

REPRODUCTIVE SUCCESS OF AMERICAN AND PACIFIC GOLDEN-PLOVERS
(*PLUVIALIS DOMINICA* AND *P. FULVA*) IN A CHANGING CLIMATE

By

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Abstract

Climate change is increasing air temperatures and altering hydrologic systems in arctic environments, which will create positive feedbacks on shrub growth and advance the phenology of arthropods, important prey for many arctic-breeding birds. Little is understood about how such climate-induced changes in habitat and prey availability may affect reproductive success of migratory birds during the short arctic breeding season. Worldwide, declines in shorebird populations, including arctic-breeding species, have recently become apparent. Projected changes in climate are expected to benefit arctic-breeding shorebirds in the short-term by increasing reproductive success and survival, primarily through prolongation of summer. Over time, however, reductions in the quantity and quality of open tundra habitat and changes in prey availability may adversely affect shorebird reproduction and exacerbate current population declines. I evaluated the reproductive success of two shorebird species, American (*Pluvialis dominica*) and Pacific (*P. fulva*) Golden-Plovers, in relation to vegetation extent and phenology. I collected data over two field seasons (2012–2013) on the Seward Peninsula, Alaska. Both species selected nest sites with less cover of tall shrubs and other tall vegetation than available at random sites within their territories. American Golden-Plovers selected territories and nest sites that were higher in elevation and had more rocky substrates and less graminoid vegetation than those selected by Pacific Golden-Plovers. Nest survival was equivalent in the two species and similar to that found in other arctic-breeding shorebirds. Over the 27-d incubation period the probability of a nest having at least one egg survive to hatch averaged 0.39 (95% CI: 0.28, 0.49). Nest survival was not explicitly associated with habitat features at nest sites; however, nest survival was lower during the year with earlier spring phenology and declined with the age of the

nest, both of which may have been at least partially related to growth of vegetation. Future research should examine reproductive success in a comprehensive manner, in which multiple aspects of a species' reproductive ecology is evaluated, allowing a more complete understanding of the effects of climate change on recruitment into populations through the combined effects of habitat structure, food resources, and climate.

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Dedication

This thesis is dedicated to my brother, David Alexander Overduijn (1984 – 2006), for his eternal influence on my life. Thank you for living your life boldly and freely, and for giving me the courage and strength to pursue my dreams.

General Introduction

The arctic tundra provides breeding habitat for hundreds of species of birds, including approximately 50 species of shorebirds. About one third of the world's shorebirds breed in the Arctic (CHASM 2004). These birds migrate to the Arctic in the spring from all over the world to take advantage of long days, abundant food resources, relatively few predators, and a lack of disease and parasites during the summer (Piersma 1997, Mouritsen and Poulin 2002, Freed et al. 2005). Many species of shorebirds have strong annual site fidelity, returning to the same breeding territories, and in some cases, even the same nest cups (Greenwood 1980, Johnson et al. 2018).

Worldwide, declines in shorebird populations have become apparent in recent decades (Brown et al. 2001, Thomas et al. 2006, Bart et al. 2007). Causes of these declines are currently unknown, but habitat alterations due to climate change in nonbreeding areas are suspected (CHASM 2004). Conversely, on arctic breeding grounds, modest temperature increases may benefit many shorebird species by increasing fitness and survival rates through prolonged summers and increased food availability. However, over time, it is expected that continued climate variation will lead to a reduction in the quantity of open habitat, and a diminishment in the quality of remaining open habitat, which may drive some of these species to extinction (Meltofte 2007). In addition, climate amelioration has led to noticeable range expansions of many species. This northward expansion of shorebird ranges could lead to interspecific competition among species for nesting habitat and food resources. Evaluating the macro-scale relationships between shorebird species and their environment will enable predictions to be made about how populations might be affected by habitat alteration as a result of climate change (Meltofte 2007).

In the Alaskan Arctic, an increase in shrubs on tundra habitats has been documented (Sturm et al. 2001, Stow et al. 2004, Tape et al. 2006), and areas near the tundra-boreal forest transition zone are particularly susceptible to shrub increase (Callaghan et al. 2005). Changes to the vertical structure and floristic composition of open-tundra habitats related to increasing height and cover of shrubs may influence the quantity and quality of potential nesting and brood-rearing areas for species that depend on these habitats. There is growing concern regarding the impact that increases in vegetation may have on the breeding habitat of shorebirds (Grishanov 2006, Brown et al. 2007). In addition to effects on shrubs, climate change in the Arctic is likely to affect arthropod communities. Specifically, the abundance and seasonality of life cycles (i.e., phenology) of invertebrates are both likely to respond to increases in temperature (Ellwood et al. 2012), moreover changes to the structure and composition of woody habitat might further influence invertebrate abundance and community diversity in northern latitudes (Rich et al. 2013). Reproductive success in shorebirds is highly dependent on the seasonal availability of invertebrates for feeding chicks (Lack 1968, Pearce-Higgins and Yalden 2004, Tulp and Schekkerman 2008). Synchrony of hatch with peak invertebrate abundance ensures that adequate resources are available to chicks for growth (McKinnon et al. 2012). In many temperate breeding bird species, asynchrony of hatch with peak invertebrate abundance results in a mismatch between the timing of hatch and peak food availability (Visser and Both 2005, Visser et al. 2006). In the Arctic, the extent to which shorebirds will be temporally decoupled from their main food resources remains unclear (Pearce-Higgins et al. 2005, Tulp and Schekkerman 2008, McKinnon et al. 2012), but the potential for trophic mismatch has been demonstrated at one site at Medusa Bay, on the Taimyr Peninsula, Siberia (Schekkerman et al. 2004).

In this thesis, I examined shorebird breeding habitat as related to nest-site selection and nest success on the Seward Peninsula, Alaska, where the juxtaposition of boreal forest with open tundra makes the tundra particularly susceptible to shrub increase (Callaghan et al. 2005). This region, located in northwestern Alaska, has pronounced longitudinal and elevational gradients of habitat. Local-scale changes in habitat types associated with elevational gradients on the Seward Peninsula are analogous to broad-scale changes in habitat associated with warming-driven shrub expansion across the Arctic. Thus, elevational gradients can function as proxies for changes in habitat related to climate warming. The Seward Peninsula is also an important breeding area for many species of shorebirds (Kessel 1989), including the American Golden-Plover (*Pluvialis dominica*; hereafter referred to as “American”) and the Pacific Golden-Plover (*P. fulva*; hereafter “Pacific”). Both species are highly territorial, are seasonally monogamous, are biparental incubators, and nest on open tundra (Johnson et al. 2001, 2018).

These two species are highly suitable choices for evaluating shorebird responses to climate-change-induced variation in habitat and food resources, because they can be found breeding sympatrically across an elevational gradient and across open habitat types. Selection of both territories and nest-sites by plovers is likely based on food availability and suitability of vegetative cover for the survival of the adults, eggs, and chicks. There are tradeoffs between visibility and concealment, because in areas where incubating adults have high visibility, physical cover may be sparse (Gotmark et al. 1995, Gómez-Serrano and López-López 2014). Breeding plovers require open-tundra habitats, which allow nonincubating mates to feed and at the same time be vigilant of their surroundings. In areas of increased vegetative cover, shorebirds have been found to increase the amount of vigilance that they exhibit. This shift in behavior allocation takes time away from other important behaviors such as feeding and could affect the

quality of the parent, potentially resulting in lower nest and brood survival (Metcalf 1984). In the absence of much vertical structure, nest survival for ground-nesting birds is often reliant on the incubation behavior of adults (Smith et al. 2007) and crypticity of both the nest and plumage of the incubating adult. This crypticity could be compromised as shrub expansion occurs and lichen-dominated substrate is replaced with more vegetated substrates.

Based on concerns regarding the increase of shrubs on open tundra, and questions about how this may impact the breeding habitat of shorebirds, I evaluated the breeding ecology of Americans and Pacifics on the Seward Peninsula in relation to nesting habitat at two different scales, territory and nest site. Little is known about nest or brood survival in these species, particularly for Pacifics (Johnson et al. 2018) and there is a need to understand these aspects of the breeding ecology before potential impacts arising from climate change can be examined. The general objectives of my research, in Chapter 1 of this thesis, were to: (1) quantify differences between habitat within territories selected by both species, (2) quantify habitat features for each species that influence the selection of nest sites, (3) determine if any of these features were related to nest success, and (4) assess whether one species may be more vulnerable to climate-related changes in the structure and composition of vegetation. In addition, I followed broods after hatch and documented the success and failure of each brood during 2012 and 2013 to determine brood survival as related to invertebrate abundance and habitat. To quantify invertebrate abundance, I collected invertebrates using pitfall traps along transects within areas used by broods during different stages of the brood-rearing period in 2013. However, due to time constraints, analyses for the brood survival and invertebrate abundance data have not been completed. I report apparent brood survival and the raw invertebrate data in Appendices A and

B. Ultimately, this research is intended to elucidate the associations between shrub extent, habitat use, and the effects of seasonal phenology on plover reproductive success.

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Chapter 1. Sympatric Plovers Partition Nesting Habitat With Minimal Effect On Nest Survival¹

1.1 Abstract

Vertical structure of vegetation and floristic composition of tundra habitats may influence the quantity and quality of potential nesting sites for avian species that breed in these habitats. Competition between sympatric species for high-quality nesting habitat may force some individuals into suboptimal habitat and lead to reduced reproductive success. We investigated the effects of vegetation structure on nest-site selection and reproductive success of two sympatrically breeding plover species, the American Golden-Plover (*Pluvialis dominica*) and Pacific Golden-Plover (*P. fulva*). Both species selected nest sites with less cover of tall shrubs and other tall vegetation than available at random sites within their territories. American Golden-Plovers selected territories and nest sites that were higher in elevation and had more rocky substrates and less graminoid vegetation than those selected by Pacific Golden-Plovers. Nest survival was equivalent in the two species and similar to that found in other arctic-breeding shorebirds: over the average 27-d incubation period the probability of a nest having at least one egg survive to hatch was 0.39 (95% CI: 0.28, 0.49). Nest survival was not associated with habitat features selected for nest sites. Nest survival was lower during the year with earlier spring phenology and declined with the age of the nest, which may have been related to growth of vegetation. Our finding that both species selected open habitat for nest sites suggests that climate-related shrub encroachment may have negative effects on reproductive success and reduce the amount of available breeding habitat for plovers in the long term. In the short term, both species may be able to adjust selection of their breeding territories and nest sites in response

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to gradual vegetation change on the tundra. Additional research is needed to quantify reproductive success during brood-rearing and subsequent life stages relative to climate-driven vegetation changes across their breeding ranges.

1.2 Introduction

Reproductive success and survival, important drivers of population dynamics, often differ among animals using habitats of varying quality (Brown 1969, Bowers 1994). Key characteristics of habitat that can influence the risk of reproductive failure for birds include vegetation structure, food resources, competition, thermal regimes, and predator abundance (Williams 1966). Habitat selection can occur across multiple spatial scales, depending on the features necessary for successful foraging and reproduction (Hildén 1965, Johnson 1980, Hutto 1985). Examining habitat selection at different spatial and temporal scales may reveal important trade-offs among survival of eggs, chicks, and adults in relation to particular characteristics (Cody 1985, Martin 1993, Colwell 2010, Chalfoun and Schmidt 2012). Quality of a habitat can best be characterized based on such demographic parameters, since measures of occupancy and abundance are sometimes misleading indicators (Van Horne 1983, Johnson 2007).

Shorebird populations are declining worldwide, including those breeding in arctic and subarctic areas (Brown et al. 2001, Thomas et al. 2006, Bart et al. 2007, Kubelka et al. 2018). To arrest or reverse such declines, it is imperative to understand how changes in the quality or abundance of key habitats may be driving demographic processes. Arctic and alpine-breeding shorebirds are deemed among the most vulnerable to changes in climate because their current breeding areas are not expected to be replaced as vegetative communities shift in response to

climate (Marcot et al. 2015). In contrast, projected changes in climate may benefit arctic-breeding shorebirds in the short-term by increasing reproductive success and survival, primarily through prolongation of the breeding season and amelioration of inclement weather. Over time, however, reductions in the quantity and quality of open tundra habitats may adversely affect shorebird reproduction and exacerbate current population declines (Meltotte et al. 2007).

Increasing air temperatures and altered hydrologic systems in arctic and subarctic environments are creating positive feedbacks on vegetation growth (Callaghan et al. 2005), which contribute to changes in the structure and composition of vegetation. As a result, tundra plant communities are expected to be lost due to stress and subsequent northward expansion of boreal communities (Huntley 1991, Hinzman et al. 2005, Settele et al. 2014, Jorgenson et al. 2015). Fire, succession, thermokarst, shrub expansion, and permafrost thaw have resulted from increasing temperatures and altered hydrologic systems and have contributed to recent shifts in habitats in northwestern Alaska, and these processes are projected to accelerate throughout the century (Jones et al. 2011, Myers-Smith et al. 2011, Jorgenson et al. 2015, Marcot et al. 2015).

In the Alaskan Arctic, shrubs are increasing in both height and areal extent on tundra habitats (Sturm et al. 2001, Stow et al. 2004, Tape et al. 2006), and areas near the tundra–boreal forest transition zone are particularly susceptible to shrub expansion (Callaghan et al. 2005). The extent of tundra habitats associated with high elevations and high latitudes is projected to decline as shrub and forest habitats increase in response to climate change (Jorgenson et al. 2015). As tundra habitats shift, structural changes to vegetation can influence the distribution and reproductive success of wildlife species (Marcot et al. 2015). For example, some tundra-obligate species, such as microtine rodents in the ecotone between the boreal biome and the arctic tundra biome, are predicted to become restricted to very small refugia in the future (Hope et al. 2013).

This raises questions regarding effects on avian species, such as shorebirds, that also rely on tundra habitats within this ecotone.

Understanding specific influences of vegetation structure on nest-site selection and its influence on reproductive success is essential for evaluating potential population-level impacts driven by regional climate change. Vegetation structure strongly influences the rate of nest predation, which is the major driver of reproductive success in many species of birds (Ricklefs 1969, Metcalfe 1984, Cresswell 1997). Many shorebirds rely on vegetation cover to conceal their nests from predators (Colwell and Oring 1990). Other species, however, rely on visual detection of potential predators and subsequent distraction displays or aggressive attacks to deter them, and for these shorebirds the absence of tall cover around the nest is important (Colwell and Oring 1990, Johnson et al. 2018, Colwell 2010). Although there is growing concern regarding the impact that increased shrub cover may have on the breeding habitat of shorebirds (Grishanov 2006, Brown et al. 2007), the extent to which individual species may be affected is unclear. For example, Whimbrels (*Numenius phaeopus*) breeding on arctic tundra avoided nesting near shrubs, suggesting that shrub and tree encroachment may reduce available nesting habitat (Ballantyne and Nol 2011). In contrast, Whimbrels nesting in the forest–tundra ecotone within the boreal forest did not avoid nesting near shrubs but nested only within large open-tundra patches (Harwood et al. 2016). Smith et al. (2007) found that shorebirds of five different species breeding in tundra habitat in Nunavut, Canada, selected nest sites with varying degrees of shrub cover, suggesting that the effects of increasing shrubs will likely be species- and habitat-specific. Given the uncertainty in the impact of increased shrub cover on productivity of tundra-nesting shorebirds, additional empirical data are required to project the consequences of increasing shrub cover on population dynamics.

In this study we focused on two closely related shorebird species that breed on tundra across northern Alaska, where shrubs have been expanding rapidly in response to climatic changes (Hinzman et al. 2005, Tape et al. 2006, Myers-Smith et al. 2011). We investigated nest-site selection and nesting success of the American Golden-Plover (*Pluvialis dominica*, hereafter "American") and Pacific Golden-Plover (*P. fulva*, "Pacific") on the Seward Peninsula in northwestern Alaska, where they breed sympatrically along an elevational gradient of moisture and vegetation (Connors et al. 1993). Both species are of high conservation concern according to the U.S. Shorebird Conservation Plan, Americans due to population declines and Pacifics due to limited breeding distribution and low abundance (Brown et al. 2001). Although the two species use similar tundra habitats composed of low vegetation and lichen for breeding, past studies have found differences in breeding habitat in their zone of sympatry, with Americans typically nesting on higher, drier slopes and Pacifics generally nesting in more mesic areas at lower elevations (Connors et al. 1993, Johnson et al. 2018). Because local-scale differences in habitat types associated with elevational gradients are often analogous to broad-scale differences in habitat associated with climate-driven shrub expansion, elevational gradients may function as spatial proxies for temporal habitat changes projected to occur in response to climate change.

For territorial species such as these, selecting nesting habitat is a two-step process that includes (1) selection of the breeding territory where nesting occurs and (2) selection of a nest site within the breeding territory. At the scale of the territory, important characteristics that may influence selection include food availability (for adults and chicks) and exposure to predators (Gotmark et al. 1995, van der Vliet et al. 2008, Colwell 2010, Gómez-Serrano and López-López 2014). At the scale of the nest site, birds may select features that enhance crypticity of the nest to reduce its detection by predators, or characteristics that maximize visibility from the nest for the

attending adult to detect predators. Many species of ground-nesting birds must balance tradeoffs between crypticity and visibility, and their patterns of habitat selection often reflect choices to reduce the probability of predation (Gotmark et al. 1995, van der Vliet et al. 2008, Colwell 2010, Gómez-Serrano and López-López 2014).

To better understand how changes in vegetation characteristics may influence nest-site selection and nesting success in these sympatric species, our primary objectives were to: (1) quantify the differences between habitat within territories selected by the two species; (2) quantify the habitat features for each species that influence the selection of nest sites within their nesting territories; (3) determine if any of these features are related to nest success; and (4) assess whether one species is likely to be more vulnerable than the other to climate-related changes in the structure and composition of vegetation. We predicted that both species would compete for and select nest sites away from tall vegetation to increase the ability of the incubating bird to visually detect potential predators. Given previous findings that Americans prefer sparsely vegetated, rocky habitat (Connors et al. 1993), we also predicted that Americans would nest in habitat that allowed better visibility than that selected by Pacifics. We were also interested in determining if interspecific differences in nest-site selection in this region of sympatry would arise primarily from differences in selection of territories, in selection of nest sites within territories, or both. Finally, we predicted higher rates of nest survival at sites with lower vegetation and better visibility. Understanding how these species select breeding habitat, and how this selection affects their reproductive success, will enable us to make predictions about the persistence of each species in response to climate-driven changes to vegetation across their tundra breeding grounds.

1.3 Methods

1.3.1 Study Sites

We studied breeding Americans and Pacifics during the summers of 2012 (May 24–August 6) and 2013 (May 23–August 20) on the southern Seward Peninsula in northwestern Alaska. The Peninsula hosts several groups of rugged, glaciated mountains that are oriented primarily east–west, with peaks of up to 1450 m; rolling hills of the southern uplands grade into low-lying coastal wetlands (Wahrhaftig 1965, Kessel 1989). The entire area is underlain by permafrost that thaws to varying depths during summer, producing numerous thaw lakes in lowland areas, and is drained by many small, meandering rivers (Wahrhaftig 1965). Mesic dwarf shrub meadows dominate the coastal lowlands and transition to drier dwarf shrub mat tundra and sparse vegetation at higher elevations; shrub thickets of varying heights occur along river drainages and on protected slopes (Kessel 1989, Thompson et al. 2016). The interior of the Peninsula has a continental climate with cold, relatively dry winters and short, warm summers; along coastal areas the climate is continental during winter due to sea ice but is maritime, with cooler temperatures and more precipitation, during the ice-free periods of summer (Swanson et al. 1985, Kessel 1989). Along the southern coast at a long-term weather station at Nome (64.5111° N, 165.44° W), 6 to 60 km from our study sites, daily low temperatures averaged 6.5 °C during June through August from 1981–2010; daily highs averaged 13.5 °C (www.usclimatedata.com).

We monitored nests of both species of golden-plover on 6 study areas across an elevational gradient, ranging from sea level to ~400 m: Woolly Lagoon (64.867° N, 166.302° W; 322 ha; elevation range 28–216 m; in 2013 only), Blume Creek (64.846° N, 166.086° W; 719 ha; 134–310 m), Feather River (64.819° N, 166.025° W; 1426 ha; 135–391 m), Mile 16 (64.628° N, 165.717° W; 200 ha; 147–239 m), Anvil Mountain (64.562° N, 165.39° W; 65 ha; 170–311 m),

and Nugget Creek (64.895° N, 165.216° W; 679 ha; 187–416 m). Three of the study areas (Feather River, Nugget Creek, Wooly Lagoon) had been included in earlier studies of golden-plover demography and speciation (Connors 1983, Johnson et al. 1993, Johnson et al. 2018). Study areas encompassed a variety of habitats, including lichen-dominated alpine meadows, ericaceous tundra, low shrubland (<3 m), tall shrubland (>3 m), grassy meadows, birch-willow hillsides, and granitic alpine ridges. Dominant plant species included dwarf birch (*Betula nana*), willow (*Salix* spp.), grasses/sedges, crowberry (*Empetrum nigrum*), blueberry (*Vaccinium uliginosum*), and mosses. In addition to the rock-dominated alpine ridges, many sites were also peppered with rocks and patches of bare ground. Nest predators included red fox (*Vulpes vulpes*), weasel (*Mustela* spp.), reindeer (*Rangifer tarandus tarandus*), gulls (*Larus* spp.), Common Raven (*Corvus corax*), Parasitic Jaegers (*Stercorarius parasiticus*), and Long-tailed Jaegers (*S. longicaudus*). Red foxes were the primary nest predators in most areas, with jaegers being an additional important nest predator at the Wooly Lagoon study area.

1.3.2 Field Methods

Nesting habitat. We systematically searched for nests from late May through late July by walking evenly spaced transects, approximately 20 m apart to ensure full overlap, across our study areas and following adults exhibiting nesting behaviors back to their nests. Nest locations were recorded using handheld GPS units. We marked nests with small rock cairns located 2 m from the nest to enable the relocation of nests while avoiding the attraction of predators. For each nest, we measured habitat characteristics within one quadrat (0.5 m × 0.5 m) centered on the nest site (to represent microhabitat at the nest) and a second quadrat at a paired point randomly selected from within a 350 m radius of the nest site (to represent habitat available in

the territory; Johnson et al. 2018). Within each quadrat, we estimated the percent cover and mean height of the following habitat components: alder (*Alnus* spp.), willow (>50 cm), dwarf willow (≤ 50 cm), dwarf birch, cinquefoil (*Potentilla* spp.), *Dryas* (*Dryas* spp.), ericaceous plants (Ericaceae), herbaceous plants, graminoids, moss, lichen, rock, and bare ground. We also estimated percent cover of water and detritus (i.e., leaf litter). We recorded cover using modified Daubenmire (1959) cover classes (0, 1–5, 6–25, 26–50, 51–75, 76–95, and 96–100%). We sampled habitat after nesting was completed to avoid disturbing nesting birds. We used geographic coordinates of nests and random points to determine their elevation from the Alaska IfSAR Digital Elevation Model (DEM) Data, which has a vertical accuracy of 3 m and horizontal accuracy of 12.2 m provided by the Geographic Information Network of Alaska (GINA, gina.alaska.edu).

Nest success. When we discovered a nest, we floated the eggs to estimate the incubation stage (Liebezeit et al. 2007). We then monitored the nest every 4–7 days throughout incubation (~27 days from laying to hatching of the first egg; Johnson et al. 2018) until eggs were within 5 days of their predicted hatch date, after which we visited them every 1–2 days until hatch occurred or the nest failed. We classified a nesting attempt as successful if at least one egg hatched or if pipped eggshell fragments were found in the nest cup. A nesting attempt was considered failed if (1) addled eggs were present in the nest cup; (2) eggs disappeared prior to the estimated hatch date (assumed lost to predation); (3) a depredation event was observed; or (4) eggs were found abandoned in the nest cup after 27 or more days of incubation had occurred.

1.3.3 Data Analyses

Breeding phenology. We used the function ‘glm’ in Program R (R Core Team 2013) to compare nest initiation dates between species and years using linear models; we analyzed ranked data because the dates were highly skewed. The candidate model set included *species*, *year*, *year+species*, *year*species*, and the null model. We used Akaike’s Information Criterion corrected for small sample size (AIC_c , Burnham and Anderson 2002) to evaluate relative support for models within the candidate set and considered models with $\Delta AIC_c < 2$ to be competitive in the absence of uninformative parameters (Arnold 2010).

Nest-site selection. To determine percent cover of each habitat component within a quadrat, we assigned the midpoint of its cover class for analysis (0, 2.5, 15, 37.5, 62.5, 85, and 97.5%); we excluded alder and water because they were rarely encountered. We collapsed height measurements of each plant species into a single variable that represented the maximum mean height of any vegetation in the quadrat. Using all quadrats from nest and random sites, we then conducted a principal components analysis to reduce highly correlated habitat variables into fewer components that represented major habitat features. All habitat measurements were standardized (mean of 0 and standard deviation of 1) before analysis. We retained the top 5 principal components (PCs) with eigenvalues > 1 and constructed a series of logistic regression models to test the following: (1) broad-scale differences between the two species in habitats selected at the territory scale using data from the random sites; (2) habitat features associated with nest-site selection within territories for each species separately using data from nest sites and random sites; and (3) differences between the two species in habitat characteristics of nest sites using nest-site habitat data only. Preliminary logistic regression analysis for each of the 4 global models (i.e., models including all 5 PCs) indicated that the 95% confidence intervals of

parameter estimates for *PC4* and *PC5* both included zero (i.e., had no association with habitat selection). We thus developed a candidate model set for each analysis that included a null model containing only an intercept, a global model with all 5 PCs, and models with all possible combinations of *PC1*, *PC2*, and *PC3*.

We used the function ‘glm’ in Program R for interspecific comparisons of random sites (representing territories) and nest sites and we conducted goodness-of-fit tests to assess model fit (R function ‘lrm’; Harrell 2015). To compare nest sites and paired random sites within territories for each species, we used a conditional logistic regression model (i.e., case-control logistic regression) that also included individual nest identification as a random effect to account for lack of independence (R function ‘clogit’; Therneau 2014). We used AIC_c to evaluate relative support for models within each candidate set. To elucidate important vegetative differences underlying the principal components analysis, we used univariate Wilcoxon tests to compare elevation, vegetation height, and cover of specific vegetation types for interspecific differences in territories and nest sites (unpaired comparisons) and between nest sites and random sites within territories for each species (paired comparisons). We corrected *P*-values for multiple comparisons within each group. We tested for homogeneity of variance for each habitat variable using Bartlett’s test for evidence of differences in selectivity other than in central tendency (Bartlett 1937).

Nest success. We developed models to estimate daily survival rates (DSR) of nests and evaluate variation associated with habitat characteristics at the nest site and other factors using the nest survival module in Program MARK (White and Burnham 1999, Dinsmore 2002). We excluded abandoned nests from nest survival analysis to preclude possible effects of observers; in total, 44 nests of Americans and 53 nests of Pacifics were included in our models. We

developed a candidate model set composed of the explanatory variables that we hypothesized to have important effects on nest survival. We included species (*species*) and 3 explanatory variables to account for temporal effects: nest age (*age*), day within season (*day*), and year (*year*). We included elevation at the nest site (*elevation*) and maximum mean height of vegetation (*maxavght*) to test for effects of inclement weather and predation related to elevation and concealment of nests. Finally, we considered *PC1*, *PC2*, and *PC3* to investigate potential effects of major habitat features. In the candidate model set, we included models with simple main effects of all 9 variables individually; 6 two-way additive combinations of species, age, day, and year; 4 two- and three-way additive combinations of *PC1*, *PC2*, and *PC3*; and the null model for a total of 20 models. We used an information theoretic approach for model selection and considered models with $AIC_c < 2$ to be competitive; we assessed the relative importance of predictor variables by summing Akaike weights (w_i) across all models in which they occurred (Burnham and Anderson 2002). Estimates for parameters are presented as (β : 95% CI).

1.4 Results

1.4.1 Weather and Breeding Phenology

Spring weather conditions during 2013 were colder and snowier than during 2012. Average daily temperatures in May 2012 (mean high of 4.8 °C, mean low of -3.5 °C), were warmer than those in May 2013 (mean high of 2.8 °C, mean low of -3.7 °C) at a nearby weather station in Nome, Alaska (www.usclimatedata.com). However, May temperatures during both years were colder than long-term average temperatures during May from 1981–2010 (mean high of 6.2 °C, mean low of -0.8 °C). Average snow depth in May 2013 (9.8 cm) was nearly double the snow depth recorded in May 2012 (5.8 cm). The same pattern held true for total precipitation (May 2012:

22.4 mm; May 2013: 45.8 mm). Total snow in May 2012 was 2.4 cm and total snow in May 2013 was 27.6 cm. The first snow-free dates were May 11, 2012, and May 25, 2013.

During the two-year study, we found a total of 114 nests: 55 Americans (26 in 2012, 29 in 2013) and 59 Pacifics (17 in 2012, 42 in 2013). The increase in Pacific nests between years can be attributed to the addition of a low-elevation study plot and a larger field crew (increase from 2 full-time crew members in 2012 to 4 in 2013). During 2012, estimated initiation dates for nests, including renests, spanned from May 21–July 9 for Americans, and from May 24–July 22 for Pacifics. During 2013, nest initiation was later and more compressed for both species, ranging from May 29–June 25 for Americans and from May 29–June 30 for Pacifics (Figure 1.1). The model with greatest support explaining variation of nest initiation dates was the interactive model *species*year* ($K = 5$, $AIC_c = 1098.55$); however, the additive model had almost equal support with $\Delta AIC_c = 0.10$. The median nest initiation date for Americans was May 29 in 2012 and June 5 in 2013; the median nest initiation date for Pacifics was June 4 in 2012 and June 7 in 2013.

1.4.2 Nesting Habitat

We measured habitat characteristics at 53 American and 58 Pacific nests. Nests were located across a range of elevations (28–416 m) and the two species overlapped in their distribution across the study area. The first 5 principal components all had eigenvalues greater than 1 and together explained 57% of the variance in the 13 variables used to describe nesting habitat (Table 1.1). *PC1* was primarily correlated with variables related to vegetation height and represented a gradient ranging from xeric, granitic, alpine sites with low-stature vegetation (negative values) to mesic, low-elevation meadows dominated by taller vegetation with mosses, graminoids, and willows (positive values). *PC2* represented a gradient ranging from lichens and ericaceous

shrubs (negative values) to rock (positive values). *PC3* represented a gradient ranging from low elevation with herbaceous vegetation to high elevation with bare ground (Figure 1.2). *PC4* represented a gradient from areas devoid of vegetation to areas covered by xeric herbs (*Dryas* and cinquefoil). Finally, *PC5* represented a gradient from tall vegetation with dwarf birch and xeric herbs to low vegetation with dwarf willows.

Interspecific comparison of territories. The best-supported model discriminating between habitat within territories of the two species included both *PC1* and *PC2*, which had 300 times more support than the null model ($\Delta AIC_c = 11.43$; Table 1.2, Figure 1.3). As evidenced by summed AIC_c weights across the model set, there was strong support for interspecific differences in *PC1* (0.99) and *PC2* (0.92) but less so for *PC3* (0.48). A goodness-of-fit test indicated that the top-ranked model fit the data well ($P = 0.41$). As *PC1* increased, the probability of use for a territory by Pacifics increased, whereas it decreased for Americans ($\beta_{PC1} = 0.33: 0.12, 0.54$). In contrast, as *PC2* increased, the probability of use for a territory by Pacifics decreased and increased for Americans ($\beta_{PC2} = -0.35: -0.62, -0.08$). Along the gradients represented by *PC1* and *PC2*, territories occupied by Americans were higher in elevation and had more rock and less graminoid vegetation than territories used by Pacifics.

Interspecific comparison of nest sites. The best-supported model discriminating between nest-site habitat of the two species included *PC1*, *PC2*, and *PC3* (Table 1.2, Figure 1.4), with strong support for all three components (AIC_c weights of 0.99, 0.99, 0.97, respectively). The null model of no interspecific differences in habitat at nest sites had virtually no support ($\Delta AIC_c = 46.65$). Nest sites were more likely to be those of Pacifics than Americans as values of *PC1* increased ($\beta_{PC1} = 1.37: 0.60, 2.13$), *PC2* decreased ($\beta_{PC2} = -1.06: -1.70, -0.41$), and *PC3* increased ($\beta_{PC3} = 1.05: 0.32, 1.78$). General characteristics of nest sites differed between the two

species in patterns that were similar to the differences found at the scale of the territory (Figure 1.5). Nest sites of Americans were significantly higher in elevation (median 268 m, range 125–416 m) than nest sites of Pacifics (median 212 m, range 28–347 m) (Figure 1.6A, Wilcoxon $P < 0.001$), corresponding to the differences in elevation in their territories. In addition, nest sites of Americans were surrounded by vegetation that was significantly lower in stature than vegetation around Pacific nests (Figure 1.6B, Wilcoxon $P < 0.001$). American nest sites had significantly more rock, more ericaceous plants, and less graminoid cover than those of Pacifics (all Wilcoxon $P < 0.001$).

Nest-site selection. There was strong evidence of nest-site selection within territories for both species ($\Delta AIC_c > 14$ for null models; Table 1.2). For Americans, the model explaining nest-site selection within territories that received the most support was $PCI+PC2+PC3$; however, the global model and $PCI+PC3$ were also competitive (Table 1.2, Figure 1.5, Figure 1.7A). Summed AIC_c weights confirmed the relative importance of PCI (1.0), $PC2$ (0.76), and $PC3$ (0.89). Although there were many differences between nest sites and random sites within territories (Figure 1.8), the strongest evidence for selection ($P < 0.001$) was for avoidance of tall vegetation and tall willows at the nest site (Table 1.3).

The model that best discriminated nest sites from random sites within territories of Pacifics included only PCI , although $PCI+PC2$ was also competitive (Table 1.2, Figure 1.5). Summed AIC_c weights indicated the greater importance of PCI (0.99) compared to $PC2$ (0.32) and $PC3$ (0.27). For Pacifics, the strongest evidence for selection ($P < 0.001$) was for nest sites with more bare ground and less tall vegetation and tall willows than available within their territories (Figure 1.9D, Table 1.3).

1.4.3 Nest Survival

There was relatively little support of DSR varying in relation to any of the explanatory variables we considered. The most parsimonious model, based on AIC_c values, included the additive effects of *year* and *age* (Table 1.4); however, 95% CIs around estimates for these parameters slightly overlapped zero ($\beta_{YEAR2013} = 0.47$: -0.14, 1.08; $\beta_{AGE} = -0.03$: -0.08, 0.01), precluding strong inference of these effects. Parameter estimates for explanatory variables in all other models with $\Delta AIC_c < 2$ included zero (i.e., no effect) in their 95% CIs, as indicated by the inclusion of the constant survival model in this group of models (Table 1.4). The most supported model that included *species* received little support from the data ($\Delta AIC_c = 2.17$) and nest DSR values estimated for each species from this model were similar (Figure 1.10). However, between years, DSR was marginally lower in 2012 than 2013. Additionally, DSR decreased with age over the course of the summer in both years (Figure 1.10). From the constant model, nest daily survival rate was 0.966 (95% CI: 0.954, 0.974). Given the average incubation period of 27 days, the probability of a nest surviving to hatch at least one egg was 0.39 (95% CI: 0.28, 0.49).

1.5 Discussion

In our study, American and Pacific Golden-Plovers breeding within the zone of sympatry selected nest sites that differed significantly in several important aspects along an elevational gradient, confirming the general patterns first described by Connors et al. (1993). The two species partitioned niches by first selecting territories that differed from one another, and then selecting nest sites that differed further in composition and structure from their surrounding nesting territories. Spatial niche partitioning, through habitat selection, is the primary way in which two very similar, competitive species can coexist (Schoener 1974). Neighboring males of

these two plover species frequently engage in interspecific territorial disputes, including aerial chases, ground displays, and fights, especially early during the breeding season, providing strong evidence of direct competition (Connors et al. 1993, K. S. Overduijn personal observation). During the year with earlier spring phenology, we found that Americans nested slightly earlier than Pacifics. Thus, temporal differences in settling patterns may also contribute to interspecific differences in selection of nesting habitat.

Contrary to our predictions, however, although niche partitioning did occur, none of the habitat features selected at nest sites and that we measured had a significant impact on nest survival. Furthermore, although features of nest sites differed between the two species, there was no interspecific difference in nest success. This was surprising because the features of nest sites most strongly selected, including preference for rocky areas and avoidance of tall willows and other vegetation, are all conducive to maximizing visibility around the nest. A study of several shorebird species nesting on arctic Alaskan tundra found that nest-site selection was commonly influenced by a combination of habitat features and social factors operating at various spatial scales (Cunningham et al. 2016). As on our study area, microscale-habitat features selected on arctic tundra by Americans likely facilitated their tactic for evading predators through early visual detection and distraction (cf. Byrkjedal 1989). Enhanced visibility would be advantageous for detecting mammalian predators within nesting territories (Gotmark et al. 1995, Koivula and Rönkä 1998, Amat and Mosero 2004, Gómez-Serrano and López-López 2014). Unlike grassland passerines, which select nest sites based on the amount of vegetation located around the nest site to aid in the concealment of the nest (Davis 2005), plovers select open nest sites on flat or gently sloping ground and avoid nesting on steep slopes (Whittingham et al. 2002, Nguyen et al. 2003). Selection for open nest sites may represent a trade-off between concealment of the nest and

increased visibility of the surrounding area to avoid predation on the incubating adult, not the eggs (Gotmark et al. 1995, van der Vliet et al. 2008, Gómez-Serrano and López-López 2014). This lack of a relationship between habitat covariates and nest success is similar to that found in some other nesting shorebirds (Nguyen et al. 2003, DeRose-Wilson et al. 2013).

Selection of nesting territories and nest sites may have little adaptive relationship to nest success in a given year. Both of our study species exhibit male-biased site fidelity to their breeding territories (Johnson et al. 1993, 1997). These long-lived, site-faithful shorebirds likely use informed site fidelity, or the “win–stay:lose–switch” rule (Schmidt 2004, Chalfoun and Schmidt 2012) when selecting their nesting territories. Use of the same nest cup between seasons has also been documented (Johnson et al. 2018). Because they are site faithful, it is possible that decisions on habitat selection are based on long-term experience rather than short-term success. Individuals may also have the plasticity to be able to select suitable nesting habitat from among many potential sites within their territories with no reproductive cost (Porzig et al. 2018).

Plovers nesting in open habitats also employ the strategy of selecting nest sites to optimize egg crypsis for concealment (Nguyen et al. 2007). Plover eggs have a mottled pattern that enable them to be camouflaged easily on rocky, bare, or lichen-covered ground (Johnson et al. 2018). The crypticity of the eggs is important because adults defend nests by leading potential predators away using a variety of distraction displays. When they do this, they often leave the open nest unattended and rely heavily on the ability of the eggs to blend in with their surroundings.

At the territory scale, open tundra habitats may allow nonincubating mates to feed and at the same time be vigilant of their surroundings. In areas of increased vegetative cover, adults may increase time devoted to vigilance, which decreases time spent on other behaviors such as

feeding; this could affect the quality of the parent, potentially resulting in lower nest and brood survival (Metcalf 1984). This could lead to a lack of congruence between nesting territory selection and reproductive success because the adaptive preference is dependent on the quality of the parent to aid in the protection of its nest and subsequently its brood (Chalfoun and Schmidt 2012). Because we did not test predation pressure or measure parental condition directly in this study, we are uncertain of the degree to which nest survival was influenced by predation or parental quality.

Selection of territories and nest sites may both have been influenced by patterns of snowmelt. In northern Alaska, snowmelt starts in the mountains and foothills and proceeds toward the coast (D. A. Walker pers. comm. 2018). Because both species typically arrive on the breeding grounds while there is still snow on the ground, it is possible that birds are selecting the first available habitats on which to nest rather than selecting for more specific attributes. For instance, open lichen habitat is the first to become free of snow in the spring and is well-drained and thus less prone to inundation from precipitation (Byrkjedal 1989), whereas lower, wetter areas are last to become snow-free (Cunningham et al. 2016). On our study area, spring conditions in 2012 were significantly warmer and tundra became snow-free earlier than in 2013. Both species began nesting concomitantly earlier during 2012, with Americans initiating nests slightly earlier than Pacifics. By comparison, nesting was delayed and more compressed for both species in 2013. Despite earlier nest initiation in 2012, nest success for both species was slightly lower that year; one explanation is that the warmer conditions in 2012 advanced plant growth to the detriment of the ability of incubating adults to detect predators. However, because we waited to measure vegetation until after the last nests had hatched to avoid disturbance, our

measurements may not have been sensitive enough to detect subtle seasonal effects of vegetation height.

Both Americans and Pacifics avoided tall willows and other tall vegetation when selecting nest sites within their nesting territories; however, patches of dense dwarf shrub cover (height ≤ 0.5 m) often occurred within territories, particularly of Pacifics. These plovers must select territories to meet multiple needs, including maximizing their own survival in addition to survival of their nests and broods. Selection of habitat at the scale of the territory may be more important than that at the nest site because selection that includes habitat and resources for the chick's survival could be driving population dynamics more than nest survival. After leaving the nest, chicks use brood-rearing territories for at least three weeks before fledging (K. S. Overduijn personal observation); therefore, food resources and ground cover that enhances crypticity of young are also important to their survival. The downy, mottled plumage of the growing chicks provides camouflage against a moss and lichen substrate. Parents sound an alarm call when a predator approaches and chicks then lie flat on the tundra, motionless, until the parents signal that it is safe. Minimal shrub cover could be important for young that are hiding, as it provides an extra barrier between the small birds and a potential predator. However, shrubs that are too tall or too dense could be detrimental because they are difficult for plover chicks to navigate and they provide more places where mammalian predators can hide, undetected by protective plover parents.

Despite the differences we found in habitat selection at two different spatial scales, Americans and Pacifics had nest survival rates (0.39, 95% CI: 0.28, 0.49) similar to those of other arctic-nesting shorebirds (sandpipers and plovers; Pearce-Higgins and Yalden 2003). In a concurrent study on the Seward Peninsula (Kwon 2016), survival rates of nests ranged between

0.34 and 0.46 for Western (*Calidris mauri*) and Semipalmated (*C. pusilla*) Sandpipers and between 0.18 and 0.33 for Red-necked Phalaropes (*Phalaropus lobatus*); these birds experienced predation pressure and weather patterns similar to those on our study area.

In both years, we found that DSR decreased slightly with age of the nest. In precocial species, analysis of nest age has shown varying results ranging from no effect to decreasing with age (DeRose-Wilson et al. 2013) to increasing with age (Wilson et al. 2007). In Mountain Plovers (*Charadrius montanus*), the increase in DSR with age of the nest was attributed to the early loss of the most vulnerable nests (Dinsmore et al. 2002). Alternatively, DSR can increase with nest age if the incubating adults become more invested in and protective of their nests as eggs develop. This is especially apparent in studies of biparental incubators (Smith and Wilson 2010). Perhaps the decrease in DSR that we observed was attributable to increases in height of vegetation as nests aged. As incubation progressed, plant growth could have led to an obstructed view for the incubating adult, thereby increasing vulnerability to predation from mesopredators that could approach nest sites undetected.

Climate-change projections in the Arctic suggest that the structure, stature, and spread of shrubs will increase as temperatures increase over time (Post et al. 2009, Myers-Smith et al. 2011, Myers-Smith and Hik 2018). Improved conditions for increased vegetation growth suggest that tundra-nesting species, such as plovers, that rely on sparsely vegetated nest sites could be adversely affected through a loss of available nesting habitat. To adjust to loss of nesting habitat, birds must have the flexibility to fine-tune habitat selection at multiple scales. Though we did not find a relationship between nest survival and habitat characteristics in this study, we did find that both plover species showed strong evidence of habitat selection in terms of avoidance of tall shrubs at nest sites. This finding (from a short-term study) may add to other long-term studies

suggesting that some species are able to adjust nesting habitat selection in relation to changing climatic conditions (Porzig et al. 2018), at least in the immediate future. Based on our examination of nest-site selection and nest survival between Americans and Pacifics, both species will likely be challenged in the future by declines in Arctic tundra habitats but may show some flexibility to adapt through multi-scale adjustments in habitat selection. However, though they may be able to make these habitat adjustments, it will be vital to continue researching other aspects of the breeding ecology of these species to gain an understanding of their overall reproductive success. For example, as areas of high latitude continue to warm, crypticity could be compromised as shrub expansion occurs and milder winters accelerate hydrological changes that cause lichen-dominated substrate (as well as bare ground and rocky substrates) to be replaced with more vegetated substrates (Vuorinen et al. 2017). The influence of habitat selection on survival during the brood-rearing period is also important to consider and may give us better insights into the population dynamics of these species in a changing climate.

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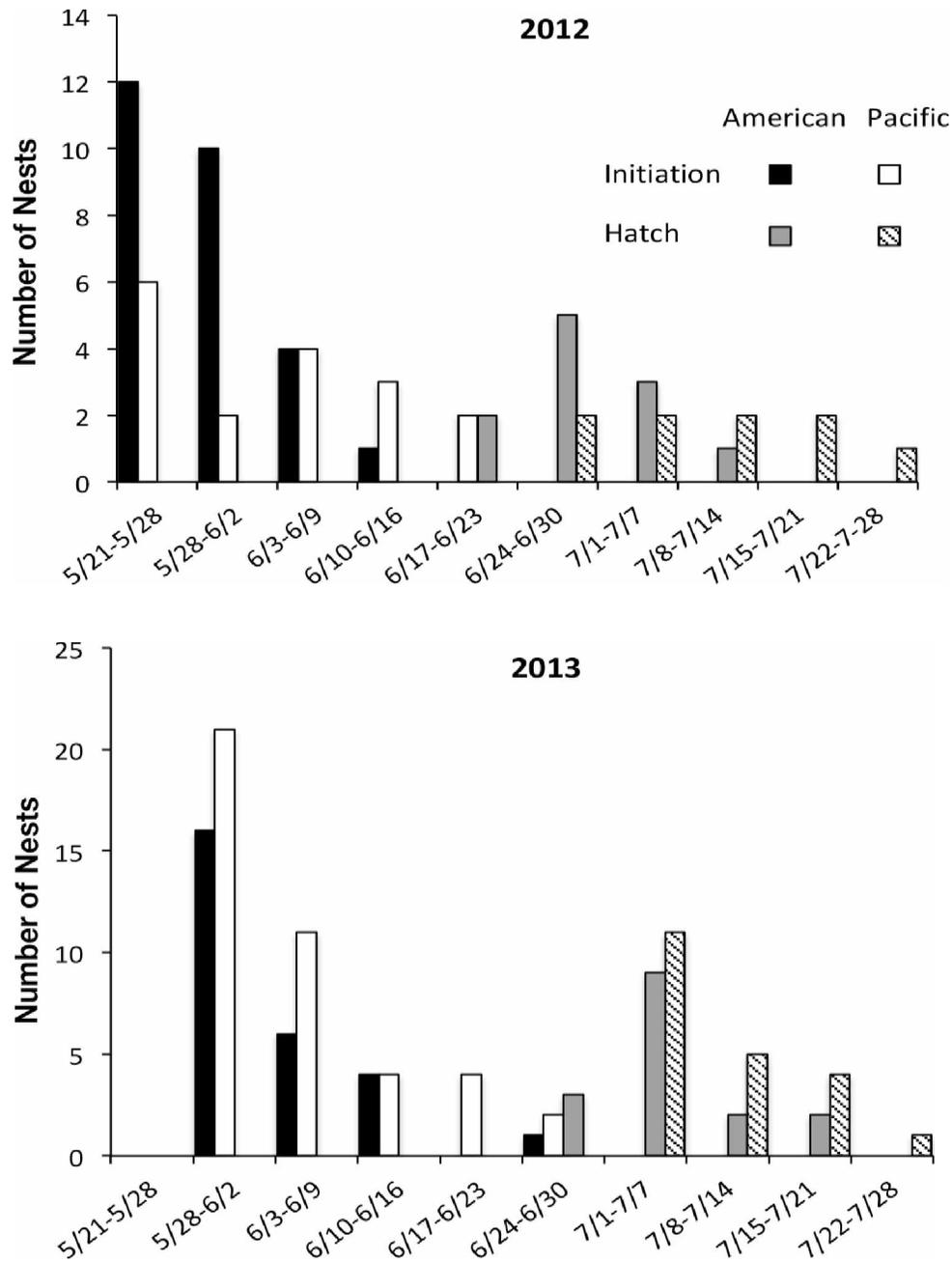


Figure 1.1. Timing of nest initiation and hatch for American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. The data were binned into 6-day intervals to correspond with how often the nests were checked (every 4 to 7 days). Initiation for both species began one week later in 2013 than in 2012. Additionally, initiation and hatch were more synchronous in 2013 than 2012.

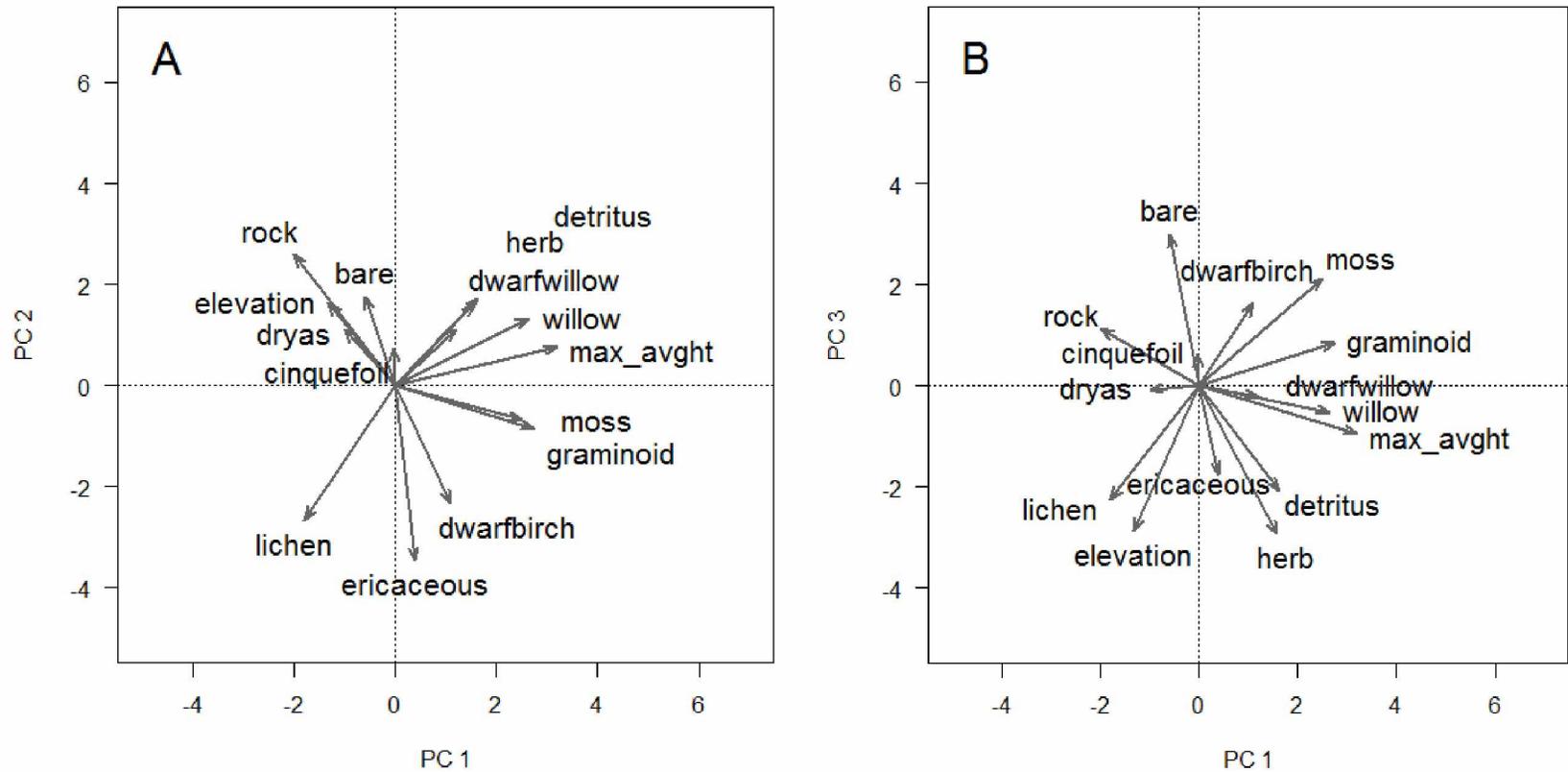


Figure 1.2. Bivariate plots of 15 habitat variables along principal component axes based on measurements at nest sites and at paired random sites within territories of American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. (A) PC1 and PC2 and (B) PC1 and PC3. Sample sizes: American ($n = 53$) and Pacific ($n = 58$).

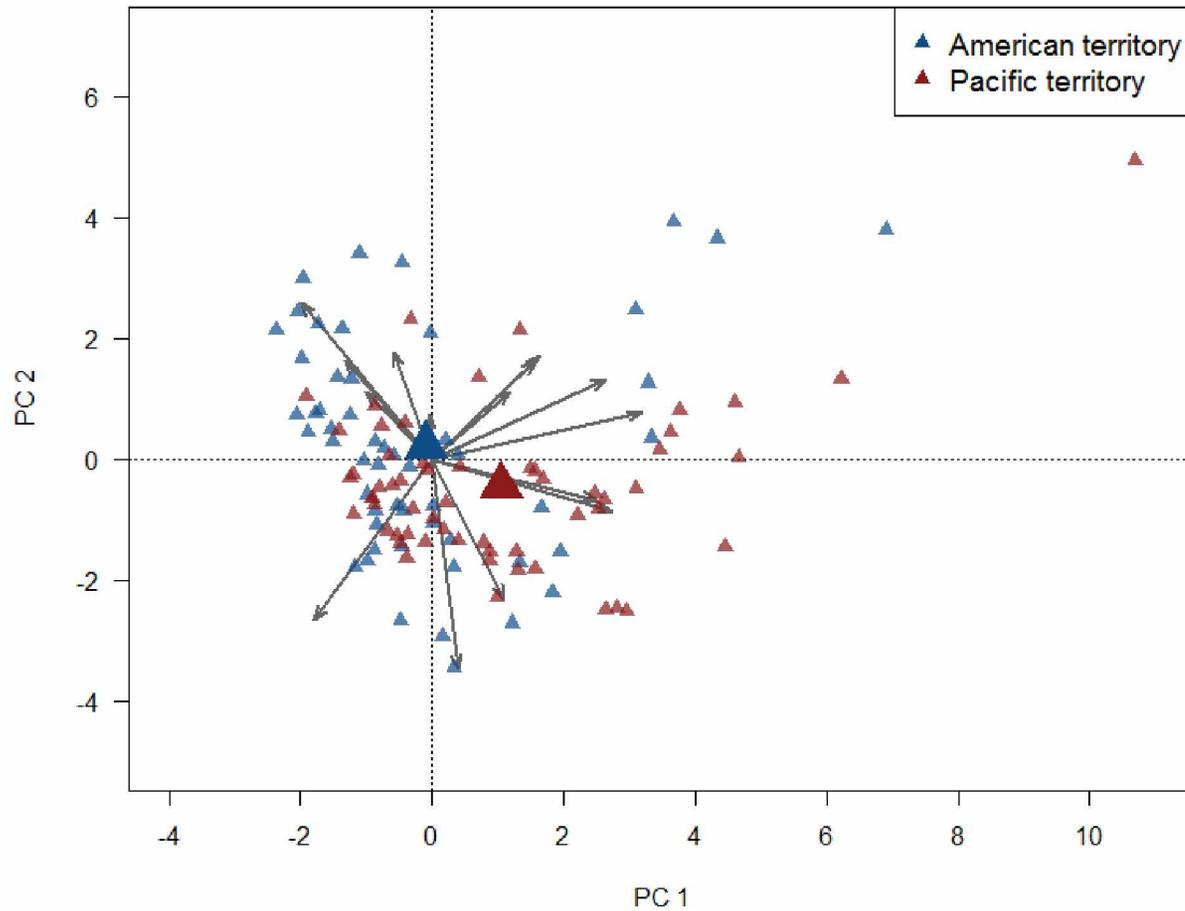


Figure 1.3. Comparison of habitat at random sites within territories used by American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013, along principal component axes PC1 and PC2. Large symbols depict median values.

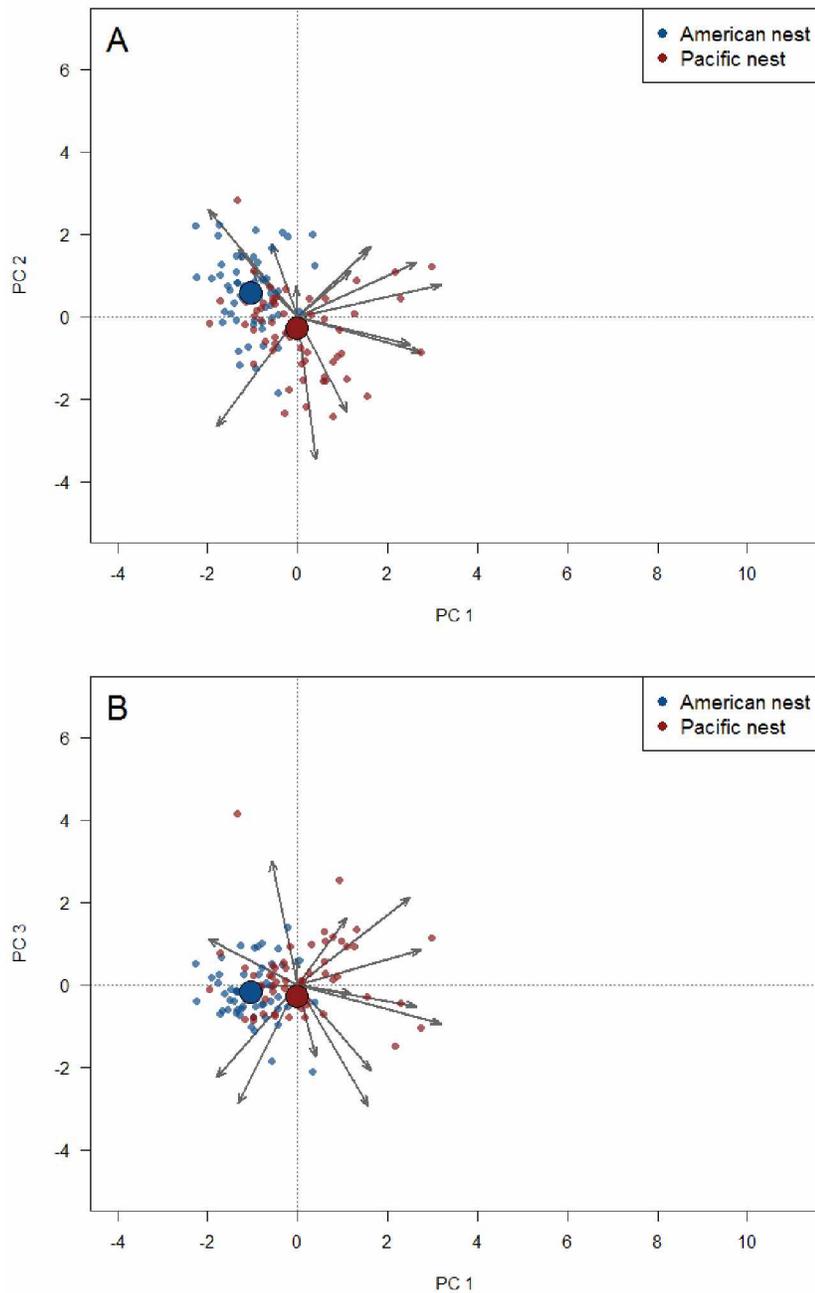


Figure 1.4. Comparison of habitat at nests of American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013, along principal component axes PC1, PC2, and PC3. (A) PC1 and PC2 and (B) PC1 and PC3. Large symbols depict median values.

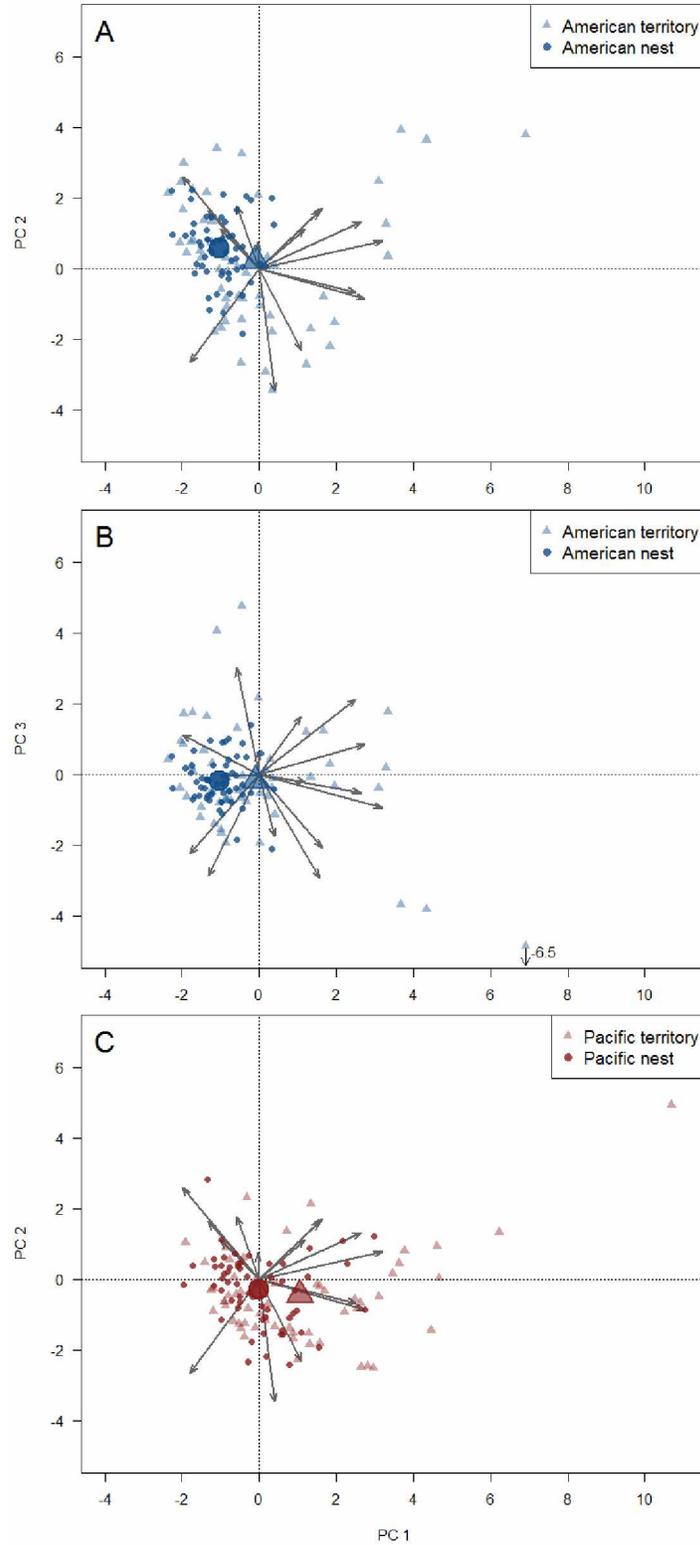


Figure 1.5. Comparison of habitat at nests and within territories of (A, B) American and (C) Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013, along principal component axes PC1, PC2, and PC3. Large symbols depict median values. Small arrow shows extreme outlier for PC3.

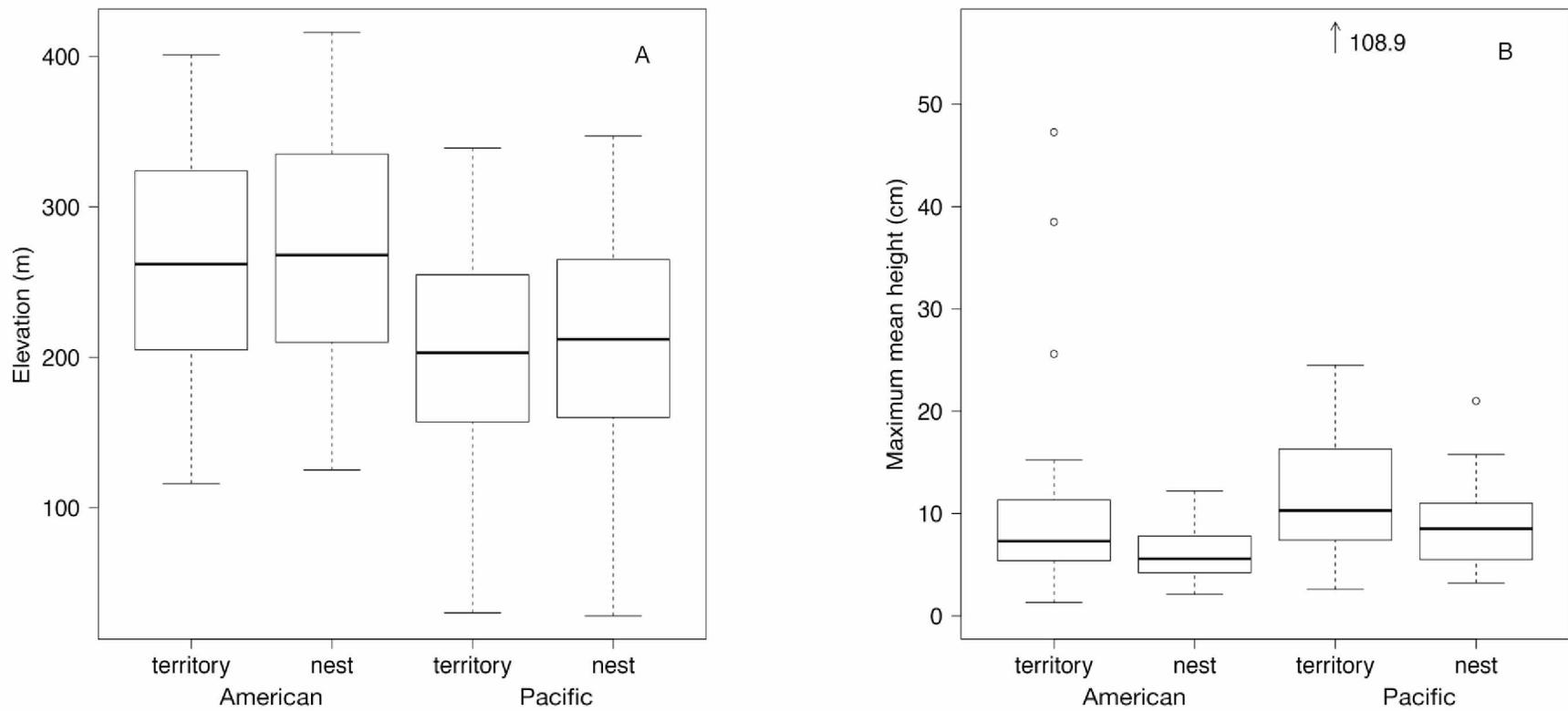


Figure 1.6. Boxplots of (A) elevation (m) and (B) maximum average height of vegetation (cm) surrounding nest sites and at paired random sites within territories of American ($n = 53$) and Pacific ($n = 58$) Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. Bold horizontal line depicts the median, box encompasses interquartile range (IQR), whiskers include 1.5 times IQR, and open circles depict outliers. The value with an arrow denotes an extreme outlier.

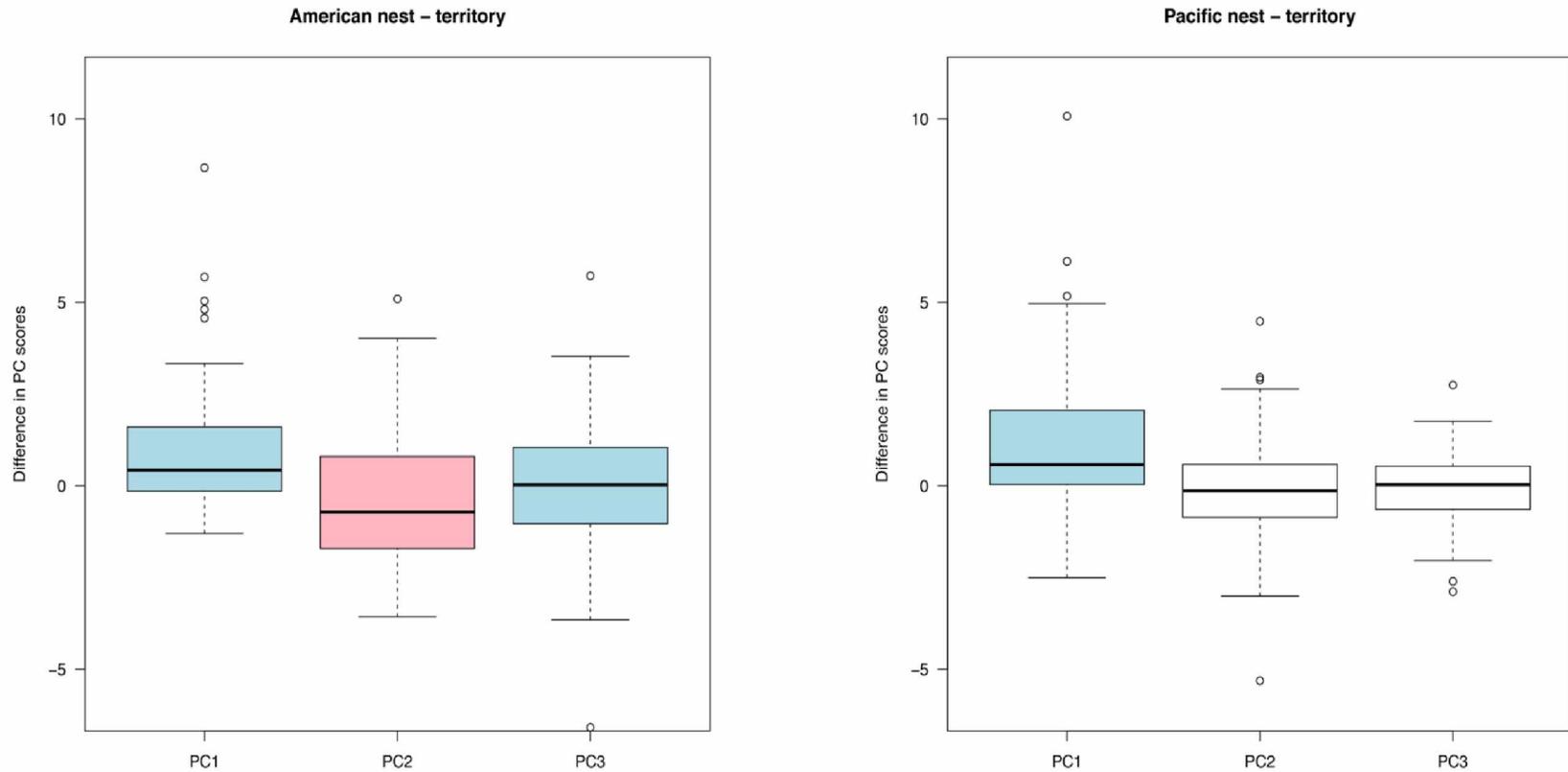


Figure 1.7. Differences in principal component (PC) scores between (A) American and (B) Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. The colors indicate that differences in PC scores between nests and territories were significantly positive (blue), significantly negative (pink), or nonsignificant (white) based on paired Wilcoxon tests.

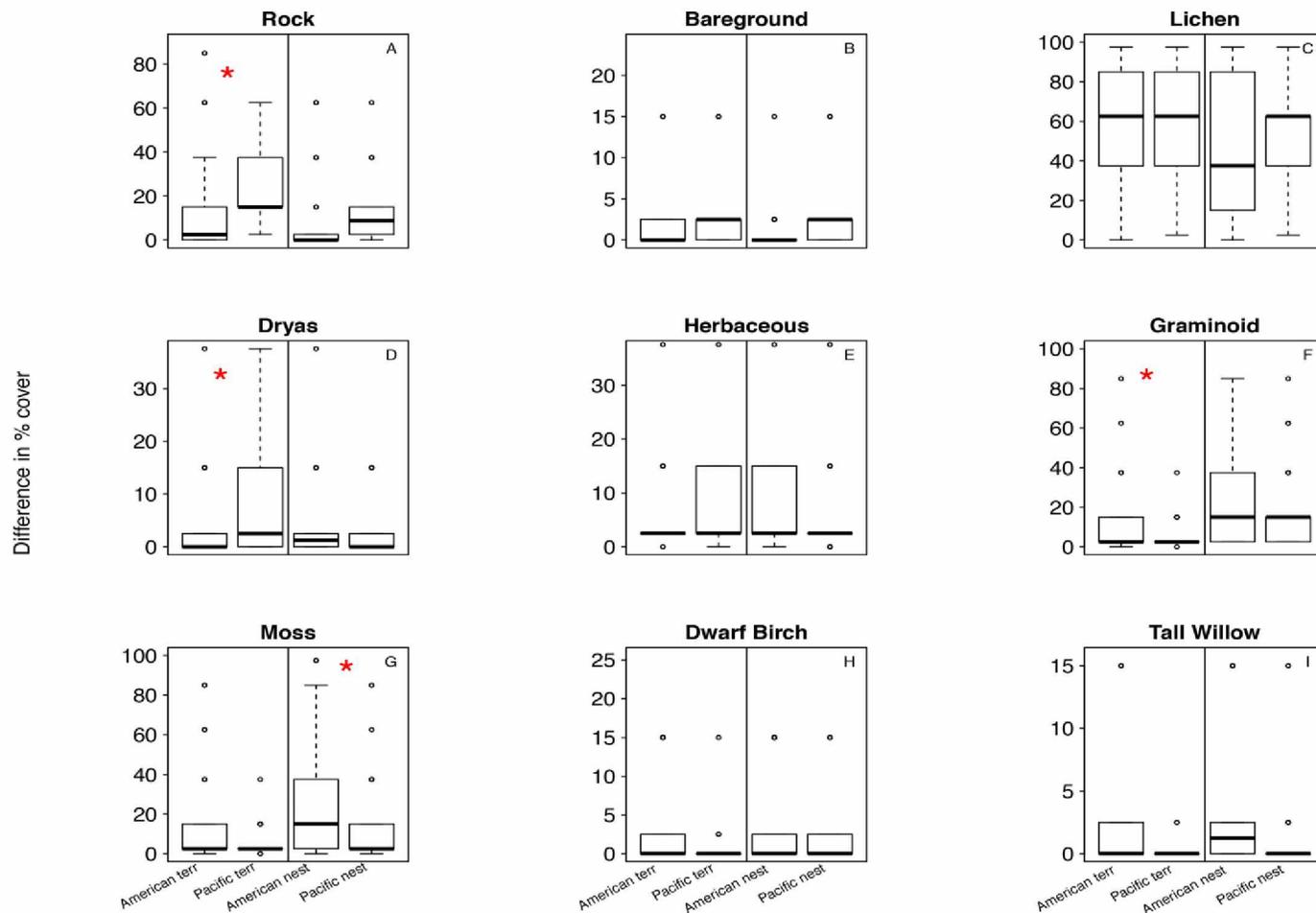


Figure 1.8. Boxplots of the most important variables that describe habitat cover around nest sites and at paired random sites within territories of American ($n = 53$) and Pacific ($n = 58$) Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. Bold horizontal line indicates the median, box encompasses interquartile range (IQR), whiskers include 1.5 times IQR, open circles represent outliers, and red asterisks indicate significant differences between species based on Wilcoxon tests.

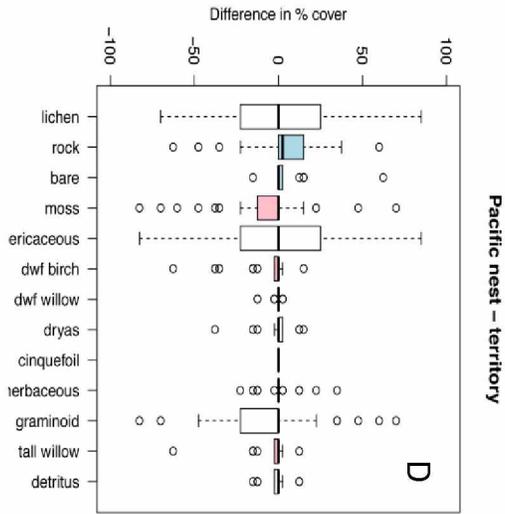
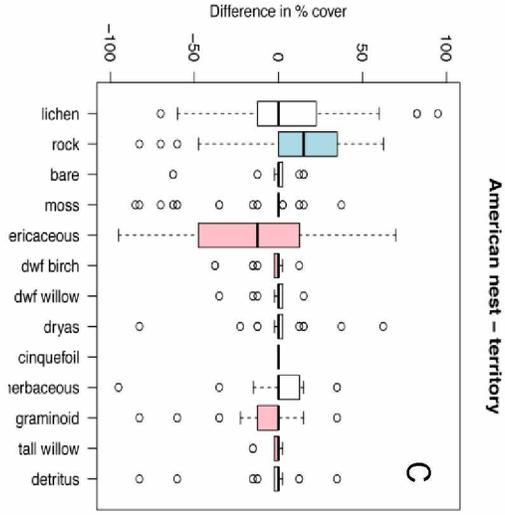
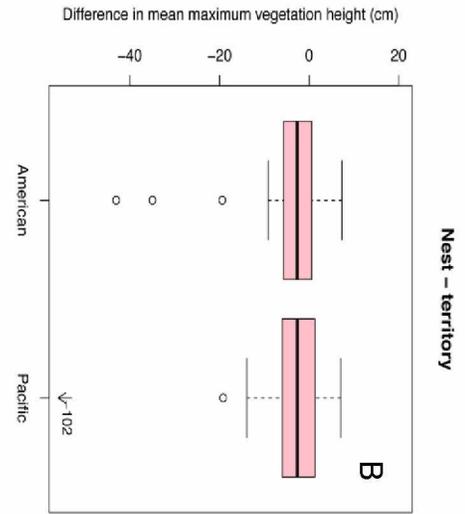
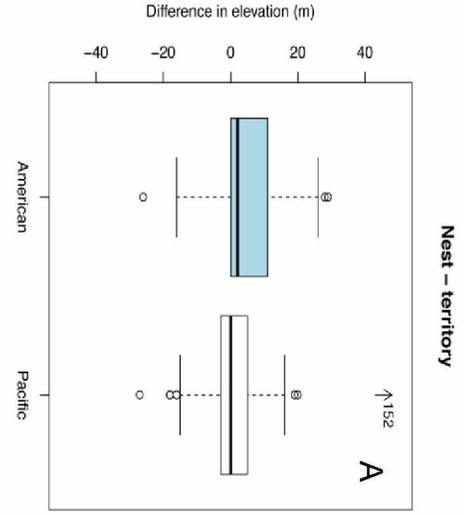


Figure 1.9. Boxplots of differences between habitat at nest sites and habitat at paired random sites within territories of American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. Bold horizontal line depicts the median difference, box encompasses interquartile range (IQR), whiskers include 1.5 times IQR, and open circles depict outliers. Values with arrows denote extreme outliers. Colors indicate that a habitat characteristic was significantly greater (blue) or lower (pink) at nest sites than within territories based on paired Wilcoxon tests. **(A)** Americans selected nest sites that were significantly higher in elevation than their surrounding territories but Pacifics did not. **(B)** Both species selected nest sites with vegetation that was significantly lower in height than was available in their surrounding territories. **(C)** Nest sites of Americans had significantly more rock and less ericaceous vegetation, dwarf birch, graminoids, and tall willow than available in territories. **(D)** Nest sites of Pacifics had significantly more rock and bare ground and less dwarf birch and tall willow than available in territories.

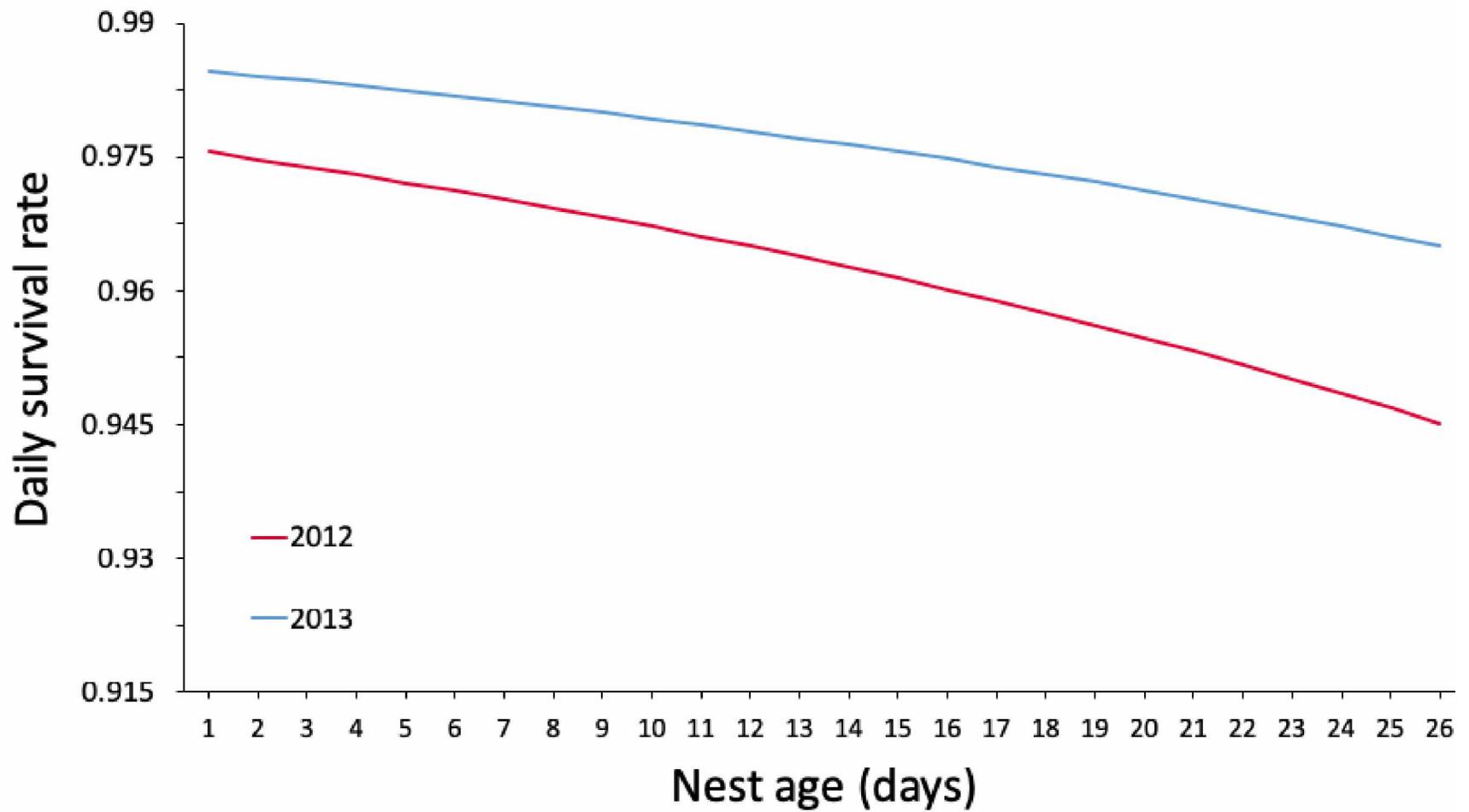


Figure 1.10. Estimated daily nest survival rates for American and Pacific Golden-Plovers (combined, due to no effect of species) on the Seward Peninsula, Alaska, during 2012 and 2013, in relation to year and age of nests (days).

Table 1.1. Principal components analysis of habitat characteristics of nest sites and paired random sites within territories of American ($n = 58$) and Pacific ($n = 53$) Golden-Plovers on the Seward Peninsula, Alaska. Values indicate factor loadings for each variable ($>|0.35|$ in boldface). The eigenvalue and percent of total variance explained are also shown for each component.

Variable	PC1	PC2	PC3	PC4	PC5
Elevation	-0.19	0.23	-0.41	0.21	-0.09
Vegetation height	0.46	0.11	-0.14	0.11	0.37
Lichen cover	-0.26	-0.38	-0.32	-0.07	0.03
Rock cover	-0.28	0.37	0.16	0.29	0.06
Bare ground cover	-0.08	0.25	0.43	0.26	0.07
Moss cover	0.36	-0.10	0.30	-0.01	-0.21
Ericaceous shrub cover	0.06	-0.49	-0.25	0.10	0.00
Dwarf birch cover	0.15	-0.33	0.23	0.10	0.26
Dwarf willow cover	0.17	0.16	-0.03	-0.24	-0.70
<i>Dryas</i> cover	-0.14	0.16	-0.01	-0.54	0.25
Cinquefoil cover	-0.01	0.11	0.09	-0.61	0.28
Herbaceous cover	0.22	0.23	-0.42	0.17	0.18
Graminoid cover	0.39	-0.12	0.12	0.01	-0.12
Willow cover	0.38	0.19	-0.07	0.03	0.21
Detritus cover	0.23	0.25	-0.30	-0.14	-0.16
Eigenvalue	3.02	1.87	1.40	1.16	1.08
Percent variance	20.10	12.47	9.33	7.73	7.22

Table 1.2. Model-selection results of logistic regressions comparing habitat selected for territories and nest sites by American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. Models with up to 5 principal components (PC) of habitat structure were tested to distinguish between territories of Americans and Pacifics, nest sites and random sites within territories for each species, and nest sites of the two species. Results of the top competitive models ($\Delta AIC_c \leq 2$) plus the global model ($PC1+PC2+PC3+PC4+PC5$) are shown relative to the null model for evidence of habitat selection. K is the number of parameters in each model and w is the relative Akaike weight for the model within each candidate set.

Comparison	Model	K	ΔAIC_c	w
American vs. Pacific territory	<i>PC1+PC2</i>	3	0.00	0.47
	<i>PC1+PC2+PC3</i>	4	0.38	0.39
	Global	6	4.65	0.05
	Null	1	11.43	0.00
American nest vs. territory	<i>PC1+PC2+PC3</i>	3	0.00	0.45
	Global	5	0.97	0.27
	<i>PC1+PC3</i>	2	1.95	0.17
	Null	0	14.39	0.00
Pacific nest vs. territory	<i>PC1</i>	1	0.00	0.49
	<i>PC1+PC2</i>	2	1.49	0.23
	Global	5	7.02	0.01
	Null	0	14.46	0.00
American vs. Pacific nests	<i>PC1+PC2+PC3</i>	4	0.00	0.86
	Global	6	4.19	0.11
	Null	1	46.65	0.00

Table 1.3. Interspecific (unpaired) and intraspecific (paired) comparisons of habitat features of territories and nest sites for American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013. Boldface *P*-values for univariate Wilcoxon tests indicate significant differences corrected for multiple comparisons within each group ($P < 0.003$).

Variable	American vs. Pacific		Nest vs. territory	
	Territory	Nest	American	Pacific
Elevation	<0.001	<0.001	0.004	0.46
Vegetation height	0.009	<0.001	<0.001	<0.001
Lichen cover	0.19	0.03	0.22	0.28
Rock cover	0.001	<0.001	0.04	0.004
Bare ground cover	0.04	0.60	0.08	<0.001
Moss cover	0.06	0.26	0.09	0.02
Ericaceous shrub cover	0.38	<0.001	0.01	0.90
Dwarf birch cover	0.35	0.006	0.004	0.009
Dwarf willow cover	0.29	0.67	0.37	0.24
<i>Dryas</i> cover	0.69	0.03	0.23	0.50
Cinquefoil cover	0.30	0.30	NA ^a	NA ^a
Herbaceous cover	0.66	0.02	0.42	0.51
Graminoid cover	<0.001	<0.001	0.03	0.07
Willow cover	0.03	0.06	<0.001	<0.001
Detritus cover	0.11	0.40	0.27	0.10

^aNA = values were zero

Table 1.4. Model selection results from analyses of nest survival of American and Pacific Golden-Plovers on the Seward Peninsula, Alaska, during 2012 and 2013 (Americans $n = 44$, Pacifics $n = 53$). K = number of parameters, ΔAIC_c = the difference in AIC_c (Akaike's Information Criterion corrected for small sample size) relative to the best model.

Model	AIC_c	ΔAIC_c	w	Model Likelihood	K	Deviance
S(<i>year+age</i>)	268.89	0.00	0.12	1.00	3	262.88
S(<i>age</i>)	269.09	0.20	0.10	0.91	2	265.08
S(<i>year</i>)	269.26	0.36	0.10	0.83	2	265.25
S(.)	269.58	0.69	0.08	0.71	1	267.58
S(<i>elevation</i>)	269.89	1.00	0.07	0.61	2	265.88
S(<i>PC2</i>)	270.09	1.20	0.06	0.55	2	266.09
S(<i>PC3</i>)	270.74	1.85	0.05	0.40	2	266.73
S(<i>PC2+PC3</i>)	270.85	1.96	0.04	0.38	3	264.83
S(<i>day</i>)	270.98	2.09	0.04	0.35	2	266.97
S(<i>age+day</i>)	271.04	2.15	0.04	0.34	3	265.02
S(<i>species+age</i>)	271.07	2.17	0.04	0.34	3	265.05
S(<i>day+year</i>)	271.13	2.24	0.04	0.33	3	265.11
S(<i>species+year</i>)	271.25	2.35	0.04	0.31	3	265.23
S(<i>maxavght</i>)	271.26	2.37	0.04	0.31	2	267.25
S(<i>PC1</i>)	271.49	2.60	0.03	0.27	2	267.48
S(<i>species</i>)	271.53	2.64	0.03	0.27	2	267.52
S(<i>PC1+PC2</i>)	271.61	2.72	0.03	0.26	3	265.60
S(<i>PC1+PC2+PC3</i>)	271.68	2.79	0.03	0.25	4	263.65
S(<i>PC1+PC3</i>)	272.54	3.65	0.02	0.16	3	266.52
S(<i>day+species</i>)	272.97	4.08	0.01	0.13	3	266.95

General Conclusion

This thesis examined the habitat selection and reproductive success of American and Pacific Golden-Plovers. Little was known about the nest or brood survival of these species, and through my work I was able to gain insight into the reproductive ecology of both Americans and Pacifics. I found that both species selected nest-sites that avoided tall vegetation and that were higher and drier than the surrounding habitat within their territories. The strong selection for nesting habitat exhibited by Americans and Pacifics highlights the importance of habitat conditions for both species and underscores the potential threat of climate-induced encroachment of shrubs onto tundra.

Differences between the two species in their nest-site selectivity and in the resulting variability of their nesting habitat suggest that Americans may have less behavioral plasticity in selecting suitable nest sites than Pacifics. Although we did not test behavioral plasticity directly in this study, Americans and Pacifics nest on tundra where cyclic fluctuations in the microtine rodent population have been observed and documented (Krebs 1996). According to the alternative prey hypothesis, predators in arctic and subarctic areas, such as arctic (*Vulpes lagopus*) and red foxes (*V. vulpes*), will switch to alternative prey during years of low rodent abundance in order to compensate for the decreased availability of their primary prey. Alternative prey often includes the eggs, nestlings, and hatchlings of nesting birds (Lack 1954, Angelstram et al. 1984). There is evidence that some birds (e.g., geese and shorebirds) can assess predation risk relative to such cyclic fluctuations and choose nest sites in accordance to this risk (Spaans et al. 1998, Larsen 2000, Forstmeier and Weiss 2004). Hence, although both plover species may be challenged in finding suitable nest sites as vegetation continues to increase in cover and height, Americans may have less ability to adapt to changing habitat conditions than Pacifics because they are already selecting nest locations that are significantly higher in elevation

at both the scale of the nest and that of the territory, giving them fewer places to go in response to predation risk.

In addition to differential responses to predation risk at the nest, I would predict that increasing shrub encroachment will result in increased competition by both species for territories at higher elevations. Spatial niche partitioning, through habitat selection, is the primary way in which two very similar, competitive species can coexist (Schoener 1974). Neighboring males of these two plover species frequently engage in interspecific territorial disputes, including aerial chases, ground displays, and fights, especially early during the breeding season, providing strong evidence of direct competition (Connors et al. 1993, K. S. Overduijn personal observation). In my study, I found that Americans nested slightly earlier than Pacifics in the year with the earlier spring, indicating that Americans were potentially able to select the best sites before Pacifics. Earlier nesting, and subsequent "first pick" of nesting territories could have been because of earlier arrival to the breeding site or competition if both species were present in the area at the same time. As a result, temporal differences in settling patterns may also contribute to interspecific differences in selection of nesting habitat. Thus, studies of interspecific behavioral interactions in current areas of overlap may shed light on the potential for competitive exclusion in the future.

Although I was surprised to find no evidence of an effect of nest-site characteristics on nest success, this result was not totally unexpected because there are numerous confounding evolutionary and ecological mechanisms that may be contributing to a lack of congruence between nest-site selection and nest success (Chalfoun and Schmidt 2012). Adult survival and brood survival are two examples of fitness components that possibly had a collaborative contribution to the selection of a nesting territory and nest site for Americans and Pacifics. These species are long-lived shorebirds with precocial young that are on the move and self-feeding

within 24 hours post-hatch (Johnson et al. 2018). Trade-offs with concealment in order to have an optimal view of ones' surroundings, and trade-offs with selective pressures such as food accessibility and nest microclimate, could also impact overall reproductive success (Chalfoun and Schmidt 2012). In the absence of much vertical vegetation structure, nest survival for these ground-nesting birds is often reliant on the incubation behavior of the adults (Smith et al. 2007) and crypticity of both the nest and plumage of the incubating adult. This crypticity could be compromised as shrub expansion occurs and lichen-dominated substrate is replaced with other vegetation. For example, in Churchill, Manitoba, Golden-Plover nests in lichen-covered substrate were more likely to hatch than those in greener and less variegated substrate due to increased concealment from predators (Byrkjedal 1989). Increased vegetation cover, as a result of climate change, could compromise the ability of ground-nesting plovers to conceal nests, chicks, and themselves in high-latitude breeding areas.

The failure to link habitat features with nest success in my study could also have been due to methodological shortcomings in the way habitat structure was measured (cf. Chalfoun and Schmidt 2012). First, my sample sizes of nests (55 Americans and 59 Pacifics over two years) may not have been large enough to detect effects of the habitat variables I measured on nest success. Second, because I characterized nesting habitat after the birds had finished incubation to minimize disturbance, measurements of vegetation at nest sites could have been biased by seasonal phenology (i.e., vegetation may have been taller and denser than at the time of nest selection), thereby masking effects that could have been at play during incubation. For example, although I did not find a direct relationship between habitat features and nest success, overall daily survival rate (DSR) was marginally lower in 2012 (earlier/warmer spring with less snow) than in 2013 (later/colder spring with more snow). The earlier and warmer breeding season could have facilitated vegetation growth compared to 2013. DSR also decreased with nest age over the

course of the summer in both years. As vegetation grew, the view of the incubating adult could have become obstructed, leading to a delayed response to predators in the breeding territory, and thus lower nest survival.

Although I focused on the influence of habitat variables on the selection of nest sites and subsequent nest success in Chapter 1, annual reproductive success encompasses more than just the survival of eggs. Habitat selection during the brood-rearing period can also influence the overall reproductive success of a bird, particularly relative to structure of the vegetation and availability of food resources for the young. Plover chicks are precocial, leave the nest at hatch, and are dependent upon their parents for shelter, finding food, and avoiding predators until they fledge at ~30 days. Broods tend to move farther from the nest site as they age; some broods have been observed moving 0.30 ± 0.10 km in the first 10 days post-hatch and up to just under 1 km 3 weeks post-hatch (Byrkjedal and Thompson 1998, Johnson et al. 2018). However, due to variability in brood-rearing territory sizes, careful consideration should be taken when determining the scale at which one measures habitat selection and resource availability for plovers (K. S. Overduijn personal observation). During brood rearing, plovers often continue to rely on crypticity for protection from predators. The downy plumage of the growing chicks provides perfect camouflage against a moss and lichen substrate. Minimal cover of low shrubs and denser vegetation could potentially provide an extra barrier between hidden chicks and a potential predator (Drury 1961, Kessel 1989, Johnson et al. 2018). Therefore, I would predict that as chicks age, habitat with some low shrub cover and ample food resources is necessary and that proximity to the nest site will determine how far broods will move to obtain these resources. However, too much vegetation could have negative effects on brood survival. For example, during the summer on the tundra, red foxes prefer vegetated habitats with more vertical structure, dominated by willows, than open habitats (Jones and Theberge 1982). Therefore, shrubs that are

too tall or too dense could be detrimental to brood survival, as these conditions provide more places where generalist mammalian predators can hide, undetected by protective adult plovers.

Habitats selected during the brood-rearing period can also strongly influence availability of food needed for the survival of chicks and recruitment of fledglings into the breeding population. Chicks of the European Golden-Plover (*Pluvialis apricaria*; hereafter referred to as "Europeans") occupy brood-rearing territories that are approximately 40 to 80 ha in size (Pearce-Higgins and Yalden 2004). From hatch until fledge, Europeans move through mosaics of habitat that vary temporally and spatially in regard to food availability (Whittingham et al. 2001, Pearce-Higgins and Yalden 2004). These movements, which can sometimes exceed 1 km in a day, enable chicks to track changes in invertebrate abundance (Pearce-Higgins and Yalden 2004). Habitat heterogeneity is important because a brood-rearing habitat that is heterogenous will accommodate different types and sizes of invertebrates for chick consumption for various stages of development from hatch until fledge (Galbraith 1988, Johansson and Blomqvist 1996, Pearce-Higgins and Yalden 2004). The diets of adults and chicks of both Americans and Pacifics are thought to be similar (Johnson et al. 2018), but there is little information on their diets where they occur together. Surface-active arthropods and berries are important for growing chicks and also maintaining the quality of adults (Pearce-Higgins and Yalden 2004). After invertebrate emergence, plovers switch from berries to protein-rich terrestrial and aquatic invertebrates such as coleopterans, dipterans (tipulids, culicids, and chironomids), lepidopteran larvae, megadrilaceans (earthworms), and hymenopterans (Bengtson et al. 1976, Byrkjedal 1980, Whittingham 1996). Tipulidae (adults and larvae), as well as Coleoptera, are of particular importance to plovers (Pearce-Higgins and Yalden 2004). Given this information, I would predict that habitat heterogeneity is important to American and Pacific chicks as they move

throughout their brood-rearing territories, tracking food availability and moving to areas with higher invertebrate abundance to meet their energetic needs.

In addition to the work I report in Chapter 1, I also tracked 52 broods of both species (25 American and 27 Pacific) by using adult behavior and vocalizations to locate them from hatch until fledge. I tracked broods every 4 days by locating individually banded adults, which remained with the chicks until fledge, to determine brood survival. I also evaluated habitat used by broods and collected invertebrates within the brood-rearing territories. Using these data, I would like to determine: (1) the importance of habitat heterogeneity to these species, (2) whether habitat heterogeneity has an effect on brood survival, (3) how habitat use changes with chick age, (4) how invertebrate biomass varies in habitats used by chicks during the brood-rearing period, and (5) whether broods track invertebrate abundance through their movements. In addition, data that I collected on invertebrate abundance could be used to examine whether there is a potential mismatch between food availability and timing of nest initiation and hatch at this low Arctic location. For instance, with the advance of spring phenology in the Arctic in response to climate change, shorebirds at one Low Arctic site in Yukon, Canada, were found to be more susceptible to mismatch than arctic-breeding passerines (Leung et al. 2018). For plovers breeding on the Seward Peninsula, Alaska, I would predict that patterns would be similar given the comparable short length of the breeding season and the vegetation conditions of the two Low Arctic sites. Although I was unable to complete these analyses in time to be included in this thesis, I plan to undertake this task in the future. I do report in this thesis, however, apparent brood survival (proportion of broods hatched that survived until fledging) of Americans and Pacifics in 2012 and 2013 (Appendix A) and summary data on the frequency and proportion of invertebrate orders found in my samples (Appendix B).

In conclusion, although my thesis focused on nest-site selection and nest success, it is also important to take into consideration other nuances of climate change such as the influence of changes in snow and permafrost on the overall reproductive success of shorebirds. Increasing temperatures in the northern hemisphere have resulted in changes in precipitation and cryospheric variables (e.g., snow and permafrost), which are having broad ecological effects (Visser and Both 2005, Møller et al. 2008). Early and disproportionately large changes in climate have been documented at high northern latitudes (Hinzman et al. 2005, AMAP 2011), yet ecological effects of climate change on high-latitude ecosystems are not well understood. One might expect that changes in snow and permafrost could impact reproductive success depending on whether or not a spring is early or late. For instance, a late spring could influence competition between sympatrically nesting species through limited availability of potential nesting territories for nest initiation. An early spring could influence the structure of vegetation and visual detection of predators throughout the breeding season. Similarly, risk of predation can also be altered in response to changes in snow and permafrost conditions in the Arctic, when patches of open tundra allow predators to easily find nesting birds early in the breeding season or when vegetation changes through altered hydrological regimes (Van Hemert et al. 2015). Documenting how species are being affected by these changes will enable us to understand some of the broad-scale impacts that climate change is having on arctic-breeding shorebirds. Future research should examine reproductive success in a comprehensive manner, in which multiple aspects of a species' reproductive ecology is evaluated, allowing a more complete understanding of the effects of climate change on recruitment into populations through the combined effects of habitat structure, food resources, and climate.

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Appendix A

Supplementary Material for Chapter

Table A-1. Samples sizes and apparent brood survival of American and Pacific Golden-Plover broods on the Seward Peninsula, Alaska during 2012 and 2013.

	American		Pacific	
	2012	2013	2012	2013
Broods	9	16	6	21
Broods that fledged at least one chick	5	11	6	13
Apparent brood survival (%)	56	69	100	62

Appendix B

Additional Supplementary Material for Chapter 1

Table B-1. Orders, frequencies, and proportion of total invertebrates collected in pitfall traps on the Seward Peninsula, Alaska, during the brood-rearing season of American and Pacific Golden-Plovers in 2013. Vouchers deposited in the University of Alaska Museum Insect Collection.

Order	Frequency	Proportion
Araneae	1941	0.1901
Centipede	78	0.0076
Coleoptera	2435	0.2385
Collembola	71	0.0070
Diptera	3869	0.3790
Enchytraeida	51	0.0050
Hymenoptera	1374	0.1346
Lepidoptera	222	0.0217
Mecoptera	5	0.0005
Neuroptera	4	0.0004
Opiliones	50	0.0049
Orthoptera	25	0.0024
Stylommatophora	1	0.0001
Trichoptera	1	0.0001
unknown	72	0.0071

Appendix C

Approval letter for project 452436-2 from the University of Alaska
Fairbanks Institutional Animal Care and Use Committee (IACUC)



Institutional Animal Care and Use Committee

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May 2, 2013

To: Abby Powell
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [452436-2] Breeding Ecology of American and Pacific Golden-Plovers

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received: April 25, 2013
Approval Date: May 2, 2013
Initial Approval Date: May 2, 2013
Expiration Date: May 2, 2014

This action is included on the May 16, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*