



## Some broad-scale effects of recent and future climate change among migratory birds in Beringia

KEVIN WINKER<sup>1,\*</sup> AND DANIEL D. GIBSON<sup>1</sup>

**Abstract.** Birds from all seven continents come to Beringia to breed in the northern summer. For birds breeding there, Beringia's position at the head of the Pacific Ocean requires substantial longitudinal (east to west and west to east) movements coming and going. These movements are most apparent to us in continental "crossover" species, Asian taxa breeding in North America and North American birds breeding in Asia. Those individuals reaching range limits in Beringia commonly travel long distances to take advantage of short summers, and many of their range limits are likely caused by time constraints: travel time plus the time required to successfully reproduce and (for most) to molt must fit into the finite constraints of the length of the summer. These constraints become most apparent when a breeding range limit is longitudinally distant from the nearest wintering area, and the most visible examples involve species whose ranges stop before the limit of apparently appropriate habitat. It is these species whose ranges we expect to change most rapidly when even small increases in the time available at high latitudes (i.e., a longer growing season) give them more time to travel farther east or west at these latitudes.

**Keywords:** Asia, Beringia, continental colonization, migration, North America, range shifts, time limitation

Projections of the effects of global warming in Alaska and northwestern Canada suggest comparatively high rates of climate change and a lengthened growing season (Tingley and Huybers 2013, Chapin et al. 2014). Even subtle changes will affect the biota of this region. Birds have long served as indicators of environmental health (e.g., canaries in coal mines, *Silent Spring*, Spotted Owl), and, because of their mobility, many bird species are likely to be among the first organisms to show changes in distribution associated with current climate change. Birds' visibility makes them relatively easy to detect, and on the basis of simple presence-absence, mapping their ranges is comparatively easy. Furthermore, unlike most of North America, Alaska and northwestern Canada represent vast, natural ecosystems with little direct anthropogenic modification. Thus any range shifts observed are not likely to be caused by direct anthropogenic modifications of habitat.

For many bird species, structural considerations of habitat are important. For example, a requisite tree nester cannot nest where there are no trees. Populations of other species probably experience range limitation due not to structure but to the amount of time available to successfully reproduce

and molt near the northern limits of the species' range. Such species, which are time-limited only in these edge populations, should show more rapid changes in distribution. Resource-limited species should show slower change, because there will be some lag time in, for example, the growth of forest where it does not presently occur. This scenario is perhaps simplistic, but in sum we expect the ranges of time-limited species to shift relatively rapidly when requisite substrate exists in an area (especially a contiguous area) not previously occupied (Figure 1). Note that this hypothesis considers only populations at the northern edge of a range, those most likely to be time limited, and it makes no predictions about changes elsewhere

Structure	Limitation	
	Time	Resources
Nonlimiting	I	II
Limiting	III	IV

**FIGURE 1.** Partitioning the limitations that species experience at the edges of their ranges in northwestern North America and northeastern Asia. Category I species will likely show most rapid change with increased growing season and are the focus of this paper.

Full citation: Winker, K., and Gibson, D. D. 2018. Some broad-scale effects of recent and future climate change among migratory birds in Beringia, in *Trends and traditions: Avifaunal change in western North America* (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 432–440. *Studies of Western Birds* 3. Western Field Ornithologists, Camarillo, CA; doi 10.21199/SWB3.23.

<sup>1</sup>University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775; \*corresponding author: kevin.winker@alaska.edu

in the range (where we expect time limitation to be a less important factor).

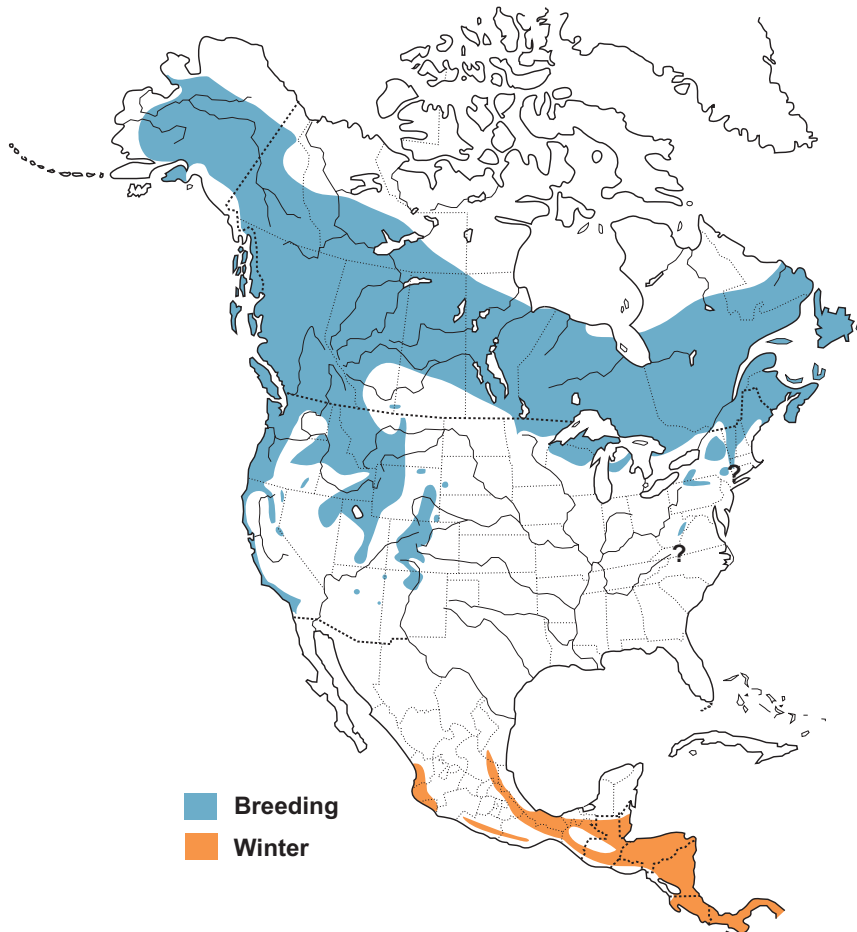
Another consideration that emphasizes the importance of continued monitoring of range shifts rather than focusing on abundance in assessing the effects of climate change is that abundance changes may be due to many factors, including phenomena acting on species' winter ranges. Range limits, on the other hand, are largely defined climatologically and physically (though in some species increased abundance can cause range expansion); range shifts generally reflect changes in the physical constraints (and the ecological conditions they produce) at the geographic limits of a species' tolerance. In many documented cases, these changes have been caused by direct anthropogenic changes opening up new habitats for a species. In the vast untouched reaches of northwestern North America, however, such

anthropogenic alterations play an insignificant role.

### RANGE EXPANSIONS

The ranges of many North American landbirds project toward the northwest, probably reflecting a prehistoric advance in the interior of the continent as environments moderated after glaciation (Figure 2). It is among these species that we might look first for continued range expansion as conditions become more favorable beyond the present northwestern edges of their ranges. Many North American species will likely spread northward, but expansion in this direction is not as easy to document as that to the west, particularly when these high latitudes have relatively few human observers.

Note that we are considering only species likely to be affected by time limitation in Beringia. This



**FIGURE 2.** North American range of Swainson's Thrush (*Catharus ustulatus*), an example of how many landbird species' breeding ranges project northwest, after occupation of regions that were covered by ice during the last glacial maximum. From Birds of North America online (birdsna.org), used by permission.

region has been rather loosely defined, but for our purposes it is roughly the area between the Lena River in Siberia and the Mackenzie River in Canada south to about the tip of the Kamchatka Peninsula (West 1998; Figure 3). Other environmental and ecological factors are important, such as habitat and prey availability and probably competitive exclusion in new avian assemblages. Thus we do not expect all species with northward range projections to spread, or for those that do to respond equivalently in distance. Indeed, numerous studies have shown that individual species respond in complex, heterogeneous ways to the multiple effects of global warming such as changes in temperature and precipitation (e.g., Angert et al. 2011, Tingley et al. 2012). Predictive models are incorporating an increasing number of potentially important factors (e.g., Huntley et al. 2008, Angert et al. 2011, Barbet-Massin et al. 2012). Because factors such as habitat and prey availability, precipitation, and competitive exclusion might affect a species' longitudinal distribution in Beringia, they may be difficult or impossible to tease out from time effects alone. Nevertheless, time constraints have thus far not been a factor in these models.

While numerous studies have documented avian range shifts associated with climate change—primarily poleward and in elevation—(e.g., Zuckerberg et al. 2009, Auer and King 2014, Virkkala and Lehikoinen 2014, Mizel et al. 2016), wider considerations of non-poleward shifts are only beginning to be addressed. For example, Gillings et al. (2015) found that range shifts among British birds have been multidirectional, with extensions to the northeast and northwest being most pronounced.

Populations of obligate migrants near the northern edges of their ranges often occupy their breeding ground for notably short periods. For example, Benson and Winker (2001), examining the median dates of spring and autumn passage of adult passerines at Fairbanks, Alaska, inferred occupancy of the breeding range as short as 48 days in the Alder Flycatcher (*Empidonax alnorum*), a species that molts after autumn migration, and 84–86 days in the Yellow Warbler, (*Setophaga petechia*), Northern Waterthrush (*Parus noveboracensis*), and Hammond's Flycatcher (*Empidonax hammondi*), species molting prior to autumn migration. Given that the vast majority of the birds recorded in this study were still in migration, these median dates may be considered to indicate the maximum average numbers of days spent on breeding grounds for populations to the

north and west of Fairbanks. This location had an average frost-free period of 105 days and, on the short side, a minimum possible period of just 51 days (at the time of the study in the 1990s). These are thermal factors affecting prey availability (especially for insectivores) and almost certainly representing strong selective forces on the timing of movements and breeding (e.g., nearly all species examined timed their movements to coincide within the long-term average frost-free period).

The main challenge that such time constraints place on these populations is on reproduction: compressing the time to obtain a territory, build a nest, lay eggs, incubate, feed young to independence, and (for most species) molt before having to migrate to wintering grounds. We can see the effects of these time constraints in several ways. One is that double brooding (successfully raising more than one clutch of offspring) is rare at high latitudes (Hussell et al. 2014). Another is a negative effect on clutch size (Rowe et al. 1994), and yet another is in the degree to which high-latitude populations overlap the energetically demanding life stages of reproduction, molt, and migration, long considered to be so energy intensive as to be separated temporally among most birds (e.g., Payne 1972, Cannell et al. 1983, Vega-Rivera et al. 1998). It is no accident that the highest levels of overlap between these energetically costly stages are being found among high-latitude populations, where evidently there is simply not enough time to spread them out as at lower latitudes (Rimmer 1988, Flockhart 2010, Benson and Winker 2015).

For example, among 17 species of passerine migrants at Fairbanks, Alaska, Benson and Winker (2015) found a negative correlation between the length of occupancy of the breeding ground (defined by the difference between median spring and autumn dates of passage) and the amount of overlap of molt and migration. In addition, they found high levels of overlap of molt with fat accumulation. Both findings are concordant with the hypothesis that time constraints promote overlap of these energetically demanding undertakings.

Here, our methods for considering time limitation likely to be affecting a migratory species' range edge included examination of migratory species' range edges in Beringia, habitat, and whether the range of likely ecological replacement species (e.g., a closely related congener) might prove a more limiting factor (through competitive exclusion). As noted above, other factors can also affect ranges; we focus on where time constraints are most likely to be active. Sources included the *Birds of North America Online* (Rodewald 2015),

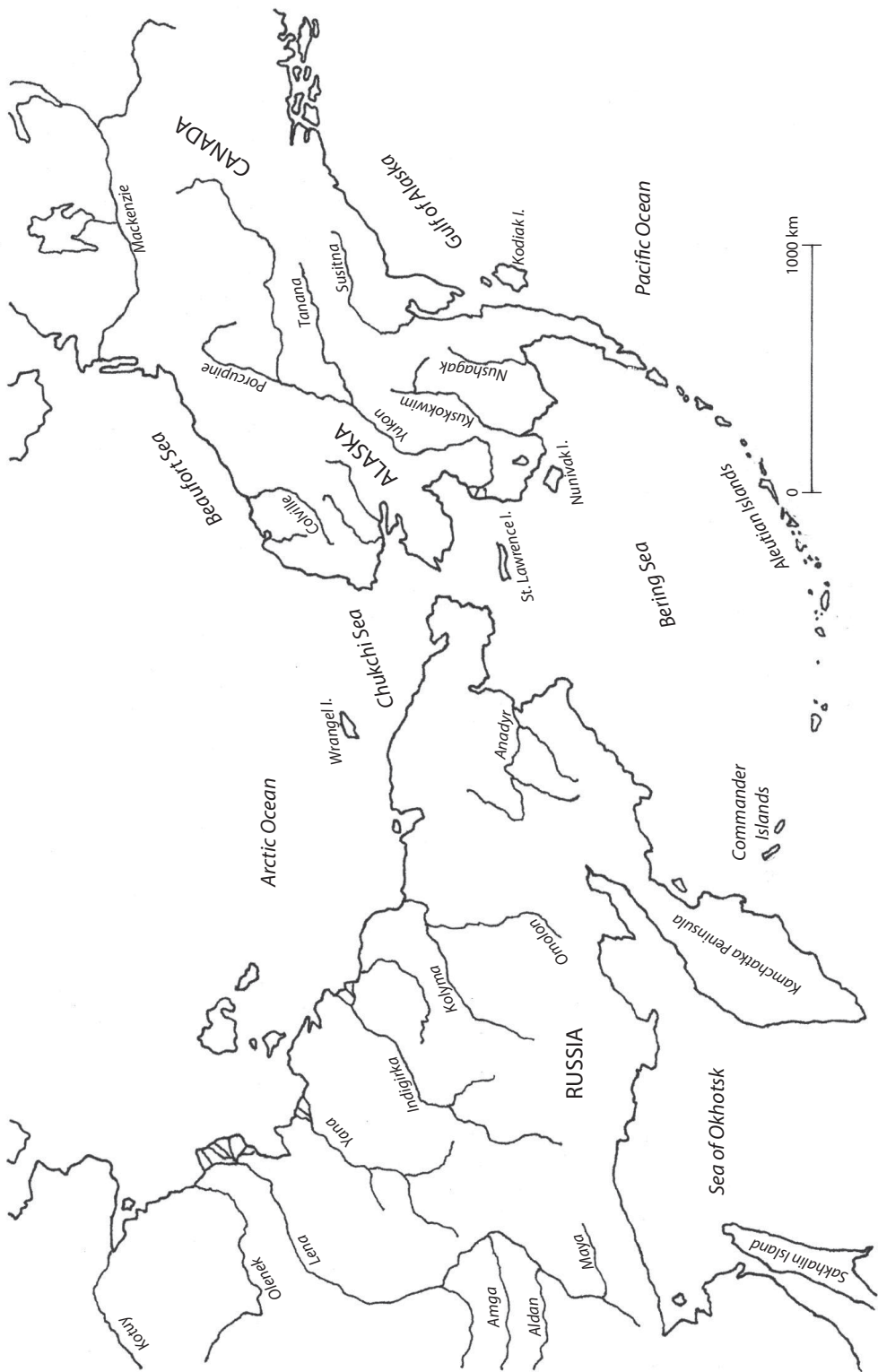


FIGURE 3. Beringia, extending roughly from the Lena River in Russia and the Mackenzie River in Canada south to about the tip of the Kamchatka Peninsula (adapted from West 1998).

National Geographic (2002), del Hoyo et al. (1992–2011), and Brazil (2009). Taxonomy follows AOU (1957, 1998), Browning (1988), and Gibson and Withrow (2015).

There are many migratory North American species whose range is likely to spread in eastern Beringia relatively quickly (over the course of decades, rather than centuries) in response to climate change (Table 1). There are also many Asian species likely to undergo relatively rapid range expansions in western Beringia in response to a longer growing season at high latitudes (Table 2). And, finally, there is a smaller subset of migratory species from both continents that have already colonized (or nearly so) the opposite continent in which we can expect range expansions farther east (for Asian species) or west (for North American species) as warming continues and breeding seasons at these latitudes lengthen (Table 3). We observe again that multiple factors affect range edges, and that time constraints alone are not likely to be able to be teased out as acting alone in relation to other factors. However, it is among these species that we most expect time limitation to play a role in Beringian range limits.

#### CONTIGUITY: STEPPING-STONE VERSUS CONTINUOUS-FRONT MODELS

Range shifts across a continent with contiguous habitat will probably proceed on a continuous front, moving gradually. This suggestion is supported by the varying positions of the northwestern (and northeastern in Asia) fronts of species' ranges currently: no clear thresholds or transitions are evident. Among islands and archipelagoes, however, an island must be able to sustain a population before a species can successfully colonize. Thus among islands and archipelagoes we can expect more stutter, or greater variance, as these relatively small patches of range become suddenly available to a species (due also to habitats being noncontiguous and the distances between them; MacArthur and Wilson 1967). Conceptually, landbird species colonizing North America from Asia may follow a similar pattern, given the important water crossing of the Bering and Chukchi seas that some species appear to make easily while others do not (yet). For a number of these, ecological replacements already on the continent being potentially colonized may exclude them through competition (particularly members of the same genus or of the same species, in cases of polytypic species with different subspecies on opposite sides of the Bering Sea). In such

cases ecological rather than climatological factors will play a more important role in determining range edges. We have excluded such taxa from our tables (e.g., the tattlers, *Tringa brevipes* and *T. incana*). Alaska, with a massive interior and a vast number of islands, is a superb natural laboratory in which these continuing and likely accelerating natural experiments might be observed.

There is a strong latitudinal component to habitat contiguity, and this has had important biogeographic consequences. The similarities of the arctic and Beringian avifaunas of Asia and North America increase with latitude (Mayr 1946, Kessel 1963, Stegmann 1963). Thus, for example, we expect less habitat contiguity and a higher threshold for intercontinental colonization and range expansion for forest-associated species than for nonforest species.

#### SOME CONSEQUENCES OF RANGE SHIFT

Most natural intercontinental colonists (e.g., Table 3) have not had any recognized negative effects on the avifauna of the continent being colonized. However, if Asian cuckoos, obligate nest parasites, colonize North America (Table 2), we're likely to see severe negative consequences among North American songbirds, particularly among the many naïve populations in much of northwestern North America.

The combination of two migration systems in Alaska makes it likely that in this region birds cause regular intercontinental exchange of pathogens (e.g., Winker et al. 2007, Pearce et al. 2011, Runstadler et al. 2013, Lee et al. 2015). The same is true of parasites. These exchanges have not been well studied, so we do not yet know the frequency of such occurrences. However, mixing of birds from these two migration systems is likely to increase with warming because longer summers at high latitudes will increase overlaps in both ranges and the time of occupancy of high latitudes. New combinations of species will also arise. Increased mixing and new combinations of vector species will provide what will essentially be dynamic new host communities, a cauldron of new opportunities for colonization of hosts, viral reassortment, and selection. Lee et al. (2015) indicated that the highly pathogenic avian influenza outbreak of 2014–15 in North America was due to wild birds introducing the virus through this intercontinental contact zone. This suggests that the consequences of the mixing of vectors, diseases, and parasites in this region could be profound for birds and humans.

SOME BROAD-SCALE EFFECTS OF CLIMATE CHANGE AMONG MIGRATORY BIRDS IN BERINGIA

**TABLE 1.** Migratory North American birds for which we might expect north and westward range expansions within or into Beringia. This list excludes North American species already breeding in Asia, but includes some that might colonize Asia. Subspecies included where relevant.

Cackling Goose	<i>Branta hutchinsii</i>	Philadelphia Vireo	<i>Vireo philadelphicus</i>
Blue-winged Teal	<i>Anas discors</i>	Red-eyed Vireo	<i>Vireo olivaceus olivaceus</i>
Canvasback	<i>Aythya valisineria</i>	Purple Martin	<i>Progne subis subis</i>
Redhead	<i>Aythya americana</i>	Tree Swallow	<i>Tachycineta bicolor</i>
Ring-necked Duck	<i>Aythya collaris</i>	Violet-green Swallow	<i>Tachycineta thalassina thalassina</i>
Lesser Scaup	<i>Aythya affinis</i>	Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis serripennis</i>
Hooded Merganser	<i>Lophodytes cucullatus</i>	Cliff Swallow	<i>Petrochelidon pyrrhonota pyrrhonota</i>
Ruddy Duck	<i>Oxyura jamaicensis rubida</i>	Barn Swallow	<i>Hirundo rustica erythrogaster</i>
Pied-billed Grebe	<i>Podilymbus podiceps podiceps</i>	House Wren	<i>Troglodytes aedon parkmanii</i>
Horned Grebe	<i>Podiceps auritus cornutus</i>	Marsh Wren	<i>Cistothorus palustris plesius</i>
American Bittern	<i>Botaurus lentiginosus</i>	Golden-crowned Kinglet	<i>Regulus satrapa amoenus</i>
Black-crowned Night-Heron	<i>Nycticorax nycticorax hoactli</i>	Ruby-crowned Kinglet	<i>Regulus calendula calendula</i>
Northern Harrier	<i>Circus cyaneus hudsonius</i>	Mountain Bluebird	<i>Sialia currucoides</i>
Sharp-shinned Hawk	<i>Accipiter striatus velox</i>	Townsend's Solitaire	<i>Myadestes townsendi townsendi</i>
Broad-winged Hawk	<i>Buteo platypterus platypterus</i>	Veery	<i>Catharus fuscescens salicicola</i>
Swainson's Hawk	<i>Buteo swainsoni</i>	Swainson's Thrush	<i>Catharus ustulatus incanus</i>
Red-tailed Hawk	<i>Buteo jamaicensis harlani</i>	Hermit Thrush	<i>Catharus guttatus euborius</i>
Yellow Rail	<i>Coturnicops noveboracensis</i>	American Robin	<i>Turdus migratorius migratorius</i>
Sora	<i>Porzana carolina</i>	Varied Thrush	<i>Isoreus naevius meruloides</i>
American Coot	<i>Fulica americana americana</i>	Gray Catbird	<i>Dumetella carolinensis</i>
Killdeer	<i>Charadrius vociferus vociferus</i>	European Starling	<i>Sturnus vulgaris vulgaris</i>
Short-billed Dowitcher	<i>Limnodromus griseus caurinus</i>	Cedar Waxwing	<i>Bombycilla cedrorum</i>
Upland Sandpiper	<i>Bartramia longicauda</i>	Smith's Longspur	<i>Calcarius pictus</i>
Wilson's Phalarope	<i>Phalaropus tricolor</i>	Ovenbird	<i>Seiurus aurocapilla aurocapilla</i>
Franklin's Gull	<i>Leucophaeus pipixcan</i>	Northern Waterthrush	<i>Parkesia noveboracensis</i>
California Gull	<i>Larus californicus albertaensis</i>	Black-and-white Warbler	<i>Mniotilta varia</i>
Caspian Tern	<i>Hydroprogne caspia</i>	Tennessee Warbler	<i>Oreothlypis peregrina</i>
Black Tern	<i>Chlidonias niger surinamensis</i>	Orange-crowned Warbler	<i>Oreothlypis celata celata</i>
Common Tern	<i>Sterna hirundo hirundo</i>	Connecticut Warbler	<i>Oporornis agilis</i>
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	MacGillivray's Warbler	<i>Geothlypis tolmiei tolmiei</i>
Northern Saw-whet Owl	<i>Aegolius acadicus acadicus</i>	Mourning Warbler	<i>Geothlypis philadelphia</i>
Common Nighthawk	<i>Chordeiles minor minor</i>	Common Yellowthroat	<i>Geothlypis trichas campicola</i>
Black Swift	<i>Cypseloides niger borealis</i>	American Redstart	<i>Setophaga ruticilla</i>
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Cape May Warbler	<i>Setophaga tigrina</i>
Anna's Hummingbird	<i>Calypte anna</i>	Magnolia Warbler	<i>Setophaga magnolia</i>
Rufous Hummingbird	<i>Selasphorus rufus</i>	Bay-breasted Warbler	<i>Setophaga castanea</i>
Belted Kingfisher	<i>Megascyle alcyon</i>	Yellow Warbler	<i>Setophaga petechia banksi</i>
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	Blackpoll Warbler	<i>Setophaga striata</i>
American Kestrel	<i>Falco sparverius sparverius</i>	Palm Warbler	<i>Setophaga palmarum palmarum</i>
Olive-sided Flycatcher	<i>Contopus cooperi cooperi</i>	Yellow-rumped Warbler	<i>Setophaga coronata hooveri</i>
Western Wood-Pewee	<i>Contopus sordidulus veliei</i>	Townsend's Warbler	<i>Setophaga townsendi</i>
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Black-throated Green Warbler	<i>Setophaga virens virens</i>
Alder Flycatcher	<i>Empidonax alnorum</i>	Canada Warbler	<i>Cardellina canadensis</i>
Least Flycatcher	<i>Empidonax minimus</i>	Wilson's Warbler	<i>Cardellina pusilla pileolata</i>
Hammond's Flycatcher	<i>Empidonax hammondii</i>	American Tree Sparrow	<i>Spizelloides arborea ochracea</i>
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Chipping Sparrow	<i>Spizella passerina arizonae</i>
Eastern Phoebe	<i>Sayornis phoebe</i>	Clay-colored Sparrow	<i>Spizella pallida</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	Brewer's Sparrow	<i>Spizella breweri taverneri</i>
Eastern Kingbird	<i>Tyrannus tyrannus</i>	Vesper Sparrow	<i>Poocetes gramineus confinis</i>
Cassin's Vireo	<i>Vireo cassinii cassinii</i>		
Blue-headed Vireo	<i>Vireo solitarius solitarius</i>		
Warbling Vireo	<i>Vireo gilvus swainsoni</i>		

(Continued)

TABLE 1. (Continued.)

Savannah Sparrow	<i>Passerculus sandwichensis sandwichensis</i>
LeConte's Sparrow	<i>Ammodramus leconteii</i>
Nelson's Sparrow-tailed Sparrow	<i>Ammodramus nelsoni</i>
Fox Sparrow	<i>Passerella iliaca zaboria</i> and <i>unalaschensis</i>
Song Sparrow	<i>Melospiza melodia merrilli</i>
Lincoln's Sparrow	<i>Melospiza lincolnii lincolnii</i>
Swamp Sparrow	<i>Melospiza georgiana ericrypta</i>
Harris's Sparrow	<i>Zonotrichia querula</i>
White-throated Sparrow	<i>Zonotrichia albicollis</i>
White-crowned Sparrow	<i>Zonotrichia leucophrys gambelii</i> and <i>Z. l. pugetensis</i>
Golden-crowned Sparrow	<i>Zonotrichia atricapilla</i>
Dark-eyed Junco	<i>Junco hyemalis hyemalis</i>
Western Tanager	<i>Piranga ludoviciana</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Red-winged Blackbird	<i>Agelaius phoeniceus arctolegus</i>
Yellow-headed Blackbird	<i>Xanthocephalus xanthocephalus</i>
Rusty Blackbird	<i>Euphagus carolinus carolinus</i>
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>
Brown-headed Cowbird	<i>Molothrus ater artemisiae</i>

### Examples

There is some evidence for current range expansions among time-limited migrants in Beringia. Whether these shifts are due in whole or in part to relaxation of time constraints is not known, but North American examples include Wilson's Phalarope (*Phalaropus tricolor*; Erwin et al. 2004), Caspian Tern (*Hydroprogne caspia*; Gibson and Withrow 2015 and citations therein), Common Nighthawk (*Chordeiles minor minor*; Sinclair et al. 2003), Yellow-bellied Flycatcher (*Empidonax flaviventris*; Benson et al. 2000, Martin et al. 2006), Cassin's Vireo (*Vireo cassinii cassinii*; DeCicco and Hajdukovich 2008), Tennessee Warbler (*Oreothlypis peregrina*; Gibson and Withrow 2015), Cape May Warbler (*Setophaga tigrina*; Tobish 2014), and White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*; Gibson and Withrow 2015). Asian examples include the Tree Swallow (*Tachycineta bicolor*), Cliff Swallow (*Petrochelidon pyrrhonota*), American Robin (*Turdus migratorius*), Fox Sparrow (*Passerella iliaca unalaschensis*), Savannah Sparrow (*Passerculus sandwichensis*), Dark-eyed Junco (*Junco hyemalis*), and American Tree Sparrow (*Spizella arborea*; Arkhipov and Ławicki 2016).

In summary, we expect climatic warming in Beringia to enable some species of migratory birds,

TABLE 2. Migratory Asian birds for which we may see eastward range expansions within or into western Beringia and, for many, possible colonization into North America. Subspecies included where relevant.

Baikal Teal	<i>Anas formosa</i>
Tufted Duck	<i>Aythya fuligula</i>
Smew	<i>Mergellus albellus</i>
Eurasian Dotterel	<i>Charadrius morinellus</i>
Terek Sandpiper	<i>Xenus cinereus</i>
Spotted Redshank	<i>Tringa erythropus</i>
Common Greenshank	<i>Tringa nebularia</i>
Black-tailed Godwit	<i>Limosa limosa melanuroides</i>
Great Knot	<i>Calidris tenuirostris</i>
Sharp-tailed Sandpiper	<i>Calidris acuminata</i>
Temminck's Stint	<i>Calidris temminckii</i>
Long-toed Stint	<i>Calidris subminuta</i>
Spoon-billed Sandpiper	<i>Calidris pygmaea</i>
Red-necked Stint	<i>Calidris ruficollis</i>
Little Stint	<i>Calidris minuta</i>
Jack Snipe	<i>Lymnocyrtus minimus</i>
Common Snipe	<i>Gallinago gallinago gallinago</i>
Pin-tailed Snipe	<i>Gallinago stenura japonica</i>
Black-headed Gull	<i>Chroicocephalus ridibundus</i>
Slaty-backed Gull	<i>Larus schistisagus</i>
Common Cuckoo	<i>Cuculus canorus canorus</i>
Oriental Cuckoo	<i>Cuculus optatus</i>
Fork-tailed Swift	<i>Apus pacificus pacificus</i>
Eurasian Kestrel	<i>Falco tinnunculus interstinctus</i>
Northern Hobby	<i>Falco subbuteo subbuteo</i>
Brown Shrike	<i>Lanius cristatus cristatus</i>
Common House-Martin	<i>Delichon urbicum lagopodum</i>
Willow Warbler	<i>Phylloscopus trochilus yakutensis</i>
Common Chiffchaff	<i>Phylloscopus collybita tristis</i>
Dusky Warbler	<i>Phylloscopus fuscatus fuscatus</i>
Pallas's Leaf Warbler	<i>Phylloscopus proregulus</i>
Yellow-browed Warbler	<i>Phylloscopus inornatus</i>
Siberian Rubythroat	<i>Luscinia calliope</i>
Red-flanked Bluetail	<i>Tarsiger cyanurus</i>
Taiga Flycatcher	<i>Ficedula albicilla</i>
Stonechat	<i>Saxicola torquatus stejnegeri</i>
Dusky Thrush	<i>Turdus naumanni eunomus</i>
Redwing	<i>Turdus iliacus iliacus</i>
Siberian Accentor	<i>Prunella montanella badia</i>
Gray Wagtail	<i>Motacilla cinerea robusta</i>
Pechora Pipit	<i>Anthus gustavi gustavi</i>
Eurasian Bullfinch	<i>Pyrrhula pyrrhula cassinii</i>
Common Rosefinch	<i>Carpodacus erythrinus grebnitskii</i>
Pallas's Rosefinch	<i>Carpodacus roseus roseus</i>
Hawfinch	<i>Coccothraustes coccothraustes japonicus</i>
Little Bunting	<i>Emberiza pusilla</i>
Rustic Bunting	<i>Emberiza rustica latifascia</i>
Yellow-breasted Bunting	<i>Emberiza aureola ornata</i>
Pallas's Bunting	<i>Emberiza pallasii polaris</i>

**TABLE 3.** Birds from North America whose breeding ranges in Asia may spread farther west, and Asian birds whose breeding ranges in North America may spread farther east. Subspecies included where relevant.

#### North American birds in Asia

Snow Goose	<i>Chen c. caerulescens</i>
Sandhill Crane	<i>Grus canadensis canadensis</i>
Baird's Sandpiper	<i>Calidris bairdii</i>
Buff-breasted Sandpiper	<i>Calidris subruficollis</i>
Pectoral Sandpiper	<i>Calidris melanotos</i>
Semipalmated Sandpiper	<i>Calidris pusilla</i>
Western Sandpiper	<i>Calidris mauri</i>
Long-billed Dowitcher	<i>Limnodromus scolopaceus</i>
Gray-cheeked Thrush	<i>Catharus minimus aliciae</i>
Savannah Sparrow	<i>Passerculus sandwichensis sandwichensis</i>

#### Asian birds in North America

Lesser Sand-Plover	<i>Charadrius mongolus stegmanni</i>
Wood Sandpiper	<i>Tringa glareola</i>
Bar-tailed Godwit	<i>Limosa lapponica</i> ssp.
Ruff	<i>Calidris pugnax</i>
Curlew Sandpiper	<i>Calidris ferruginea</i>
Sky Lark	<i>Alauda arvensis pekinensis</i>
Arctic Warbler	<i>Phylloscopus borealis</i>
Lanceolated Warbler	<i>Locustella lanceolata</i>
Bluethroat	<i>Luscinia svecica svecica</i>
Northern Wheatear	<i>Oenanthe oenanthe oenanthe</i>
Eastern Yellow Wagtail	<i>Motacilla tschutschensis tschutschensis</i>
White Wagtail	<i>Motacilla alba ocularis</i>
Olive-backed Pipit	<i>Anthus hodgsoni yunnanensis</i>
Red-throated Pipit	<i>Anthus cervinus</i>
Brambling	<i>Fringilla montifringilla</i>

those that are probably time-limited at their range edges, to substantially expand their ranges in this region, on a primarily east–west axis. While other factors will affect birds' range shifts in Beringia, we highlight the taxa we consider most likely to respond to longer growing seasons and a corresponding relaxation of time constraints.

#### ACKNOWLEDGMENTS

We thank Colleen M. Handel, Steven C. Heinl, and the editors for helpful comments on an earlier draft. We also thank the Cornell Laboratory of Ornithology for permission to reproduce Figure 2.

#### LITERATURE CITED

American Ornithologists' Union (AOU). 1957. Check-list of North American Birds, 5th ed. Am. Ornithol. Union, Port City Press, Baltimore.  
 AOU. 1998. Check-list of North American Birds, 7th ed. Am. Ornithol. Union, Washington, DC.  
 Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S.

E., Tewksbury, J. J., and Chunco, A. J. 2011. Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* 14:677–689; doi 10.1111/j.1461-0248.2011.01620.x.  
 Arkhipov, V. Yu, and Ławicki, Ł. 2016. Nearctic passerines in Russia. *Dutch Birding* 38:201–214.  
 Auer, S. K., and King, D. I. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Global Ecol. Biogeogr.* 23:867–875; doi 10.1111/geb.12174.  
 Barbet-Massin, M., Thuiller, W., and Jiguet, F. 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biol.* 18:881–890; doi 10.1111/j.1365-2486.2011.02552.x.  
 Benson, A. M., Pogson, T. H., and Doyle, T. J. 2000. Updated geographic distribution of eight passerine species in central Alaska. *W. Birds* 31:100–105.  
 Benson, A. M., and Winker, K. 2001. Timing of breeding range occupancy among high-latitude passerine migrants. *Auk* 118:513–519; doi 10.1642/0004-8038(2001)118 [0513:TOBROA]2.0.CO;2.  
 Benson, A. M., and Winker, K. 2015. High-latitude passerine migrants overlap energetically demanding events in autumn. *Wilson J. Ornithol.* 127:601–614; doi 10.1676/14-034.1.  
 Brazil, M. 2009. *Birds of East Asia*. Princeton Univ. Press, Princeton, NJ.  
 Browning, M. R. 1988. A new subspecies of *Carpodacus roseus*. *Bull. Br. Ornithol. Club* 108:177–179.  
 Cannell, P. F., Cherry, J. D., and Parkes, K. C. 1983. Variation and migration overlap in flight feather molt of the Rose-breasted Grosbeak. *Wilson Bull.* 95:621–627.  
 Chapin, F. S., III, Trainor, S. F., Cochran, P., Huntington, H., Markon, C., McCammon, M., McGuire, A. D., and Serreze, M. 2014. Climate Change Impacts in the United States: The Third National Climate Assessment (J. M. Melillo, Terese (T.C.) Richmond, and G. W. Yohe, eds.), Alaska: chap. 22, pp. 514–536. U.S. Global Change Research Program, Washington, DC; doi 10.7930/J00Z7150.  
 DeCicco, L. H., and Hajdukovich, N. [R.]. 2008. First record of the Cassin's Vireo nesting in Alaska. *W. Birds* 39:36–38.  
 Del Hoyo, J., Elliott, A., Sargatal, J., and Christie, D. 1992–2011. *Handbook of the Birds of the World*, Vols. 1–16. Lynx Edicions and BirdLife Int., Barcelona.  
 Erwin, C. A., Rozell, K. B., and DeCicco, L. H. 2004. Update on the status and distribution of Wilson's Phalarope and Yellow-bellied Sapsucker in Alaska. *W. Birds* 35:42–44.  
 Flockhart, D. T. T. 2010. Timing of events on the breeding grounds for five species of sympatric warblers. *J. Field Ornithol.* 81:373–382; doi 10.1111/j.1557-9263.2010.00293.x.  
 Gibson, D. D., and Withrow, J. J. 2015. Inventory of the species and subspecies of Alaska birds. *W. Birds* 46:94–185.



- Gillings, S., Balmer, D. E., and Fuller, R. J. 2015. Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biol.* 21:2155–2168; doi 10.1111/gcb.12823.
- Huntley, B., Collingham, Y. C., Willis, S. G., and Green, R. E. 2008. Potential impacts of climatic change on European breeding birds. *PLoS One* 3(1): e1439; doi 10.1371/journal.pone.0001439.
- Hussell, D. J. T., Bairlein, F., and Dunn, E. H. 2014. Double brooding by the Northern Wheatear on Baffin Island. *Arctic* 67:167–172.
- Kessel, B. 1963. West-east relationships of the birds of northern Alaska, *in* Pacific Basin Biogeography (J. L. Gressitt, ed.), pp. 79–84. Bishop Museum Press, Honolulu.
- Lee, D.-H., Torchetti, M. K., Winker, K., Ip, H., Song, C.-S., and Swayne, D. E. 2015. Intercontinental spread of Asian-origin H5N8 to North America through Beringia by migratory birds. *J. Virol.* 89:6521–6524; doi 10.1128/JVI.00728-1.5.
- MacArthur, R. H., and Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, NJ.
- Martin, P. R., Bonier, F., and Gibson, D. D. 2006. First nest of the Yellow-bellied Flycatcher for Alaska, with notes on breeding biology. *W. Birds* 37:8–22.
- Mayr, E. 1946. History of the North American bird fauna. *Wilson Bull.* 58:3–41.
- Mizel, J. D., Schmidt, J. H., McIntyre, C. L., and Roland, C. A. 2016. Rapidly shifting elevational distributions of passerine species parallel vegetation change in the subarctic. *Ecosphere* 7(3): e01264; doi 10.1002/ecs2.1264.
- National Geographic. 2002. *Field Guide to the Birds of North America*, 4th ed. Nat. Geogr. Soc., Washington, DC.
- Payne, R. B. 1972. Mechanisms and control of molt. *Avian Biol.* 2:103–105.
- Pearce, J. M., Reeves, A. B., Ramey, A. M., Hupp, J. W., Ip, H. S., Bertram, M., Petrula, M. J., Scotton, B. D., et al. 2011. Interspecific exchange of avian influenza virus genes in Alaska: The influence of trans-hemispheric migratory tendency and breeding ground sympatry. *Mol. Ecol.* 20:1015–1025; doi 10.1111/j.1365-294X.2010.04908.x.
- Rimmer, C. C. 1988. Timing of the definitive prebasic molt in Yellow Warblers at James Bay, Ontario. *Condor* 90:141–146.
- Rodewald, P. (ed.). 2015. *The Birds of North America Online*. Cornell Lab. Ornithol., Ithaca, NY; birdsna.org.
- Rowe L., Ludwig, D., and Schluter, D. 1994. Time, condition and the seasonal decline of avian clutch size. *Am. Nat.* 143:698–722; doi 10.1086/285627.
- Runstadler, J., Hill, N., Hussein, I. T. M., Puryear, W., and Keogh, M. 2013. Connecting the study of wild influenza with the potential for pandemic disease. *Infect. Genet. Evol.* 17:162–187; doi 10.1016/j.meegid.2013.02.020.
- Sinclair, P. H., Nixon, W. A., Eckert, C. D., and Hughes, N. L. (eds.). 2003. *Birds of the Yukon Territory*. Univ. of British Columbia Press, Vancouver.
- Stegmann, B. 1963. The problem of the Beringian continental land connection in the light of ornithogeography, *in* Pacific Basin Biogeography (J. L. Gressitt, ed.), pp. 65–78. Bishop Museum Press, Honolulu.
- Tingley, M. P., and Huybers, P. 2013. Recent temperature extremes at high northern latitudes unprecedented in the last 600 years. *Nature* 496:201–205; doi 10.1038/nature11969.
- Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C., and Beissinger, S. R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biol.* 18:3279–3290; doi 10.1111/j.1365-2486.2012.02784.x.
- Tobish, T. [G. Jr.]. 2014. Alaska region (summer 2013). *N. Am. Birds* 67:638–641.
- Vega-Rivera, J. H., McShea, W. J., Rappole, J. H., and Haas, C. A. 1998. Pattern and chronology of pre-basic molt for the Wood Thrush and its relation to reproduction and migration departure. *Wilson Bull.* 110:384–392.
- Virkkala, R., and Lehikoinen, A. 2014. Patterns of climate-induced density shifts of species: Poleward shifts faster in northern boreal birds than in southern birds. *Global Change Biol.* 20:2995–3003; doi 10.1111/gcb.12573.
- West, F. H. (ed.). 1998. *American Beginnings: The Prehistory and Palaeoecology of Beringia*. Univ. of Chicago Press, Chicago.
- Winker, K., McCracken, K. G., Gibson, D. D., Pruett, C. L., Meier, R., Huettmann, F., Wege, M., Kulikova, I. V., et al. 2007. Movements of birds and avian influenza from Asia into Alaska. *Emerging Infect. Dis.* 13:547–552.
- Zuckerberg, B., Woods, A. M., and Porter, W. F. 2009. Poleward shifts in breeding bird distributions in New York state. *Global Change Biol.* 15:1866–1883; doi 10.1111/j.1365-2486.2009.01878.x.