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Spatial and temporal variation in climate change: a bird's eye view

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Abstract Recent changes in global climate have dramatically altered worldwide temperatures and the corresponding timing of seasonal climate conditions. Recognizing the degree to which species respond to changing climates is therefore an area of increasing conservation concern as species that are unable to respond face increased risk of extinction. Here we examine spatial and temporal heterogeneity in the rate of climate change across western North America and discuss the potential for conditions to arise that may limit the ability of western migratory birds to adapt to changing climates. Based on 52 years of climate data, we show that changes in temperature and precipitation differ significantly between spring migration habitats in the desert southwest and breeding habitats throughout western North America. Such differences may ultimately increase costs to individual birds and thereby threaten the long-term population viability of many species.

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1 Introduction

Global climate change has dramatically altered seasonal climate conditions and led to corresponding advances in phenology (Root et al. 2003). In migratory species, however, advances in phenology are often less than expected (Møller et al. 2008), indicating there may be significant trade-offs with other sources of natural selection. For example, in migratory birds the benefit of advancing breeding must be weighed against the cost of advancing migration (Alerstam 1991). Because many bird species stop en route to refuel, food availability at stopover locations directly influences survival and future reproduction (Alerstam 1991). Given the degree of heterogeneity in climate change across landscapes and differences in the responses of local communities (IPCC 2001), changes in resource phenology at stopover and breeding locations may differ greatly. However, despite the importance of migration in limiting populations (Alerstam 1991), and clear evidence that climate change is both spatially and temporally heterogeneous (IPCC 2001), we know little about the relative rates of climate change at migratory versus breeding locations and thus the potential for selection during migration to limit phenological responses to changing climates (Ahola et al. 2004).

As an important step in addressing this issue, we analyzed the degree of spatial and temporal variation in the rate of climate change between migratory and breeding regions used by > 200 species of migratory birds (Electronic Supplementary Table 1) known to travel through the desert southwest en route to breeding locations throughout western North America. Addressing climate change in the desert southwest may be particularly informative because it's an important wintering area for many short-distance migrants and acts as a migratory funnel for long-distance migrants traveling from the Neotropics.

2 Materials and methods

We gathered unadjusted data from the U.S. Historical Climatology Network (Williams et al. 2007), Alaska Climate Research Center (2009), and Canadian National Climate Data and Information Archive (2009) for 82 weather stations representing 10 states and 4 provinces (Electronic Supplementary Table 2). To minimize missing data we limited our analysis to monthly climate data for March–September of 1954–2006. We focused on minimum temperature and accumulated precipitation because plant and insect phenology, and thus the majority of avian food resources, appear most sensitive to these climate variables (e.g. Crimmins et al. 2008). We also recorded latitude and elevation for each station.

Utilizing complete case regression analysis, we estimated rates of change in temperature and precipitation over the 52-year period for each month, at each climate station. We tested whether rates of climate change were spatially and temporally variable using an ANCOVA that included month as a factor and latitude and elevation as covariates; however, because we were interested in comparing rates of change among regions when each is occupied by migrants, we categorized data by region and time as spring migration, summer breeding, or fall migration 'habitat categories' which we then added to the ANCOVA. Habitat categories were assigned based

on generalities about when western birds migrate (Spring: March–May, Fall: July–September) and breed (Summer: May–July) and what regions are predominately used during migration (desert southwest: 31.35°–34.77°) versus breeding (western North America 37.28°–71.28°). The overlap in timing (May and July) and the close proximity of regions (280 km) makes this test highly conservative for detecting differences in the rate of climate change among habitat categories. Analyses were conducted on the complete data set, but for visual simplicity, where appropriate graphs represent mean changes for each station.

3 Results

Over the 52-year period, changes in precipitation varied among the 82 stations from an 18% decline to a 28% increase; however the rate of change was not influenced by latitude (Fig. 1a; $F_{1,574} = 1.361$, $p = 0.244$) elevation (Fig. 1b; $F_{1,574} = 0.29$, $p = 0.590$), or month (Fig. 2a; $F_{1,574} = 1.403$, $p = 0.211$). Changes in minimum temperature also varied among stations from a 5% decline to a 24% increase, but unlike precipitation, temperature changes were influenced by latitude (Fig. 1c;

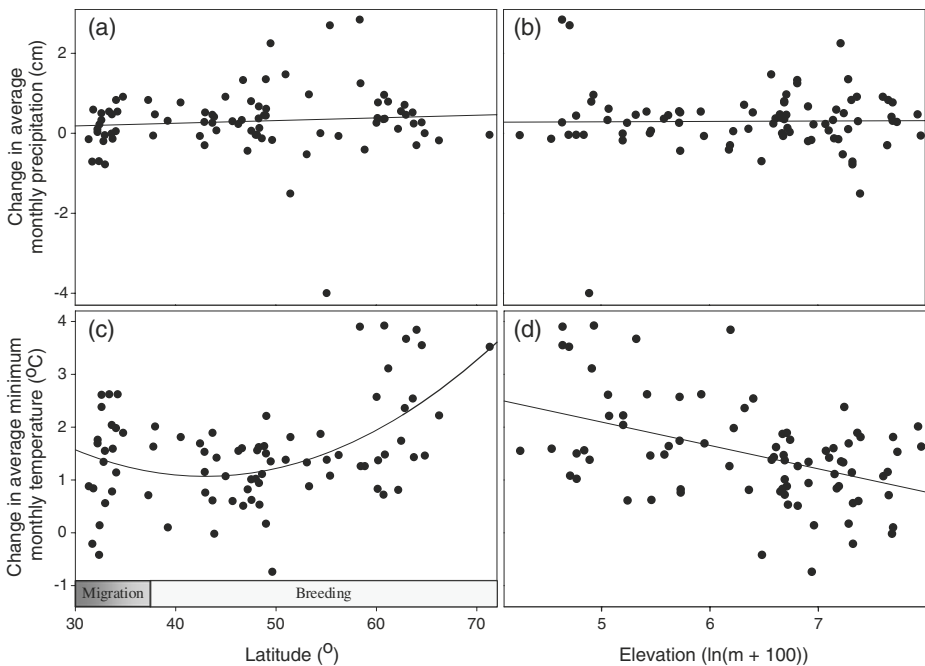


Fig. 1 Changes in temperature, but not precipitation, vary with latitude and elevation. Changes in precipitation are consistent across (a) latitudes ($r^2 = 0.008$) and (b) elevations ($r^2 < 0.001$); but changes in minimum temperature are more extreme at (c) higher latitudes ($r^2 = 0.256$) and (d) lower elevations ($r^2 = 0.212$). Elevations were natural-log transformed to correct for higher variance at lower elevations

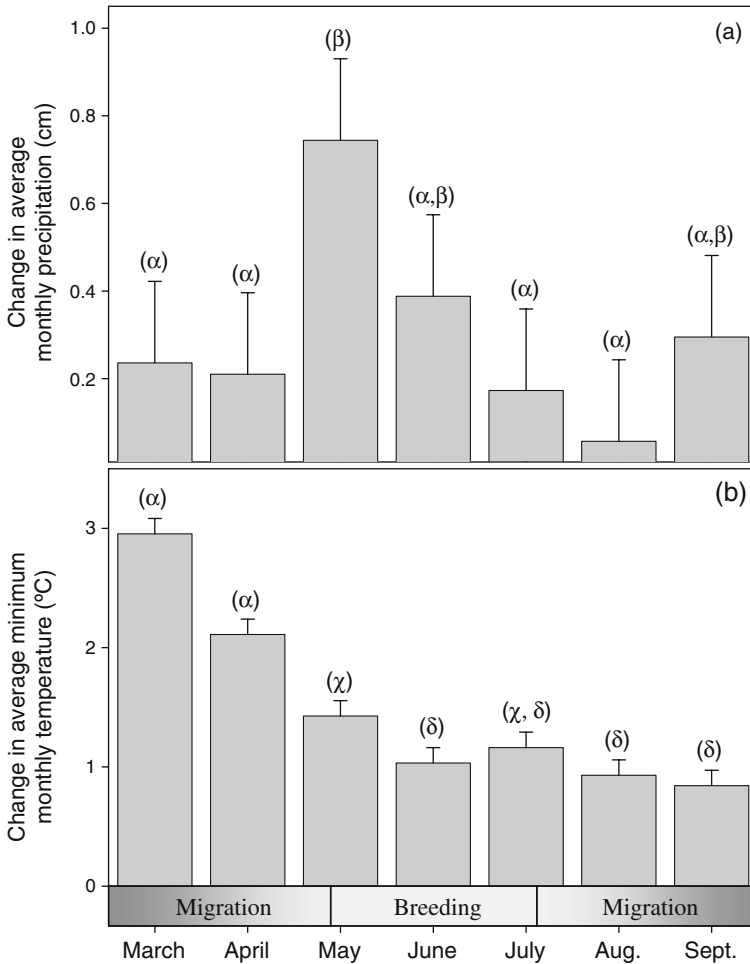
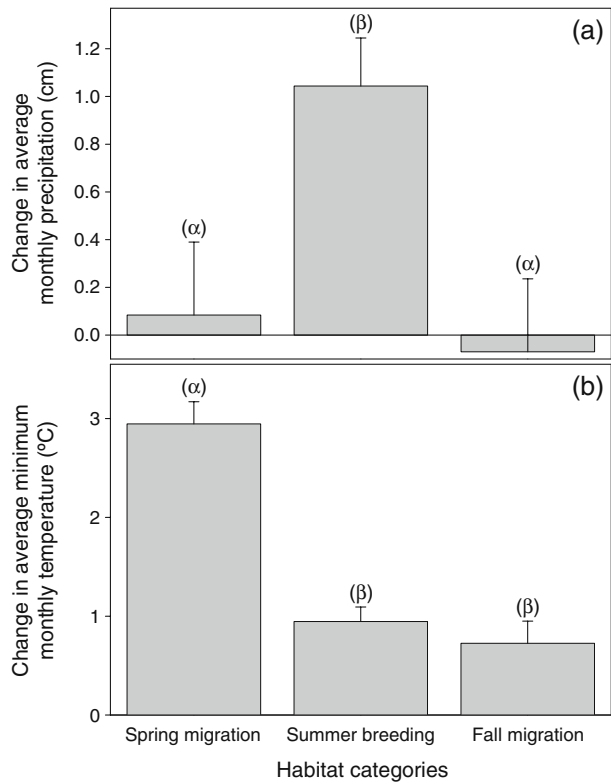


Fig. 2 Changes in temperature, but not precipitation, show a clear seasonal trend. Change in precipitation (a) did not differ among months or show any predictable seasonal pattern, but changes in temperature (b), differed among months resulting in a clear seasonal decline in the degree of warming. Columns are estimated marginal means (\pm s.e.m.) uniquely identified when significantly different at the 0.05 level according to an LSD post-hoc test

$F_{2,574} = 17.853$, $p < 0.001$), elevation (Fig. 1d; $F_{1,574} = 48.610$, $p < 0.001$), and month (Fig. 2b; $F_{1,574} = 35.765$, $p < 0.001$), with higher latitudes, lower elevations, and earlier months experiencing more drastic increases in temperature.

When adjusted to consider when birds are present in each region, there was a significant effect of habitat category on precipitation (Fig. 3a; $F_{1,306} = 4.769$, $p = 0.009$), with breeding habitats becoming significantly wetter, driven primarily by increasing May precipitation, as evident by the significant month effect ($F_{1,306} = 2.440$, $p = 0.026$). Habitat category also influenced the rate of temperature change (Fig. 3b; $F_{1,306} = 26.587$, $p < 0.001$), with spring migration habitats warming

Fig. 3 Migratory birds experience differences in climate change among spring migration, summer breeding, and fall migration habitats. After accounting for when birds are present at breeding versus migratory habitats, climate change differed significantly between habitats, with birds experiencing relatively wetter breeding (a) and warmer spring migration habitats (b). Columns are estimated marginal means (\pm s.e.m.) uniquely identified when significantly different at the 0.05 level according to an LSD post-hoc test



significantly more than breeding or fall migration habitats. Moreover the effect of latitude ($F_{1,306} = 12.667$, $p < 0.001$), elevation ($F_{1,306} = 36.274$, $p < 0.001$), and month ($F_{1,306} = 2.067$, $p = 0.038$) continued to be prevalent within each category.

4 Discussion

Our findings show that despite consistent increases in temperature throughout western North America, the relative rate of temperature change varied widely among locations. Although the latitudinal pattern (Fig. 1c) would predict more extreme temperature changes at breeding habitats, we found that spring migration habitats experienced the most extreme increases in temperature (Fig. 3b). This result emphasizes the importance of seasonal declines in temperature change across western North America (Fig. 2b). Moreover, although we failed to find consistent patterns explaining changes in precipitation (Figs. 1a, b; 2a), habitat categories did differ significantly, with breeding locations becoming relatively wetter (Fig. 3a). In combination these findings demonstrate that not only are migratory birds experiencing climate change, but they are experiencing different rates of change throughout their migratory cycle.

To successfully manage future wildlife populations we must understand how climate change alters trade-offs between sources of selection to predict how individuals may respond, populations may evolve, and management actions may ameliorate increasing costs. In a critical first step in addressing this question, we demonstrated that climate change patterns, and thus potential sources of selection, vary significantly among the habitats occupied by birds migrating across western North America. From a bird's perspective, differing rates of climate change may have important fitness consequences. For example, that spring migration habitats are warming faster than breeding habitats likely creates discordance in plant and insect phenology between locations. If phenology is advancing faster at migratory stopover locations than at breeding locations, then individuals are faced with a difficult trade-off: 1) migrate when food availability is optimal en route (McGrath et al. 2009) and arrive at breeding grounds early when food is limited and risk of severe weather is high (e.g. Decker and Conway 2009), or 2) migrate after food availability has peaked en route, but arrive at breeding locations when reproductive potential is optimal. In both scenarios, increased costs to individuals are likely to have important implications for migratory bird populations by reducing survival en route, reproductive potential at breeding locations, or potentially both. Moreover, because costs are additive from one location to another, discordance in the phenology of even two locations may have cascading effects throughout an individual's migratory cycle (Alerstam 1991).

Here, we clearly demonstrate that rates of climate change vary substantially among locations occupied during the migratory cycle of western birds, and in doing so we highlight the importance of considering the potential for climate change *per se* to impact migratory populations, and perhaps more importantly, how differing rates of climate change throughout the migratory cycle may alter multiple sources of selection acting on individuals. Future research focused on relating spatial and temporal variation in climate change to the timing, duration, and patterns of migration for specific species will elucidate the overall costs of climate change to individuals and help identify species and populations of particular conservation concern.

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Table 1: Species with populations that may face differential selection between migratory and breeding locations due to discordance in the rate of climate change.

Grebes	Clark's Grebe	<i>Aechmophorus clarkii</i>
	Western Grebe	<i>Aechmophorus occidentalis</i>
	Eared Grebe	<i>Podiceps nigricollis</i>
	Pied-billed Grebe	<i>Podilymbus podiceps</i>
	Least Grebe	<i>Tachybaptus dominicus</i>
Pelicans	American White Pelican	<i>Pelecanus erythrorhynchos</i>
Cormorants	Double-crested Cormorant	<i>Phalacrocorax auritus</i>
Wading Birds	Great Egret	<i>Ardea alba</i>
	Great Blue Heron	<i>Ardea herodias</i>
	American Bittern	<i>Botaurus lentiginosus</i>
	Cattle Egret	<i>Bubulcus ibis</i>
	Green Heron	<i>Butorides virescens</i>
	Snowy Egret	<i>Egretta thula</i>
	Marbled Godwit	<i>Limosa fedoa</i>
	Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>
White-faced Ibis	<i>Plegadis chihi</i>	
Waterfowl	Wood Duck	<i>Aix sponsa</i>
	Northern Pintail	<i>Anas acuta</i>
	American Wigeon	<i>Anas americana</i>
	American Green-winged Teal	<i>Anas c. carolinensis</i>
	Northern Shoveler	<i>Anas clypeata</i>
	Green-winged Teal	<i>Anas crecca</i>
	Cinnamon Teal	<i>Anas cyanoptera</i>
	Blue-winged Teal	<i>Anas discors</i>
	Mallard	<i>Anas platyrhynchos</i>
	Gadwall	<i>Anas strepera</i>
	Greater White-fronted Goose	<i>Anser albifrons</i>
	Lesser Scaup	<i>Aythya affinis</i>
	Redhead	<i>Aythya americana</i>
	Ring-necked Duck	<i>Aythya collaris</i>
	Canvasback	<i>Aythya valisineria</i>
	Canada Goose	<i>Branta canadensis</i>
	Bufflehead	<i>Bucephala albeola</i>
	Common Goldeneye	<i>Bucephala clangula</i>
	Snow Goose	<i>Chen caerulescens</i>
	Ross's Goose	<i>Chen rossii</i>
Hooded Merganser	<i>Lophodytes cucullatus</i>	
Common Merganser	<i>Mergus merganser</i>	
Red-breasted Merganser	<i>Mergus serrator</i>	
Ruddy Duck	<i>Oxyura jamaicensis</i>	

Raptors	Cooper's Hawk Sharp-shinned Hawk Golden Eagle Red-tailed Hawk Ferruginous Hawk Swainson's Hawk Turkey Vulture Northern Harrier Merlin Prairie Falcon Peregrine Falcon American Kestrel Bald Eagle Osprey	<i>Accipiter cooperii</i> <i>Accipiter striatus</i> <i>Aquila chrysaetos</i> <i>Buteo jamaicensis</i> <i>Buteo regalis</i> <i>Buteo swainsoni</i> <i>Cathartes aura</i> <i>Circus cyaneus</i> <i>Falco columbarius</i> <i>Falco mexicanus</i> <i>Falco peregrinus</i> <i>Falco sparverius</i> <i>Haliaeetus leucocephalus</i> <i>Pandion haliaetus</i>
Rails	American Coot Sora Virginia Rail	<i>Fulica americana</i> <i>Porzana carolina</i> <i>Rallus limicola</i>
Cranes	Whooping Crane Sandhill Crane	<i>Grus americana</i> <i>Grus canadensis</i>
Shorebirds	Spotted Sandpiper Sanderling Dunlin Western Sandpiper Least Sandpiper Mountain Plover Semipalmated Plover Killdeer Common Snipe Black-necked Stilt Short-billed Dowitcher Long-billed Dowitcher Long-billed Curlew Whimbrel Red-necked Phalarope Wilson's Phalarope American Golden Plover Black-bellied Plover American Avocet Lesser Yellowlegs Greater Yellowlegs Willet Solitary Sandpiper	<i>Actitis macularius</i> <i>Calidris alba</i> <i>Calidris alpina</i> <i>Calidris mauri</i> <i>Calidris minutilla</i> <i>Charadrius montanus</i> <i>Charadrius semipalmatus</i> <i>Charadrius vociferus</i> <i>Gallinago gallinago</i> <i>Himantopus mexicanus</i> <i>Limnodromus griseus</i> <i>Limnodromus scolopaceus</i> <i>Numenius americanus</i> <i>Numenius phaeopus</i> <i>Phalaropus lobatus</i> <i>Phalaropus tricolor</i> <i>Pluvialis dominica</i> <i>Pluvialis squatarola</i> <i>Recurvirostra americana</i> <i>Tringa flavipes</i> <i>Tringa melanoleuca</i> <i>Tringa semipalmata</i> <i>Tringa solitaria</i>
Gulls	Herring Gull California Gull Ring-billed Gull Bonaparte's Gull Franklin's Gull	<i>Larus argentatus</i> <i>Larus californicus</i> <i>Larus delawarensis</i> <i>Larus philadelphia</i> <i>Larus pipixcan</i>

Terns	Black Tern Caspian Tern Forster's Tern	<i>Chilidonias niger</i> <i>Sterna caspia</i> <i>Sterna forsteri</i>
Doves	Mourning Dove	<i>Zenaida macroura</i>
Cuckoos	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>
Owls	Burrowing Owl	<i>Athene cunicularia</i>
Nightjars	Common Nighthawk Common Poorwill	<i>Chordeiles minor</i> <i>Phalaenoptilus nuttallii</i>
Swifts	White-throated Swift Vaux's Swift Black Swift	<i>Aeronautes saxatalis</i> <i>Chaetura vauxi</i> <i>Cypseloides niger</i>
Hummingbirds	Black-chinned Hummingbird Anna's Hummingbird Broad-tailed Hummingbird Rufous Hummingbird Allen's Hummingbird Calliope Hummingbird	<i>Archilochus alexandri</i> <i>Calypte anna</i> <i>Selasphorus platycercus</i> <i>Selasphorus rufus</i> <i>Selasphorus sasin</i> <i>Stellula calliope</i>
Kingfishers	Belted Kingfisher	<i>Ceryle alcyon</i>
Woodpeckers	Lewis's Woodpecker Red-naped Sapsucker Williamson's Sapsucker	<i>Melanerpes lewis</i> <i>Sphyrapicus nuchalis</i> <i>Sphyrapicus thyroideus</i>
Flycatchers	Olive-sided Flycatcher Western Wood-Pewee Pacific-slope Flycatcher Western Flycatcher Hammond's Flycatcher Least Flycatcher Dusky Flycatcher Cordilleran Flycatcher Willow Flycatcher Gray Flycatcher Ash-throated Flycatcher Say's Phoebe Eastern Kingbird Western Kingbird	<i>Contopus cooperi</i> <i>Contopus sordidulus</i> <i>Empidonax difficilis</i> <i>Empidonax difficilis/occid.</i> <i>Empidonax hammondii</i> <i>Empidonax minimus</i> <i>Empidonax oberholseri</i> <i>Empidonax occidentalis</i> <i>Empidonax traillii</i> <i>Empidonax wrightii</i> <i>Myiarchus cinerascens</i> <i>Sayornis saya</i> <i>Tyrannus tyrannus</i> <i>Tyrannus verticalis</i>
Shrikes	Loggerhead Shrike	<i>Lanius ludovicianus</i>

Vireos	Cassin's Vireo Warbling Vireo Plumbeous Vireo	<i>Vireo cassinii</i> <i>Vireo gilvus</i> <i>Vireo plumbeus</i>
Swallows	Barn Swallow Cliff Swallow Purple Martin Bank Swallow Northern Rough-winged Swallow Tree Swallow Violet-green Swallow	<i>Hirundo rustica</i> <i>Petrochelidon pyrrhonota</i> <i>Progne subis</i> <i>Riparia riparia</i> <i>Stelgidopteryx serripennis</i> <i>Tachycineta bicolor</i> <i>Tachycineta thalassina</i>
Wrens	Marsh Wren Rock Wren House Wren	<i>Cistothorus palustris</i> <i>Salpinctes obsoletus</i> <i>Troglodytes aedon</i>
Kinglets	Ruby-crowned Kinglet Golden-crowned Kinglet	<i>Regulus calendula</i> <i>Regulus satrapa</i>
Gnatcatchers	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Thrushes	Hermit Thrush Swainson's Thrush Townsend's Solitaire Mountain Bluebird Western Bluebird American Robin	<i>Catharus guttatus</i> <i>Catharus ustulatus</i> <i>Myadestes townsendi</i> <i>Sialia currucoides</i> <i>Sialia mexicana</i> <i>Turdus migratorius</i>
Thrashers	Sage Thrasher Brown Thrasher	<i>Oreoscoptes montanus</i> <i>Toxostoma rufum</i>
Pipits	American Pipit Sprague's Pipit	<i>Anthus rubescens</i> <i>Anthus spragueii</i>
Waxwings	Cedar Waxwing	<i>Bombycilla cedrorum</i>

Wood-Warblers	Audubon's Warbler Myrtle Warbler Yellow-rumped Warbler Black-throated Gray Warbler Hermit Warbler Yellow Warbler Townsend's Warbler Common Yellowthroat Yellow-breasted Chat Black-and-white Warbler MacGillivray's Warbler Ovenbird Northern Waterthrush American Redstart Orange-crowned Warbler Tennessee Warbler Nashville Warbler Virginia's Warbler Wilson's Warbler	<i>Dendroica c. auduboni</i> <i>Dendroica c. coronata</i> <i>Dendroica coronata</i> <i>Dendroica nigrescens</i> <i>Dendroica occidentalis</i> <i>Dendroica petechia</i> <i>Dendroica townsendi</i> <i>Geothlypis trichas</i> <i>Icteria virens</i> <i>Mniotilta varia</i> <i>Oporornis tolmiei</i> <i>Seiurus aurocapilla</i> <i>Seiurus noveboracensis</i> <i>Setophaga ruticilla</i> <i>Vermivora celata</i> <i>Vermivora peregrina</i> <i>Vermivora ruficapilla</i> <i>Vermivora virginiae</i> <i>Wilsonia pusilla</i>
Tanagers	Western Tanager	<i>Piranga ludoviciana</i>
Grosbeaks	Blue Grosbeak Rose-breasted Grosbeak Black-headed Grosbeak	<i>Guiraca caerulea</i> <i>Pheucticus ludovicianus</i> <i>Pheucticus melanocephalus</i>
Buntings	Lazuli Bunting	<i>Passerina amoena</i>
Sparrows	Cassin's Sparrow Baird's Sparrow Grasshopper Sparrow Sage Sparrow Black-throated Sparrow Lark Bunting McCown's Longspur Chestnut-collared Longspur Lark Sparrow Dark-eyed Junco Swamp Sparrow Lincoln's Sparrow Song Sparrow Savannah Sparrow Fox Sparrow Green-tailed Towhee Spotted Towhee Vesper Sparrow American Tree Sparrow Brewer's Sparrow Clay-colored Sparrow Chipping Sparrow White-throated Sparrow Golden-crowned Sparrow White-crowned Sparrow Harris's Sparrow	<i>Aimophila cassinii</i> <i>Ammodramus bairdii</i> <i>Ammodramus savannarum</i> <i>Amphispiza belli</i> <i>Amphispiza bilineata</i> <i>Calamospiza melanocorys</i> <i>Calcarius mccownii</i> <i>Calcarius ornatus</i> <i>Chondestes grammacus</i> <i>Junco hyemalis</i> <i>Melospiza georgiana</i> <i>Melospiza lincolni</i> <i>Melospiza melodia</i> <i>Passerculus sandwichensis</i> <i>Passerella iliaca</i> <i>Pipilo chlorurus</i> <i>Pipilo maculatus</i> <i>Poocetes gramineus</i> <i>Spizella arborea</i> <i>Spizella breweri</i> <i>Spizella pallida</i> <i>Spizella passerina</i> <i>Zonotrichia albicollis</i> <i>Zonotrichia atricapilla</i> <i>Zonotrichia leucophrys</i> <i>Zonotrichia querula</i>

Blackbirds

Red-winged Blackbird
Brewer's Blackbird
Bullock's Oriole
Scott's Oriole
Orchard Oriole
Brown-headed Cowbird
Common Grackle
Western Meadowlark
Yellow-headed Blackbird

Agelaius phoeniceus
Euphagus cyanocephalus
Icterus bullockii
Icterus parisorum
Icterus spurius
Molothrus ater
Quiscalus quiscula
Sturnella neglecta
Xanthocephalus
xanthocephalus

Finches

Lesser Goldfinch
American Goldfinch
Cassin's Finch

Carduelis psaltria
Carduelis tristis
Carpodacus cassinii

Table 2: Weather stations

	State/Province	Location	Lat.(°)	Elev.(m)	State/Province	Location	Lat.(°)	Elev.(m)	
Migration	Arizona	Ajo	32.37	549	California	Blythe	33.63	81	
		Buckeye	33.38	271		Brawley	32.95	-30	
		Douglas	31.35	1231		Cuyamaca	32.98	1414	
		Parker	34.22	125		Indio	33.73	-6	
		Roosevelt	33.67	672		Redlands	34.05	402	
		Safford	32.82	900		New Mexico	Carlsbad	32.42	951
		Tombstone	31.70	1405			El Paso	31.80	1194
		Tucson	32.23	742			Gage	32.22	1344
	Yuma	32.62	58	Jornada	32.62		1300		
						Los Lunas	34.77	1475	
						Socorro	34.08	1398	
	Breeding	Alaska	Anchorage	61.18	35	Idaho	Caldwell	43.67	722
			Annette	55.05	33		Kellogg	47.53	707
			Barrow	71.28	10		Moscow	46.73	811
Beaver Falls			55.38	11	Priest River		48.35	725	
Bethel			60.78	38	Sandpoint		48.28	640	
Big Delta			64.00	386	Montana		Bozeman	45.67	1480
Fairbanks			64.82	132			Cut Bank	48.60	1170
Gulkana			62.17	479			Hamilton	46.25	1076
Juneau			58.35	4			Helena	46.60	1167
								Kalispell	48.30
					Northwest Territories	Ft. Good	66.24	82	
						Ft. Smith	60.02	205	
Alberta		Beaver Mines	49.47	1257		Hay River	60.84	165	
		Calmar	53.29	720		Yellow	62.46	206	
		Carway	49.00	1354	Oregon	Bend	44.07	1116	
		Empress	50.96	612		Crater Lake	42.90	1974	
		Lake Louise	51.43	1524		Drain	43.67	89	
		Lethbridge	49.63	929		Grant Pass	42.43	282	
		British Columbia	Abbotsford	49.03	59		Riddle	42.95	207
			Barkerville	53.07	1283	Washington	Blaine	49.00	18
		Cowichan Lake	48.82	177	Buckley		47.17	209	
		Dease Lake	58.43	807	Everett		47.98	18	
Fort Nelson		58.84	382	Port Angeles	48.12		27		
		Fort St. James	54.43	686		Snoqualmie	47.55	134	
		Fort St. John	56.24	695	Wyoming	Moran	43.85	2072	
Colorado		Cheesman	39.22	2097			Pinedale	42.87	2187
		Durango	37.28	2011			Yellowstone	44.97	1899
		Hermit	37.77	2743	Yukon	Mayo	63.62	504	
		Steamboat	40.50	2084		Pelly Ranch	62.82	454	
		Telluride	37.95	2643		Teslin	60.17	705	
				Watson		60.12	687		
						Whitehorse	60.71	706	