Projected changes in wildlife habitats in Arctic natural areas of northwest Alaska

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Abstract We project the effects of transitional changes among 60 vegetation and other land cover types ("ecotypes") in northwest Alaska over the 21st century on habitats of 162 bird and 39 mammal species known or expected to occur regularly in the region. This analysis, encompassing a broad suite of arctic and boreal wildlife species, entailed building wildlifehabitat matrices denoting levels of use of each ecotype by each species, and projecting habitat changes under historic and expected accelerated future rates of change from increasing mean annual air temperature based on the average of 5 global climate models under the A1B emissions scenario, and from potential influence of a set of 23 biophysical drivers. Under historic rates of change, we project that 52 % of the 201 species will experience an increase in medium- and high-use habitats, 3 % no change, and 45 % a decrease, and that a greater proportion of mammal species (62 %) will experience habitat declines than will bird species (50 %). Outcomes become more dire (more species showing habitat loss) under projections made from effects of biophysical drivers and especially from increasing temperature, although species generally associated with increasing shrub and tree ecotypes will likely increase in distribution. Changes in wildlife habitats likely will also affect trophic cascades, ecosystem function, and ecosystem services; of particular significance are the projected declines in habitats of most small mammals that form the prey base for mesocarnivores and raptors, and habitat declines in 25 of the 50 bird and mammal species used for subsistence hunting and trapping.

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1 Introduction

Climate warming is leading to major changes in arctic ecosystems, including redistributions of vegetation to different physiognomic classes and significant increases in woody vegetation cover (Pearson et al. 2013). Implications are striking for wildlife habitat and populations, with many species-specific responses to changing phenologies of snowmelt and breeding cycles (Grabowski et al. 2013). The present study was motivated by the U.S. Department of Interior's need to project potential future changes in land and water cover types and associated wildlife species on their public lands in northwest Alaska. In this study, we projected the availability of wildlife habitat in northwest Alaska through the 21st century by relating recent and projected changes in the extent of land cover types (Jorgenson et al. 2015) to habitat of bird and mammal species of the region.

2 Study area

The study area in Alaska comprised portions of the North Slope, West Coast, and Central Interior Climate Divisions (Bieniek et al. 2012), and encompassed 1,629 km² including five national park units (Bering Land Bridge National Preserve, Cape Krusenstern National Monument, Gates of the Arctic National Park and Preserve, Kobuk Valley National Park, Noatak National Preserve), one national wildlife refuge (Selawik), and a 10-km buffer along their borders (Jorgenson et al. 2015). Terrestrial and aquatic cover types ("ecotypes") of the study area span coastal, lacustrine, riverine, lowland, upland, alpine, and anthropogenic landscapes occurring within several major river drainages, found in the northern Seward Peninsula and much of the Brooks Range (Jorgenson et al. 2009). Because the region borders the Bering Strait and includes some of the northernmost montane areas on the continent, its fauna comprises a unique assemblage of species with Panboreal, Old World, Beringian, and North and South American affinities (Kessel 1989).

3 Methods

We used analyses of recent historic rates of change in, and transitions among, ecotypes (Jorgenson et al. 2009, 2015; DeGange et al. 2014) to project the future area of each ecotype to the end of the century under three related modeling approaches that provided a range of values of each ecotype as a depiction of uncertainty of future climate and biophysical conditions. (1) A "time-dependent model" with linear extrapolation assumed that recent historic (past 30 years) rates of ecotype changes will continue at the same rates without additional influence of increasing temperature. (2) A "temperature-dependent model" related recent historic rates (past 30 years) of ecotype changes to recent historic trends in mean annual air temperature (MAAT). (3) A "rate-adjusted model" adjusted ecotype transition rates ± 50 % based on perceived feedbacks and lags associated with 23 biophysical drivers (Jorgenson et al. 2015), without projected changes in MAAT. The time-dependent model generally provides the most conservative projections as a base from which effects of temperature and biophysical drivers can be evaluated. In the temperature-dependent model, we developed linear regressions of MAAT vs. year derived from data from the nearest 10 weather stations (Western Regional Climate Center, www.wrcc.dri.edu/summary/Climsmak.html), and we applied the ecotypetemperature change rates to an expected 6C increase in temperature over the 21st century for the study area (Scenarios Network for Alaska Planning, www.snap.uaf.edu) based on an average of the five best-performing global climate models for Alaska (Walsh et al. 2008) under the intermediate A1B carbon-emissions scenario (IPCC 2007).

We developed matrices of wildlife species-ecotype relationships depicting use by each species at three ordinal use levels (low, moderate, and high), following existing procedures (Patton 1992; Johnson and O'Neil 2001; Morrison et al. 2006). Results presented in this paper are based on moderate- and high-use levels which depict more consistent usage and higher probability of species occurrence. The matrices were developed from a combination of published literature, field data, and expert knowledge, and include species known or suspected to breed within or immediately adjacent to the study area (Supplemental Material). The full set of ecotypes used by a species constituted that species' habitat within the study area. The total areal coverage of all ecotypes used by a species describes the species' total habitat area; the number of ecotypes used by a species constitutes the species' habitat use breadth; and the number of species using a given ecotype constitutes that ecotype's associated species richness. We used linear and polynomial regression to examine relationships for birds and mammals between the percent change in habitat projected to occur for each species during this century under the temperature-dependent model, and species' habitat use breadth (number of ecotypes used) and habitat rarity (percent of the study area in habitat in 2010). We also denoted species used for subsistence or regularly harvested in the study area. We did not attempt to model and quantify species interactions, however, which are poorly known within the study area, although we do discuss examples of several species' key ecological functions.

4 Results

The study area intersects the Arctic tundra and boreal forest biomes and is dominated by seven shrub and meadow (57 % of the total study area), two forest (9 %), and two alpine barrens (9%) ecotypes. In lowlands, the dominant shrub ecotype (lowland birch-ericaceous-willow low shrub) is projected to decline in area by 65 % and black spruce forest is projected to double during this century; similarly, dominant meadow, dwarf shrub, and low shrub ecotypes in upland and alpine areas are projected to decline by 15 % whereas tall shrub and white spruce forest ecotypes are projected to increase by 31 and 19 %, respectively. Dominant alpine barrens ecotypes are projected to remain largely unchanged. Other currently less-extensive ecotypes projected to greatly expand in area (>300 %) include lacustrine meadow and willow shrub; lowland birch and spruce-birch forests; human-modified barrens; and various upland ecotypes including thermokarst barrens, sagebrush shrub, aspen forest, and several types of mixed white spruce forest (see Supplementary Material for species names). Additional, lessextensive ecotypes each projected to greatly decline in area (>25 %) include coastal brackish sedge-grass meadow, alder-willow tall shrub, dryas dwarf shrub, white spruce-willow forest in riverine areas, lakes and alder tall shrub in lowlands, landslide barrens and birch forest in uplands, and alpine snowfields and glaciers (Jorgenson et al. 2015).

Associated increases in wildlife habitats pertain mostly to projected spread of lowland sedge fen and dryas meadow, black and white spruce forest, and some upland shrub ecotypes, as well as lacustrine bogs, fens, and meadows resulting from drying and drainage of tundra lakes. Decreases in wildlife habitats pertain mostly to projected major decline of upland sedgedryas meadow, upland birch shrub, and some lowland shrub ecotypes. The major biophysical processes anticipated to drive changes in ecotypes and associated extent of wildlife habitat over the century include increases in thermokarst, fire, post-fire succession, shrub and forest expansion, lake drainage, soil drainage, and river erosion and deposition (Jorgenson et al. 2015; Higuera et al. 2011; Jones et al. 2011; Suarez et al. 1999). Birds of the study area include a wide variety of water- and wetland-associated waterfowl, loons, grebes, shorebirds, and gulls; a distinct complement of raptors, shorebirds, jaegers, ptarmigan, and passerines associated with barrens and dwarf-shrub ecotypes in upland and alpine areas; and additional raptors, grouse, and near-passerines and passerines strongly associated with low-shrub, tall-shrub, and forest ecotypes. Present avian distribution across the landscape in this region is aligned primarily along gradients of moisture, elevation, and vertical structure of the habitat but is also constrained by zoogeographic history (Kessel 1989; Tibbitts et al. 2006). Mammals include a variety of large and small carnivores; mostly herbivorous rodents associated with open habitats; forest-associated sciurids and medium-size species; large ungulates such as caribou, moose, and sheep; and others (Cook and MacDonald 2006; MacDonald and Cook 2009).

Birds and mammals differ in their current patterns of ecotype use breadth and ecotype specialization. Only 4 bird species (3 %; rock ptarmigan, mew gull, glaucous gull, savannah sparrow) each occur in ≥ 25 % of all 60 ecotypes, whereas 42 bird species (25 %) each occur in only ≤ 5 % of all ecotypes. However, rock ptarmigan's high usage is explained by its being one of the few resident bird species using high, largely unvegetated alpine habitats during summer and lower-elevation shrub habitats during winter. Also, mew and glaucous gulls use a variety of wetland, coastal, and lacustrine ecotypes, as well as barrens and meadows during breeding and non-breeding seasons. Mammals are more ecotype-generalist than are birds; 10 mammal species (26 %) each use ≥ 25 % of all ecotypes, and only 5 mammal species (13 %; arctic fox, least weasel, American mink, muskrat, northern river otter) each use ≤ 5 % of all ecotypes.

The median richness among all ecotypes is 16 (10 %) bird species and 5 (13 %) mammal species. The most bird species-rich (\geq 30 species) ecotypes currently include sedge meadows and fens, spruce-poplar forests, grass and dryas meadows, and tussock-shrub ecotypes, with riverine, lake and bog ecotypes also providing for significant richness. The most mammal species-rich (\geq 10 species) environments include various upland low- and tall-shrub, tussock-shrub, sedge-dryas meadow, and various spruce-forest ecotypes, as well as the lowland birchericaceous –willow low shrub ecotype. Species-poor environments for both birds and mammals constitute 16,230 ha (10 % of the study area), primarily consisting of various low-productivity and highly-disturbed sites, such as snowfields and glaciers, and barrens created by landslides, thermokarst, human activities, and mafic and sandy conditions.

Under the time-dependent model, habitats of 45 and 3 bird species, and 5 and 4 mammal species are projected to increase and decrease, respectively, by at least 10 % in area by the end of the century. Among species whose habitats are currently less widespread in the region (current habitat is <5 % of the total study area), habitats of 29 and 1 bird species, and 0 and 5 mammal species are projected to increase and decrease, respectively, by at least 10 % in area by the end of the century. Habitat-gainer species generally include forest, tall-shrub, and fen associates such as some raptors, grouse, woodpeckers, passerines, gulls, porcupine, tree squirrels, mustelids, and black bears; and habitat-loser species generally include meadow, dwarf-shrub, and low-shrub associates such as several raptors, shorebirds, ptarmigan, passerines, a few waterfowl, lemmings, voles, shrews, open-ground squirrels, and caribou.

The greatest degree of habitat change projected for birds and mammals resulted from the temperature-dependent model (Figs. 1 and 2). Under this model, habitats of 64 and 44 bird species, and 6 and 16 mammal species are projected to increase and decrease, respectively, by at least 10 % in area by the end of the century. Among species whose habitats are currently less widespread in the region (current habitat is <5 % of the total study area), habitats of 36 and 7 bird species, and 0 and 5 mammal species are projected to increase and decrease, respectively, by at least 10 % in area by the end of the century.

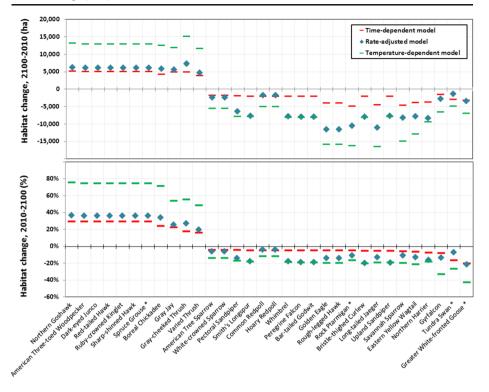


Fig. 1 Bird species projected to incur the greatest gain or loss of their habitats in northwest Alaska from climate change over the 21st century, under projections based on historic trends (*time model*), increases in mean annual air temperature (*temperature model*), and influence of 23 biophysical drivers (*rate-adjusted model*). Shown are selected species with habitat that constituted ≥ 10 % of the total study area in 2010 and that is projected to change at least ± 10 % (gain or loss) by 2100 (i.e., projected changes of the more common species). * = major subsistence species (regularly hunted or eggs collected)

Among the 33 bird species of major subsistence value in the region, under the timedependent model 13 show an increase in habitat and 20 show a decrease, and under the temperature-dependent model 26 show an increase and 7 show a decrease (examples in Fig. 1). In contrast, among the 17 mammal species of major subsistence value in the region, under the time-dependent model 9 show an increase in habitat and 8 show a decrease, but under the temperature-dependent model only 5 show an increase and 12 show a decrease (Fig. 2). By the end of the century, under the temperature-dependent model, subsistence species gaining habitat the most (\geq 20 % gained) include bufflehead, common goldeneye, spruce and ruffed grouse, harlequin duck, black, surf, and white-winged scoter, common loon, American marten, and moose; and subsistence species losing habitat the most (\geq 20 % lost) include white-fronted goose, tundra swan, arctic fox, river otter, muskrat, mink, and caribou.

We hypothesized that, in general, specialists with low habitat breadth (species that use the fewest number of ecotypes) and rare species (with habitat consisting of the smallest extent of the study area) may be more vulnerable to climate change. Our results under the temperaturedependent model, however, suggested non-significant relationships for mammals and generally inverse relationships for birds (Figs. 3 and 4). The effects, however, vary widely among species that are currently rare and that have narrow habitat breadth, with outcomes depending on expected trends in specific ecotypes contributing to each species' habitat. Upland- and

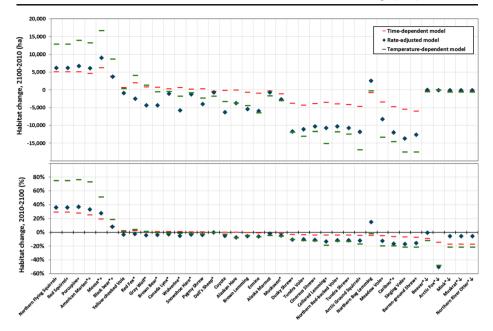


Fig. 2 Changes in habitat area of mammal species in northwest Alaska over the 21st century, under projections based on historic trends (*time model*), increases in mean annual air temperature (*temperature model*), and influence of 23 biophysical drivers (*rate-adjusted model*). Shown are all mammal species included in this study; * = major subsistence species (regularly hunted); + = habitat constituting ≥ 10 % of the total study area in 2010 and projected to change at least ± 10 % (gain or loss) by 2100 (i.e., projected changes of the more common species); $\downarrow =$ habitat <5 % of the total study area in 2010 and projected to decrease ≥ 10 % by 2100 (i.e., projected reductions of the less common species)

alpine-breeding shorebirds, passerines, ptarmigan, and raptors are among the most vulnerable avian species because of projected large losses to key, currently common habitats in the region that will not likely be replaced elsewhere. Among these birds, species with Beringian affinities, such as bristle-thighed curlew, bar-tailed godwit, red knot, and eastern yellow wagtail, are especially at risk because of paleohistorically-limited distributions within the region. However, mammal species with habitat currently comprising <5 % of the study area – beaver, American mink, muskrat, northern river otter, and arctic fox – are projected to experience habitat losses of 5–33 % over the century because of expected declines in rare habitat types (specific coastal habitats in the case of arctic fox) or declines in habitats associated with fresh water (wet meadows, lowland lakes, and riverine shrub habitat).

Differential trends in ecotypes and changes in species' habitats likely will affect the trophic structure and ecosystem dynamics of the region. The projected decline in habitats for small terrestrial, burrowing, and subnivian (beneath snow cover) mammals may reduce the distribution of these small mammals leading to population declines of raptors, mammalian carnivores, and other secondary consumers dependent on them as key prey. Declines in the associated burrowing functions of small mammals also may compromise ecological conditions of the active (seasonally thawed) soil layer (Pike and Mitchell 2013; Yoshihara et al. 2010). Loss of lichens from increased fire and loss of upland dwarf birch tussock-shrub from thermokarst and shrub expansion will reduce foraging habitat for caribou (Joly et al. 2011). Loss of lowland lakes will have a major effect on waterbirds and aquatic mammals. Concomitantly, a shift to more forested conditions may result in habitat increases of resident large

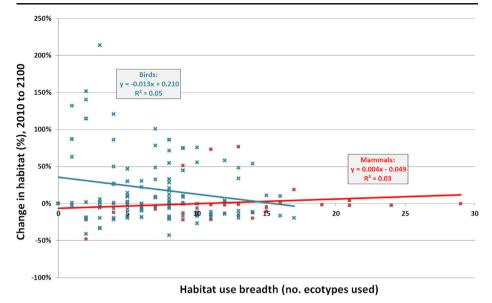
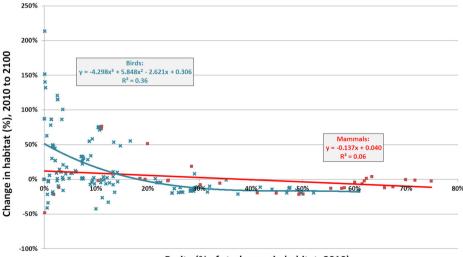


Fig. 3 Relationship between species' projected change in habitat from 2010 to 2100 under the temperaturedependent model, and species' habitat use breadth

ungulates, principally moose. More extensive distributions of resident ungulates would also lead to more resident predators such as wolves, which may then impact other prey species such as Dall's sheep.

Impending changes in American beavers are less clear. Reduction in beaver habitat may create a negative feedback as declining habitats would result in less ecosystem engineering through stream-damming, an ecological function that creates lentic and wetland habitat for



Rarity (% of study area in habitat, 2010)

Fig. 4 Relationship between species' projected change in habitat from 2010 to 2100 under the temperaturedependent model, and species' habitat rarity many other species (Wright 2009). However, beavers are a recent addition to northern and northwestern Alaska and are currently expanding their range. This may be a case where suitable beaver habitat is declining but beavers may be expanding at least locally and temporarily, and their damming function could continue to block passage of subsistence fish such as salmon and whitefish.

Other effects of projected changes in overall habitats on food webs, trophic dynamics, and ecosystem functions of the region are unknown but likely to occur (Ims and Fuglei 2005; McKinnon et al. 2013).

Our analysis also considered potential future incursion by southern or eastern parapatric species, as their preferred habitats become more established and spread north and west into the study area. Such species include meadow jumping mouse, hairy woodpecker, red-breasted nuthatch, and ruffed grouse. Also, some nine bird species included in the analysis—four waterfowl (snow goose, Steller's eider, spectacled eider, and king eider), four shorebirds (sanderling and white-rumped, stilt, and buff-breasted sandpipers), and one alcid (black guillemot)—currently breed primarily to the north along the Arctic Coastal Plain, although historic breeding records exist for several of these in the study area during the 20th century. Reasons for recent northward range contractions are not clear, but these species are not likely to extend their breeding range southward with climate change. Importantly, however, the study area may still provide them with migration habitat.

5 Discussion and conclusions

As an initial investigation into potential climate-induced changes of wildlife habitats of northwest Alaska, this study provides a framework for future refinements and identifies species, habitats, and ecotypes most likely to change the most over the century. Such projected changes can be viewed as testable hypotheses, as a basis for prioritizing research and monitoring studies, and perhaps as information useful for climate adaptation planning (Ledee et al. 2011).

Key assumptions, uncertainties, and accuracy in ecotype mapping and change analyses are presented elsewhere (Jorgenson et al. 2009, 2015; DeGange et al. 2014). Our wildlife projections are first approximations based mostly on habitat associations and some knowledge of species interactions. We do not distinguish resident from hibernating mammals and, because of lack of knowledge, the species-ecotype associations we developed for this study did not differentiate season or manner of use by each species (e.g., for breeding, feeding, migration, resting), nor do they account for how topography may contribute to habitat use such as influencing ungulate migration corridors, use of ridgetops or snowfields for insect relief (Witter et al. 2012), locations used for calving, etc. We suspect that contemporary patterns of animal migration may be quite vulnerable to disruption from changes in habitat distribution and abundance, and possibly also to changes in the distribution of their predators (Hansen et al. 2013). Examples include declines in lacustrine environments in Bering Land Bridge National Preserve and Selawik National Wildlife Refuge, potentially affecting migratory birds; and decline in suitability of seasonal migration habitats for the ecologically and culturally important caribou of the Western Arctic Herd (currently estimated at 235,000 animals, Alaska Department of Fish and Game 2014).

Changes in ecotype categories, particularly expansion of shrub and forest types, could be modified by herbivory by muskoxen, caribou, rodents, lagomorphs, ptarmigan, and other species (Gough et al. 2012; Olofsson et al. 2009; Post and Pedersen 2008; Ravolainen et al. 2014). Caribou in particular, even though in decline globally (Vors and Boyce 2009), have

been implicated as agents thwarting the expansion of arctic shrub cover in Nunavik, Canada (Plante et al. 2014). Whether, and the degree to which, herbivores will modify shrub and tree expansion in the study area is unknown and may deserve monitoring.

Our wildlife habitat summaries and areal projections should not be interpreted as or extrapolated to population size or trend. The structure and dynamics of food webs in the study area are incompletely known, as are potential behavioral responses and plasticity of individual species to changes in their prey and food base or to climate-affected distributions of disease and parasites (e.g., Callaghan et al. 2004). As well, shifts in abundance and distribution of subsistence species may have as yet unknown social and cultural implications for local human communities dependent on their availability.

With further field research on the abundance, distribution, and ecology of wildlife in the study area, we expect improvements in our depictions of species-habitat associations and our change projections. We anticipate that the coming century also will reveal many surprises in changing composition and structure of biotic communities, and in the distributions of plant and animal species and their ecology, seasonality, and migration patterns under climate-induced and anthropogenic drivers. We expect that new and unique species-habitat associations, and appearance of species new to the area, will result from forthcoming environmental changes.

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