**Small Mammal and Avian Range Shifts**

Certain birds and mammals are found at different elevations in the Sierra Nevada mountains today compared to a century earlier. Almost 75 percent of the small mammal species and over 80 percent of the bird species surveyed in this region have shifted ranges. While high-elevation mammals tended to shift their range upslope, birds and low-elevation mammals shifted downslope as frequently as upslope. Range responses of both taxa differed across montane portions of California.

![Figure 1. Shifts in elevational range limits over the past century for three regions in the Sierra Nevada: Northern (Lassen), Central (Yosemite) and Southern (Sequoia/Kings Canyon)](image)

A. Small mammal range shifts

<table>
<thead>
<tr>
<th>Proportion of species</th>
<th>Upper Limit</th>
<th>Lower Limit</th>
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<tbody>
<tr>
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<td>No change</td>
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Across all regions

- Species with range shift: 26%
- Species with no range shift: 74%

B. Bird range shifts

<table>
<thead>
<tr>
<th>Proportion of species</th>
<th>Upper Limit</th>
<th>Lower Limit</th>
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<tbody>
<tr>
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<td>No change</td>
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Across all regions

- Species with no range shift: 16%
- Species with range shift: 84%

Based on data from: Rowe et al., 2015 (mammals); Tingley et al, 2012 (birds)

Bars show the proportion of species that have shifted their upper or lower elevational limits to higher (“shift up”) or lower (“shift down”) elevations, or that have shown no elevational change (“no change”) over the past century.

Pie charts show the percentages of species that shifted in any direction in any region (green) and that did not shift at all (gray).
What does the indicator show?
Significant changes have occurred in the elevational range of small mammals (Figure 1A) and birds (Figure 1B) in three study regions in the Sierra Nevada: the northern (Lassen), central (Yosemite) and southern (Sequoia and King’s Canyon) regions (see map, Figure 2). The shifts reflect changes that have occurred since a survey conducted by Joseph Grinnell and a team of scientists in the early 20th century. Current ranges are based on resurveys of the same field sites conducted between 2003 and 2010. (See Technical Considerations for more information.)

Of the 34 mammalian species surveyed, 25 were found to have shifted their elevational ranges in at least one region (Figure 1A). A shift involves a contraction or expansion of the upper and/or lower limits of a species’ elevational range. About two-thirds of the species ranges across the three regions remained unchanged at either or both the upper and lower elevational limits. Of the 22 species found in the three regions, none shifted both their upper and lower limits consistently in the same direction in all the regions (see Appendix, Figure A1). Across the three regions, elevational limits were more than twice as likely to have moved upslope as downslope (Figure 2). High-elevation species were more likely to contract their ranges (typically as a result of an upslope shift of their lower limits) than to expand them, whereas low-elevation species were just as likely to have contracted their limits as expanded them (Rowe et al., 2015).

Shifts in elevation among birds were more frequent than among mammals; 84 percent of bird species shifted their elevational distribution (Figure 1B). Upslope shifts occurred in 46 percent of lower elevation limits (resulting in range contraction), and 53 percent of upper limits (resulting in range expansion) (Figure 2). Downward shifts were as common as upward shifts (Tingley et al., 2012).
Why is this indicator important?
Animals reproduce, grow and survive within specific ranges of climatic and environmental conditions. Species may respond to changes in these conditions by, among other things, a shift in range boundaries. Globally, broad patterns of species shifts in response to warming temperatures have occurred over historical time scales ranging from years to millennia. Models project with high confidence that species movement will be a common phenomenon with continued warming (Settele et al., 2014).

Species respond uniquely to climatic and other environmental changes. This indicator shows both upslope and downslope shifts in elevation for small mammals and birds, demonstrating the idiosyncratic nature of species' responses to climate change. Range shifts can change community composition as the abundance of some species decreases or increases (Settele et al., 2014). Changes in species occurrence can lead to competitive displacement, intensification of predation or new predator-prey interactions and ultimately a decline in biodiversity (Blios et al., 2013). In general, climate change should favor species that are better able to tolerate warmer and more variable climatic conditions.
Certain species may not be able to shift their ranges fast enough to migrate to suitable environments, particularly where has been loss or fragmentation of habitat or barriers to species movement (see What factors influence this indicator? below). Declines in population abundance can result. In extreme cases, extirpation (eradication) or extinction of species may occur (Settele et al., 2014). For example, the American pika, a small mammal adapted to high altitudes and cold temperatures, has disappeared from a 64-square-mile span of habitat from Mount Shasta to the southern Sierra Nevada (Stewart et al., 2015). Resurveys of historical pika locations over six years found they no longer occurred at 10 of 67 (15 percent) historical sites. The authors suggested that pikas have experienced climate-mediated range contraction over the past century tied to increasing summer temperatures.

The indicator presented here tracks changes in the elevation at which species are found today, compared to earlier in the century. This information will help in understanding and anticipating the long-term dynamics of the distribution of small mammals and birds in California, and examining the factors that influence them. This knowledge is crucial in efforts to identify which species are resilient or sensitive to climate change and, thus, to guide efforts to maintain species diversity in the face of regional warming. Models project with high confidence that species movement will be a common phenomenon with continued warming. The data from this indicator are useful in research to test the performance of model-based predictions of species’ responses to changes in climate and land cover. Such research will improve predictions of future species’ responses.

Changes in the composition of ecological communities, such as the loss of species, can change the ways in which ecosystems function (Hooper et al., 2005). Altered biodiversity has led to widespread concern for both economic (e.g., food sources) and non-economic (e.g., ethical, aesthetic) reasons. Wildlife and habitat conservation programs, government agencies and international scientific programs are taking steps to understand and minimize biodiversity loss and species invasions in an effort towards preserving ecosystems. This is important for our national parks, where scientists predict future warming will cause substantial turnover of species (Moritz et al., 2008).

What factors influence this indicator?
Range shifts are in part a response to the stresses of climate change (temperature and precipitation). Both the magnitude and the rate of climate change can impact a species’ ability to adapt and survive. Recent research suggests that the picture is complex: temperature, precipitation and habitat may force range shifts in multiple directions and affect upper and lower range limits differently, with the relative contribution of different factors varying by elevation (Santos et al., 2017). The mixed or heterogeneous responses described here may reflect a species’ intrinsic sensitivity to temperature, precipitation or other physical factors, as well as altered interactions with biological elements of the community (such as food sources, vegetation, and competitors) — all of which are changing in different ways in the three regions.

Changes in climate over the past century differed among the three study regions (Tingley et al., 2012; Rowe et al., 2015). The Central region reported the greatest and
the Northern region the least increase in mean annual temperature. Across all three regions, the maximum temperature of the warmest month was relatively constant, while the minimum temperature of the coldest month increased. The Yosemite Valley record indicates a substantial increase in monthly minimum temperatures of greater than 3 degrees centigrade (°C). This temperature increase is also evident from tree ring data and analyses of vegetation change (Millar et al., 2004), snowmelt data, and retraction of the Mt. Lyell glacier. Precipitation increased most in the Northern region, which also cooled, and also in the Central region, but not in the Southern region. These kinds of spatially variable changes in climate over the past century in California can be seen in other ecosystem indicators, such as actual evapotranspiration and climatic water deficit (Rapacciuolo et al., 2014).

Small mammals may respond differently to changes in minimum and maximum temperatures based on differences in species traits, such as lifespan, dietary breadth, and reproduction habitat (Moritz et al., 2008). Increased temperatures have been identified as a likely cause of the contractions of the high-elevation small mammal species and at least some of the upwards expansions of lower elevation species, although temperature effects on lower elevation species are less predictable. The effect of temperature is especially pronounced at higher elevations where changes in minimum temperature can affect thermoregulatory capacity, hibernation, behavior, and food-web structure (Santos et al., 2017). The average increase in elevation of about 500 meters for affected species in the Yosemite re-survey is consistent with what would be expected with the estimated temperature increase of 3°C, assuming that the species ranges are limited primarily by physiology (Moritz et al., 2008). The mechanisms explaining downslope shifts and the variable responses among related species are not well understood. Other factors also could be at play, including community structure and competitive interactions. The effects of changing precipitation on small mammals are not as clear but include challenges in finding water or cover (e.g., below the snow pack). Changes in moisture can also have metabolic impacts, such as difficulties in thermoregulation through transpiration when relative humidity is high (Santos et al., 2017). Moreover, some species may be able to persist in refugia (that is, areas in which individuals can survive through a period of unfavorable conditions) created by anthropogenic changes to the habitat, such as campgrounds where food and water are available (Morelli et al., 2012 and 2017).

Birds showed more heterogeneous elevational range shifts within species and among the three study regions over the past century (Tingley et al., 2012). In general, birds shifted upslope with increasing temperatures and shifted downslope with increased precipitation. Species-specific factors were also associated with the elevational changes: species were more likely to shift elevational ranges if they had small clutch sizes, defended all-purpose territories (i.e., where courtship, mating nesting, foraging all occur), and were non-migratory. The greatest changes to composition of montane bird communities occurred in the highest and lowest elevations (Tingley and Beissinger, 2013).
Birds have also been shown to respond to warming by breeding earlier to reduce the temperatures to which nests are exposed during breeding and to track shifting peaks in the availability of resources (Socolar et al., 2017). Using data from the Grinnell Resurvey Project, researchers found that breeding dates in the Sierra Nevada and the Coast Range (from the Oregon border to north of San Luis Obispo) shifted 5 to 12 days earlier over the last century. These findings suggest that earlier breeding might reduce both the need and the opportunity to shift geographically.

A group of researchers have studied biogeographic responses in birds, mammals and plants in California along with regional patterns of climate data during the 20th century to better understand species responses to a warming climate (Rapacciuolo et al., 2014). Although the expected response with warming is upward elevational shifts, they describe how downslope shifts are as common as upslope shifts. One common finding (noted above) was contractions of lower limits of high-elevation mammal species occurring primarily in response to warmer temperatures. They suggested that the substantial heterogeneity in response to warming with low elevation species may be due to influences such as interspecific competition and the spread of invasive species. In addition to temperature alone, species responses were also reportedly affected by the shifting seasonal balance of temperature and precipitation (water availability). They found that species-specific sensitivities to local-scale trophic interactions and habitat changes can also influence range shift dynamics, highlighting a need to adopt a more multifaceted and finer-scale understanding of climate change impacts.

The topography of a habitat can play a role in how an animal is impacted by climate change. Topographically complex areas provide potential climate change “refugia” whereas low-relief topography can exacerbate climate change impacts as organisms must travel further to remain in the same climate space (Maher et al., 2017). Mountains provide an extremely important climate refuge for many species because the rate of displacement required to track climate is low (i.e., they can disperse relatively short distances upslope to track favorable environmental conditions). However, species that already occur near mountaintops are among the most threatened by climate change because they cannot move upwards. The consequences of losing favorable climate space are not yet well understood (Settele et al., 2014).

In addition to topographic influences, research suggests that climate change effects on animals during the 20th century in California may have been largely affected by changes in vegetation rather than, or in addition to, direct physiological effects (Rapacciuolo et al., 2014), although warming winter temperatures are sometimes clearly important (Morelli et al., 2012). Substantial vegetation changes within the Central region (Yosemite National Park) have occurred since the early 1900’s due to a number of factors, including fires, fire suppression efforts, and temperature changes. Of the 23 small mammal species in Yosemite National Park, 11 shifted their elevational ranges in the same direction as shifts in vegetation, six species shifted in a different direction, and the rest showed no relationship (Santos et al., 2015). Species that shifted in the same direction as vegetation were mostly inhabitants of low to intermediate elevations, while species that shifted in different direction inhabited high elevations. Vegetation change
appears to directly affect some of the changes in the range of small mammals. For example, the expansion of the upper limit of the ranges of the California pocket mouse and the Piñon mouse (on the west slope) can be attributed to stand-replacing fires in the lower areas of the park. The large downwards shift in the elevation of the Montane shrew is probably related to its preference for wet meadows and the recovery of wet meadow systems in Yosemite Valley, following cessation of grazing and intense restoration efforts (Moritz et al., 2008).

**Technical Considerations**

**Data Characteristics**

Resurveys of small mammals and birds were conducted between 2003 through 2010 along three elevational transects in the Sierra Nevada Mountains that spanned four National Parks (see map above) and numerous other state, federal and private land holdings. The surveys revisited sites that were originally studied between 1911-1920 by Joseph Grinnell and staff of the Museum of Vertebrate Zoology (MVZ), University of California at Berkeley (Grinnell, 1930). The resurveys provide updated information on habitat and community changes at each site over the past century, while documenting the presence as well as ranges (geographic and habitat) of species of special concern to the lay and scientific communities. Detailed information on the Grinnell Resurvey Project can be found at: [http://mvz.berkeley.edu/Grinnell/index.html](http://mvz.berkeley.edu/Grinnell/index.html).

Small mammal surveys were conducted at 166 locations: 38 in the Northern, 81 in the Central and 47 in the Southern region. Species were categorized as low elevation, high elevation or widespread for purposes of observing how species at different elevations respond. Statistical analyses of range shifts were restricted to 34 species that were detected at more than 10 percent of sites for at least one region in both eras. Details can be found in Rowe et al. (2014).

The resurvey of bird species for the three regions was conducted during breeding season. Observers collected data with temporal sampling as follows: Lassen, 2006-07; Yosemite, 2003-04; Southern Sierra, 2008-09. A total of 251 modern surveys were conducted at 84 sites, with each site surveyed a maximum of 5 times. Over 87 percent of the survey sites were located on permanently protected lands. All sites contained “west slope Sierran” vegetation communities. Habitat descriptions were matched to historic field notes wherever possible. The data from this resurvey can be found at: [http://arctos.database.museum](http://arctos.database.museum). Details can be found in Tingley et al. (2012).

**Strengths and Limitations of the Data**

Detailed maps and field notes from the Grinnell investigators facilitated the relocation of actual sites, transects and trap lines. The position of all generalized sites, based on documentation of the actual campsite, has been reasonably well established.

Substantial differences in small mammal survey methodologies between the two survey periods may result in biases in trapability. The Grinnell team used shotguns and snap traps for all mammal surveys, while the recent survey used live traps. To assess the comparability of survey success for each species across the time periods, statistical
“Occupancy”) analyses were conducted. For the 34 species of small mammals considered above, detectability probabilities were sufficiently high across the survey periods to yield robust results. The analysis of changes in elevational range of mammals incorporates differences in detectability between study periods.

Natural year-to-year fluctuations in species’ abundances may affect the detection of particularly rare species, and hence the comparisons between the study periods.

For purposes of examining possible climate change impacts on species shifts, field surveys were conducted in protected areas where other human influences (e.g., land use changes) were limited.

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References:


Figure A1. Small mammal range limit shifts, by species*

Red bars — range contractions; yellow bars — range expansions; gray bars — non-significant contractions; white bars — non-significant expansions (white); black bars — historic range. (Lack of a bar indicates that species is not found in that region.)

*List of common names follows.

Source: Modified from Rowe et al., 2015
Common names for the species listed in Figure A-1 are as follows:

01  Sorex ornatus (Ornate shrew)  
02  Dipodomys heermannii (Heermann's kangaroo rat)  
03  Microtus californicus (Amargosa vole)  
04  Reithrodontomys megalotis (Western harvest mouse)  
05  Chaetodipus californicus (California pocket mouse)  
06  Neotoma macrotis (Big-eared woodrat)  
07  Neotoma fuscipes (Dusky-footed woodrat)  
08  Peromyscus truei (Pinyon mouse)  
09  Sciurus griseus (Western gray squirrel)  
10  Dipodomys agilis (Agile kangaroo rat)  
11  Tamias merriami (Merriam's chipmunk)  
12  Peromyscus boylii (Brush mouse)  
13  Thomomys bottae (Botta's pocket gopher)  
14  Otospermophilus beecheyi (California ground squirrel)  
15  Peromyscus maniculatus (Deer mouse)  
16  Sorex trowbridgii (Trowbridge's shrew)  
17  Tamias quadrimaculatus (Long-eared chipmunk)  
18  Sorex vagrans (Vagrant shrew)  
19  Tamias senex (Allen's chipmunk)  
20  Tamiasciurus douglasii (Douglas' squirrel)  
21  Zapus princeps (Western jumping mouse)  
22  Microtus montanus (Montane vole)  
23  Microtus longicaudus (Long-tailed vole)  
24  Thomomys monticola (Mountain pocket gopher)  
25  Neotoma cinerea (Bushy-tailed woodrat)  
26  Tamias speciosus (Lodgepole chipmunk)  
27  Tamias amoenus (Yellow-pine chipmunk)  
28  Sorex palustris (American water shrew)  
29  Marmota flaviventris (Yellow-bellied marmot)  
30  Urocitellus beldingi (Belding's ground squirrel)  
31  Callospermophilus lateralis (Golden-mantled ground squirrel)  
32  Sorex monticolus (Dusky shrew)  
33  Ochotona princeps (American pika)  
34  Tamias alpinus (Alpine chipmunk)
Figure A2. Bird range limit shifts, by species*

Source: Tingley et al., 2012

Red bars — range contractions; green bars — range expansions; gray bars — historical range.
(Lack of a bar indicates that species is not found in that region.)

*Numbers along the x-axis correspond to the species list that follows.
Species are presented in Figure A-2 in the following order:

01 American Crow (Corvus brachyrhynchos)
02 American Goldfinch (Spinus tristis)
03 Yellow-breasted Chat (Icteria virens)
04 House Sparrow (Passer domesticus)
05 Horned Lark (Eremophila alpestris)
06 Northern Mockingbird (Mimus polyglottos)
07 Western Kingbird (Tyrannus verticalis)
08 Cliff Swallow (Pterochelidon pyrrhonota)
09 Common Yellowthroat (Geothlypis trichas)
10 Blue Grosbeak (Passerina caerulea)
11 Willow Flycatcher (Empidonax traillii)
12 Nuttall's Woodpecker (Picoides nuttallii)
13 Acorn Woodpecker (Picus formicivora)
14 Black-chinned Hummingbird (Archilochus alexandri)
15 Blue-gray Gnatcatcher (Polioptila caerulea)
16 Western Meadowlark (Sturna neglectus)
17 Bullock's Oriole (Icterus bullockii)
18 Bewick's Wren (Thryomanes bewickii)
19 California Towhee (Melozona crissalis)
20 House Finch (Haemorhous mexicanus)
21 Lark Sparrow (Chondestes grammacus)
22 Oak Titmouse (Baeolophus inornatus)
23 California Quail (Callipepla californica)
24 Ash-throated Flycatcher (Myiarchus cinerascens)
25 Black Phoebe (Sayornis nigricans)
26 Bushtit (Psaltiparus minimus)
27 Western Scrub-Jay (now split into Apheloma californica, Apheloma insularis, and Apheloma woodhouseii)
28 Anna's Hummingbird (Calypte anna)
29 Downy Woodpecker (Picoides pubescens)
30 Mourning Dove (Zenaida macroura)
31 Yellow Warbler (Setophaga petechia) *formerly Dendroica petechia
32 Red-winged Blackbird (Agelaius phoeniceus)
33 Tree Swallow (Tachycineta bicolor)
34 Western Bluebird (Sialia mexicana)
35 Song Sparrow (Melospiza melodia)
36 Pacific-slope Flycatcher (Empidonax difficilis)
37 Lesser Goldfinch (Spinus psaltria)
38 Black-headed Grosbeak (Pheucticus melanocephalus)
39 Canyon Wren (Catherpes mexicanus)
40 Spotted Towhee (Pipilo maculatus)
41 Wrentit (Chamaea fasciata)
42 Lazuli Bunting (Passerina amoena)
43 Violet-green Swallow (Tachycineta thalassina)
44 Brewer's Blackbird (Euphagus cyanocephalus)
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<th>No.</th>
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<th>Scientific Name</th>
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<td>Lawrence’s Goldfinch</td>
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<td>Savannah Sparrow</td>
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<tr>
<td>87</td>
<td>Yellow-rumped Warbler</td>
<td><em>Setophaga coronata</em></td>
</tr>
<tr>
<td>88</td>
<td>Lincoln’s Sparrow</td>
<td><em>Melospiza lincolnii</em></td>
</tr>
<tr>
<td>89</td>
<td>Sooty Grouse</td>
<td><em>Dedragapus fuliginosus</em></td>
</tr>
<tr>
<td>90</td>
<td>Pine Siskin</td>
<td><em>Spinus pinus</em></td>
</tr>
</tbody>
</table>
91 Dusky Flycatcher (*Empidonax oberholseri*)
92 Hermit Thrush (*Catharus guttatus*)
93 Pygmy Nuthatch (*Sitta pygmaea*)
94 Cassin's Finch (*Haemorhous cassinii*)
95 Clark's Nutcracker (*Nucifraga columbiana*)
96 Ruby-crowned Kinglet (*Regulus calendula*)
97 Mountain Bluebird (*Sialia currucoides*)
98 Williamson's Sapsucker (*Sphyrapicus thyroideus*)
99 White-crowned Sparrow (*Zonotrichia leucophrys*)