**Airborne laser scanning and spectral remote sensing give a bird's eye perspective on arctic
tundra breeding habitat at multiple spatial scales**

Authors: Boelman, N.T.¹⁺, Holbrook, J.D.², Greaves, H.E.^{3*}, Krause, J.S.^{4*}, Chmura, H.E.⁴,
Magney, T.S.³, Perez, J.H.⁴, Eitel, J.U.H.^{3,5}, Gough, L.⁶, Vierling, K.T.², Wingfield, J.C.⁴, and
Vierling, L.A.^{3,5}

¹ Lamont-Doherty Earth Observatory, and Department of Earth and Environmental Sciences,
Columbia University, Palisades NY, 10964.

²Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, USA 83844-1136

³ Geospatial Laboratory for Environmental Dynamics, University of Idaho, Moscow, ID, USA
83844-1133;

⁴ Department of Neurobiology, Physiology and Behavior, University of California at Davis,
Davis CA, 95616.

⁵ McCall Outdoor Science School, University of Idaho, McCall, ID, USA, 83638

⁶ Department of Biological Sciences, Towson University, 8000 York Road, Towson, MD 21252

* Indicates that these authors contributed equally to the study.

⁺ Author to whom correspondence should be addressed; E-Mail: nboelman@ldeo.columbia.edu;
Tel.: +1-845-365-8480

Running head: ALS reveals arctic bird-habitat associations

ABSTRACT. The effects of climate change are more acute in the Arctic than any other region, and as such, arctic tundra wildlife habitats are changing in ways that are not yet well understood. Remote sensing tools are capable of assessing dynamics in wildlife-habitat associations over a wide range of spatial scales and in a variety of ecosystems. As already well-established in other ecosystems, Light Detection and Ranging (LiDaR) technology has the potential to greatly expand our understanding of tundra wildlife-habitat associations because unlike the most commonly used spectral vegetation index - the Normalized Difference Vegetation Index (NDVI) - LiDaR directly quantifies three-dimensional (3-D) vegetation structure. Only recently has airborne laser scanning (ALS) technology evolved to having vertical resolution and point densities high enough to quantify small differences in vegetation structure which characterize the physical structure of arctic tundra ecosystems. Our objective was to employ ALS metrics, airborne spectral data (for NDVI), and Landsat 7 ETM+ data (for snow cover) to determine the relative importance of a suite of ecological characteristics - considered at multiple spatial scales - on habitat use and reproductive success of two of the most common migratory songbird species breeding in northern Alaska. Our novel and important findings include (1) combining ALS metrics - but not NDVI - with Landsat derived snow cover data provided useful information, revealing that while Gambel's white-crowned sparrows use breeding territories in areas with high canopy volume and large snow-free areas, Lapland longspurs will establish territories in areas with low canopy volume, small patches of snow-free tundra, and minimal surface wetness and; (2) while habitat characteristics were important determinants of habitat use for both species at the territory scale, those in the immediate vicinity of nest-sites were not. Contrary to expectation, we also found that the reproductive success of both species was unaffected by variation in our hypothesized metrics of shelter and food availability (canopy volume, standard

deviation of micro-terrain height) at both the nest-site or territory scales. Our study is the first arctic demonstration of how ALS yields novel insights into wildlife-habitat associations, suggesting it has great potential in other ecosystems with similarly small - yet often ecologically important - ranges in 3-D vegetation structure.

KEYWORDS. airborne laser scanning (ALS); arctic tundra; breeding habitat; Gambel's white-crowned sparrow; Lapland longspur; Light Detection and Ranging (LiDaR); Normalized Difference Vegetation Index (NDVI); remote sensing; snow; songbirds; vegetation structure; wildlife

1. INTRODUCTION.

1.1 Remote sensing of arctic tundra wildlife habitat.

The effects of climate change are more acute in the Arctic than any other region (Callaghan et al., 2004). Considering the myriad current and expected future changes in vegetation cover (Pearson et al., 2013; Zhang et al., 2013) and phenology (Zeng et al., 2011), snow cover dynamics (Stone et al., 2002; Derksen and Brown, 2012), and seasonality in environmental conditions (Chapman and Walsh, 1993; Serreze et al., 2000; Bintanja and van der Linden 2013; Overland et al., 2004); the spatial and temporal characteristics of current wildlife habitats are also expected to change considerably (Zockler and Lysenko 2000; Post et al., 2009; Henden et al., 2011; Ehrich et al., 2012; Boelman et al., 2014). While some species are likely to benefit or adapt to these changes, others will shift their geographic range or be extirpated (Wingfield et al. *in press*; Boelman et al., 2014). In order to better predict how a particular species will respond to changing tundra conditions, it is necessary to determine the relative importance of ecological characteristics that define its habitat (Bowler and Benton 2005; Clobert 2009; Cote 2010; Wingfield et al. *in press*; Parmesan and Yohe 2003; Parmesan 2007). Although field surveys are often an essential first step towards understanding wildlife-habitat associations, for practical reasons they are typically limited in their spatial scope. However, combining animal surveys with remote sensing and predictive modeling techniques can not only broaden the spatial applicability of field-derived findings, but can also enable examination of the importance of key ecological characteristics at multiple spatial scales (Hurlbert and Haskell 2003; Turner et al., 2003; Swatantran et al., 2012), and is particularly useful for studies of remote and inaccessible regions – such as most of the Arctic.

Although various types of spectral, RADAR (RADio Detection And Ranging) and LiDaR based remote sensing products have been employed (Turner et al., 2003; Vierling et al., 2008; Bergen et al., 2009; Swatantran et al., 2012; Wood et al., 2013), the Normalized Difference Vegetation Index (NDVI, Rouse et al., 1974) is by far the most commonly used in wildlife ecology (as reviewed in Hurlbert and Haskell 2003; and Pettorrelli et al., 2011). For example, arctic studies employing NDVI have been used to examine ungulate-vegetation interactions (Griffith et al., 2002; Bremset-Hansen et al., 2009; Couturier et al., 2009; Virtanen et al., 2013) and avian ecology (Pedersen et al., 2007; Tombre et al., 2008; Shariatinajafabadi et al., 2014). The success of NDVI can be in large part attributed to the fact that because it is a good proxy for spatial and temporal dynamics in primary productivity in many contexts, it often correlates with abundance and distribution patterns of animals (as reviewed in Hurlbert and Haskell 2003; and Pettorrelli et al., 2011). While these studies have provided valuable insight, it is likely that inherent measurement limitations of the vegetation index itself fail to elucidate some of the most important wildlife-vegetation associations on the tundra. For example, although the majority of tundra ecosystems are currently dominated by short stature sedge, shrub, moss and lichen cover (Leaf Area Index (LAI) < 1), tall deciduous shrub dominated communities (LAI $\leq$ 2) are becoming taller, denser, and more ubiquitous in many arctic regions (Myers-Smith et al., 2011; Elmendorf et al., 2012). As this shift in vegetation cover continues, LAI-NDVI relationships are likely to become less informative in tundra because NDVI tends to be insensitive to variation in green leaf area for canopies in which LAI exceeds values between 2 and 6, depending on the type of vegetation being measured (Hatfield et al., 1985; Chen et al., 2004) – meaning that animal responses to increasing shrub dominance may go undetected or misinterpreted. In addition, due to the non-linear contribution of various tissue types (ie. live green tissue, standing

litter, stem) to canopy reflectance properties, it has proven challenging to accurately apply the NDVI as a remote proxy for tundra vegetation cover characteristics without use of rarely available *a priori* knowledge of the vegetation community type dominant within a given pixel (Boelman et al., 2005; Street et al., 2007). Further, NDVI measurements in the tundra will be confounded by temporal variations in rapidly changing vegetation phenology and standing water – which will dilute the NDVI signal, making repeat passive remote sensing measurements difficult to interpret unless taken under identical conditions in space and time (i.e., Gamon et al., 2013). Perhaps the most critical limitation from a wildlife habitat perspective however, is that the NDVI does not directly provide information on the tundra’s inherently small – yet ecologically important (Henden et al., 2011; Ehrich et al., 2012; Boelman et al., 2014; Sweet et al., 2015) – range in vegetation 3-D structural characteristics (Vierling et al., 1997; Boelman et al., 2011).

1.2 LiDaR for arctic tundra wildlife studies.

Light Detection and Ranging (LiDaR) sensors have the potential to greatly expand our understanding of tundra wildlife-habitat associations because LiDaR directly quantifies the three-dimensional (3-D) structure of vegetation (Lefsky et al., 2002; Zolkos et al., 2013). In fact, many studies have found that the additional inclusion of remotely sensed datasets derived from other sensor types often provide ecological information that is complementary to LiDaR, thus providing more comprehensive characterization of wildlife habitats compared to LiDaR alone (e.g. Holmgren et al., 2008; Orka et al., 2013; Davies and Asner, 2014; Nijland et al., 2015; Zald et al., 2016). As such, LiDaR technology is increasingly being used in ecosystems with high structural complexity (i.e forests) for wildlife habitat characterization and mapping (Hill et al., 2004; Hyde et al., 2005, 2006; Hinsley et al., 2002, 2006; Boelman et al., 2007; Goetz et al., 2007, 2010, 2014; Clawges et al., 2008; Vierling et al., 2008; Bergen et al., 2009; Vogeler et al.,

2014; Zellweger et al., 2013; Davies and Asner 2014), as well as studies of wildlife behavior (Trainor et al., 2013; Melin et al., 2013; Loarie et al., 2015). To date however, the use of LiDaR technology in ecological studies in low stature ecosystems (ie. < 2m tall) - such as characterizes the arctic tundra - is extremely limited (Streutker and Glenn, 2006; Greaves et al., 2015; Greaves et al. *in review*). This is due to technological limitations in vertical resolution and point density of LiDaR systems that were previously too coarse to quantify small differences in vegetation structure (Zolkos et al., 2013). It is therefore not surprising that, to our knowledge, LiDaR technology has never been used in wildlife ecology in arctic tundra. Given that the physical structure of tundra vegetation is changing quickly as deciduous shrubs become increasingly tall, dense and abundant (Boelman et al., 2011; Myers-Smith et al., 2011) and the forest-tundra ecotone expands northward, current advances in LiDaR technology are likely to prove critical to uncovering tundra wildlife-vegetation interactions.

LiDaR technology has proven particularly insightful to the field of avian ecology (see recent reviews by Hill et al., 2004; Müller and Vierling 2014; Davies and Asner 2014) because birds are often highly sensitive to the 3-D structure of vegetation cover (e.g. MacArthur and MacArthur 1961; Lesak et al., 2011). Given that every year, billions of songbirds migrate to breed in the Arctic (Pielou 1994), LiDaR is likely to be equally informative in the study of arctic-breeding species that exhibit high species specificity in terms of the 3-D structural characteristics of the vegetation communities in which they prefer to nest. In a recent study, Boelman et al. (2014) used field-surveys to determine how vegetation community composition and height were associated with nest-site preferences in two arctic-breeding songbird species, but were subsequently limited in their ability to accurately predict habitat availability at the regional scale. This was partially attributed to the fact that the 3-D structural properties of mapped vegetation

cover types are only coarsely known, while it was the fine-scale variations in vegetation structure - that can now be resolved using airborne laser scanning (ALS) (Greaves et al., 2015; Greaves et al. *in review*) - that were determined to be very important to the birds. In addition to vegetation properties, ground-nesting songbirds generally select breeding habitats based on other ecological factors that can be assessed using state of the art ALS technology, including areas where certain micro-topographical characteristics prevail or where surface water does not accumulate during the breeding season (Rodrigues 1994; Norment 1993; Oakeson 1954).

1.3 Objectives and hypotheses.

Our goal was to use airborne laser scanning (ALS), as well as spectral reflectance data from both an airborne sensor and the Landsat 7 ETM+ sensor, to determine the relative importance of key ecological characteristics - considered at multiple spatial scales - on habitat use and reproductive success of two of the most common migratory songbird species breeding in northern Alaska - Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*) and Lapland longspurs (*Calcarius lapponicus*). Using a suite of spectral reflectance products and ALS derived metrics, we addressed three major objectives: (1) to determine the influence of a suite of ecological variables on patterns of habitat use by GWCS and LALO; (2) to make spatially explicit predictions of the probability of habitat use for each species at the larger landscape scale in the vicinity of field-study sites, and; (3) to examine relationships between key habitat characteristics and metrics of reproductive success (nestling condition, nest success, and number of fledglings) for each species.

Our general hypotheses were that: (1) only ALS-derived vegetation metrics would provide useful information on habitat use at the nest-site scale (64 - 512 m²), while both ALS and NDVI would provide insight into habitat use at the territory scale (1,127 - 28,300 m², depending

on species); (2) based on existing knowledge of songbird-breeding habitat associations, our remotely sensed measures of micro-topography, surface wetness, and snowmelt patterns would be critical co-determinants of habitat use at territory and nest-site scales (see Table 1 for detailed hypotheses and predictions), and; (3) since vegetation provides both shelter and food resources at the territory and nest-site scales, respectively, and micro-topography provides shelter at the nest-site scale in areas with little shrub cover, we expected reproductive success to vary with differences in canopy volume (GWCS) and standard deviation of micro-terrain height (LALO).

Table 1. We evaluated hypotheses and predictions for Gambel’s white-crowned sparrow (GWCS) and Lapland longspur (LALO) at the territory and nest-site scale in the vicinity of Toolik Lake, Alaska, USA. We used a variety of covariates in multiple Random Forest models to evaluate our predictions for each species and scale. We summarized all covariates (with the exception of distance to snow free zones) at multiple spatial extents.

Scale	Species	Extents	Tested hypotheses	Predictions	Remotely sensed covariates in Random Forest Model
Territory	GWCS	1,127 - 3,470 m ²	Vast and structurally diverse shrub habitats in snowfree areas with minimal standing water will be used (Blanchard Oakeson & Erickson 1949; Norment 1993; Chilton et al. 1995; Wingfield et al. 2004; Boelman et al. 2014)	(1) positive relationship between use and both vegetation structural complexity and greenness (2) negative relationship between use and both standing water and snowcover	LiDAR canopy volume (vegetation structural complexity); NDVI (vegetation greenness); Distance to snow-free zones (snowcover); LiDAR return intensity (surface wetness)
	LALO	10,900 - 28,300 m ²	Open habitats in snowfree areas with minimal standing water will be used (Rodrigues 1994; Hunt et al. 1995; Hussell & Montgomerie 2002; Boelman et al. 2014)	(1) negative relationship between use and each of vegetation structural complexity and greenness, snowcover and standing water	LiDAR canopy volume (vegetation structural complexity); NDVI (vegetation greenness); Distance to snow-free zones (snowcover); LiDAR return intensity (surface wetness)
Nest-site	GWCS	64 - 512 m ²	Areas with tall, dense shrubs and minimal standing water will be used (Blanchard Oakeson & Erickson 1949; Norment 1993; Chilton et al. 1995; Wingfield et al. 2004; Boelman et al. 2014)	(1) positive relationship between use and vegetation structural complexity (2) negative relationship between use and standing water	LiDAR canopy volume (vegetation structural complexity); LiDAR return intensity (surface wetness)
	LALO	64 - 512 m ²	Open habitats with high micro-topographical variability and minimal standing water will be used (Williamson 1968; Boal & Anderson 2005; Rodrigues 1994; Boelman et al. 2014)	(1) negative relationship between use and both vegetation structural complexity and standing water (2) positive relationship between use and micro-topographical variation	LiDAR canopy volume (vegetation structural complexity); LiDAR return intensity (surface wetness); LiDAR standard deviation of terrain height (micro-topographical variation)

2. MATERIALS AND METHODS

2.1 Overview.

We collected data on nest locations and reproductive success for two songbird species (GWCS and LALO) in northern Alaska during 2011-2014. Coincident with these data, we collected habitat covariates using remote sensing tools (i.e., ALS and spectral imagery). We

employed a ‘used and available’ design to assess which remotely sensed covariates were important for use at both territory and nest-site scales for each bird species using Random Forest models (Breiman 2001). We then generated predicted probabilities of habitat use for models that performed well. In addition, we evaluated how covariates at the territory and nest-site scale influenced reproductive success following hypotheses related to food resources and habitat structure respectively. This approach allowed us to assess songbird-habitat relationships at multiple spatial scales (i.e., territory and nest-site), as well as to determine relationships between characteristics of used habitats and reproduction.

2.2 Study area.

The study area includes tundra in the vicinity of the Arctic Long Term Ecological Research (ARC LTER) site at Toolik Field Station in the arctic foothills region of Alaska (68°38’ N, 149°34’ W, elevation 760 m) (Fig. 1). The four research sites include Roche Mountonee (ROMO), Toolik Lake Field Station (TLFS), Imnavait Creek (IMVT), and Sag River-Department of Transportation Camp (SDOT). Sites were chosen in May 2010 to represent the most common tundra types in the northern foothills of the Brooks Range. Moist-acidic tundra (MAT) communities - in which Lapland longspurs typically nest (Boelman et al., 2014) - are composed of short (< 30 cm) tussock-forming sedges (e.g. *Eriophorum vaginatum*), forbs (e.g. *Polygonum* spp. and *Pedicularis* spp.), dwarf evergreen shrubs (e.g. *Vaccinium vitis-idaea*), occasional dwarf deciduous shrubs (e.g. *Betula nana*, *Salix pulchra*), mosses, and lichens. Shrub dominated tundra (typically > 30 cm) - in which White-crowned sparrows typically nest (Boelman et al., 2014) - is composed of either dwarf or erect-deciduous shrub vegetation, dominated by a mixture of *S. pulchra*, *Salix glauca*,

Salix alaxensis, *Salix richardsonii*, *B. nana*, and *Vaccinium uliginosum*, with a mixture of sedges, evergreens, and other herbaceous perennials, or, riparian shrub tundra vegetation dominated by taller shrubs, mainly *S.alaxensis* and *B. nana*.

Figure 1. A) Location of our 4 study sites in the vicinity of Toolik Field Station, AK, USA; B) TLFS study site; C) IMVT study site; D) SDOT study site; E) ROMO study site. White triangles B, D and E indicate nest locations of Gambel’s white-crowned sparrow found during 2011-2014. Yellow pentagons within B and C are nest locations of Lapland longspur found during 2011-2014.

2.3 Songbird datasets.

Nest locations. Lapland longspur (hereafter LALO) and Gambel’s White-crowned sparrow nests (hereafter GWCS) were located by searching the areas surrounding each of our four research sites (Fig. 1), during the month of June. Only nests that were located within the ALS and aerial NDVI image footprints (Fig. 1) were included in this study. Nest searching was conducted along

a full range of vegetation community heights (< 20 cm to > 2 m tall) that are found in the foothills region of the Brooks Range. Nests were found by flushing incubating birds or following birds to their nests. Of the nests used in this study, 46 GWCS nests were found at three study sites and 68 LALO nests at two study sites during 2011-2014 (Figure 1). Nest locations were recorded with a handheld GPS so that they could be easily relocated. Our GPS accuracy was ≤ 8 m.

Metrics of reproductive success. Nests were located by following females to the nest during nest building or incubation, or flushing females from the nest. Nests were checked at least every other day, with most nests checked daily. A nest was determined to be successful if at least one nestling was raised to fledging. The number of fledglings in each successful nest was recorded. All nests that were depredated or had nestlings that did not fledge were determined to have failed. At six days of age, nestling tarsus was measured to the nearest 0.1 mm with micro-calipers. Nestlings were weighed to nearest 0.1 g using a portable Ohaus scale. Mean nestling condition per nest was calculated by dividing the mass (g) by tarsus length (mm) for each nestling. Each bird was banded with an aluminum band provided by the United States Geological Survey.

2.4 Remotely sensed covariates for habitat modeling.

2.4.1 Acquisition of ALS and NDVI.

ALS data and digital imagery were acquired August 1st, 2013 (Vierling et al., 2013a, 2013b). ALS data were collected with a Riegl VQ-480i sensor (wavelength 1550 nm) mounted on a small airplane flying at 365 m above ground level. The altitude of the airplane and the laser beam divergence (0.3 milliradians) yielded an estimated laser spot size of 11 cm. Local ground

control yielded vertical accuracy of 8-10 cm. Laser return density was nominally 13.5 points m⁻², and flight lines were overlapped 60% to achieve a nominal aggregated density of 27 points m⁻². Four-band digital imagery (RGB + near infrared, used to calculate NDVI) was collected simultaneously from a Leica RCD30 60MP camera mounted to the aircraft, and was processed by the vendor (Kodiak Mapping Incorporated, www.kodiakmapping.com) to produce orthorectified image mosaics with a pixel resolution of 4.25 cm.

2.4.2. *Data Processing: ALS metrics.*

Canopy volume was calculated at a resolution of 0.80 m following Greaves et al. (2015 *in review*). In brief, following identification of the lowest and highest data points at each sample location, each set of points was rasterized using the las2dem tool in LAStools (Isenburg 2015). A canopy volume surface was calculated by subtracting the ‘lowest’ raster from the ‘highest’ raster and multiplying the result by the square of the raster resolution. We also calculated laser return intensity, maximum canopy height, and standard deviation of canopy height (a measure of canopy surface roughness), using LAStools (Isenburg, 2015). Laser return intensity and maximum canopy height were created at a resolution of 0.80 m to match canopy volume resolution, while standard deviation of canopy height was calculated at a resolution of 2.4 m to ensure that each pixel included enough laser returns to produce meaningful statistics.

In this study, laser return intensity was not radiometrically calibrated against reflectance standards (Kaasalainen et al., 2009; Eitel et al., 2010), or accounted for differences in laser beam incidence angle or distance between the ALS instrument and the surveyed object (Kukko et al., 2008; Kaasalainen et al., 2011). While we did not consider a robust calibration in our analysis, we included laser return intensity as a metric for surface wetness in our predictive models because: 1) a visual examination of the laser return intensity data shows little evidence of

‘striping’ in the data due to angular-distance effects between different passes (e.g. points returned near nadir in one pass vs. returned at the edge of the scan swath in the next pass); 2) areas where we know there is a small amount of standing water and/or high surface wetness had correspondingly low return intensity values (data not shown); and 3) the difference in terrain altitude relative to flight altitude is relatively small for this dataset. Although ALS return intensity is an imperfect measure of soil moisture, it has been shown to correlate with gravimetric soil water content (Garroway et al., 2011; Nield et al., 2014) and has proven useful in distinguishing cover types that differ in surface wetness (Goodale et al., 2007; Korpela et al., 2009). For these reasons, our interpretation of low laser return intensity values are the result of increased absorption in the NIR due to increased surface wetness.

Standard deviation of terrain height (a measure of micro-topographical variation) was calculated in R version 3.0.1 (R Core Team, 2015) using the package “raster” (Hijmans, 2015) by aggregating ground rasters (native resolution 0.15 m) to 2.4 m resolution.

2.4.3. Data processing: NDVI.

We used the RGB + near-infrared orthoimagery to calculate NDVI (Tucker, 1979), which is commonly used to characterize vegetation in the Arctic (e.g. Shippert et al., 1995; Simms and Ward 2013). We used the R package “raster” to calculate NDVI at the native imagery resolution (4.25 cm) and then resampled to 0.80 m.

2.4.4. Data Processing: 15 m resolution snow cover map.

We produced a snow cover map using the 15 m resolution panchromatic band from the Landsat 7 Enhanced Thematic Mapper plus (ETM+) sensor. ETM+ image data (Path 72, Row 12) were retrieved from the global Landsat archive via the USGS EarthExplorer interactive

server (earthexplorer.usgs.gov). We used a scene collected on 29 May 2001 because it was cloud free, occurred before the 2003 malfunction of the ETM+ scan line correction mechanism (therefore providing contiguous data across the full area of interest; Markham et al., 2004), and captured the landscape during the midpoint of snow melt which is similar to that typically experienced by birds as they use territories and nest locations. Although the image pre-dated our field data collection, landscape level snowmelt patterns on the North Slope of Alaska during the mid-point of snowmelt (i.e. time at which the landscape is ~50 % snowfree) are consistent across years (Konig and Sturm 1998), and thus we utilized the 2001 scene of our study area to coarsely characterize annual snowmelt patterns during the time when migratory songbirds typically arrive in northern Alaska. We mapped areas of snow and no-snow using a panchromatic band reflectance threshold. Use of the appropriate threshold was supported by cross-referencing with a 30 m resolution snow map produced from the same ETM+ image using the multispectral Normalized Difference Snow Index (NDSI; Dozier 1989). Given the approximate nature of our “snow free” delineation (caused by fine-scale variation in snowmelt patterns among years and inter-annual differences in snowcover extent during songbird territory and nest-site use), we generated a distance to snow free zones raster (range = 0-1480 m) - rather than a snow/no snow raster - to better represent the fuzzy boundaries around snow free locations.

2.5 Data Analysis.

We summarized habitat covariates (with the exception of distance to snow free zones) at multiple spatial extents at both territory and nest-site scales. To our knowledge, no information from remote sensing techniques existed concerning the importance of spatial extent of any ecological variables in territory or nest-site use for either species. Previous research indicated that LALO and GWCS have territories ranging in size from 10,900 to 28,300 m² (Seastedt and

MacLean 1979) and 1,127 to 3,460 m² (Ralph and Pearson 1971; Patterson and Petrinovich 1978), respectively. Thus, we characterized the appropriate variables for LALOs at 10,900, 17,400, and 28,300 m², and at 1,127, 2,294, and 3,460 m² for GWCS (Summary in Table 1). We implemented an exploratory approach at the nest-site scale and summarized data across the following four extents for both study species: 64, 128, 256, and 512 m². Our GPS accuracy of ≤ 8 m set the lower bounds of the extents at 64 m². The three larger nest-site extents were chosen so that a range of areas surrounding each nest could be considered in our analyses (i.e., each area was doubled up to 512 m²). We used a moving window analysis (i.e., focal statistics tool) in ArcMap 10.2 to summarize covariates at the mean for each species at each scale and extent (See Table 1). Distance to snow-free zones was only characterized for the territory scale because of 1) the low spatial resolution of the imagery used (225 m²), and 2) we expected snow patterns to largely drive territory establishment rather than nest-site placement within territories.

Our main objective was to use remotely sensed covariates to understand what habitat characteristics are most important for use at the territory and nest-site scales. We therefore implemented a ‘used and available’ design at the suite of territory and nest-site extents (as listed above for each species) and characterized differences in remotely measured ecological characteristics between used versus available habitats. We considered habitat use, as opposed to habitat selection, because we recognized that not all available locations may be encountered by each species (Lele et al., 2013). At the territory scale, we measured available habitat by randomly allocating approximately 1000 potential territory locations throughout the study area. This allocation corresponded to a density of 1 available territory location every 100 m $\times$ 100 m cell. At the nest-site scale, we used the largest reported territory extent to set available buffers (i.e. GCWS = 3,460 m², LALO = 28,300 m²), and randomly generated 20 potential nest locations

per buffer. This allocation corresponded to a density of 1 available nest location every $\sim 170 \text{ m}^2$ for each GWCS buffer, and 1 available nest location every $\sim 1,400 \text{ m}^2$ for each LALO buffer. Because we wanted to compare the habitat characteristics between used versus available territories and nest locations, we extracted all remotely sensed covariates for each species, scale (according to hypotheses listed in Table 1), and extent for both used and available locations using standard functions in ArcMap. Collinearity among different covariates was assessed to identify variables that represented distinct gradients. Because both standard deviation (SD) of canopy heights and maximum canopy height were highly correlated with canopy volume ($r = 0.97$ and 0.97 , respectively), we used only canopy volume in subsequent analyses. All other covariates exhibited relatively low pairwise correlations ($|r| < 0.38$) and were thus included in subsequent analyses.

We used a Random Forest approach (Breiman 2001; Cutler et al., 2007) to assess and predict habitat use at the territory and nest-site scale for both GWCSs and LALOs. Random Forests is an ensemble technique, and can be applied within a classification or regression framework (Liaw and Wiener 2002; Cutler et al., 2007). The Random Forest algorithm is increasingly used in ecology (e.g., Martinuzzi et al., 2009; Baruch-Mordo et al., 2013) because it easily handles many covariates (which can be correlated), is non-parametric, naturally includes interactions, and is predictive in nature (e.g., Evans and Cushman 2009; Genuer et al., 2010; Evans et al., 2011). For classification, the Random Forest technique involves: (1) random selection of bootstrap samples, (2) for each sample, an unpruned tree is grown to classify outcomes (used and available habitat in our case) where the nodes are defined by the best split or information gain using a random sample of covariates, and (3) prediction of the outcome for new data by applying the bootstrapped model (Liaw and Wiener 2002; Cutler et al., 2007; Evans et

al., 2011). Observations excluded from the bootstrap sample are referred to as the ‘out-of-bag’ observations, and are used to assess the predictive performance of the trees grown from the ‘in-bag’ or bootstrapped observations (Breiman 2001). Combining the out-of-bag predictions (i.e. majority vote across trees) generates an estimate of the total out-of-bag prediction error (OOBE), which indicates model performance (Liaw and Wiener 2002; Cutler et al., 2007). Covariate importance within Random Forests is assessed by permuting the values of the covariate for the out-of-bag observations and passing the modified data down the tree to generate new predictions. The difference between the predictive performance of the permuted and original data provides a measure of variable importance (referred to as the mean decrease in accuracy), with higher values indicating higher importance (Cutler et al., 2007). Finally, the effect of covariates on the predicted probabilities of habitat use can be visualized using partial dependence plots, which show the dependency of the probability of habitat use on a covariate after averaging the effects of the other covariates (Cutler et al., 2007).

We used Random Forests in a multi-stage fashion (similar to Genuer et al., 2010) with in the R package randomForest (Liaw and Wiener 2002). First, we included our hypothesized covariates (see Table 1) at both scales and all spatial extents to identify the most influential extent at the territory and nest-site scales. However, for the reasons aforementioned, distance to snow free zones was not summarized at the nest-site scale, nor across territory extents because the values would have been nearly identical across extents. We used the extent identified as most important for each covariate - as determined by the mean decrease in accuracy - and built a reduced model that included only this 1 extent per covariate. We evaluated model performance through assessment of both OOBE and variable importance values. Because our used and available design resulted in a large imbalance between available compared to used locations (i.e.

available>>used), we applied the approach of Evans and Cushman (2009) as implemented in the rfUtilities R package to generate a more appropriate estimate of OOB. For models with an OOB $\leq 30\%$, we assessed partial dependence plots and predicted the probability of habitat use by including only those covariates with high (e.g., ≥ 20) importance values. We then used the reduced model to map the predicted probability of habitat use on a per species basis, and only for study sites where we observed nests of that species to allow for easy visualization of model performance. In all models, we used default values (e.g., number of variables randomly sampled at each split in a tree) within the randomForest (see Liaw and Wiener 2002) and rfUtilities (Evans and Cushman 2009) R package, and constructed 1,000 bootstrapped trees.

To examine our hypotheses concerning habitat characteristics and reproductive success, we used linear regression to assess the relationship between nestling condition and habitat covariates, and calculated means and 90% CIs for habitat covariates with categories of nest success (e.g., no fledglings or 2 fledglings). When we assessed the effect of a covariate on nestling condition, we controlled for the days from clutch initiation to account for differences in hatch dates. For GWCS, we assessed the relationship between canopy volume at both the territory and nest-site scales and mean nestling condition, nest success, and number of fledglings. For LALO, we examined the relationship between canopy volume at the territory scale, and terrain height diversity at the nest-site scale, and mean nestling condition, nest success, and number of fledglings.

3. RESULTS

3.1 Relative importance of covariates and spatial scale in determining habitat use.

Models at the territory scale - but not at the nest-site scale - generally produced informative

results for both GWCSs and LALOs. First, models incorporating all extents for GWCS indicated that the 2,294 m² extent for canopy volume, and the 1,127 m² extent for both NDVI and ALS intensity were the most supported based on variable importance (Table 2). As such, these three

Table 2. Variable importance and out-of-bag error (OOBE) values generated from Random Forest models at the territory and nest-site scale for Gambel's white-crowned sparrow (GWCS) and Lapland longspur (LALO) in the vicinity of Toolik Lake, Alaska, USA. Spatial extents most supported by models are indicated in parenthesis following variable names.

Scale	Gambel's white-crowned sparrow (GWCS)	Lapland longspur (LALO)
	<i>Variable Importance:</i>	<i>Variable Importance:</i>
	Canopy Volume (2,294m ²) = 43	Canopy Volume (28,300m ²) = 27
Territory	Distance to snow-free zone = 28	Distance to snow-free zone = 24
	LiDAR Intensity (1,127m ²) = 13	LiDAR Intensity (28,300m ²) = 26
	NDVI (1,127m ²) = 9	NDVI (28,300m ²) = 16
	<i>Model OOBE = 14%</i>	<i>Model OOBE = 28%</i>
	<i>Variable Importance:</i>	<i>Variable Importance:</i>
	Canopy Volume (256m ²) = -1	Canopy Volume (256m ²) = 15
Nest-site	LiDAR Intensity (256m ²) = -4	LiDAR Intensity (64m ²) = 6
		SD of micro-topography (256m ²) = 12
	<i>Model OOBE = 42%</i>	<i>Model OOBE = 38%</i>

scale-specific covariates, plus distance of nest to snow free zones, were then included in a reduced model that yielded a relatively low OOBE of 14% and indicated that canopy volume and distance to snow free zones were the most important variables for GWCS habitat use (Table 2). While the probability of use increased with canopy volume, it decreased as distance to snow free zones exceeded a few hundred meters, highlighting GWCS use of dense and structurally diverse shrub communities in snow free areas (Figure 2).

Second, models incorporating all extents for LALO indicated that the most supported extent was 28,300 m² for canopy volume, NDVI, and ALS intensity (Table 2). The reduced model suggested that canopy volume, ALS intensity, and distance to snow free zones were the most important variables to LALO habitat use, however, the OOBE was 28%, indicating weaker predictive performance for the LALO model compared to GWCS model (Table 2). The probability of use for LALO decreased both as distance to snow free zones increased and canopy

Figure 2. Gambel's white-crowned sparrow (GWCS) nest locations at TLFS and important habitat covariates. A) Left and middle panes show nest locations of GWCS and proximity to snow-free zones (blue). Right pane shows the probability of habitat use by GWCS is high at short distances to snow-free zones, and sharply declines as distance from snow free zones increases; B) Left and middle panes show nest locations for GWCS and canopy volume (light colors = low values, dark colors = high values). Right pane shows the probability of habitat use by GWCS is low at low canopy volume and sharply increases as canopy volume increases. Nest locations are indicated by 'x'.

volume increased, indicating the use of short vegetation and snow free habitats (Figure 3). Relative to GWCS, the mean distance of LALO nests from snow free zones was larger (138 m vs. 26 m, respectively). Further, the probability of habitat use by LALO increased with ALS intensity, suggesting greater use of areas with minimal cover of surface wetness (Figure 3).

Models at the nest-site scale generally produced uninformative results for both GWCS and LALO. For GWCS, models with all covariates and extents suggested that canopy volume and ALS intensity were both supported at the 256 m² extent (Table 2). However, the OOB of the reduced model was high (42%) and the variable importance values were negative, indicating

weak predictive performance and covariate relationships. For LALO, both canopy volume and SD of terrain height were supported at the 256 m² extent, while ALS intensity was supported at the 64 m² extent (Table 2). Similar to GWCS, the OOB E for the reduced LALO model was high (38%) and all variable importance values were ≤ 21 , indicating weak predictive ability and covariate effects. Because of the weak performance at the nest-site scale for both species we did not map predicted probabilities of nest-site use.

Figure 3. Lapland-longspur (LALO) nest locations at TLFS and important habitat covariates. A) Left and middle panes show nest locations of LALO and proximity to snow-free zones (blue). Right pane shows the probability of habitat use by LALO is higher at shorter distances to snow free areas, and reduces as distance from snow-free zones increases; B) Left and middle panes show nest locations of LALO and canopy volume (light colors = low values, dark colors = high values). Right pane shows the probability of habitat use is high at low canopy volume and sharply declines as canopy volume increases; C) Left and middle panes show nest locations of LALO and LiDaR intensity (light colors = low values, dark colors = high values). Right pane shows the probability of habitat use is low at low LiDaR intensity values and increases as LiDaR intensity increases. Nest locations are indicated by 'x'.

3.2 Predictions for probability of habitat use at the territory scale.

The predicted probability of use at the territory scale (based on canopy volume and distance to snow free zones) for GWCSs indicated relatively strong discrimination between low and high probability locations (Figure 4A and 5AB). However, the predicted probability of use at the territory scale for LALOs (based on canopy volume, ALS intensity, and distance to snow free zones) indicated comparatively weaker discrimination between low and high probability locations (Figure 4B and 5C).

Figure 4. Predicted probability of habitat use at TLFS for: A) Gambel's white-crown sparrow (GWCS), and; B) Lapland longspur (LALO). Predicted probabilities were based on Random Forest models. Differences in grid cell size between A and B corresponds to different territory sizes between species. Nest locations are indicated by 'x'.

Figure 5. Predicted probability of habitat use for Gambel’s white-crown sparrow (GWCS) at: A) SDOT, and (B) ROMO; C) Predicted probability of habitat use for Lapland longspur (LALO) at IMVT. Predicted probabilities were based on Random Forest models. Differences in grid cell size between A and B corresponds to different territory sizes between species. Nest locations are indicated by ‘x’.

3.3 Relationship between habitat and reproductive success.

Of the 46 GWCS nests found, we calculated mean nestling condition for 15 (mean = 0.73), and determined nest success for 42 (37 were successful, and mean number of fledglings = 3.76). Of the 68 LALO nests, we calculated mean nestling condition for 17 (mean = 0.86), and determined nest success for 61 (37 were successful, and mean number of fledglings = 2.18).

For GWCS, linear regressions suggested a positive albeit insignificant relationship between canopy volume and nestling condition at both the territory and nest site scales (Figure 6A). Indeed, after accounting for the days since clutch initiation, the effect of canopy volume on nestling condition indicated no statistically significant effect (Territory: t -value of the slope =

1.35, p -value = 0.20; Nest-Site: t -value of the slope = 1.45, p -value = 0.17). Similarly, the mean estimates of canopy volume ($\pm 90\%$ CIs) were not different between successful and unsuccessful nests, and there was no effect on the number of nestlings fledged (Figure 6B and C). For LALO, linear regression indicated no effect of canopy volume (at the territory scale) or SD of terrain height (nest-site scale) on nestling condition (Figure 7A). Indeed, after accounting for the days since clutch initiation, neither both canopy volume nor SD of terrain height had any significant effect on nestling condition (canopy volume: t -value of the slope = 1.15, p -value = 0.27; SD terrain height: t -value of the slope = 1.50, p -value = 0.95). Similarly, the mean estimates of canopy volume and SD of terrain height ($\pm 90\%$ CIs) were not different between successful and unsuccessful nests, and there was no effect on the number of nestlings fledged (Figure 7B and C).

Figure 6. A) Linear relationship between nestling condition (mass/tarsus length) of Gambel's white-crowned sparrow and canopy volume at the territory (top) and nest-site (bottom) scales, ($n = 15$). B) Mean ($\pm 90\%$ CI) canopy volume at successful and unsuccessful nests of Gambel's white-crowned sparrow at the territory (top) and nest-site (bottom) scales ($n = 37$ successful and 5 unsuccessful). C) Mean ($\pm 90\%$ CI) canopy volume across the number of fledglings per nest for Gambel's white-crowned sparrow at the territory (top) and nest-site (bottom) scales ($n_{\text{five}} = 17$, $n_{\text{four}} = 14$, $n_{\text{three}} = 3$, $n_{\text{two}} = 2$, $n_{\text{zero}} = 5$).

Figure 7. A) Linear relationship between nestling condition (mass/tarsus length) of Lapland longspur and canopy volume at the territory scale (top) and SD of terrain height at the nest-site scale (bottom), ($n = 17$). B) Mean ($\pm 90\%$ CI) canopy volume at the territory scale (top) and SD of terrain height at the nest-site scale (bottom) at successful and unsuccessful Lapland longspur nests ($n = 37$ successful and 24 unsuccessful). C) Mean ($\pm 90\%$ CI) canopy volume at the territory scale (top) and SD of terrain height at the nest-site scale (bottom) across the number of fledglings per nest for Lapland longspur ($n_{\text{five}} = 9$, $n_{\text{four}} = 11$, $n_{\text{three}} = 13$, $n_{\text{two}} = 2$, $n_{\text{zero}} = 24$). We observed only one nest with 1 fledgling and did not include a 1 fledgling group in this plot.

4. DISCUSSION

4.1 ALS reveals that neighborhood appeal is more important than backyard charm. In

partial agreement with our first hypothesis, ALS-derived metrics, but not NDVI, yielded useful information on the relative importance of distinct habitat characteristics that were generally known to be important determinants of breeding habitat use by LALOs and GWCS (Norment 1993; Chilton et al., 1995; Hunt et al., 1995; Hussell and Montgomerie 2002; Boelman et al., 2014). Contrary to expectation, ALS metrics were only important at the territory scale ($\leq 28,300 \text{ m}^2$), and not in the immediate vicinity of nests ($\leq 512 \text{ m}^2$). Our findings support many studies conducted in temperate and tropical ecosystems, while also contributing the first Arctic

demonstration, showing that ALS provides significantly more insight relative to NDVI into understanding wildlife-habitat associations in tundra.

Since NDVI has proven capable of identifying areas of high versus low tundra productivity (Vierling et al., 1997; Boelman et al., 2003, 2005, 2011; Street et al., 2007), we expected to find that songbird habitat use would be associated to some degree with variation in NDVI at the territory scale since our two study species nest exclusively in two very distinct tundra types: GWCS nest in tall shrub tundra communities where LAI typically is typically ≤ 2 (GWCS), while LALOs nest in short sedge dominated tundra communities where LAI is typically < 1 and (LALO) (Williams and Rastetter 1999). We attribute the discrepancy between our expectations and findings to the fact that NDVI-vegetation relationships tend to be community-specific, with significant overlap among them, so that different measured values of LAI, aerial plant cover, canopy height, or aboveground biomass from a range of community types are often associated with the same NDVI value (i.e. Boelman et al., 2005 and 2011).

Given that GWCS are known to place nests under the shelter of taller stature deciduous shrubs (Boelman et al., 2014), we expected that within their chosen territories, this species would place nests in locations where deciduous shrubs were larger (ie. higher canopy volume) and where surface wetness was low (ie. higher ALS intensity). Similarly, because LALOs nest exclusively in areas of low-lying tundra vegetation (< 20 cm tall) where variation in canopy height is minimal (Boelman et al., 2014), we expected that within their chosen territories this species would place nests in locations of micro-topographically diverse terrain (ie. higher SD of terrain height) that would provide superior insulation from harsh environmental conditions and predation (Kern 1984; Rodrigues et al., 1994; Norment 1995; Morton 2002). In partial disagreement with these hypotheses, multi-scale analysis of ALS metrics revealed that although

ecological characteristics at the territory scale are important determinants to breeding habitat use, neither species showed preferences towards any of our measured ecological characteristics in the immediate vicinity of nest-sites. This finding is consistent with several previous studies from other ecosystems, and may be partially explained by the observation that animals such as birds may respond to multiple habitat characteristics being considered at multiple spatial scales (Wiens 1989). Studies that have explicitly considered ecological characteristics at different spatial scales (i.e. nest-site, territory and landscape scales) have found that the variables in the immediate vicinity of nest sites are not always as influential as variables considered over larger spatial scales (e.g. Chalfoun and Martin 2007). For instance, Saab (1999) found that landscape context was a more important predictor of nest site use for over 30 species of riparian nesting birds as compared to habitat characteristics occurring at the nest-site scale.

4.2 What makes a neighborhood worth fighting for?

In partial agreement with our second hypothesis, territory use for GWCS was found to be strongly associated with areas of high canopy volume, while that for LALOs is associated with areas of both low canopy volume and high ALS intensity (i.e. low surface wetness). Considering previous field-based work on these species, our finding that LALO and GWCS territories are characterized by either very low or high canopy volumes, respectively, is not surprising (Norment 1993; Chilton et al., 1995; Hunt et al., 1995; Hussell and Montgomerie 2002; Boelman et al., 2014). Instead, our study findings highlight the unique ability of ALS remote sensing to both contribute to understanding critical wildlife-vegetation associations in arctic tundra, and, to scaling up this understanding to predict habitat use over large regions. Similarly, the fact that ALS was able to show that LALOs, but not GWCS, use breeding territories with low surface wetness provides further incentive to employ ALS as a tool for wildlife studies in tundra

ecosystems where standing water is a ubiquitous landscape feature due to annual flooding and thawing of the soil active layer each summer (Shaver and Chapin 1991; Tape et al., 2006; Naito and Cairns 2011). However, because both of our study species are ground nesters, and must avoid areas prone to inundation, we expected that both would exhibit a strong positive relationship between territory use and ALS intensity. We attribute the species-specific responses to the fact that the tall-shrub communities in which GWCS nest are often, but not exclusively, associated with areas of flowing surface water (i.e. zones of low ALS intensity) where tall shrubs are dominant (Sweet et al., 2014), while nesting LALO avoid these areas entirely due to exclusive preferences of short, sedge-dominated tundra communities.

In addition, our assessment of the role of snow cover patterns in determining territory use yielded slightly different conclusions for GWCS and LALO. We found that while GWCS nests were located in or near typically snow-free zones - suggesting a preference for snow-free areas of greater extent - LALO nests were found at a range of distances from large snow-free zones - suggesting that they will nest more readily within snow-free areas of smaller extent that were likely not resolved by the Landsat 7 panchromatic sensor (pixel size=225 m²). These findings agree with our hypothesis that both species establish territories near snow-free zones, but offer the additional insight that relative to GWCS, LALOs will establish territories in areas with smaller patches of snow-free tundra. This difference between species may be partly attributed to the fact that LALO's breeding in our study region typically arrive a few days prior to GWCS (Boelman et al. *in review*), and thus during a time when snow cover is generally higher and patches of snowfree tundra are both smaller and less abundant. In addition, while GWCSs are a largely boreal species, LALO are arctic specialists - having arrived in Alaska following the retreat of the last glaciation (Williamson and Emison 1971) - that may be better able to cope with

high snow cover conditions that often characterize early springtime on the tundra (Wingfield et al., 2004). One caveat associated with our assessment of the role of spring snow cover patterns in determining territory use is that our study region unavoidably included anthropogenic features (i.e. roads) that are typically snowfree earlier than areas with little human impact, and as such, these features may have influenced our results to some extent.

Finally, our modeled spatial predictions were able to better discriminate between high and low habitat use probabilities for GWCSs compared to LALOs. This suggests that GWCS exhibit stronger habitat use relative to LALOs, and/or that ecological variables other than those considered in our analysis are important additional determinants of LALO breeding habitat use.

4.3 Reproductive success is unrelated to the degree of neighborhood appeal.

Contrary to our final hypothesis, we found that reproductive success of GWCS and LALOs was unaffected by differences in either canopy volume or SD of micro-terrain height among territories. This finding supports those of studies in other ecosystems that have found that variables that influenced songbird breeding habitat use did not have strong influences on reproduction. For example, Sadoti and Vierling (2010) found that although habitat characteristics at the territory scale were influential in determining nest-site use by Red-naped sapsuckers (*Sphyrapicus nuchalis*), the characteristics of the specific tree in which a nest was placed were the most influential in driving nest productivity. Similarly, Chalfoun and Martin (2007) found that breeding habitat use for Brewer's sparrows (*Spizelli breweri*) was influenced largely by landscape scale characteristics, but the specific ecological characteristics in the near vicinity of nests seemed to more strongly influence nest success. The fact that reproductive success of both species in our study were not influenced by canopy volume or SD of micro-terrain height suggests that in addition to the spatial characteristics examined herein, several

other factors - such as parental effects, nest quality, and inter-annual variation in both environmental conditions and predator pressure - likely affected reproductive success over our study period (Norment et al., 1995; Mutzel et al., 2013; Perez et al. *in revision*).

5. CONCLUSIONS

Through the use of ALS technology to examine wildlife habitat characteristics in arctic tundra, our study broadens current understanding of songbird-habitat associations, and to our knowledge is the first arctic demonstration of how integrating LiDaR technology with field surveys and predictive modeling enables accurate mapping of tundra breeding territories. In addition, the demonstrated utility of ALS in arctic tundra suggests that it is likely to be informative in other low stature ecosystems with similarly small ranges in 3-D structural attributes and where seemingly uniform canopies may provide distinct breeding habitats that are critical to faunal communities. Although the collection of ALS data is currently restricted to highly tailored, one-time, and costly airborne surveys, a handful of studies have examined the potential usefulness of a now-inactive space-borne LiDaR system (Geoscience Laser Altimeter System, GLAS) for modeling animal habitat (Vierling et al., 2013; Goetz et al., 2014). Although there are no space-borne LiDaR systems currently active, multiple authors have noted the importance of broader airborne coverage for biodiversity studies (Bergen et al., 2011; Goetz et al., 2011), as well as the next generation of spaceborne LiDaR instruments that are currently in design (e.g. GEDI, IceSAT-2). As an alternative to LiDaR, existing and next generation synthetic aperture radar (SAR) instruments (e.g. UAVSAR, TanDEM-X) also yield information on the physical structure of vegetation, and thereby serve as an attractive alternative or complementary

tool to LiDaR (Swatantran et al. 2012). Similarly, spectral image texture has proven to be a surrogate for vegetation structure (e.g. Wood et al., 2013).

Our most important ALS-enabled finding with respect to songbird-habitat associations is that the ecological characteristics we found to be most important in determining breeding habitat use - canopy volume, spring snowmelt patterns, and surface wetness - were only important at the territory scale (2,294 - 28,300 m², depending on species), suggesting that variation in characteristics in the immediate vicinity of nests (64 - 512 m²) are not important to the birds. Since Gambel's white-crowned sparrows and Lapland longspurs represent two broad groups of arctic breeding songbirds with contrasting habitat requirements - shrub tundra nesters vs. open tundra nesters, respectively - our findings inform how songbirds with similar breeding territory and nest-site preferences rely on specific ecological characteristics in rapidly changing arctic tundra ecosystems.

6. ACKNOWLEDGEMENTS

We thank Ashley Asmus, Shae Bowman, Kathryn Daly, Adam Formica, Jessica Gersony, Kathleen Hunt, Michaela McGuigan, Simone Meddle, Lisa Quach, Jake Schas, Shannan Sweet and Marley Tran for field assistance. We thank Toolik Field Station (TFS) (Institute of Arctic Biology, University of Alaska Fairbanks) and CH2M HILL for providing support and logistics. This project has been funded by NASA Terrestrial Ecology grant (NNX12AK83G) to L. Vierling, and a collaborative NSF grant from the Office of Polar Programs (ARC 0908444 to N. Boelman, ARC 0908602 to L. Gough, and ARC 0909133 to J. Wingfield).

7. REFERENCES

- Baruch-Mordo, S., J.S. Evans, J.P. Severson, D.E. Naugle, J.D. Maestas, J.M. Kiesecker, M.J. Falkowski, C.A. Hagen, and K.P. Reese. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. *Biological Conservation* 167:233-241.
- Bergen, K. M., S. J. Goetz, R. O. Dubayah, G. M. Henebry, C. T. Hunsaker, M. L. Imhoff, R. F. Nelson, G. G. Parker, and V. C. Radeloff. 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for LiDaR and radar spaceborne missions. *Journal of Geophysical Research: Biogeosciences* 114:1–13.
- Bintanja, R., and E. C. van der Linden. 2013. The changing seasonal climate in the Arctic. *Scientific reports* 3:1556.
- Boelman, N.T., L. Gough, J. Wingfield, S. J. Goetz, A. Asmus, H. Chmura, J. Krause, P. Jonathan, S. Sweet, and K. Guay. 2014. Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology in review*:1–13.
- Boelman, N. T., G. P. Asner, P. J. Hart, and R. E. Martin. 2007. Multi-trophic invasion resistance in Hawaii: Bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications* 17:2137–2144.

705 Boelman, N. T., L. Gough, J. R. McLaren, and H. Greaves. 2011. Does NDVI reflect variation in
 706 the structural attributes associated with increasing shrub dominance in arctic tundra?
 707 Environmental Research Letters 6:035501.

708 Boelman, N. T., M. Stieglitz, K. L. Griffin, and G. R. Shaver. 2005. Inter-annual variability of
 709 NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra.
 710 Oecologia 143:588–597.

711 Boelman, N. T., M. Stieglitz, H. M. Rueth, M. Sommerkorn, K. L. Griffin, G. R. Shaver, and
 712 J.A., Gamon. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term
 713 warming and fertilization in wet sedge tundra. Oecologia 135:414–21.

714 Boelman, N.T., J.C. Wingfield, L. Gough, J.S. Krause, S.K. Sweet, H.E. Chmura, and J.H. Perez.
 715 *in review*. Long-distance migratory songbirds adjust timing of clutch initiation in response
 716 to unpredictable and dynamic spring conditions in the Arctic

717 Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies:
 718 relating individual behaviour to spatial dynamics. Biological reviews of the Cambridge
 719 Philosophical Society 80:205–225.

720 Breiman, L. 2001. Random Forests. Machine Learning 45:5-32.

721 Callaghan T.V., L.O. Björn, Y. Chernov, T. Chapin, T.R. Christensen, B. Huntley, R.A. Ims, M.
 722 Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S.
 723 Schaphoff and SS. 2004. Effects of changes in climate on landscape and regi, and S. S.

2004. Effects of changes in climate on landscape and regional processes, and feedbacks to
 the climate system. *Ambio* 33:459–468.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend
 on spatial scale and metrics of fitness. *Journal of Applied Ecology* 44:983–992.

Chapman, W., and J. Walsh. 1993. Recent variations of sea ice and air temperature in high
 latitudes. *Bulletin of the American Meteorological Society* 74:33–47.

Chen, X., L. Vierling, E. Rowell, and T. DeFelice. 2004. Using LiDaR and effective LAI data to
 evaluate IKONOS and Landsat 7 ETM+ vegetation cover estimates in a ponderosa pine
 forest. *Remote Sensing of Environment* 91:14–26.

Chilton, G., M. C. Baker, C. D. Barrentine and M. A. Cunningham. 1995. White-crowned
 Sparrows (*Zonotrichia leucophrys*). In *The Birds of North America*, No. 183 (A. Poole,
 Ed.). The Birds of North America Online, Ithaca, New York.

Clawges, R., K. Vierling, L. Vierling, and E. Rowell. 2008. The use of airborne LiDaR to assess
 avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sensing of*
Environment 112:2064–2073.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal,
 heterogeneity in animal dispersal syndromes and the dynamics of spatially structured
 populations. *Ecology Letters* 12:197–209.

Cote, J., J. Clobert, T. Brodin, S. Fogarty, and a Sih. 2010. Personality-dependent dispersal:
 characterization, ontogeny and consequences for spatially structured populations.

744 Philosophical transactions of the Royal Society of London. Series B, Biological sciences
745 365:4065–4076.

746 Couturier, S., S. D. Côté, R. D. Otto, R. B. Weladji, and J. Huot. 2009. Variation in Calf Body
747 Mass in Migratory Caribou: The Role of Habitat, Climate, and Movements. *Journal of*
748 *Mammalogy* 90:442–452.

749 Cutler, D.R., T.C. Edwards Jr., K.H. Beard, A. Cutler, K.T. Hess, J. Gibson, and J.J. Lawler.
750 2007. Random forests for classification in ecology. *Ecology* 88:2783-2792.

751 Davies, A. B., and G. P. Asner. 2014. Advances in animal ecology from 3D-LiDaR ecosystem
752 mapping. *Trends in Ecology & Evolution* 29:681–691.

753 Derksen, C., and R. Brown. 2012. Spring snow cover extent reductions in the 2008-2012 period
754 exceeding climate model projections. *Geophysical Research Letters* 39:1–6.

755 Dozier, J. 1989. Spectral signature of alpine snow cover from the Landsat Thematic Mapper.
756 *Remote Sensing of Environment* 22:9–22.

757 Ehrich, D., J.A. Henden, R. A. Ims, L. O. Doronina, S. T. Killengren, N. Lecomte, I. G.
758 Pokrovsky, G. Skogstad, A.A. Sokolov, V.A. Sokolov, and N. G. Yoccoz. 2012. The
759 importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better?
760 *Oecologia* 168:141–51.

761 Eitel, J. U. H., L.A. Vierling, and D. S. Long. 2010. Simultaneous measurements of plant
762 structure and chlorophyll content in broadleaf saplings with a terrestrial laser scanner.
763 *Remote Sensing of Environment* 114:2229–2237.

764 Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan,
 765 L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. a. Day, A. M. Fosaa, W. a. Gould, J.
 766 Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F.
 767 Keuper, K. Klanderud, J. a. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J.
 768 Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post,
 769 C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø.
 770 Totland, T. Troxler, C. H. Wahren, P. J. Webber, J. M. Welker, and P. a. Wookey. 2012.
 771 Global assessment of experimental climate warming on tundra vegetation: Heterogeneity
 772 over space and time. *Ecology Letters* 15:164–175.

773 Emison, W. B. 1971. Lapland Longspur (*Calcarius lapponicus*) in Alaska ., *Bioscience* 21:701–
 774 707.

775 Evans, J.S., M.A. Murphy, Z.A. Holden, and S.A. Cushman. 2011. Modeling species distribution
 776 and change using Random Forests. Pages 139-159 *in* Predictive species and habitat
 777 modeling in landscape ecology: concepts and applications. Drew, A.C., Y. Wiersma, and F.
 778 Huettmann, editors. Springer, New York.

779 Evans, J.S., and S.A. Cushman. 2009. Gradient modeling of conifer species using Random
 780 Forest. *Landscape Ecology* 24:673-683.

781 Gamon, J.A., K. F. Huemmrich, R. S. Stone, and C. E. Tweedie. 2013. Spatial and temporal
 782 variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation
 783 growth following earlier snowmelt. *Remote Sensing of Environment* 129:144–153.

784 Garroway, K., Hopkinson, C., & Jamieson, R. (2011). Surface moisture and vegetation
785 influences on LiDaR intensity data in an agricultural watershed. *Canadian Journal of*
786 *Remote Sensing*, 37(3), 275–284. doi:10.5589/m11-036

787 Genuer, R., J.M. Poggi, and C. Tuleau-Malot. 2010. Variable use using random forests. *Pattern*
788 *Recognition Letters* 31:2225-2236.

789 Goetz, S. J., D. Steinberg, M. G. Betts, R. T. Holmes, P. J. Doran, R. Dubayah, and M. Hofton.
790 2010. LiDaR remote sensing variables predict breeding habitat of a Neotropical migrant
791 bird. *Ecology* 91:1569–1576.

792 Goetz, S. J., M. Sun, S. Zolkos, A. Hansen, and R. Dubayah. 2014. The relative importance of
793 climate and vegetation properties on patterns of North American breeding bird species
794 richness. *Environmental Research Letters* 9:034013.

795 Goetz, S., D. Steinberg, R. Dubayah, and B. Blair. 2007. Laser remote sensing of canopy habitat
796 heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA.
797 *Remote Sensing of Environment* 108:254–263.

798 Goodale, R., C. Hopkinson, D. Colville, and D. Amirault-Langlais. 2007. Mapping piping plover
799 (*Charadrius melodus melodus*) habitat in coastal areas using airborne LiDaR data. *Canadian*
800 *Journal of Remote Sensing* 33:519–533.

801 Greaves, H. E., L.A. Vierling, J. U. H. Eitel, N. T. Boelman, T. S. Magney, C. M. Prager, and K.
802 L. Griffin. 2015. Estimating aboveground biomass and leaf area of low-stature Arctic
803 shrubs with terrestrial LiDaR. *Remote Sensing of Environment* 164:26–35.

804 Greaves, H., L.A., Vierling, J.U.H., Eitel, N.T., Boelman, T.S., Magney, C.M., Prager, and K.L.,
805 Griffin. *in review*. Fine-scale mapping of aboveground shrub biomass in Arctic tundra using
806 terrestrial and airborne LiDaR.

807 Griffith, B., D.C. Douglas, N.E. Walsh, D.D. Young, T.R. McCabe, D.E. Russell, R.G. White,
808 R.D. Cameron, and K.R. Whitten. 2002. Section 3: The Porcupine Caribou Herd, from
809 Biological Science Report USGS/BRD 2002-0001: Arctic refuge coastal plain terrestrial
810 wildlife research summaries, 8-37.

811 Hansen, B. B., R. Aanes, I. Herfindal, B. E. Sæther, and S. Henriksen. 2009. Winter habitat-
812 space use in a large arctic herbivore facing contrasting forage abundance. *Polar Biology*
813 32:971–984.

814 Hatfield, J. L., E. T. Kanemasu, G. Asrar, R. D. Jackson, P. J. Pinter, R. J. Reginato, and S. B.
815 Idso. 1985. Leaf-area estimates from spectral measurements over various planting dates of
816 wheat. *International Journal of Remote Sensing* 1161.

817 Henden, J.-A., R. A. Ims, N. G. Yoccoz, R. Sørensen, and S. T. Killengreen. 2011. Population
818 dynamics of tundra voles in relation to configuration of willow thickets in southern arctic
819 tundra. *Polar Biology* 34:533–540.

820 Hijmans, R. J. 2015. Introduction to the ' raster ' package (version 2 . 4-20):1–27.

821 Hill, R.A., S.A. Hinsley, D. L. a. Gaveau, and P. E. Bellamy. 2004. With Airborne Laser
822 Scanning Data. *International Journal of Remote Sensing* 25:4851–4855.

- 823 Hinsley, S.A., R.A.A. Hill, D. L.A. Gaveau, and P. E. Bellamy. 2002. Quantifying woodland
824 structure and habitat quality for birds using airborne laser scanning. *Functional Ecology*
825 16:851–857.
- 826 Hinsley, S.A., R.A. Hill, P. E. Bellamy, and H. Balzter. 2006. The application of LiDaR in
827 woodland bird ecology: climate, canopy structure and habitat quality. *Photogrammetric*
828 *Engineering and Remote Sensing* 72:1399–1406.
- 829 Holmgren, J., A. Persson, and U. Soderman. 2008. Species identification of individual trees by
830 combining high resolution LiDAR data with multi-spectral images. *International Journal of*
831 *Remote Sensing* 29:1537-1552.
- 832 Hunt, K., J. Wingfield, L. B. Astheimer, W. A. Buttemer, and T. P. Hahn. 1995. Temporal
833 Patterns of Territorial Behavior and Circulating Testosterone in the Lapland Longspur and
834 Other Arctic Passerines 1. *American Zoologist* 284:274–284.
- 835 Hurlbert, A. H., A. H. Hurlbert, J. P. Haskell, and J. P. Haskell. 2003. The effect of energy and
836 seasonality on avian species richness and community composition. *The American naturalist*
837 161:83–97.
- 838 Hyde, P., R. Dubayah, B. Peterson, J. B. Blair, M. Hofton, C. Hunsaker, R. Knox, and W.
839 Walker. 2005. Mapping forest structure for wildlife habitat analysis using waveform
840 LiDaR: Validation of montane ecosystems. *Remote Sensing of Environment* 96:427–437.
- 841 Hussell, D. J. T., and R. Montgomerie. 2002. Lapland Longspurs (*Calcarius lapponicus*). *In* The
842 Birds of North America, No. 656 (A. Poole and F. Gill, eds.). The Birds of North America,

843 Inc., Philadelphia, PA.

844 Hyde, P., R. Dubayah, W. Walker, J. B. Blair, M. Hofton, and C. Hunsaker. 2006. Mapping
845 forest structure for wildlife habitat analysis using multi-sensor (LiDaR, SAR/InSAR,
846 ETM+, Quickbird) synergy. *Remote Sensing of Environment* 102:63–73.

847 Kaasalainen, S., A. Jaakkola, M. Kaasalainen, A. Krooks, and A. Kukko. 2011. Analysis of
848 incidence angle and distance effects on terrestrial laser scanner intensity: Search for
849 correction methods. *Remote Sensing* 3:2207–2221.

850 Kaasalainen, S., A. Krooks, A. Kukko, and H. Kaartinen. 2009. Radiometric Calibration of
851 Terrestrial Laser Scanners with External Reference Targets. *Remote Sensing* 1:144–158.

852 Kern, D. 1984. Racial Differences in nests of White-crowned sparrows. *The Condor* 86:455–
853 466.

854 König, M., and M. Sturm. 1998. Mapping snow distribution in the Alaskan Arctic using aerial
855 photography and topographic relationships. *Water Resources Research* 34:3471.

856 Korpela, I., M. Koskinen, H. Vasander, M. Holopainen, and K. Minkkinen. 2009. Airborne
857 small-footprint discrete-return LiDaR data in the assessment of boreal mire surface patterns,
858 vegetation, and habitats. *Forest Ecology and Management* 258:1549–1566.

859 Kukko, A., S. Kaasalainen, and P. Litkey. 2008. Effect of incidence angle on laser scanner
860 intensity and surface data. *Applied optics* 47:986–992.

861 Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002. LiDaR remote sensing for
862 ecosystem studies. *Bioscience* 52:19–30.

863 Lele, S.R., E.H., Merrill, J. Keim, and M.S. Boyce. 2013. Use, choice and occupancy: clarifying
864 concepts in resource use studies. *Journal of Animal Ecology* 82:1183-1191.

865 Lesak, A.A., V. C. Radeloff, T. J. Hawbaker, A. M. Pidgeon, T. Gobakken, and K. Contrucci.
866 2011. Modeling forest songbird species richness using LiDaR-derived measures of forest
867 structure. *Remote Sensing of Environment* 115:2823–2835.

868 Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R news* 2: 18-22.

869 Loarie, S. R., C. J. Tambling, and G. P. Asner. 2013. Lion hunting behaviour and vegetation
870 structure in an African savanna. *Animal Behaviour* 85:899–906.

871 Macarthur, R. H., and J. W. Macarthur. 1961. On Bird Species Diversity Published by :
872 Ecological Society of America Linked references are available on JSTOR for this article :
873 *Ecology* 42:594–598.

874 Maltamo, M., E. Næsset, and J. Vauhkonen. 2014. *Forestry Applications of Airborne Laser*
875 *Scanning*. Springer.

876 Markham, B. L., J. C. Storey, D. L. Williams, and J. R. Irons. 2004. Landsat sensor performance:
877 history and current status. *IEEE Transactions on Geoscience and Remote Sensing* 42:2691–
878 2694.

879 Martinuzzi, S., L.A. Vierling, W.A. Gould, M.J. Falkowski, J.S. Evans, A.T. Hudak, and K.T.
 880 Vierling. 2009. Mapping snags and understory shrubs for a LiDaR-based assessment of
 881 wildlife habitat suitability. *Remote Sensing of the Environment* 113:2533-2546.

882 Melin, M., P. Packalén, J. Matala, L. Mehtätalo, and J. Pusenius. 2013. Assessing and modeling
 883 moose (*alces alces*) habitats with airborne laser scanning data. *International Journal of*
 884 *Applied Earth Observation and Geoinformation* 23:389–396.

885 Morton, M. L. 2002. The Mountain White-crowned Sparrow: Migration and reproduction at high
 886 altitude. *Studies in Avian Biology*.

887 Mutzel, a, N. J. Dingemanse, Y. G. Araya-Ajoy, and B. Kempenaers. 2013. Parental
 888 provisioning behaviour plays a key role in linking personality with reproductive success.
 889 *Proceedings of the Royal Society B: Biological Sciences* 280:20131019–20131019.

890 Myers-Smith, I. H., S. C. Elmendorf, P. S. a. Beck, M. Wilmking, M. Hallinger, D. Blok, K. D.
 891 Tape, S. a. Rayback, M. Macias-Fauria, B. C. Forbes, J. D. M. Speed, N. Boulanger-
 892 Lapointe, C. Rixen, E. Lévesque, N. M. Schmidt, C. Baittinger, A. J. Trant, L. Hermanutz,
 893 L. S. Collier, M. a. Dawes, T. C. Lantz, S. Weijers, R. H. Jørgensen, A. Buchwal, A. Buras,
 894 A. T. Naito, V. Ravolainen, G. Schaepman-Strub, J. a. Wheeler, S. Wipf, K. C. Guay, D. S.
 895 Hik, and M. Vellend. 2015. Climate sensitivity of shrub growth across the tundra biome.
 896 *Nature Climate Change* 5, 887–891 doi:10.1038/nclimate2697

897 Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M.
 898 Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A.
 899 Trant, L. S. Collier, S. Weijers, J. Rozema, S. a Rayback, N. M. Schmidt, G. Schaepman-

900 Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S.
 901 Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub
 902 expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental*
 903 *Research Letters* 6:045509.

904 Naito, A. T., and D. M. Cairns. 2011. Relationships between Arctic shrub dynamics and
 905 topographically derived hydrologic characteristics. *Environmental Research Letters*
 906 6:045506.

907 Nijland, W., N. C. Coops, S. E. Nielsen, and G. Stenhouse. 2015. Integrating optical satellite
 908 data and airborne laser scanning in habitat classification for wildlife management.
 909 *International Journal of Applied Earth Observation and Geoinformation* 38:242–250.

910 Nield, J. M., J. King, and B. Jacobs. 2014. Detecting surface moisture in aeolian environments
 911 using terrestrial laser scanning. *Aeolian Research* 12:9–17.

912 Norment, C. J. 1993. Nest-Site Characteristics and Nest Predation in Harris ' Sparrows and
 913 White-Crowned Sparrows in the Northwest Territories , Canada. *The Auk* 110:769–777.

914 Norment, C. J. 1995. Incubation Patterns in Harris ' Sparrows and White-Crowned Sparrows in
 915 the Northwest. *Journal of Field Ornithology* 66:553–563.

916 Oakeson, B. B. 1954. The Gambel's sparrow at Mountain Village, Alaska. *Auk* 71(4) 351-65.
 917

918 Orka, H.O., M. Dalponte, T. Gobakken, E. Naesset, and L.T. Ene. 2013. Characterizing forest
 919 species composition using multiple remote sensing data sources and inventory approaches.

920 Scandinavian Journal of Forest Research 28:677-688.

921 Overland, J. E., M. C. Spillane, D. B. Percival, M. Wang, and H. O. Mofjeld. 2004. Seasonal and
922 regional variation of pan-Arctic surface air temperature over the instrumental record.
923 Journal of Climate 17:3263–3282.

924 Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of
925 phenological response to global warming. Global Change Biology 13:1860–1872.

926 Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts
927 across natural systems. Nature:37–42.

928 Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. a. Beck, T. Damoulas, S. J. Knight, and S. J.
929 Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change.
930 Nature Climate Change 3:673–677.

931 Pedersen, a Ø., J. U. Jepsen, N. G. Yoccoz, and E. Fuglei. 2007. Ecological correlates of the
932 distribution of territorial Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Canadian
933 Journal of Zoology 85:122–132.

934 Perez, J.H., J.S., Krause, H.E., Chmura, S., Bowman, M., McGuigan, A., Asmus, S.L., Meddle,
935 K.E., Hunt, L., Gough, N.T., Boelman, J.C., Wingfield. *in revision*. Nestling growth rates in
936 relation to food abundance and weather in the Arctic.

937 Petrinovich, L, Patterson, T. 1982. The White-crowned sparrow: Stability, recruitment, and
938 population structure in the Nuttall subspecies. The Auk 99:1–14.

939 Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud.
 940 2011. The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in
 941 animal ecology. *Climate Research* 46:15–27.

942 Pielou, E.G.. 1994. *A Naturalist's Guide to the Arctic*. University of Chicago Press, Chicago.

943 Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V Callaghan, T. R. Christensen, B. Elberling,
 944 A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R.A. Ims, E. Jeppesen, D. R. Klein, J. Madsen,
 945 A.D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R.
 946 van der Wal, J. Welker, P.A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological
 947 dynamics across the Arctic associated with recent climate change. *Science* (New York,
 948 N.Y.) 325:1355–1358.

949 Ralph, C. J., and C. A. Pearson. 1971. Correlation of Age, Size of Territory , Plumage , and
 950 Breeding Success in White-Crowned Sparrows. *The Condor* 73:77–80.

951 Rodrigues, R. 1994. Microhabitat Variables Influencing Nest-Site Selection by Tundra Birds.
 952 *Ecological Applications* 4:110–116.

953 Rouse, J.W., R.H. Haas, J. A. Schell, and D.W. Deering. 1974. Monitoring the vernal
 954 advancement and retrogradation (greenwave effect) of natural vegetation.

955 Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a
 956 hierarchical analysis. *Ecological Applications* 9:135–151.

957 Sadoti, G., and K. T. Vierling. 2010. Nonideal habitat selection by a North American cavity
 958 excavator: pecking up the wrong tree? *Canadian Journal of Zoology* 88:527–535.

959 Seastedt, T. R., and S. F. Maclean. 1979. Territory size and composition in relation to resource
 960 abundance in Lapland longspurs breeding in Arctic Alaska. *The Auk* 96:131–142.

961 Serreze, M. C., J.E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W.
 962 C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent
 963 change in the northern high latitude environment. *Climatic Change* 46:159–207.

964 Shariatinajafabadi, M., T. Wang, A. K. Skidmore, A. G. Toxopeus, A. Kölzsch, B. a. Nolet, K.-
 965 M. Exo, L. Griffin, J. Stahl, and D. Cabot. 2014. Migratory Herbivorous Waterfowl Track
 966 Satellite-Derived Green Wave Index. *PLoS ONE* 9:e108331.

967 Shaver, G. R., and F. S. Chapin. 1991. Production : Biomass Relationships and Element Cycling
 968 in Contrasting Arctic Vegetation Types. *Ecological Monographs* 61:1–31.

969 Shippert, M. M., D.A. Walker, N.A. Auerbach, and B. E. Lewis. 1995. Biomass and leaf-area
 970 index maps derived from SPOT images for Toolik Lake and Innavait Creek areas, Alaska.
 971 *Polar Record* 31:147.

972 Stone, R. S. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change.
 973 *Journal of Geophysical Research* 107.

974 Street, L. E., G. R. Shaver, M. Williams, and M. T. Van Wijk. 2007. What is the relationship
 975 between changes in canopy leaf area and changes in photosynthetic CO₂ flux in arctic
 976 ecosystems? *Journal of Ecology* 95:139–150.

977 Streutker, D., and N. Glenn. 2006. LiDaR measurement of sagebrush steppe vegetation heights.
 978 *Remote Sensing of Environment* 102:135–145.

979 Swatantran, A., R. Dubayah, S. Goetz, M. Hofton, M. G. Betts, M. Sun, M. Simard, and R.
 980 Holmes. 2012. Mapping migratory bird prevalence using remote sensing data fusion. PLoS
 981 ONE 7.

982 Sweet, S. K., L. Gough, K. L. Griffin, and N. T. Boelman. 2014. Tall deciduous shrubs offset
 983 delayed start of growing season through rapid leaf development in the Alaskan arctic
 984 tundra. *Arctic, Antarctic, and Alpine Research* 46:682–697.

985 Sweet, S. K., K. L. Griffin, H. Steltzer, L. Gough, and N. T. Boelman. 2015. Greater deciduous
 986 shrub abundance extends tundra peak season and increases modeled net CO₂ uptake. *Global
 987 Change Biology*

988 Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska
 989 and the Pan-Arctic. *Global Change Biology* 12:686–702.

990 Tombre, I. M., K.A. Høgda, J. Madsen, L. R. Griffin, E. Kuijken, P. Shimmings, E. Rees, and C.
 991 Verschuur. 2008. The onset of spring and timing of migration in two arctic nesting goose
 992 populations: The pink-footed goose *Anser bachyrhynchus* and the barnacle goose *Branta
 993 leucopsis*. *Journal of Avian Biology* 39:691–703.

994 Trainor, A. M., J. R. Walters, W. F. Morris, J. Sexton, and A. Moody. 2013. Empirical
 995 estimation of dispersal resistance surfaces: A case study with red-cockaded woodpeckers.
 996 *Landscape Ecology* 28:755–767.

997 Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote
 998 sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* 18:306–
 999 314.

1000 Vierling, L.A., J.U.H. Eitel, N.T. Boelman, K.L. Griffin, H. Greaves, T.S. Magney, C. Prager,
 1001 M., Ajayi, and R. Gibson. 2013a. Bare earth LiDaR dataset for Toolik Field Station, AK,
 1002 and nearby field sites along Dalton Highway. doi: 10.7923/G4057CV5.

1003 Vierling, L.A., J.U.H. Eitel, N.T. Boelman, K.L. Griffin, H. Greaves, T.S. Magney, C. Prager,
 1004 M., Ajayi, and R. Gibson. 2013b. Four-band, 5cm resolution orthophotographs of Toolik
 1005 Field Station, AK, and nearby field sites along Dalton Highway. doi:
 1006 10.7923/G4VD6WCW.

1007 Vierling, K. T., L.A. Vierling, W. a Gould, S. Martinuzzi, and R. M. Clawges. 2008. LiDaR:
 1008 shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the*
 1009 *Environment* 6:90–98.

1010 Vierling, L. a., K. T. Vierling, P. Adam, and A. T. Hudak. 2013. Using satellite and airborne
 1011 LiDaR to model woodpecker habitat occupancy at the landscape scale. *PLoS ONE* 8.

1012 Vierling, LA, Deering D.W., Eck, T. 1997. Differences in arctic tundra vegetation type and
 1013 phenology as seen using bidirectional radiometry in the early growing season. *Remote*
 1014 *Sensing of Environment* 60:71–82.

1015 Virtanen, R., J. A. Grytnes, J. Lenoir, M. Luoto, J. Oksanen, L. Oksanen, and J. C. Svenning.
 1016 2013. Productivity-diversity patterns in arctic tundra vegetation. *Ecography* 36:331–341.

- 1017 Vogeler, J. C., A. T. Hudak, L. a. Vierling, J. Evans, P. Green, and K. T. Vierling. 2014. Terrain
1018 and vegetation structural influences on local avian species richness in two mixed-conifer
1019 forests. *Remote Sensing of Environment* 147:13–22.
- 1020 Wiens, J. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- 1021 Williams, M., and E. B. Rastetter. 1999. Vegetation characteristics and primary productivity
1022 along an arctic transect: implications for scaling-up. *Journal of Ecology* 87:885–898.
- 1023 Wingfield, J. C., J. S. Krause, J. H. Perez, H. E. Chmura, Z. Németh, K. R. Word, R. M. Calisi,
1024 and S. L. Meddle. *accepted*. A Mechanistic Approach to Understanding Range Shifts in a
1025 Changing World: What Makes a Pioneer? *General and Comparative Endocrinology*.
- 1026 Wingfield, J. C., N. Owen-Ashley, Z. M. Benowitz-Fred-Ericks, S. E. Lynn, T. P. Hahn, H.
1027 Wada, C. Breuner, S. L. Meddle, and L. M. Romero. 2004. Arctic spring: the arrival
1028 biology of migrant birds. Pages 948–960 *Acta Zoologica Sinica*.
- 1029 Wood, E. M., A. M. Pidgeon, V. C. Radeloff, and N. S. Keuler. 2013. Image Texture Predicts
1030 Avian Density and Species Richness. *PLoS ONE* 8.
- 1031 Zald, H. S. J., M. a. Wulder, J. C. White, T. Hilker, T. Hermosilla, G. W. Hobart, and N. C.
1032 Coops. 2016. Integrating Landsat pixel composites and change metrics with lidar plots to
1033 predictively map forest structure and aboveground biomass in Saskatchewan, Canada.
1034 *Remote Sensing of Environment* 176:188–201.

1035

1036 Zellweger, F., F. Morsdorf, R. S. Purves, V. Braunisch, and K. Bollmann. 2014. Improved
 1037 methods for measuring forest landscape structure: LiDaR complements field-based habitat
 1038 assessment. *Biodiversity and Conservation* 23:289–307.

1039 Zeng, H., G. Jia, and H. Epstein. 2011. Recent changes in phenology over the northern high
 1040 latitudes detected from multi-satellite data. *Environmental Research Letters* 6:045508.

1041 Zhang, W., P.A., Miller, B. Smith, R. Wania, T. Koenigk, and R. Döscher. 2013. Tundra
 1042 shrubification and tree-line advance amplify arctic climate warming: results from an
 1043 individual-based dynamic vegetation model. *Environmental Research Letters* 8:034023.

1044 Zöckler, C., and I. Lysenko. 2000. Water birds on the edge. Retrieved March 20, 2014, from
 1045 <http://sea.unep-wcmc.org/climate/waterbirds/report.pdf>.

1046 Zolkos, S. G., S. J. Goetz, and R. Dubayah. 2013. A meta-analysis of terrestrial aboveground
 1047 biomass estimation using LiDaR remote sensing. *Remote Sensing of Environment* 128:289–
 1048 298.

1049
 1050
 1051
 1052
 1053

Figure 1. A) Location of our 4 study sites in the vicinity of Toolik Field Station, AK, USA; B) TLFS study site; C) IMVT study site; D) SDOT study site; E) ROMO study site. White triangles B, D and E indicate nest locations of Gambel's white-crowned sparrow found during 2011-2014. Yellow pentagons within B and C are nest locations of Lapland longspur found during 2011-2014.

Figure 2. Gambel's white-crowned sparrow (GWCS) nest locations at TLFS and important habitat covariates. A) Left and middle panes show nest locations of GWCS and proximity to snow-free zones (blue). Right pane shows the probability of habitat use by GWCS is high at short distances to snow-free zones, and sharply declines as distance from snow free zones increases; B) Left and middle panes show nest locations for GWCS and canopy volume (light colors = low values, dark colors = high values). Right pane shows the probability of habitat use by GWCS is low at low canopy volume and sharply increases as canopy volume increases. Nest locations are indicated by 'x'.

Figure 3. Lapland-longspur (LALO) nest locations at TLFS and important habitat covariates. A) Left and middle panes show nest locations of LALO and proximity to snow-free zones (blue). Right pane shows the probability of habitat use by LALO is higher at shorter distances to snow free areas, and reduces as distance from snow-free zones increases; B) Left and middle panes show nest locations of LALO and canopy volume (light colors = low values, dark colors = high values). Right pane shows the probability of habitat use is high at low canopy volume and sharply declines as canopy volume increases; C) Left and middle panes show nest locations of LALO and LiDaR intensity (light colors = low values, dark colors = high values). Right pane

shows the probability of habitat use is low at low LiDaR intensity values and increases as LiDaR intensity increases. Nest locations are indicated by 'x'.

Figure 4. Predicted probability of habitat use at TLFS for: A) Gambel's white-crown sparrow (GWCS), and; B) Lapland longspur (LALO). Predicted probabilities were based on Random Forest models. Differences in grid cell size between A and B corresponds to different territory sizes between species. Nest locations are indicated by 'x'.

Figure 5. Predicted probability of habitat use for Gambel's white-crown sparrow (GWCS) at: A) SDOT, and (B) ROMO; C) Predicted probability of habitat use for Lapland longspur (LALO) at IMVT. Predicted probabilities were based on Random Forest models. Differences in grid cell size between A and B corresponds to different territory sizes between species. Nest locations are indicated by 'x'.

Figure 6. A) Linear relationship between nestling condition (mass/tarsus length) of Gambel's white-crowned sparrow and canopy volume at the territory (top) and nest-site (bottom) scales, ($n = 15$). B) Mean ($\pm 90\%$ CI) canopy volume at successful and unsuccessful nests of Gambel's white-crowned sparrow at the territory (top) and nest-site (bottom) scales ($n = 37$ successful and 5 unsuccessful). C) Mean ($\pm 90\%$ CI) canopy volume across the number of fledglings per nest for Gambel's white-crowned sparrow at the territory (top) and nest-site (bottom) scales ($n_{\text{five}} = 17$, $n_{\text{four}} = 14$, $n_{\text{three}} = 3$, $n_{\text{two}} = 2$, $n_{\text{zero}} = 5$).

1098 **Figure 7.** A) Linear relationship between nestling condition (mass/tarsus length) of Lapland
1099 longspur and canopy volume at the territory scale (top) and SD of terrain height at the nest-site
1100 scale (bottom), ($n = 17$). B) Mean ($\pm 90\%$ CI) canopy volume at the territory scale (top) and SD
1101 of terrain height at the nest-site scale (bottom) at successful and unsuccessful Lapland longspur
1102 nests ($n = 37$ successful and 24 unsuccessful). C) Mean ($\pm 90\%$ CI) canopy volume at the
1103 territory scale (top) and SD of terrain height at the nest-site scale (bottom) across the number of
1104 fledglings per nest for Lapland longspur ($n_{\text{five}} = 9$, $n_{\text{four}} = 11$, $n_{\text{three}} = 13$, $n_{\text{two}} = 2$, $n_{\text{zero}} = 24$). We
1105 observed only one nest with 1 fledgling and did not include a 1 fledgling group in this plot.

Figure 1

Figure 2

Figure 3

Figure 4

a) GWCS probability of use at TLFS

b) LALO probability of use at TLFS

Figure 5

a) GWCS probability of use at SDOT

b) GWCS probability of use at ROMO

c) LALO probability of use at IMVT

Figure 6

Figure 7