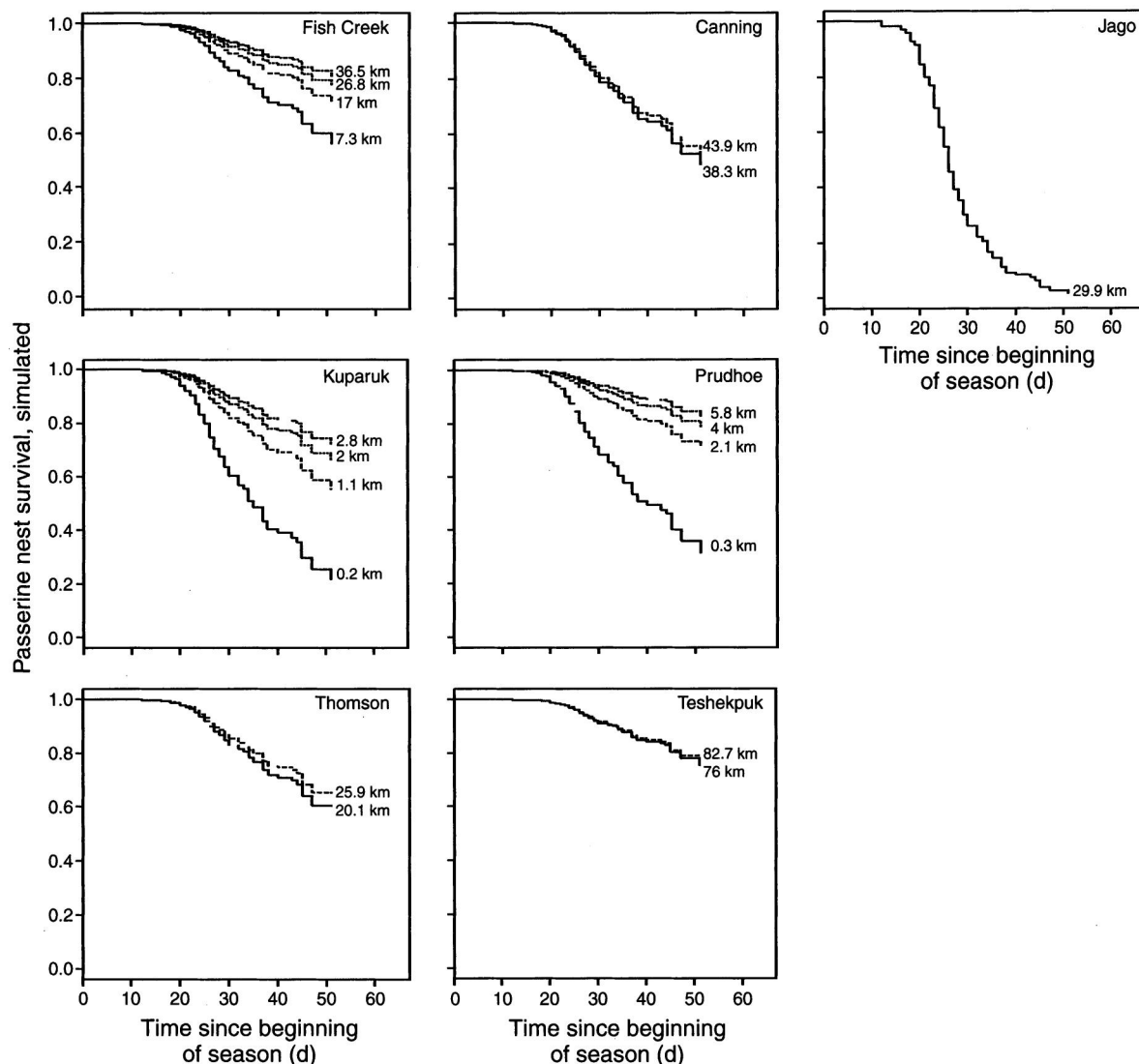


FIG. 4. Simulated survival of passerine nests at varying distances from high-value infrastructure within each study site predicted by the best-fitting proportional hazards model containing SITE, CONCEALMENT, and LN.HIGHSTRUCT. Covariates are described in Table 2. Nest concealment was set at 70%.

conspicuous. Therefore our index of subsidized predator abundance reflects mainly Glaucous Gull and Common Raven activity and provides little useful information to the model if fox predation is actually the dominant cause of nest failure in the oil fields, as suggested by others (Troy 2000, Johnson et al. 2007, Liebezeit and Zack 2008). Arctic fox predation has had devastating effects on some colonies of nesting waterfowl in Alaska (Quinlan and Lehnhausen 1982, Anthony et al. 1991, Johnson 2000) and was a major factor affecting wader populations breeding in the Russian Arctic (Summers and Underhill 1987, Martin and Baird 1988, Underhill et al. 1989, 1993). An ongoing study in Barrow, Alaska suggests that arctic fox removal may result in enhanced shorebird nest survival (R. Lancot, *unpublished data*). Therefore, the predator species most likely to have been

undercounted in our study is also likely to be the most important nest predator of shorebirds and passerines on the ACP.

Our modeling approach may have resulted in failure to detect some infrastructure and subsidized predator effects if they were correlated with study site. If this were the case, inclusion of SITE.YEAR and SITE covariates in the first stage of modeling would reduce the additional explanatory power of covariates related to infrastructure and subsidized predator abundance in the second stage. We therefore may have attributed an infrastructure effect to natural among-site variation. Alternative approaches ran the opposite risk of erroneously attributing natural variation among sites and years to infrastructure effects; thus we chose the more conservative approach to testing our hypothesis.

Our hypothesis that predation of nesting birds would be higher near human infrastructure that attracted predators was derived from observations of concentrations of predators in the oil fields in the 1980s and early 1990s by several of the authors, as well as from corroborating studies (Eberhardt et al. 1983, Burgess et al. 1993, Murphy and Anderson 1993). However, baseline population data for predators on the ACP have not been available or adequate to clearly demonstrate increases from pre-development levels (Truett et al. 1997, Noel et al. 2006). The most abundant subsidized predators in the oil fields, arctic foxes and Glaucous Gulls, may no longer be as concentrated as during the first two decades of oil development. Waste-handling practices in the oil fields improved during the mid-1990s, reducing access to human food waste (CPAI and BP 2005). Subsidized predators that previously were attracted to food waste may have declined over the last decade, but populations have not been monitored closely to judge the effectiveness of these new management practices. The most compelling case of a sustained increase is for Common Ravens, the species for which artificial nesting structures are most important (A. Powell and S. Backensto, *unpublished data*; Conoco-Phillips Alaska, Inc., *unpublished data*). Raven numbers from Audubon Christmas Bird Counts increased from 1988 to 2007 at Prudhoe Bay (Patuxent Wildlife Research Center, Laurel, Maryland, USA; data *available online*).¹¹ Even so, Common Ravens still occur in relatively low numbers (18–25 nests in a 1400-km² area of the Prudhoe Bay and Kuparuk oil fields; A. Powell and S. Backensto, *unpublished data*).

Our results confirm that substantial temporal and spatial variability in nest survival occurs in the arctic (Summers and Underhill 1987, Troy 2000). We attempted to control for this natural variability by modeling environmental covariates (Wiens and Parker 1995), but met with limited success. A development (infrastructure) effect, if present, may be small relative to natural variability in the arctic, rendering such effects difficult to detect. It is not unusual for environmental disturbance studies to be complicated by natural variability (Underwood 1994, Wiens and Parker 1995).

Nonetheless, we did detect higher predation risk for passerine nests near oil field facilities. This result, along with evidence of the predator effects from elsewhere in the Arctic (Restani et al. 2001; R. Lanctot, *unpublished data*), is sufficient to warrant continued efforts to minimize predator subsidies. We recommend that new oil field infrastructure and other residential or industrial development in this region be designed to reduce artificial nesting, perching, and denning sites and managed to limit access to food wastes. Because the predation impact that we detected was limited (in terms of affected species and spatial extent), and because the

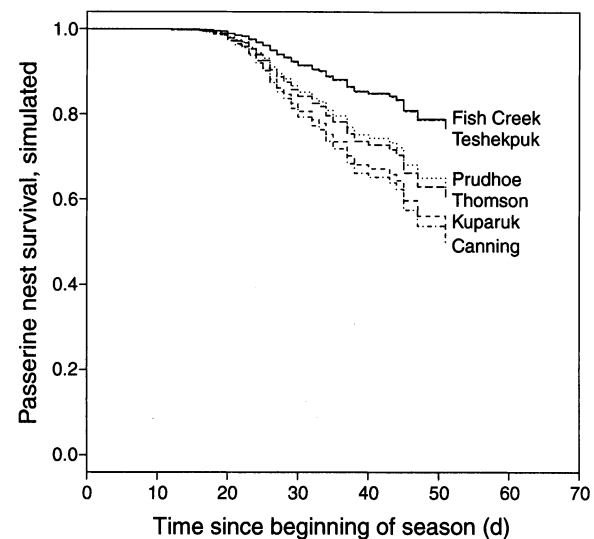


FIG. 5. Passerine nest survival for all study sites predicted by best-fitting proportional hazards model containing SITE, CONCEALMENT, and LN.HIGHSTRUCT. Nest concealment was set to 70%, and distance was set to the median distance to the nearest high-value structure on each study site. The Jago study site is not included because it had only one passerine nest.

difficulty and cost of redesigning or managing existing artificial nesting and perching structures (e.g., powerlines, buildings, communication towers) is potentially large, we recommend targeted efforts to minimize the influence of individual nest predators when they can be identified. We recommend that predator management always be conducted in conjunction with monitoring to judge effectiveness.

Questions raised by this study could be addressed through research on other components of the system. Many factors other than proximity to infrastructure influence populations of predators in the arctic environment. Disease, intraspecific competition, and especially natural food availability play significant roles in predator abundance and distribution (Maher 1974, Underwood and Mosher 1982, Smits et al. 1989). Further research on demography of predator populations and their relative importance with respect to nest survival is needed. In particular, follow-up studies to those in the 1990s on predator abundance in the oil fields (e.g., Burgess et al. 1993, Murphy and Anderson 1993) are needed to assess the efficacy of current waste-control techniques in locations where predators were previously concentrated. Follow-up studies on nest survival should be considered, with special attention paid to study designs that better address the challenges posed by high natural variability. Artificial nest experiments (e.g., Wilson et al. 1998, Kristan and Boarman 2003) should be considered because they allow better control of natural variability, are not as restricted by sample size as natural nest studies, and can be designed to test the importance of specific point sources of infrastructure.

¹¹ (<http://www.audubon.org/bird/cbc/hr/index.html>)



PLATE 1. Arctic fox (*Vulpes lagopus*) with a Greater White-fronted Goose (*Anser albifrons*) egg, near Prudhoe Bay, Alaska, USA. Photo credit: S. Zack.

Finally, we recommend long-term (i.e., ≥ 10 years) monitoring of nest survival using a balanced design (all sites monitored in all years) to evaluate an anthropogenic effect that, if present, may be difficult to detect against the background variability inherent in this arctic predator-prey system.

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LITERATURE CITED

- Andersen, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100–1120.
- Anthony, R. M., P. L. Flint, and J. S. Sedinger. 1991. Arctic fox removal improves nest success of Black Brant. *Wildlife Society Bulletin* 19:176–184.
- Bart, J., S. Brown, B. Harrington, and R. I. G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? *Journal of Avian Biology* 38:73–82.
- Burgess, R. M., and P. W. Banyas. 1993. Inventory of arctic fox dens in the Prudhoe Bay region, 1992. Unpublished report to BP Exploration (Alaska) Inc., Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Burgess, R. M., J. R. Rose, P. W. Banyas, and B. E. Lawhead. 1993. Arctic fox studies in the Prudhoe Bay Unit and adjacent undeveloped areas, 1992. Unpublished report to BP Exploration (Alaska) Inc., Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Clayton, D. G., and J. Cuzick. 1985. Multivariate generalizations of the proportional hazards model (with discussion). *Journal of the Royal Statistical Society Series A* 148:82–117.
- Cox, D. R. 1972. Regression models and life tables (with discussion). *Journal of the Royal Statistical Society Series B* 34:187–220.
- Cox, D. R., and D. Oakes. 1984. Analysis of survival data. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- CPAI and BP (ConocoPhillips Alaska and BP Exploration [Alaska]). 2005. North slope environmental field handbook. CPAI and BP, Anchorage, Alaska, USA.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–565.

- Day, R. H. 1998. Predator population and predation intensity on tundra-nesting birds in relation to human development. Unpublished report to Northern Alaska Ecological Services, U.S. Fish and Wildlife Service, Fairbanks, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Derksen, D., T. C. Rothe, and W. D. Eldridge. 1981. Use of wetland habitat by birds in the National Petroleum Reserve: Alaska. Resource publication (U.S. Fish and Wildlife Service) 141:1–27.
- Eberhardt, L. E., R. A. Garrott, and W. C. Hanson. 1983. Den use by arctic foxes in northern Alaska. *Journal of Mammalogy* 64:97–102.
- Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson. 1982. Arctic fox home range characteristics in an oil-development area. *Journal of Wildlife Management* 46:183–190.
- George, T. L. 1987. Greater land bird densities on island vs. mainland: relation to nest predation level. *Ecology* 68:1393–1400.
- Grambsch, P., and T. Therneau. 1994. Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–526.
- Gray, R. J. 1992. Flexible methods for analyzing survival-data using splines, with applications to breast-cancer prognosis. *Journal of the American Statistical Association* 87:942–951.
- Haskell, D. G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Animal Behaviour* 57: 893–901.
- Haskell, D. G., A. M. Knupp, and M. C. Schneider. 2001. Nest predator abundance and urbanization. Pages 243–257 in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Howe, M. A., H. Geissler, and B. A. Harrington. 1989. Population trends of North American shorebirds based on the International Shorebird Survey. *Biological Conservation* 49:185–199.
- Hussell, D. J. T., and R. Montgomerie. 2002. Lapland Longspur (*Calcarius lapponicus*). Number 656 in A. Poole and F. Gill, editors. *The Birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington, D.C., USA.
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727–737.
- Johnson, C. B., R. M. Burgess, B. E. Lawhead, J. Neville, J. P. Parrett, A. K. Prichard, J. R. Rose, A. A. Stickney, and A. M. Wildman. 2003. Alpine avian monitoring program, 2001. Unpublished report to ConocoPhillips Alaska, Inc., and Anadarko Petroleum Corporation, Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Johnson, C. B., J. P. Parrett, and P. E. Seiser. 2007. Spectacled Eider monitoring at the CD-3 development, 2006. Unpublished report to ConocoPhillips Alaska, Inc., and Anadarko Petroleum Corporation, Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Johnson, S. R. 2000. Lesser Snow Goose. Pages 233–257 in J. C. Truett and S. R. Johnson, editors. *The natural history of an Arctic oil field, development and biota*. Academic Press, San Diego, California, USA.
- Klein, J. P., and M. L. Moeschberger. 1997. *Survival analysis, techniques for censored and truncated data*. Springer, New York, New York, USA.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Addison-Wesley Educational, Menlo Park, California, USA.
- Kristan, W. B., and W. I. Boarman. 2003. Spatial patterns of risk of Common Raven predation on desert tortoises. *Ecology* 84:2432–2443.
- Kristan, W. B., and W. I. Boarman. 2007. Effects of anthropogenic developments on Common Raven nesting biology in the West Mojave Desert. *Ecological Applications* 17:1703–1713.
- Lahiri, S. N. 2003. *Resampling methods for dependent data*. Springer, New York, New York, USA.
- Lancot, R. B., and C. D. Laredo. 1994. Buff-breasted Sandpiper (*Tryngites subruficollis*). Number 91 in A. Poole and F. Gill, editors. *The Birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington, D.C., USA.
- Leech, S. M., and M. L. Leonard. 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology* 8:644–646.
- Liebezeit, J. R., et al. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* 109:32–47.
- Liebezeit, J. R., and S. Zack. 2008. Point counts underestimate the importance of arctic foxes as avian nest predators: evidence from remote video cameras in Arctic Alaskan oil fields. *Arctic* 61:153–161.
- Mabee, T. 1997. Using eggshell evidence to determine nest fate of shorebirds. *Wilson Bulletin* 109:307–313.
- Mabee, T. J., A. M. Wildman, and C. B. Johnson. 2006. Using egg flotation and eggshell evidence to determine age and fate of Arctic shorebird nests. *Journal of Field Ornithology* 77: 163–172.
- Maher, W. 1974. Ecology of pomarine, parasitic, and long-tailed jaegers in northern Alaska. *Pacific Coast Avifauna* 37: 1–157.
- Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117:615–626.
- Martin, A. P., and D. Baird. 1988. Lemming cycles: which Palearctic migrants are affected? *Bird Study* 35:143–145.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. *Breeding Biology Research and Monitoring Database (BBIRD)*. Montana Cooperative Wildlife Research Unit, Missoula, Montana, USA.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society B* 267:2287–2293.
- Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–47 in M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology and conservation in an urbanizing world*. Kluwer, Dordrecht, The Netherlands.
- Monda, M. J., J. T. Ratti, and T. R. McCabe. 1994. Reproductive ecology of Tundra Swans on the Arctic National Wildlife Refuge, Alaska. *Journal of Wildlife Management* 58:757–773.
- Morrison, R. I. G., B. J. McCaffery, R. E. Gill, S. K. Skagen, S. L. Jones, G. W. Page, C. L. Gratto-Trevor, and B. A. Andres. 2006. Population estimates of North American shorebirds, 2006. *Wader Study Group Bulletin* 111:67–85.
- Murphy, S. M., and B. A. Anderson. 1993. *Lisburne Terrestrial Monitoring Program: The effects of the Lisburne Development Project on geese and swans, 1985–1989*. Unpublished report to ARCO Alaska, Inc., Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- Murphy, S. M., B. A. Anderson, C. L. Cranor, and R. H. Day. 1987. *Lisburne terrestrial Monitoring Program: The effects of the Lisburne Development Project on geese and swans*. Unpublished report for Atlantic Richfield Co., Anchorage, Alaska, USA, prepared by ABR, Inc., Fairbanks, Alaska, USA.
- NAS (National Academy of Sciences). 2003. *Cumulative environmental effects of oil and gas activities on Alaska's North Slope*. National Research Council of the National

- Academies. National Academies Press, Washington, D.C., USA.
- Noel, L. E., S. R. Johnson, and W. J. Gazey. 2006. Oilfield development and Glaucous Gull (*Larus hyperboreus*) distribution and abundance in central Alaskan Beaufort Sea lagoons, 1970–2001. *Arctic* 59:65–78.
- Nur, N., A. L. Holmes, and G. R. Geupel. 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. *Condor* 106:457–471.
- Pitelka, F. A. 1974. An avifaunal review for the Barrow region and North Slope of Arctic Alaska. *Arctic and Alpine Research* 6:161–184.
- Poole, A. F., P. Stettenheim, and F. B. Gill, editors. 2003. *The Birds of North America: life histories for the 21st century*. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington, D.C., USA.
- Quinlan, S. E., and W. A. Lehnhausen. 1982. Arctic fox predation on nesting common eiders at Icy Cape, Alaska. *Canadian Field-Naturalist* 96:462–466.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. General Technical Report PSW-GTR-144. Pacific Southwest Research Station, USDA Forest Service, Albany, California, USA.
- Restani, M., J. M. Marzluff, and R. E. Yates. 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of Common Ravens in the Arctic. *Condor* 103:399–404.
- Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *Journal of Wildlife Management* 53:137–142.
- Smits, C. M. M., B. G. Slough, and C. A. Yasui. 1989. Summer food habits of sympatric arctic foxes, *Alopex lagopus*, and red foxes *Vulpes vulpes*, in the Northern Yukon Territory. *Canadian Field-Naturalist* 103:363–367.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Soric, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75–92.
- Summers, R. W., and L. G. Underhill. 1987. Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study* 34:161–171.
- Therneau, T. M., P. M. Grambsch, and V. S. Pankratz. 2003. Penalized survival models and frailty. *Journal of Computational and Graphical Statistics* 12:156–175.
- Troy, D. M. 1993. Population dynamics of birds in the Pt. McIntyre Reference Area: 1981–1992. Unpublished report to BP Exploration (Alaska), Inc., Anchorage, Alaska, USA, prepared by Troy Ecological Research Associates, Anchorage, Alaska, USA.
- Troy, D. M. 2000. Shorebirds. Pages 277–303 in J. C. Truett and S. R. Johnson, editors. *The natural history of an Arctic oil field: development and biota*. Academic Press, San Diego, California, USA.
- Truett, J. C., M. E. Miller, and K. Kertell. 1997. Effects of Arctic Alaska oil development on Brant and Snow Geese. *Arctic* 50:138–146.
- Underhill, L. G., R. P. Prys-Jones, E. E. Syroechkovski, Jr., N. M. Groen, V. Karpov, H. G. Lappo, M. W. J. van Roomen, A. Rybkin, H. Schekkerman, H. Spiekman, and R. W. Summers. 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135:277–292.
- Underhill, L. G., M. Waltner, and R. W. Summers. 1989. Three-year cycles in breeding productivity of Knots *Calidris canutus* wintering in southern Africa suggest Taimyr Peninsula provenance. *Bird Study* 36:83–87.
- Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* 4:3–15.
- Underwood, L., and J. A. Mosher. 1982. Arctic fox. Pages 491–503 in J. Chapman and G. Feldhammer, editors. *Wild mammals of North America*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- U.S. Fish and Wildlife Service. 2005. Arctic National Wildlife Refuge bird list. U.S. Fish and Wildlife Service, Fairbanks, Alaska, USA.
- Walker, D. A., K. R. Everett, P. J. Webber, and J. Brown. 1980. *Geobotanical atlas of the Prudhoe Bay region, Alaska*. U.S. Army Corps of Engineers. Cold Regions Research and Engineering Laboratory. CRREL report 80-14. Hanover, New Hampshire, USA.
- Weather Underground. 2008. Daily weather recorded at Deadhorse Airport, Prudhoe Bay, Alaska 2002–2005. (<http://www.wunderground.com/history/airport/PASC/>)
- Wiens, J. A., and K. R. Parker. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecological Applications* 5:1069–1083.
- Wilson, G. R., M. C. Brittingham, and L. J. Goodrich. 1998. How well do artificial nests estimate success of real nests? *Condor* 100:357–364.