vol. 188, no. 6 the american naturalist december 2016

American Society of Naturalists Address

The Natural History of the South Hills Crossbill in Relation to Its Impending Extinction*

Craig W. Benkman[†]

Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071

Submitted May 6, 2016; Accepted July 28, 2016; Electronically published October 5, 2016

Dryad data: http://dx.doi.org/10.5061/dryad.cm586.

abstract: Increasingly, the species that we discover will be uncommon, area restricted, and vulnerable to extinction. I describe the natural history of a newly discovered seed-eating finch from the Rocky Mountain region, the South Hills crossbill (*Loxia curvirostra* complex). It relies on seeds in the closed cones of the fire-adapted Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) and is found only in the higher elevations of two small mountain ranges in southern Idaho. Here crossbills and pine are engaged in a coevolutionary arms race. Although most of the seeds remain secured within the cones for decades until the heat of a stand-replacing fire causes the cone scales to separate, seeds become accessible to crossbills slowly as cones weather and gaps form between some of the scales. However, hot days (≥32°C), especially four or more hot days, seem to mimic the effect of fire, apparently causing the immediate release of a fraction of the seeds. Such events caused a 20% annual decline in crossbills that lasted up to 4 years and an 80% decline in the population between 2003 and 2011. This is an example of a novel trophic mismatch between a consumer and its resource caused by a shift in the phenology of the resource arising from climate change. Not only do these phenological shifts have the potential to cause seed consumers to decline, these shifts are also likely to cause reduced recruitment of the plants. The South Hills crossbill is especially vulnerable and will likely go extinct this century before lodgepole pine is extirpated from the South Hills.

Keywords: climate change, *Loxia*, phenological mismatch, population decline, range-restricted, serotiny.

> One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. (Leopold 1987, p. 286)

Introduction

Some species, especially generalists, have been increasing recently, but many others are declining (Butchart et al. 2010; Pearce-Higgins et al. 2015). The declines are worrisome. The causes of these declines are diverse, including invasive species (Bellard et al. 2016), habitat loss (Gaston et al. 2003; Schipper et al. 2008), climate change (Parmesan and Yohe 2003; Parmesan 2006; Pearce-Higgins et al. 2015), and the interactions among these factors (Brook et al. 2008; Mantyka-Pringle et al. 2012). Although the evidence for adverse effects from climate change is mounting (Pearce-Higgins and Green 2014; Urban 2015), relatively few studies have documented mechanisms by which species have declined from climate change (Cahill et al. 2013; Ockendon et al. 2014). An understanding of mechanisms not only helps evaluate alternative hypotheses for decline but also provides insight into both the dynamics of populations and future impacts (Cahill et al. 2013; Ockendon et al. 2014). Moreover, such an understanding informs the generality and feasibility of management and mitigation (Ockendon et al. 2014; Pearce-Higgins and Green 2014).

Below I describe the discovery and natural history of a range-restricted specialist and the evidence for a mechanism by which it is imperiled and unlikely to persist as a species. Like the majority of evidence for declines from climate change (Cahill et al. 2013; Ockendon et al. 2014; Pearce-Higgins and Green 2014), ours supports causes mediated through trophic interactions. It also suggests a mechanism by which a life-history trait of woody plants, serotiny, might be vulnerable to extreme temperature events to the detriment of the plants and to animals that rely on their canopy seed banks. Serotiny is characterized by the reten-

---

* Craig W. Benkman received the 2014 Edward O. Wilson Naturalist Award. The Wilson Award is given to an active investigator in midcareer who has made significant contributions to the knowledge of a particular ecosystem or group of organisms and whose research and writing illuminate principles of evolutionary biology and an enhanced appreciation of natural history.

[†] E-mail: cbenkman@uwyo.edu.

ORCIDs: Benkman, http://orcid.org/0000-0002-9714-4064.

Am. Nat. 2016. Vol. 188, pp. 589–601. © 2016 by The University of Chicago. 0003-0147/2016/18806-56975$15.00. All rights reserved.
DOI: 10.1086/688904

tion of seeds in woody fruits (e.g., *Banksia*, *Eucalyptus*, and *Protea*) or cones (e.g., conifers) until hot temperatures, usually rom a stand-replacing fire, cause the seeds to be shed to the ground, where the conditions and resources postfire are especially favorable for seedling recruitment (Lamont et al. 1991).

While collecting serotinous cones of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) in two isolated mountain ranges in southern Idaho in 1996, I discovered a distinct ecotype of red crossbill (Aves: *Loxia curvirostra* complex), the South Hills crossbill. Armed with evidence that variation in crossbill beak structure was related to variation in cone structure (fig. 1*A*, 1*B*; Newton 1972; Benkman 1993), my observations in 1996 of distinctive cones in the South Hills provided clues that the crossbill also would be distinct. Indeed, based on the structure of the cones, I was able to predict and then confirm the size of the crossbill's beak when I returned to capture and measure some the next year.

This was a thrilling discovery. First, it proved to illustrate coevolution between crossbills and conifers (Benkman 1999; Benkman et al. 2001, 2003, 2013). Second, the South Hills crossbill behaved as a distinct species (Smith and Benkman 2007; Benkman et al. 2009). More recently, we have found that it is the most genetically distinct taxon in the North American red crossbill complex (Parchman et al., forthcoming), further consistent with its recognition as a species (*L. sinesciurus*; Benkman et al. 2009). The discovery of a new bird species in the continental United States neither collected previously nor based on elevating known variation has occurred rarely in the past century or more.

This discovery, however, is bittersweet. In the late 1990s, the South Hills crossbill was common within the 70 km^2 of lodgepole pine forest in the South Hills and Albion Mountains. It was especially common because of the absence of its main competitor for seeds in lodgepole pine cones, the American red squirrel (*Tamiasciurus hudsonicus*). Fortu-

Figure 1: Crossbills and lodgepole pine cones in the South Hills of southern Idaho: male biting between slightly open cone scales (*A*); female laterally abducting her lower mandible to spread scales and expose seeds (*B*); close-up of a several-year-old serotinous cone whose seeds are inaccessible to crossbills (*C*); and branch with increasingly older cones (from left to right), several of which toward the right have been foraged on by crossbills (*D*).

nately, red squirrels remain absent, unlike in Newfoundland, where they were introduced in 1963, nearly causing the extinction of the Newfoundland crossbill (*Loxia curvirostra percna*; Benkman 1989; Parchman and Benkman 2002). However, following the heat wave during the summer of 2003, which caused human misery, death (Dhainaut et al. 2004), and declines in bird populations in Europe (Jiguet et al. 2006), the South Hills crossbill also began declining (Santisteban et al. 2012). Many animal species worldwide are declining (Butchart et al. 2010; Urban 2015). With the notable exceptions of Old World vultures (Oaks et al. 2004; Ogada et al. 2015), bats in eastern North America (Frick et al. 2010), and a frightening number of frog species (Crawford et al. 2010; Alroy 2015), relatively few species have been observed declining so precipitously as the South Hills crossbill. It declined by more than 60% between 2003 and 2008 (Santisteban et al. 2012) and by 80% by 2011 (Hart 2013).

Up to 2008, the best predictor of the South Hills crossbill's decline was mean spring temperature (Santisteban et al. 2012). The higher the temperature, the lower the annual survival, which could account for the decline in the population; other factors such as West Nile virus could be eliminated as a cause of decline (Santisteban et al. 2012). However, unlike lizards, where there is a plausible mechanism by which higher spring temperatures cause population declines (Sinervo et al. 2010), it has been difficult to envision a mechanism by which higher spring temperatures adversely affect South Hills crossbills (Santisteban et al. 2012). We argued that the correlation between spring temperature and annual survival was spurious and that, instead, the lagged effects from hot summer days (≥32°C) in the previous 3–5 years were responsible for the decline (Santisteban et al. 2012). This fit with the sharp increase in the number of hot days in 2003 (fig. 2), and we could envision a plausible mechanism based on the natural history of this system. Below, I provide additional context and discuss the hypothesized mechanism that makes South Hills crossbills vulnerable to an increase in hot summer days. I then evaluate this and alternative mechanisms.

Natural History of the South Hills Crossbill

The South Hills crossbill is one of 10 ecotypes (call types) in the North American red crossbill complex (Groth 1993; Benkman 1999; Irwin 2010); each ecotype is adapted for foraging on seeds in the cones of a single species of conifer that reliably holds seeds from fall to spring (Benkman 1993, 2003; Parchman and Benkman 2002). South Hills crossbills feed virtually exclusively on seeds in lodgepole pine cones (Benkman et al. 2009, 2012), which are available year-round in serotinous cones (fig. 1). Rocky Mountain lodgepole pine trees produce either serotinous cones that remain closed for up to several decades or longer or nonserotinous cones that open and shed their seeds in autumn several weeks after the seeds mature (Koch 1996). Only about 6% of the seeds in 1–10-year-old serotinous cones are eaten by crossbills because the scales are hard and securely bonded (fig. 1*C*; Benkman et al. 2013). But as the cones weather, small gaps form between scales that crossbills widen further so that the seeds can be extracted with their tongue (fig. 1*A*, 1*B*). Crossbills rely on seeds in these gradually opening serotinous cones (Smith and Benkman 2007; Benkman et al. 2012).

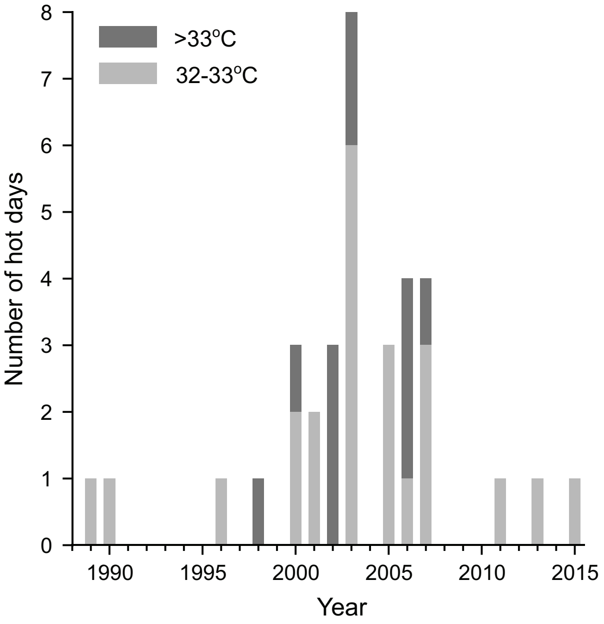

Figure 2: Number of hot (≥32°C) days in the South Hills of southern Idaho (data from Magic Mountain Snow Telemetry site, station ID 610) between 1989 and 2015.

Older serotinous cones are especially plentiful in the South Hills because of the absence of red squirrels, which elsewhere are the dominant predispersal seed predator, removing and caching a large fraction of the closed cones (Smith 1970; Elliott 1988). Because the probability of seed predation by red squirrels is much higher for a seed that remains in a serotinous cone for an extended time period (years) than a seed in a nonserotinous cone that is vulnerable to harvest for the few weeks before the cones open, red squirrels exert strong selection against serotiny (Talluto and Benkman 2014). On the other hand, increasing frequency of fire favors a higher frequency of serotiny (Enright et al. 1998; Talluto and Benkman 2014), with the local frequency of serotiny representing a balance of conflicting selection exerted by red squirrels and fire (Talluto and Benkman 2014). For example, the frequency of serotiny among trees averages about 30% in the presence of red squirrels but around 90% in their absence, as in the South Hills (Benkman and Siepielski 2004). Consequently, in the absence of red squirrels, more serotinous cones are produced and a higher proportion of them accumulate and weather on the branches, becoming accessible to crossbills (fig. 1*D*).

This process of gradual accumulation and weathering apparently results in an almost constant rate of renewal of accessible seeds, especially as annual variation in cone production in the South Hills is small (Benkman et al. 2012); masting is no longer an effective or favored defense in the absence of a seed predator such as red squirrels (Fletcher et al. 2010; Summers 2011). However, the one condition that greatly alters the availability of seeds in serotinous cones is high temperatures. They melt the resins holding the scales together, causing cones to open and release seeds quickly (Koch 1996). Although seeds in open cones are readily accessible to crossbills, they are an ephemeral resource. Extensive and synchronous cone opening depletes many of the seeds that would have become available more gradually. The possibility of the synchronous opening of cones and release of seeds following a series of hot days (see Nathan et al. 1999; Teste et al. 2011), especially from cones whose bonds between their scales were already weakened due to weathering and whose seeds would have become accessible to crossbills in the next several months or years, is why we hypothesized that hot summer days were inimical to South Hills crossbills (Santisteban et al. 2012). We used a maximum daily temperature threshold of ≥32°C in our analyses (Santisteban et al. 2012), because 32°C was near the upper limit of temperatures at the Magic Mountain Snow Telemetry (SNOTEL) site, which is 2.6 km from where most of our mark-and-recapture efforts were conducted, and because the number of cones susceptible to cone opening should be greatest at the highest temperatures (Nathan et al. 1999; Teste et al. 2011). Temperatures reached or exceeded 32°C on 21 days between 2003 and 2015 (fig. 2); data underlying figure 2 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm586 (Benkman 2016). During 14 (two-thirds) of these days, the maximum temperature was between 32.0°C and 32.8°C. Temperatures reached 34°C only twice, with a maximum of 35.1°C.

This hypothesis for cone opening and crossbill decline deserves further testing because many species are thought to be vulnerable to increasing temperatures (Urban 2015), yet mechanistic understanding of population declines related to climate change remains elusive (Cahill et al. 2013; Ockendon et al. 2014; Pearce-Higgins and Green 2014). Here, I consider further the population dynamics of the South Hills crossbill by including seven additional years of data (2009–2015) beyond our previous study (Santisteban et al. 2012). I also examine whether temperatures experienced by cones when air temperatures exceed 31°C might cause the opening of cones. However, first I consider the impact of increasing tree mortality as a potential cause of crossbill declines.

Conifer mortality has increased in the western United States (van Mantgem et al. 2009), and because lodgepole pine is at its warm-edge range margin in the South Hills, it should be especially vulnerable (Reich et al. 2015). Warm conditions are also favorable for mountain pine beetle (*Dendroctonus ponderosae*; Bentz et al. 2010), which between 2003 and 2013 caused massive mortality to lodgepole pine in the Rocky Mountains (fig. 3*A*; Carswell 2014). Pine die-off in the South Hills could represent the beginning of the projected disappearance within this century of lodgepole pine from the South Hills and Albion Mountains (Coops and Waring 2011).

Beetle-Kill, and Trophic and Trait-Mediated Indirect Interactions

Although mountain pine beetles have killed numerous lodgepole pine in the South Hills during the past decade (C. W. Benkman, personal observation), the mortality rate appears much less than in many areas in the Rocky Mountains (fig. 3). In 2002 and 2013, several of my students measured the number and diameter at breast height of all lodgepole pine within a 20-m radius at each of 67 locations in the South Hills used for crossbill surveys. From these data, I estimated the basal area (m^2 of stem at breast height/m^2 of area) at each location for both years to determine whether there had been a decline in the volume of lodgepole pine (fig. 4), which should reflect the overall level of cone production as cones are produced at the tips of branches; data underlying figure 4 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm586 (Benkman 2016). Although there were considerable differences between the two years at many of the locations (fig. 4), basal area did not differ consistently between years (mean [SE] basal area in 2002 and 2013 was .0267 [.0010] and .0272 [.0012], respectively; paired *t*-test: $t = .49$, $P = .63$), nor was the trend consistent (reduced major axis regression: intercept did not differ from 0 [95% CI: −.013–0.001], and slope did not differ from 1 [95% CI: .982–1.480]). Consequently, changes in forest volume or structure were unlikely to account for the 80% decline in crossbills between 2003 and 2011.

This raises the question of why more pine did not die from mountain pine beetles, especially as the South Hills is on the border of the Great Basin Desert, with abiotic conditions highly favorable to mountain pine beetle outbreaks (Bentz et al. 2010). I believe the answer is related to the absence of red squirrels and their cascading effects. Red squirrels both directly and indirectly depress the densities of insectivorous birds. First, red squirrels are a dominant nest predator in Rocky Mountain conifer forests (Tewksbury et al. 1998), and in their absence, the density of aboveground open-cup nesting birds averages more than twice as high as in ranges with red squirrels (Siepielski 2006). These birds include warblers, tanagers, and flycatchers, all

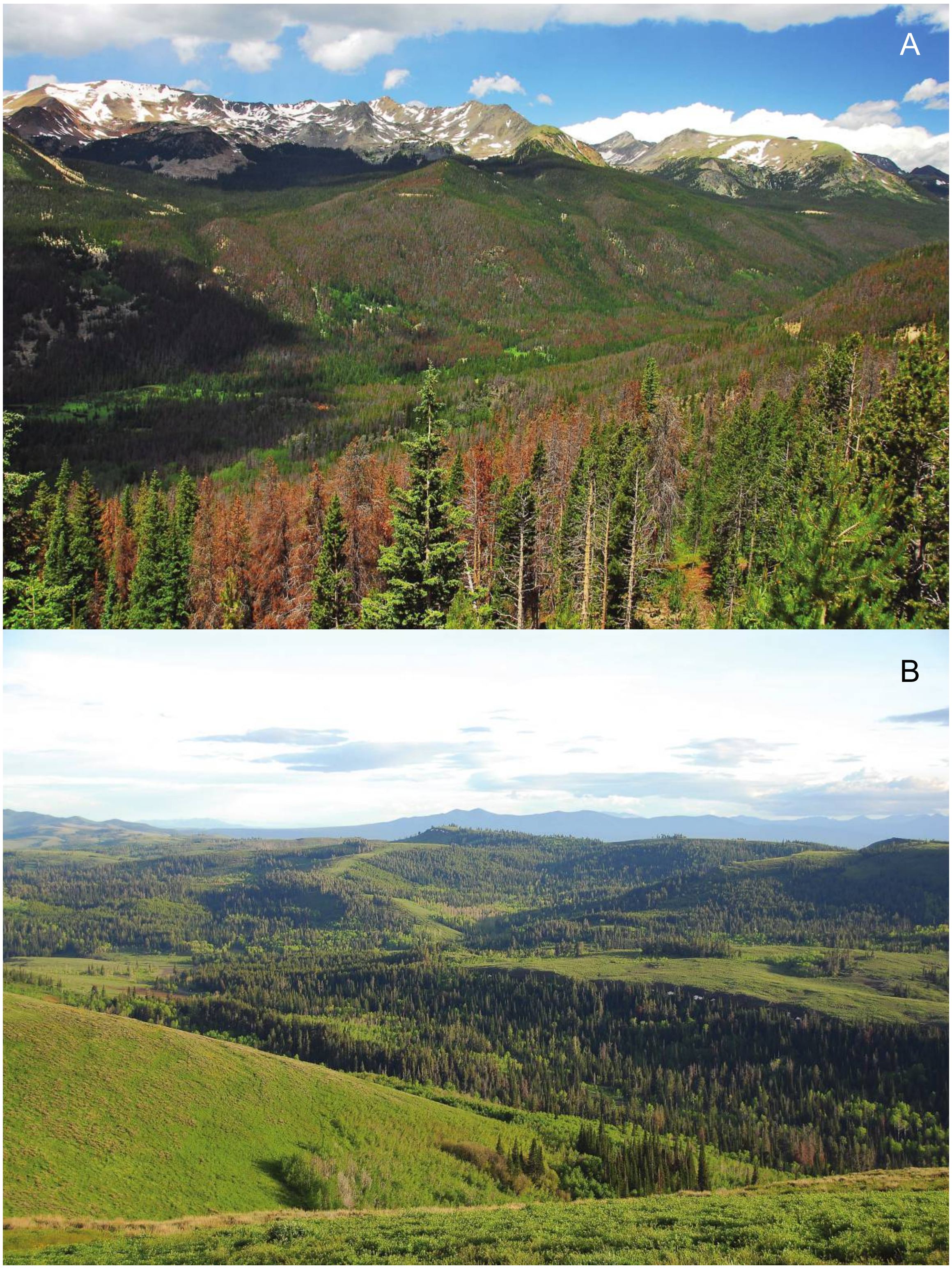

Figure 3: Lodgepole pine mortality from mountain pine beetle was much greater in many locations in the Rocky Mountains (*A*; dying trees have orange needles; Rocky Mountain National Park, CO) than in the South Hills, southern Idaho (*B*). Photographs taken by C. W. Benkman in July 2010 and June 2009, respectively.

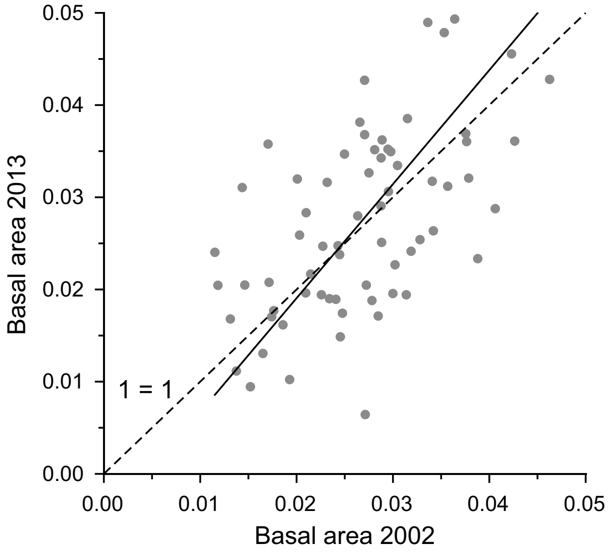

Figure 4: Basal area (m^2 of stem at breast height/m^2 of area) within a 20-m radius at each of 67 locations within the South Hills, southern Idaho, in 2013 in comparison to 2002. The solid line represents a reduced major axis regression, and the dashed line represents the 1 : 1 ratio.

of which could prey on mountain pine beetles moving on and between trees. Second, hairy woodpeckers (*Picoides villosus*)—which are cavity nesters and an important predator on pine beetles when they are on the bark and burrowing in the tree (Fayt et al. 2005)—are about five times more abundant in the South Hills than in lodgepole pine forests with red squirrels (Benkman et al. 2013). Hairy woodpeckers forage on seeds in lodgepole pine cones and prefer the same cone traits that red squirrels prefer (especially more seeds per unit cone mass). Thus, with the relaxation of defenses directed at red squirrels as in the South Hills, hairy woodpeckers increase in abundance (a trait-mediated indirect effect; Benkman et al. 2013). Overall, higher levels of beetle predation by the various insectivorous birds could limit mountain pine beetle outbreaks in the South Hills. Such a hypothesis is consistent with studies showing that increases in insectivorous birds result in decreases in herbivory (e.g., Marquis and Whelan 1994; Mäntylä et al. 2011) and with studies suggestive of the potential for relatively high densities of woodpeckers to prevent beetle epidemics (Fayt et al. 2005).

Recent Population Changes and Their Relationship to Temperature

Although high temperatures are likely to increase in frequency throughout this century (Duffy and Tebaldi 2012; Christidis et al. 2014), there have been few hot summer days (≥32°C) in the South Hills during the past 8 years (only three during 2008–2015; fig. 2). If crossbills declined between 2003 and 2008 because of hot summer days during the previous 3–5 years (Santisteban et al. 2012), then the South Hills crossbill should have rebounded in numbers since 2010–2012. To evaluate whether crossbill numbers have rebounded, I used similar methods for estimating crossbill densities using point transects, as described in Santisteban et al. (2012). Briefly, the observations of crossbills at 74 10-min point transects in the South Hills were right truncated at 84 m and grouped into three intervals for analyses (0–16 m, 16–42 m, and 42–84 m). I used the remaining 669 crossbill observations between 2003 and 2015 to estimate a single detection function and to estimate yearly population density using Distance 6.2 Release 1 (Thomas et al. 2010). Our density estimates are biased upward (Santisteban et al. 2012), but it does not affect trends among years because this bias is consistent among years.

As predicted, crossbills have rebounded since 2010–2012 (fig. 5); data underlying figure 5 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm586 (Benkman 2016). An analysis of the annual change in crossbill population size (i.e., annual change in estimated densities; because area is fixed) in relation to the number of hot days in the previous 4 years indicates that crossbills declined when there were >3 hot days but increased when there were <3 hot days (fig. 6). The relationships between population change and the number of hot days in the previous 3 or 5 years were less strong ($r^2 < .75$) than that for the previous 4 years ($r^2 = .87$, $P < .0001$). In an earlier analysis including data up to 2008, the best predictor of

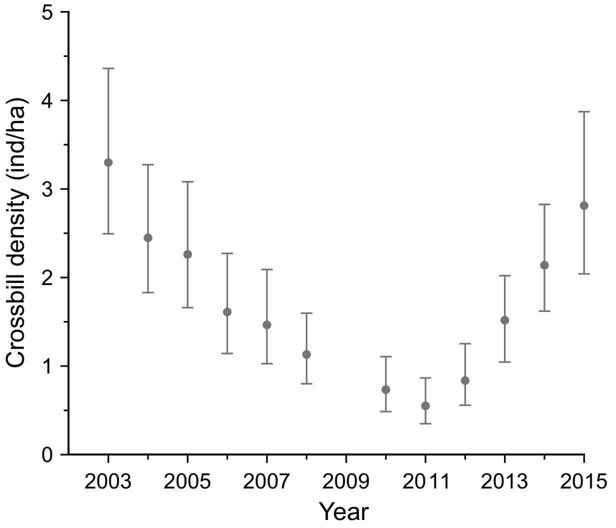

Figure 5: Estimated densities of crossbills in late summer (July–August) in the South Hills of southern Idaho from 2003 to 2015 based on 74 10-min point transects conducted each year; 95% confidence limits are plotted around the mean. Data from 2009 are missing.

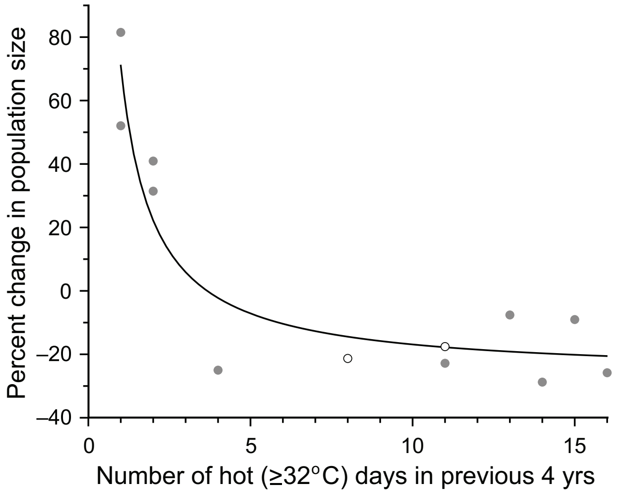

Figure 6: Crossbills decreased in population size when there were more than three hot days (≥32°C) in the previous 4 years, whereas they increased when there were less than three hot days. The curve represents the following regression: percent population change = $-26.66 + 97.69/(\text{no. hot days in previous 4 years} + 0.0001)$, $r^2 = .87$, df = 8, $P < .0001$).Open symbols represent estimates of population change assuming that the population density in 2009 was intermediate between that in 2008 and 2010 (see fig. 5); these two estimates (changes between 2008 and 2009 and between 2009 and 2010) were not included in the regression.

declines in annual adult survival—which, using a simple demographic model, could account for the decline in crossbill density—was mean spring temperature (March–May; Santisteban et al. 2012). In a subsequent analysis including data up to 2012, the best predictor was mean annual temperature (July–June; Hart 2013). Now neither spring nor annual temperature was correlated with the annual change in population size (pairwise correlations: $r < .14$, $P > .70$). Earlier we reported an annual decline in cone production from 1991 to 2007 and could not rule out its contribution to crossbill declines up to 2008 (Santisteban et al. 2012). However, with a more accurate estimate of annual cone production (Hart 2013), no trend in annual cone production was detected between 1997 and 2011 (fig. 7; correlation between mean number of cones and year: $r = .33$, $n = 15$, $P = .22$), indicating that there has not been a decline in cone production and that variation in annual cone production cannot account for the variation in crossbill density. Data underlying figure 7 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm586 (Benkman 2016).

One interpretation of the results (fig. 6) is that the cumulative effect of four or more hot days during one summer (2003, 2006, or 2007; fig. 2) caused approximately 20% of the seeds that would normally become accessible over the next 4 years to be shed. This could cause the 20% annual decline in crossbills during the following 4 years (fig. 6) and suggests that repeated exposure to temperatures at or just above 32°C (one day reached 34°C, and one day reached 35°C since 2003) was critical. The necessity of multiple hot summer days perhaps reflects the importance of an increasing duration of high temperatures for cone opening when near the cone-opening-temperature threshold (Alexander and Cruz 2012). Consecutive days of hot temperatures might be especially effective in causing cone opening: temperatures of ≥32°C occurred in two bouts of 2 and one bout of 3 consecutive days (each bout separated by 1–2 weeks) in 2003 and in one bout of 3 and one bout of 2 consecutive days in 2006 and 2007, respectively. Unfortunately, I do not have survey data for crossbills prior to 2003 that are comparable to those collected beginning in 2003 to evaluate whether, alternatively, declines follow a total of four or more hot days occurring in successive summers (e.g., the five hot days during 2000–2001; fig. 2). However, 2000–2002 point counts based on the number of crossbills perched within 50 m do not indicate a decline in the crossbills between 2001 and 2002 (Benkman et al. 2012). Thus, I conclude that the cumulative effect of four or more hot days during relatively brief periods (18–36 days in 2003, 2006, and 2007) caused a substantial fraction of seeds to be released. Whether air temperatures of ≥32°C potentially cause at least a fraction of the serotinous cones to open and release their seeds deserves consideration.

Are Cones Likely to Open When Air Temperatures Exceed 31°C?

Serotinous lodgepole pine cones open at cone temperatures of 45°–60°C (Perry and Lotan 1977), but whether cones in

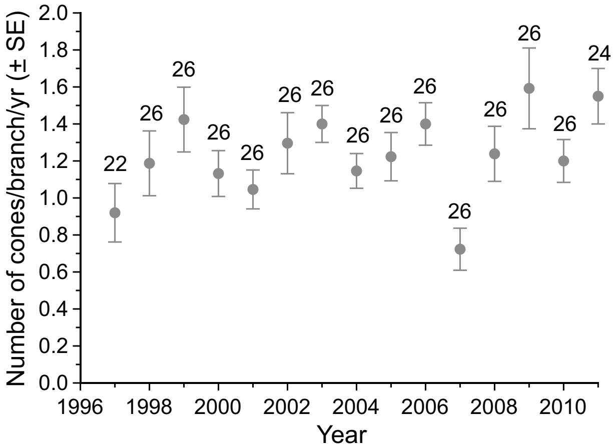

Figure 7: Annual lodgepole pine cone production did not vary in a consistent manner between 1996 and 2011. The numbers above the error bars represent the number of trees sampled. Cones were counted on five branches from the upper third of recently fallen trees (needles still green; Hart 2013).

direct sunlight experience such temperatures when air temperatures exceed only 31°C is unknown. Consequently, I evaluated whether cone-opening temperatures of lodgepole pine cones from the South Hills might overlap the surface temperatures of cones when air temperatures exceed 31°C (temperature recorded at the Magic Mountain SNOTEL site). The temperature at which cone scales begin to open was measured for 1–10-year-old cones (2–3 cones from each age class for a total of 28–30 cones per tree) from 30 trees and 15–20 year-old cones from 32 trees (two cones from 1 tree, three cones from 31 trees) in a digital drying oven (myTemp Mini Digital Incubators, model H2200-H, Benchmark Scientific, Edison, NJ). The oven temperature was set at 40°C, and after the temperature remained at 40°C for 20 min, the temperature was raised 2°C and allowed to stabilize at that temperature for 10 min. This was repeated for each 2°C incremental rise in temperature until all the cones had opened or the temperature reached 60°C, the maximum temperature for the oven. Cones were viewed through a window in the oven so that the temperature at which a cone began to open could be recorded. For the few cones that did not open (9 out of 897 cones from the 1–10-year-old cones [an average of 0.3 of the 29.9 cones per tree]; all 15–20-year-old cones opened), a 62°C cone-opening temperature was recorded for them. I used the mean temperature at which the cones began to open as the tree's cone-opening temperature.

Between June 9 and 18, 2015, I recorded the maximum surface temperature of cones in direct sunlight at approximately 1.5–2 m aboveground on one lodgepole pine tree (42°10′03.62″N, 114°15′53.17″W; elevation 2,112 m) in the South Hills using a FLIR420 thermal-imaging camera (fig. 8). During each time period, I recorded the maximum temperature on the surface of 10 haphazardly chosen cones and compared these temperatures to the respective air temperature recorded every half hour 2.6 km away at the Magic Mountain SNOTEL site. These data are plotted in figure 9 along with the mean cone-opening temperatures for 62 trees. Cone temperatures increased with increases in air temperature up to 25°C and then decreased (fig. 9; the quadratic term to a quadratic regression fit to the data was not significant: $P = .092$; data underlying fig. 9 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm586 [Benkman 2016]). The decline at higher temperatures was probably the result of wind during these measurements causing turbulence over the cones. Wind tends to occur during warmer afternoons, although during some of the hot days in, for example, 2003, there was very little wind (C. W. Benkman, personal observation). However, I note that the maximum cone surface temperatures were limited to a small fraction of the cone surface (fig. 8), and only some cones will experience direct sunlight during the hottest times of the day. Nevertheless, the results suggest the potential for an increasing overlap between cone temperatures and cone-opening temperatures as air temperatures increase (fig. 9). Such an overlap might be sufficient to cause cone scales to open when ambient temperatures exceed 31°C, especially for cones that are weathered and already prone to open, thereby depleting a fraction of the seeds that would likely become accessible to crossbills over the next several years. That crossbill declines only followed summers with four or more hot days implies that the cumulative impact of multiple hot days is critical.

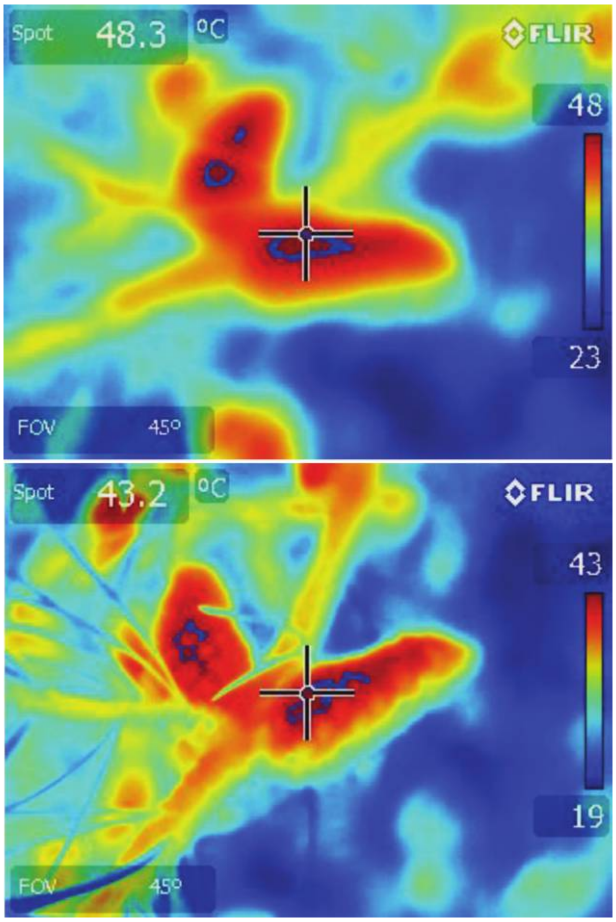

Figure 8: Thermal images of lodgepole pine cones in direct sunlight in June 2015.

Concluding Comments

Climate change will cause large changes in the abundances and distributions of species (Parmesan 2006), and many will decline and ultimately go extinct (Pearce-Higgins and Green 2014; Urban 2015). Especially problematic are those species like the South Hills crossbill that are specialized on a single food resource restricted to a small amount of habitat (~70 km^2) atop isolated mountains and, consequently, unable to track climate changes (Parmesan 2006; Dirnböck et al. 2011; Santisteban et al. 2012; Payne and Bro-Jørgensen

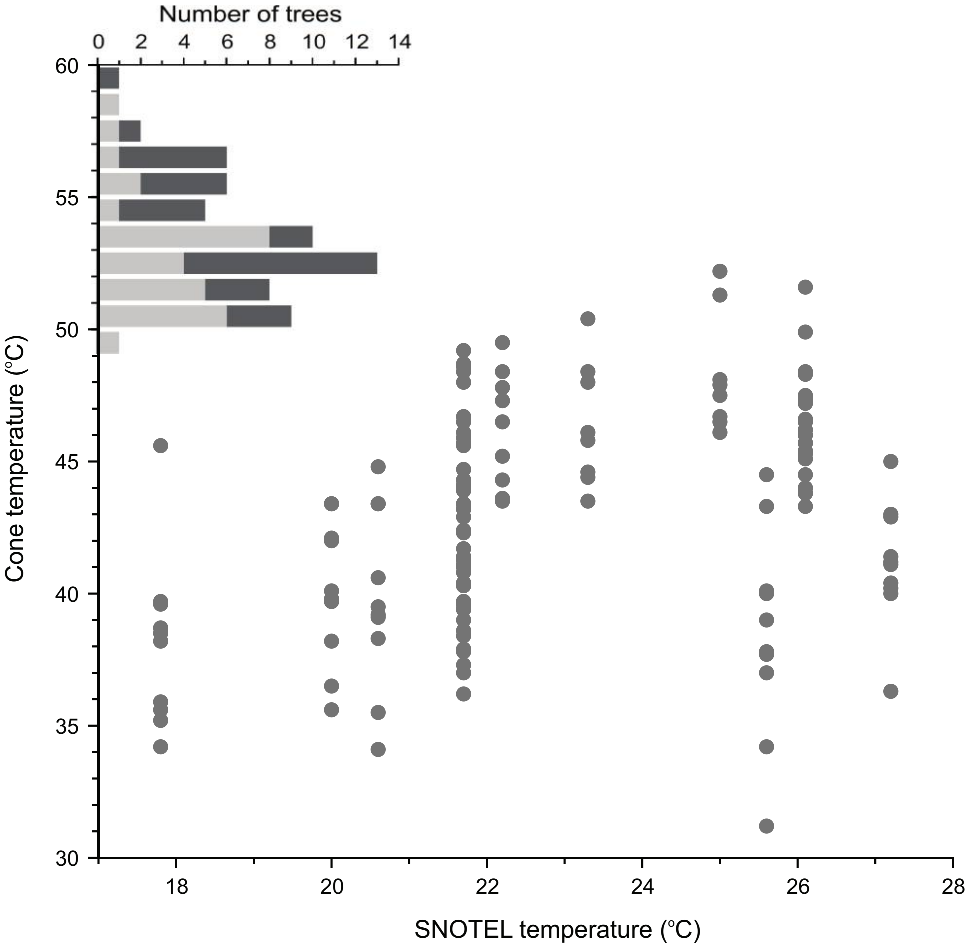

Figure 9: Maximum surface temperatures of cones (circles) in relation to air temperatures at the Magic Mountain Snow Telemetry (SNOTEL) site in June 2015. The histogram shows mean cone-opening temperatures for 62 trees based on experiments using an oven: light gray bars represent values for 1–10-year-old cones for 30 trees; dark bars represent values for 15–20-year-old cones for 32 trees.

2016). Lodgepole pine is projected to disappear not only from the South Hills and Albion Mountains but also from extensive areas to the north and east by the end of this century (Coops and Waring 2011). South Hills crossbills cannot move north and survive. There, red squirrels occupy lodgepole pine forests where a smaller-beaked crossbill is more efficient (Benkman et al. 2001; Benkman 2003).

While lodgepole pine persists in the South Hills, it is conceivable that evolution by either crossbills or pine could reduce the extent of food limitation experienced by crossbills following hot summer days. For example, larger beak sizes might improve access to seeds in more closed and better-defended cones that are now avoided; crossbills consume only 6% of the seeds in 1–10-year-old serotinous cones (Benkman et al. 2013). Larger beaked crossbills are found in, for example, Mexico (*Loxia curvirostra stricklandi*) and Europe (e.g., *Loxia pytyopsittacus*), so that a genetic constraint is unlikely to prevent the evolution of larger beaks. However, larger beaks are associated with larger bodies and greater energy requirements (Benkman 1991). Presumably, the limited accessibility of seeds in tightly closed cones even for large-beaked crossbills—plus their associated greater daily energy demands—prevents the evolution of larger beaks in the South Hills.

Alternatively, seed availability in the canopy seed bank could increase if selection favored trees that produce cones that remained closed during the hottest summer days. Such selection is likely because seedling recruitment should be higher following a stand-replacing fire that frees up resources than after a summer with multiple hot days (Koch 1996; Kolb and Robberecht 1996; Enright et al. 2015). Indeed, a potential management option to facilitate this evolution—and thereby benefit both the pines and crossbills—is to reforest using seeds from trees whose cones have the highest opening temperatures (fig. 9), assuming cone-opening temperature is heritable. This strategy would be more effective if reforestation was focused on sites having the coldest summer temperatures (e.g., north-facing slopes) within the South Hills and Albion Mountains. Such a choice of sites is analogous to the recommended conservation strategy of protecting the most climatically favorable or resilient habitats (e.g., Pearce-Higgins and Green 2014; Maron et al. 2015).

This reforestation strategy alone, however, is unlikely to prevent the South Hills crossbill from going extinct. As mentioned earlier, lodgepole pine is projected to disappear from the South Hills and Albion Mountains as well as from extensive areas to the north and east by the end of this century (Coops and Waring 2011). Climate change is also expected to result in more frequent fires in the region of the South Hills (Westerling et al. 2011) and a greater potential for very large fires (Barbero et al. 2015), which would be devastating to the crossbills if a large fraction of the pine forests were to burn at once. Decreasing fire intervals will limit the time over which a canopy seed bank accumulates, thus further reducing both the number of seeds in the canopy seed bank and recruitment following fire (Brown and Johnstone 2012; Enright et al. 2015). Moreover, a dramatic decrease in fire intervals is likely to be sufficient to favor plants other than lodgepole pine (Johnstone and Chapin 2006; Westerling et al. 2011). Such adverse consequences will not be limited to lodgepole pine and crossbills in the South Hills. Serotiny is a common life-history trait of woody plants in Australia, South Africa, and North America (Lamont et al. 1991), and climate change is likely to be unfavorable for the recruitment of many serotinous plants (Enright et al. 2015) and to the various seed predators including other taxa of crossbills and the many Australian parrots that rely on seeds in serotinous fruits (Joseph 1986; Low 2014).

An earlier release of seeds might also be partly responsible for the 3.7% annual decline in red crossbills throughout the Northern Rocky Mountain region between 1966 and 2012 (Sauer et al. 2014). Crossbill specialization and evolution are sensitive to the phenology of seed retention, as crossbills rely on conifers that retain seeds in cones through winter and into spring (Benkman 1993). Thus, increases in temperature that would cause cones (e.g., nonserotinous Douglas fir *Pseudotsuga menziesii* and ponderosa pine *Pseudotsuga ponderosa*) to open further and more rapidly shed seeds (Krugman and Jenkinson 1974) would be inimical to crossbills. Consistent with a decline in seed resources in late winter and spring, red crossbills are coming to bird feeders (number of crossbills day^{-1} feeder^{-1}) during this time period in the Rocky Mountain region at an accelerating rate, with a greater than 20-fold increase between 1988 and 2010 (data from the Cornell Laboratory of Ornithology's Project FeederWatch). This increase of crossbills at feeders occurred in spite of a concurrent decrease in the crossbill population as assessed along survey routes (Sauer et al. 2014).

More generally, our study adds to mounting evidence that adverse effects of climate change are mostly indirect and mediated through trophic interactions (Cahill et al. 2013; Ockendon et al. 2014) and that the interaction of greatest importance, at least for birds, is from reduced food availability (Pearce-Higgins and Green 2014). An additional example where hot temperatures cause a subsequent decline in the abundance and availability of a key food resource is the Eurasian golden plover (*Pluvialis apricaria*; Pearce-Higgins et al. 2010). Critical to plover reproductive success is the emergence of adult craneflies (Diptera: Tipulidae) in May and early June. During this period, warm temperatures are advantageous for the emergence of the craneflies and to breeding plovers. However, higher temperatures in August depress survival of early larval instars of cranefly in the soil and thereby depress the abundance of adults emerging the next year, causing a decline in the plover population (Pearce-Higgins et al. 2010). In the case of the plover, hot Augusts cause a decline in the abundance of a key food resource, whereas in the South Hills crossbill, hot days in late July and August do not alter the abundance of seeds produced but rather the phenology of seed release. This altered timing of the release of seeds could be considered an example of climate change causing a phenological mismatch (Both and Visser 2001). Phenological mismatches include shifts in resource phenology such as fruiting in plants (Butt et al. 2015) or the timing of peak abundance of arthropods (Both et al. 2006) that result in mismatches in the availability of resources relative to demand by their consumers. In the case of serotiny, the shift in phenology will likely adversely affect plant recruitment, thus further contributing to the collapse of the consumer populations. Unfortunately, evolution in long-lived woody plants in response to climate change that would lessen the impact on their recruitment and on their seed consumers might not be rapid enough to prevent large declines and extinctions.

Finally, that a bird species like the South Hills crossbill can be missed for so long in the well-explored continental United States—and could have gone extinct without notice—further indicates that we underappreciate the diversity that might have or will go extinct in the near future (Ceballos and Ehrlich 2009). Much as Aldo Leopold (1949) lamented in *A Sand County Almanac*, the accrual of knowledge is ever more bittersweet.

Acknowledgments

I thank the many students who have contributed to fieldwork in the South Hills, especially N. Behl, J. Colquitt, T. Fetz, J. Hart, P. Keenan, A. Siepielski, and J. Smith. I thank K. Benkman for measuring cone-opening temperatures and D. Bonter for making Project FeederWatch data available. I also thank J. Bronstein, J. Pearce-Higgins, A. Siepielski, and an anonymous reviewer for helpful suggests on the manuscript. I acknowledge the Sawtooth National Forest and the Idaho Department of Fish and Game for allowing us to conduct this research. I am very thankful for the financial support provided by the National Science Foundation and the Robert Berry Chair Endowment.

Literature Cited

Alexander, M. E., and M. G. Cruz. 2012. Modelling the effects of surface and crown fire behaviour on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21:709–721.

Alroy, J. 2015. Current extinction rates of reptiles and amphibians. Proceedings of the National Academy of Sciences of the USA 112: 13003–13008. http://dx.doi.org/10.1073/pnas.1508681112.

Barbero, R., J. T. Abatzoglou, N. K. Larkin, C. A. Kolden, and B. Stocks. 2015. Climate change presents increased potential for very large fires in the contiguous United States. International Journal of Wildland Fire 24:892–899. http://dx.doi.org/10.1073/pnas.1508681112.

Bellard, C., P. Cassey, and T. M. Blackburn. 2016. Alien species as a driver of recent extinctions. Biology Letters 12:20150623. http://dx.doi.org/10.1098/rsbl.2015.0623.

Benkman, C. W. 1989. On the evolution and ecology of island populations of crossbills. Evolution 43:1324–1330.

———. 1991. Predation, seed size partitioning and the evolution of body size in seed-eating finches. Evolutionary Ecology 5:118–127.

———. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecological Monographs 63:305–325.

———. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. American Naturalist 154(suppl.): S75–S91.

———. 2016. Data from: The natural history of the South Hills crossbill in relation to its impending extinction. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.cm586.

Benkman, C. W., T. Fetz, and M. V. Talluto. 2012. Variable resource availability when resource replenishment is constant: the coupling of predators and prey. Auk 129:115–123. http://dx.doi.org/10.1525/auk.2011.11069.

Benkman, C. W., W. C. Holimon, and J. W. Smith. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. Evolution 55:282–294.

Benkman, C. W., T. L. Parchman, A. Favis, and A. M. Siepielski. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. American Naturalist 162:182–194.

Benkman, C. W., and A. M. Siepielski. 2004. A keystone selective agent? pine squirrels and the frequency of serotiny in lodgepole pine. Ecology 85:2082–2087.

Benkman, C. W., J. W. Smith, P. C. Keenan, T. L. Parchman, and L. Santisteban. 2009. A new species of red crossbill (Fringillidae: *Loxia*) from Idaho. Condor 111:169–176.

Benkman, C. W., J. W. Smith, M. Maier, L. Hansen, and M. V. Talluto. 2013. Consistency and variation in phenotypic selection exerted by a community of seed predators. Evolution 67:157–169.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613. http://dx.doi.org/10.1525/bio.2010.60.8.6.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83. http://dx.doi.org/10.1038/nature04539.

Both, C., and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migratory bird. Nature 411:296–298.

Brook, B., N. Sodhi, and C. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23:453–460. http://dx.doi.org/10.1016/j.tree.2008.03.011.

Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. Forest Ecology and Management 266:34–41. http://dx.doi.org/10.1016/j.foreco.2011.11.006.

Butchart, S. H. M., M. Walpole, B. Collen, A. Van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, et al. 2010. Global biodiversity: indicators of recent declines. Science 328:1164–1168. http://dx.doi.org/10.1126/science.1187512.

Butt, N., L. Seabrook, M. Maron, B. S. Law, T. P. Dawson, J. Syktus, and C. A. McAlpine. 2015. Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. Global Change Biology 21:3267–3277. http://dx.doi.org/10.1111/gcb.12869.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Yeong Ryu, G. C. Sbeglia, et al. 2013. How does climate change cause extinction? Proceedings of the Royal Society B 280:20121890. http://dx.doi.org/10.1098/rspb.2012.1890.

Carswell, C. 2014. Don't blame the beetles. Science 346:154–156.

Ceballos, G., and P. R. Ehrlich. 2009. Discoveries of new mammal species and their implications for conservation and ecosystem services. Proceedings of the National Academy of Sciences of the USA 106: 3841–3846.

Christidis, N., G. S. Jones, and P. A. Stott. 2014. Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. Nature Climate Change 5:46–50. http://dx.doi.org/10.1038/nclimate2468.

Coops, N. C., and R. H. Waring. 2011. A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change. Climatic Change 105:313–328. http://dx.doi.org/10.1007/s10584-010-9861-2.

Crawford, A. J., K. R. Lips, and E. Bermingham. 2010. Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. Proceedings of the National Academy of Sciences of the USA 107:13777–13782.

Dhainaut, J. F., Y. E. Claessens, C. Ginsburg, and B. Riou. 2004. Unprecedented heat-related deaths during the 2003 heat wave in Paris: consequences on emergency departments. Critical Care 8:1–2.

Dirnböck, T., F. Essl, and W. Rabitsch. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 17:990–996. http://dx.doi.org/10.1111/j.1365-2486.2010.02266.x.

Duffy, P. B., and C. Tebaldi. 2012. Increasing prevalence of extreme summer temperatures in the U.S. Climatic Change 111:487–495. http://dx.doi.org/10.1007/s10584-012-0396-6.

Elliott, P. F. 1988. Foraging behavior of a central-place forager: field tests of theoretical predictions. American Naturalist 131:159–174.

Enright, N. J., J. B. Fontaine, D. M. J. S. Bowman, R. A. Bradstock, and R. J. Williams. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Frontiers in Ecology and the Environment 13:265–272. http://onlinelibrary.wiley.com/doi/10.1890/140231/abstract.

Enright, N. J., R. Marsula, B. B. Lamont, and C. Wissel. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. Journal of Ecology 86:946–959.

Fayt, P., M. M. Machmer, and C. Steeger. 2005. Regulation of spruce bark beetles by woodpeckers—a literature review. Forest Ecology and Management 206:1–14. http://dx.doi.org/10.1016/j.foreco.2004.10.054.

Fletcher, Q. E., S. Boutin, J. E. Lane, J. M. LaMontagne, A. G. McAdam, C. J. Krebs, and M. M. Humphries. 2010. The functional response of a hoarding seed predator to mast seeding. Ecology 91:2673–2683.

Frick, W. F., J. F. Pollock, A. C. Hicks, K. E. Langwig, D. S. Reynolds, G. G. Turner, C. M. Butchkoski, and T. H. Kunz. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682. http://dx.doi.org/10.1126/science.1188594.

Gaston, K. J., T. M. Blackburn, and K. K. Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society B 270:1293–1300. http://dx.doi.org/10.1098/rspb.2002.2303.

Groth, J. G. 1993. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American red crossbill (*Loxia curvirostra*) complex. University of California Publications in Zoology 127:1–143.

Hart, J. A. 2013. Are South Hills crossbills declining with increasing temperatures? PhD diss. University of Wyoming, Laramie.

Irwin, K. 2010. A new and cryptic call type of the red crossbill. Western Birds 41:10–25.

Jiguet, F., R. Julliard, C. D. Thomas, O. Dehorter, S. E. Newson, and D. Couvet. 2006. Thermal range predicts bird population resilience to extreme high temperatures. Ecology Letters 9:1321–1330. http://dx.doi.org/10.1111/j.1461-0248.2006.00986.x.

Johnstone, J. F., and F. S. Chapin III. 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems 9:268–277.

Joseph, L. 1986. Seed-eating birds of southern Australia. Pages 85–93 *in* H. A. Ford and D. C. Paton, eds. The dynamic partnership: birds and plants in southern Australia. Government Printer, Adelaide.

Koch, P. 1996. Lodgepole pine in North America. Forest Product Society, Madison, WI.

Kolb, P. F., and R. Robberecht. 1996. High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. Tree Physiology 16:665–672.

Krugman, S. L., and J. L. Jenkinson. 1974. *Pinus* L., pine. Pages 598–638 *in* C. S. Schopmeyer, ed. Seeds of woody plants in the United States. USDA Forest Service Handbook 450. USDA Forest Service, Washington, DC.

Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. Botanical Review 57: 277–317.

Leopold, A. 1987. Foreword. Pages 281–288 *in* J. B. Callicott, ed. Companion to *A Sand County Almanac*: interpretative & critical essays. University of Wisconsin Press, Madison, WI.

Low, T. 2014. Where song began: Australia's birds and how they changed the world. Penguin Random House Australia, Docklands.

Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology 18:1239–1252. http://dx.doi.org/10.1111/j.1365-2486.2011.02593.x.

Mäntylä, E., T. Klemola, and T. Laaksonen. 2011. Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia (Berlin) 165:143–151. http://dx.doi.org/10.1007/s00442-010-1774-2.

Maron, M., C. A. McAlpine, J. E. M. Watson, S. Maxwell, and P. Barnard. 2015. Climate-induced resource bottlenecks exacerbate species vulnerability: a review. Diversity and Distributions 21: 731–743. http://dx.doi.org/10.1111/ddi.12339.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007–2014. http://dx.doi.org/10.2307/1941605.

Nathan, R., U. N. Safriel, I. N. Meir, and G. Schiller. 1999. Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. Journal of Ecology 87:659–669.

Newton, I. 1972. Finches. Collins, London.

Oaks, J. L., M. Gilbert, M. Z. Virani, R. T. Watson, C. U. Meteyer, B. A. Rideout, H. L. Shivaprasad, et al. 2004. Diclofenac residues as the cause of vulture population decline in Pakistan. Nature 427: 630–633. http://dx.doi.org/10.1038/nature02317.

Ockendon, N., D. J. Baker, J. A. Carr, E. C. White, R. E. A. Almond, T. Amano, E. Bertram, et al. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20:2221–2229. http://dx.doi.org/10.1111/gcb.12559.

Ogada, D., P. Shaw, R. L. Beyers, R. Buij, C. Murn, J. M. Thiollay, C. M. Beale, et al. 2015. Another continental vulture crisis: Africa's vultures collapsing toward extinction. Conservation Letters 9:89–97. http://dx.doi.org/10.1111/conl.12182.

Parchman, T. L., and C. W. Benkman. 2002. Diversifying coevolution between crossbills and black spruce on Newfoundland. Evolution 56:1663–1672.

Parchman, T. L., C. A. Buerkle, V. Soria-Carrasco, and C. W. Benkman. Forthcoming. Genome divergence and diversification within a geographic mosaic of coevolution. Molecular Ecology.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37:637–669. http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Payne, B. L., and J. Bro-Jørgensen. 2016. Disproportionate climate-induced range loss forecast for the most threatened African antelopes. Current Biology 26:1200–1205. http://dx.doi.org/10.1016/j.cub.2016.02.067.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12–23. http://dx.doi.org/10.1111/j.1365-2486.2009.01883.x.

Pearce-Higgins, J. W., S. M. Eglington, B. Martay, and D. E. Chamberlain. 2015. Drivers of climate change impacts on bird communities. Journal of Animal Ecology 84:943–954. http://dx.doi.org/10.1111/1365-2656.12364.

Pearce-Higgins, J. W., and R. E. Green. 2014. Birds and climate change: impacts and conservation responses. Cambridge University Press, Cambridge.

Perry, D. A., and J. E. Lotan. 1977. Opening temperatures in serotinous cones of lodgepole pine. USDA Forest Service Research Note INT-228.

Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change 5:148–152.

Santisteban, L., C. W. Benkman, T. Fetz, and J. W. Smith. 2012. Survival and population size of a resident bird species are declining as temperature increases. Journal of Animal Ecology 81:352–363. http://dx.doi.org/10.1111/j.1365-2656.2011.01918.x.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2014. The North American breeding bird survey, results and analysis 1966–2012. Version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225–230.

Siepielski, A. M. 2006. A possible role for red squirrels in structuring breeding bird communities in lodgepole pine forests. Condor 108: 232–238.

Sinervo, B., F. Mendez-De-La-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagran-Santa Cruz, R. Lara-Resendiz, et al. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899. http://dx.doi.org/10.1126/science.1184695.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349–371.

Smith, J. W., and C. W. Benkman. 2007. A coevolutionary arms race causes ecological speciation in crossbills. American Naturalist 169: 455–465.

Summers, R. W. 2011. Patterns of exploitation of annually varying *Pinus sylvestris* cone crops by seed-eaters of differing dispersal ability. Ecography 34:723–728. http://dx.doi.org/10.1111/j.1600-0587.2010.06498.x.

Talluto, M. V., and C. W. Benkman. 2014. Conflicting selection from fire and seed predation drives fine-scaled phenotypic variation in a widespread North American conifer. Proceedings of the National Academy of Sciences of the USA 111:9543–9548. http://dx.doi.org/10.1073/pnas.1400944111.

Teste, F. P., V. J. Lieffers, and S. M. Landhausser. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecological Applications 21:150–162.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14. http://dx.doi.org/10.1111/j.1365-2664.2009.01737.x.

Urban, M. C. 2015. Accelerating extinction risk from climate change. Science 348:571–574.

Van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524. http://dx.doi.org/10.1126/science.1165000.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the USA 108:13165–13170. http://dx.doi.org/10.1073/pnas.1110199108.

Editor: Judith L. Bronstein

A female South Hills crossbill foraging on the ground for seeds in a lodgepole pine cone. Cones that fall from trees open during hot summer days when in direct sunlight, and apparently this occurs for cones in trees during summers with four or more hot days (≥32°C). Photo credit: Craig W. Benkman.