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Supplementary material is appended to the end of this article

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LETTER

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

Joseph J. Fontaine · Karie L. Decker · Susan K. Skagen · Charles van Riper III

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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.

Electronic supplementary material The online version of this article (doi:10.1007/s10584-009-9644-9) contains supplementary material, which is available to authorized users.

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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;

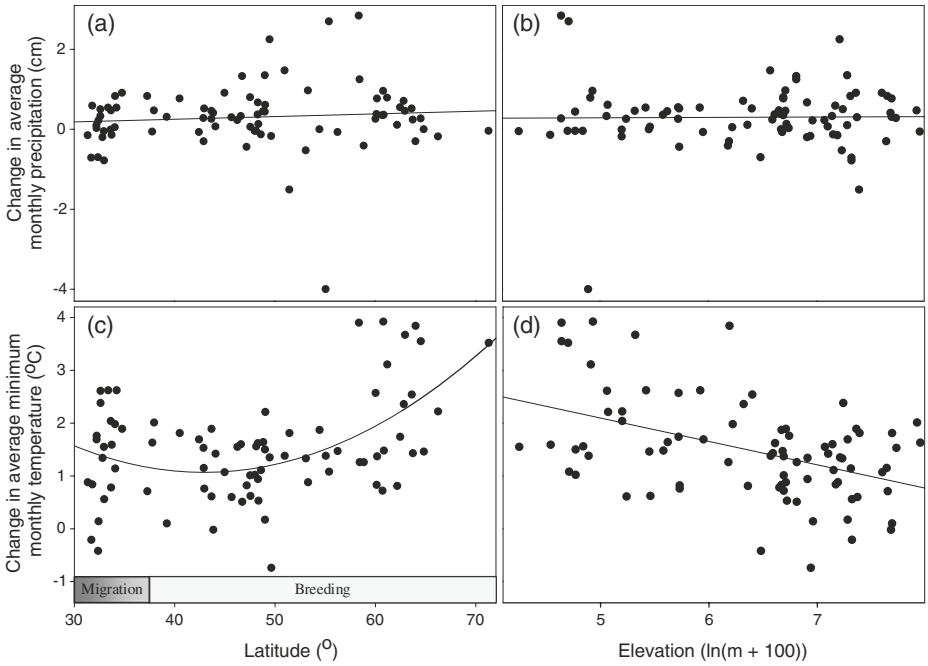

Fig. 1 Changes in temperature, but not precipitation, vary with latitude and elevation. Changes in precipitation are consistent across (**a**) latitudes ($r^2 = 0.008$) and (**b**) elevations ($r^2 < 0.001$); but changes in minimum temperature are more extreme at (**c**) higher latitudes ($r^2 = 0.256$)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

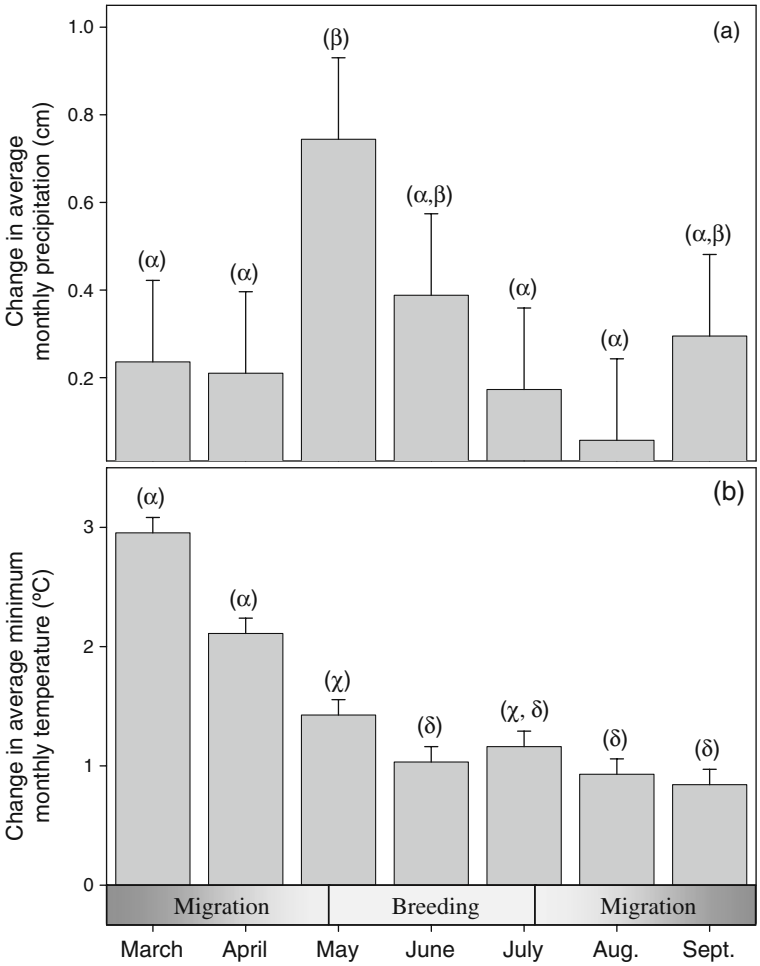

Fig. 2 Changes in temperature, but not precipitation, show a clear seasonal trend. Change in precipitation (**a**) did not differ among months or show any predictable seasonal pattern, but changes in temperature (**b**), differed among months resulting in a clear seasonal decline in the degree of warming. Columns are estimated marginal means (±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

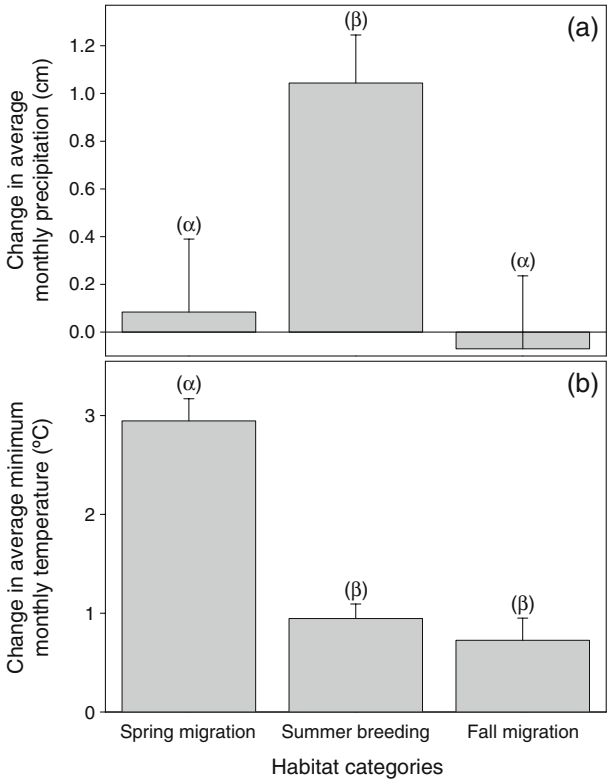

Fig. 3 Migratory birds experience differences in climate change among spring migration, summer breeding, and fall migration habitats. After accounting for when birds are present at breeding versus migratory habitats, climate change differed significantly between habitats, with birds experiencing relatively wetter breeding (**a**) and warmer spring migration habitats (**b**). Columns are estimated marginal means (±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	*Aechmophorus clarkii*
	Western Grebe	*Aechmophorus occidentalis*
	Eared Grebe	*Podiceps nigricollis*
	Pied-billed Grebe	*Podilymbus podiceps*
	Least Grebe	*Tachybaptus dominicus*
Pelicans	American White Pelican	*Pelecanus erythrorhynchos*
Cormorants	Double-crested Cormorant	*Phalacrocorax auritus*
Wading Birds	Great Egret	*Ardea alba*
	Great Blue Heron	*Ardea herodias*
	American Bittern	*Botaurus lentiginosus*
	Cattle Egret	*Bubulcus ibis*
	Green Heron	*Butorides virescens*
	Snowy Egret	*Egretta thula*
	Marbled Godwit	*Limosa fedoa*
	Black-crowned Night-Heron	*Nycticorax nycticorax*
	White-faced Ibis	*Plegadis chihi*
Waterfowl	Wood Duck	*Aix sponsa*
	Northern Pintail	*Anas acuta*
	American Wigeon	*Anas americana*
	American Green-winged Teal	*Anas c. carolinensis*
	Northern Shoveler	*Anas clypeata*
	Green-winged Teal	*Anas crecca*
	Cinnamon Teal	*Anas cyanoptera*
	Blue-winged Teal	*Anas discors*
	Mallard	*Anas platyrhynchos*
	Gadwall	*Anas strepera*
	Greater White-fronted Goose	*Anser albifrons*
	Lesser Scaup	*Aythya affinis*
	Redhead	*Aythya americana*
	Ring-necked Duck	*Aythya collaris*
	Canvasback	*Aythya valisineria*
	Canada Goose	*Branta canadensis*
	Bufflehead	*Bucephala albeola*
	Common Goldeneye	*Bucephala clangula*
	Snow Goose	*Chen caerulescens*
	Ross's Goose	*Chen rossii*
	Hooded Merganser	*Lophodytes cucullatus*
	Common Merganser	*Mergus merganser*
	Red-breasted Merganser	*Mergus serrator*
	Ruddy Duck	*Oxyura jamaicensis*

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

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

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

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

Blackbirds	Red-winged Blackbird	*Agelaius phoeniceus*
	Brewer's Blackbird	*Euphagus cyanocephalus*
	Bullock's Oriole	*Icterus bullockii*
	Scott's Oriole	*Icterus parisorum*
	Orchard Oriole	*Icterus spurius*
	Brown-headed Cowbird	*Molothrus ater*
	Common Grackle	*Quiscalus quiscula*
	Western Meadowlark	*Sturnella neglecta*
	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Finches	Lesser Goldfinch	*Carduelis psaltria*
	American Goldfinch	*Carduelis tristis*
	Cassin's Finch	*Carpodacus cassinii*

Table 2: Weather stations

	State/Province	Location	Lat.(º)	Elev.(m)	State/Province	Location	Lat.(º)	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
		McGrath	62.95	105		Kalispell	48.30	904
		McKinley	63.73	631	Northwest	Ft. Good	66.24	82
		Nome	64.52	4	Territories	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	Abbotsford	49.03	59		Riddle	42.95	207
	Columbia	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