

Survival and population size of a resident bird species are declining as temperature increases

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Summary

1. A large number of migratory bird species appear to be declining as the result of climate change, but whether resident bird species have or will be adversely affected by climate change is less clear. We focus on the South Hills crossbill (*Loxia curvirostra* complex), which is endemic to about 70 km² of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) forest in southern Idaho, USA.

2. Our results indicate that the South Hills crossbill has declined by over 60% between 2003 and 2008, and that decreasing adult survival drives this population decline.

3. We evaluated the relative support for multiple hypotheses linking crossbill survival to climate, an ectoparasitic mite (scaly-leg mites *Knemidokoptes jamaicensis*), and the recent emergence of West Nile virus. Changes in adult apparent survival rate were closely associated with average spring and annual temperatures, and with high temperatures (≥ 32 °C) during summer, which have increased during the last decade. In contrast, there was little evidence that scaly-leg mites or West Nile virus contributed to recent declines in adult survival.

4. The most probable mechanism causing the decline in adult survival and population size is a decrease in the availability of their primary food resource, seeds in serotinous pine cones. Cone production has declined with increasing annual temperatures, and these cones appear to be prematurely opening owing to increasingly hot summer conditions releasing their seeds and reducing the carrying capacity for crossbills later in the year.

5. In light of regional climate change forecasts, which include an increase in both annual temperature and hot days (> 32 °C), and the likely disappearance of lodgepole pine from southern Idaho by the end of this century, additional research is needed to determine how to maintain lodgepole pine forests and their supply of seeds to conserve one of the few bird species endemic to the continental United States.

Key-words: apparent annual survival, climate change, crossbills, Great Basin, *Loxia*, *Pinus contorta*, population decline, trophic interactions

Introduction

Numerous bird species are declining globally. Recent evidence demonstrates that a large fraction of bird species in North America have declined over the past several decades (Sauer, Hines & Fallon 2008), mirroring large declines in migratory bird species in Europe (Berthold *et al.* 1998; Sanderson *et al.* 2006). Highly migratory species are in greatest decline, and the hypothesized mechanism with the most support for these declines is the phenology mismatch hypothesis (Both *et al.* 2006, 2010; Møller, Rubolini & Lehikoinen 2008;

Jones & Cresswell 2010). Those populations or species with the greatest mismatch between the timing of breeding and the availability of food resources are in greatest decline. Although the mismatch hypothesis is likely to be less relevant to resident species (Jones & Cresswell 2010), climate change could potentially affect resident species via other mechanisms given the strong links between populations and climate (e.g. Newton 1998; Walther *et al.* 2002; Parmesan 2006). For example, the impacts of recent, accelerated global climate change on physiology, phenology and distribution have all been well documented (e.g. Stenseth *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Bradshaw & Holzapfel 2006), and the potential for altered trophic interactions is

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immense and not limited to migratory species (Harrington, Woiwod & Sparks 1999; Stenseth *et al.* 2002; Van der Putten, Macel & Visser 2010).

Specialist species in particular are especially vulnerable to environmental change (Kotiaho *et al.* 2005; Shultz *et al.* 2005; Jiguet *et al.* 2007). Among the most specialized vertebrates in the world is the South Hills crossbill, recognized as a 'call type' of the red or common crossbill (*Loxia curvirostra* L. complex) and characterized as a distinct species (*L. sine-sciurus*; Benkman *et al.* 2009). The South Hills crossbill feeds almost exclusively on seeds in the cones of Rocky Mountain lodgepole pine (*Pinus contorta latifolia* Engelm.) (Benkman *et al.* 2009); it is endemic to about 70 km² of lodgepole pine at the higher elevations of two small mountain ranges (South Hills and Albion Mountains) in southern Idaho (USA) and is unable to survive in competition with other crossbills for seeds elsewhere (Benkman, Holimon & Smith 2001). The South Hills crossbill is well studied with respect to ecological and evolutionary processes mediating co-evolutionary interactions between it and lodgepole pine (Benkman 1999, 2003; Benkman, Holimon & Smith 2001; Benkman *et al.* 2003, 2009; Smith & Benkman 2007), but relatively little work has been conducted on its demography.

Range-restricted species should be especially susceptible to extinction processes owing to demographic and environmental stochasticity (Hannah, Midgely & Millar 2002; Thomas *et al.* 2004; Ringsby *et al.* 2006; Jenouvrier *et al.* 2009). Indeed, range-restricted species that are confined near mountaintops, like the South Hills crossbill, have been the most likely to decline and go extinct as the result of recent climate change (Parmesan 2006). Moreover, regional climate change forecasts for the Western United States indicate dramatic changes in plant distributions, such as a 50% or more reduction in the distribution of lodgepole pine including extirpation from the South Hills and Albion Mountains (Thompson *et al.* 1998). Because the South Hills crossbill is restricted to such a small area of high-elevation pine forest in the northeast corner of the Great Basin Desert, increasing temperature or drought is likely to have large impacts on this species. Nevertheless, determining the actual extinction risk of range-restricted species requires a comprehensive understanding of the species' response to local climate change (Davis *et al.* 1998; Stenseth *et al.* 2002; Schwartz *et al.* 2006a).

The goals of our study were to assess population trends of the South Hills crossbill and identify potential factors influencing its population dynamics. The primary focus was on the role of climate-related factors and their influence on annual survival, with a secondary focus on the possible effects of parasites. Benkman *et al.* (2005) showed that the presence of an ectoparasite (scaly-leg mites *Knemidokoptes jamaicensis* Turk) lowered annual survival rates for adult crossbills. However, whether scaly-leg mites continue to impact adult survival is unknown. In addition, the Centers for Disease Control and Prevention (CDC) identified the first human case of West Nile virus (WNV) in southern Idaho in 2003. WNV has led to the decline in several avian host populations in North America, primarily through its impact on

survival rates, including species closely related to crossbills (Komar 2003; Kilpatrick, LaDeau & Marra 2007; LaDeau, Kilpatrick & Marra 2007). Here, we evaluate the relative support for multiple hypotheses relating crossbill survival to climate, scaly-leg mites, and WNV. We do not consider major habitat changes, as nearly all the lodgepole pine forests in the South Hills and Albion Mountains are managed by the Sawtooth National Forest, and there is only very limited logging with relatively little annual variation. In addition, the mountain bark beetle (*Dendroctonus ponderosae* Hopkins), causing massive die-offs of lodgepole pine elsewhere in the range, has had a limited impact in the South Hills and Albion Mountains (CWB, personal observation).

Materials and methods

ESTIMATING CROSSBILL ABUNDANCE

All surveys were conducted by one of us (LS) using distance-sampling methods and point transects to estimate population density from 2003 to 2008 (Buckland *et al.* 2001). Seventy-four survey locations (point transects) were established in lodgepole pine stands of varying age and density, with most points occurring in mature stands in the South Hills. Analyses were confined to the late summer surveys (July and August), when survey data were most extensive across years. This period coincides with the end of the breeding season for crossbills (Smith & Benkman 2007) and is when most crossbills were captured for the mark-recapture studies. Population surveys consisted of 10-min point transects conducted from dawn until 11.00 h. Surveys were postponed if it was raining or windy (> 3 on the Beaufort scale). Because point-transect locations were not selected randomly in terms of forest age (most were in mature forests), and the relative amounts of different-aged stands are unknown in the South Hills, our density estimates are restricted to survey areas (Buckland *et al.* 2001; Thomas *et al.* 2010).

Point-transect surveys make three important assumptions: (i) birds at the point are detected with certainty; (ii) birds that are moving are detected at their initial location; and (iii) distance measurements from observer to birds are exact (Buckland *et al.* 2001; Buckland 2006). Crossbills are readily detected in the field because they vocalize frequently, and even when not vocalizing, visual and other auditory cues indicate their presence. For example, the sound of pine cones being pried open or seed wings falling from tree canopies are indicators of crossbills. Crossbills are also gregarious and frequently found in noisy family groups during July and August. These factors reduce the likelihood of violating assumptions 1 and 2. However, the long duration of point transects (10 min) potentially leads to violating assumption 2, because individuals may move into the survey area during the interval. This results in an upward bias in density estimates (Buckland 2006). Crossbills fly long distances between foraging areas and water sources, so individuals flying overhead during surveys were not included in the analyses, because a bird in flight is more likely to be detected as it approaches the point further biasing abundance estimates upward (Buckland *et al.* 2001).

Violation of assumption 3 (exact distance measurements) likely occurred during the first year of the study (2003) when distances were visually estimated. A laser rangefinder (Bushnell Yardage Pro Scout, Kansas, USA) was used in subsequent years to reduce the problems with this assumption. Observations recorded during surveys in 2003 were grouped into one of the three distance categories (i.e. bins; 0–25 m, 25–50 m, 50+ m) in the field. The mid-point of observations

within each bin was used for analyses (Buckland *et al.* 2001). Observations were right-truncated for analyses at 84 m, which is where the best-fitting detection function was approximately equal to 0.10 (Buckland *et al.* 2001). As a result, 69 observations (14.8% of total) made beyond 84 m were not included in density estimates. The mid-point for the third bin was therefore 67 m (i.e. the mid-point between 50 and 84 m).

The gregarious nature of crossbills meant that the density of crossbill groups must be estimated (Buckland *et al.* 2001). We therefore recorded the size of groups (clusters) encountered during surveys as well as the distance from the point to the centre of each cluster. Although larger clusters are frequently more detectable at greater distances than smaller clusters (Buckland *et al.* 2001), we found no evidence for a relationship between distance from the point and the size of detected clusters ($t_{394} = 0.47$, $P = 0.32$). We multiplied estimated density of clusters by mean cluster size to estimate the density of individual crossbills (Buckland *et al.* 2001).

Survey data were analysed with Program DISTANCE (Version 5.0, release 2; Thomas *et al.* 2010) to estimate population density. Preliminary analyses suggested that there was evidence of heaping – observations being disproportionately assigned to certain distances (e.g. 30, 35, 40, 45 m). Observations were therefore grouped into four equal distance intervals for analyses because goodness-of-fit tests are sensitive to heaping, and grouping the data improves analyses of model fit (Buckland *et al.* 2001). Year-specific estimates of the mean probability of detecting a crossbill during surveys were highest in 2007 (0.59 ± 0.07 SE) and lowest in 2003 (0.29 ± 0.03 SE) when it was significantly smaller ($P < 0.05$) than in 2005, 2006 and 2008 (0.49 ± 0.03 SE, 0.59 ± 0.07 SE and 0.49 ± 0.04 SE, respectively), as indicated by nonoverlapping 95% confidence intervals around the annual point estimates. Because no other between-year comparison differed significantly ($P > 0.05$), we used all 396 observations recorded during 434 point transects to estimate a single detection function. The starting model set consisted of the uniform, half-normal and hazard-rate key functions to model the detection function in conjunction with cosine, simple polynomial and hermite polynomial series expansions (Buckland *et al.* 2001). The half-normal (cosine) key function was selected for density estimation because of its desired properties as a robust model, particularly its shape near the point (i.e. at zero distance; Buckland *et al.* 2001), and because the difference in Akaike Information Criterion (AIC; Akaike 1992; Burnham & Anderson 2004) between this detection function and the most parsimonious model (uniform cosine) was small ($\Delta\text{AIC} = 0.21$). A Chi-square goodness-of-fit test indicated a suitable fit of the observations made across years to the half-normal detection function ($\chi^2 = 0.88$, d.f. = 2, $P = 0.64$).

ANNUAL SURVIVAL

Mist-netting and resighting We used mark–recapture–resighting methods (hereafter mark–recapture) to quantify annual survival rates for adult and juvenile (hatch-year) South Hills crossbills. Crossbills were captured with mist nets during summer from 2000 to 2007 in the South Hills, Idaho ($42^\circ 10' 6.8''$ N, $114^\circ 15' 52.5''$ N). Nets were opened between 06.00 and 13.00 h where crossbills came down to the ground for water, charcoal or salts. Crossbills were aged, sexed and examined for the presence of scaly-leg mites. Adult males were recognized by yellow to red plumage on their breast and throat, whereas females were generally olive-grey to greenish with grey throat feathers. Juvenile crossbills were easily recognized by their heavily brown-streaked breast and belly. Mite infestation was evident in the condition and coloration of the tarsi. Smooth, horn-coloured tarsi were

considered free of mites. Infected tarsi were ash-coloured, scaly and swollen, depending on the degree of infection (Latta 2003; Benkman *et al.* 2005). Adult crossbills were banded with a unique combination of coloured leg bands. Juvenile crossbills were banded with only a USFWS metal band. Only adults were colour-banded upon initial capture because of the relatively low recapture rate of juveniles and the finite number of band combinations (Benkman *et al.* 2005). We excluded juveniles identified to call types other than South Hills and the few exhibiting symptoms of mite infestation. We assumed that the remaining unclassified juveniles were South Hills crossbills because >95% of breeding crossbills were South Hills crossbills (Smith & Benkman 2007).

Resighting was attempted at and away from netting areas. Spotting scopes ($40 \times$ Questar [New Hope, PA], $20\text{--}60 \times$ Kowa [Tokyo] and $20\text{--}60 \times$ Swarovski [Austria] scopes) were used to identify and record band combinations whenever possible between 2000 and 2007. Resightings occurred during two or more weeks during each of the following months: July 2000; June through September 2001 and 2002; March–August 2003; March–July, September 2004; May–August 2005 and 2006; and May–June 2007. Ninety-two per cent of all recaptures and resightings occurred during May to August (4 months).

We developed two sets of candidate models to evaluate potential causes of variation in annual survival rates, one including juveniles and adults ('age models'), and another including only adults. We analysed a second set of models using data only from adults because we were unable to accommodate 'sex' and occurrence of scaly-leg mites in the age models. We could not incorporate 'sex' as a grouping variable in the age models because we were unable to determine the sex of most individuals captured as juveniles. Few individuals captured as juveniles had evidence of scaly-leg mites (2 of 936 juveniles), whereas we evaluated the influence of scaly-leg mites on adult survival by including the presence or absence of mites upon initial capture as an individual covariate that is assumed to remain invariant over the lifetime of the individual.

Age models and potential causes of variation

Some types of weather are more likely to directly impact annual survival through its effects on the availability of food resources. For example, rain followed by freezing temperatures may lead to cones becoming saturated and then freezing. Similarly, freezing rain may result in cones being covered by a layer of ice, making it difficult for crossbills to access seeds (CWB and LS, personal observations) and increasing the risk of starvation. We therefore quantified the occurrence of cold and wet days (mean daily temperature $< 5^\circ\text{C}$ and rainfall > 1 mm) between November and June. Climate data were gathered from an automated US Department of Agriculture Natural Resources Conservation Service climate data collection system (SNOTEL) located at the Magic Mountain ski area (site number: 610), which is *c.* 2 km from where most crossbills were captured. Daily precipitation and temperature readings are available dating back to October 1980 and June 1989, respectively.

We also conducted analyses focused on evaluating the potential effects of hot and dry weather on survival. The scales of serotinous pine cones are sealed by resin (Perry & Lotan 1979) and open when the resin melts in response to fire (pyriscence) or high ambient temperatures (xerisence), thereby releasing the enclosed seeds (Teste, Lieffers & Landhäusser 2011). Serotinous lodgepole pine cones open when temperatures exceed $40\text{--}45^\circ\text{C}$ (Perry & Lotan 1979; Knapp & Anderson 1980; Hellum & Barker 1981). Although maximum daily temperature at a weather station in the South Hills exceeded 35°C on only two occasions between 1989 and 2007, cone surface

temperatures may reach higher temperatures (Teste, Lieffers & Landhäusser 2011), and anecdotal observations indicate that increasing proportions of the serotinous cones in the South Hills have been opening in the last decade (CWB, pers. obs.). In addition, lodgepole pine trees in the South Hills retain serotinous cones for decades (see Benkman *et al.* 2003). These older serotinous cones with weakened resin bonds (Hellum & Barker 1981) may be more prone to open as temperatures increase. A high incidence of xeriscence owing to hot and dry conditions in 1 year would result in reduced food availability in subsequent years because South Hills crossbills rely on the gradual weathering of older (> 5 years old) serotinous cones (Benkman *et al.* 2003; Smith & Benkman 2007; Benkman, Fetz & Talluto, in press). We explored the relationship between annual adult survival rates and conditions favouring xeriscence by developing models incorporating weighted and unweighted moving averages of the number of hot (≥ 32 °C) and dry days occurring in the preceding 3 or 5 years. We evaluated the support for three moving-average models: (i) an unweighted 3- and 5-year average of hot/dry days; (ii) a weighted average with a 50% year-to-year decline in weight; and (iii) a weighted average with a 33% year-to-year decline in weight. For the weighted average models, the greatest weight was given to the summer at the beginning of the interval over which survival was to be estimated.

We also included three other climate variables. These variables were average daily temperature during: (i) the year (1 July–30 June to coincide with the year between most captures and recaptures and the period over which survival was estimated); (ii) spring (March–May), which also corresponds to the first half of the breeding season (Smith & Benkman 2007); and (iii) nonbreeding season (September–March). We did not have a priori expectations that average daily temperature, especially increasing average daily temperatures, would be particularly detrimental to South Hills crossbills, so we include these variables in the model set more for exploratory purposes.

We tested for a change in annual survival rates as a function of the number of WNV cases reported to the CDC and US Geological Survey in the immediate vicinity of the South Hills. We tallied the number of avian, human, mosquito, sentinel and veterinary WNV cases reported from the two southern Idaho counties encompassing the South Hills (Twin Falls and Cassia) and two adjacent counties in north-western Utah (Box Elder) and north-eastern Nevada (Elko). This approach assumes that the number of reported cases reflects the risk of WNV-driven mortality for crossbills in the South Hills. Other studies show a close relationship between reports of WNV-infected dead birds and subsequent reported cases of WNV in humans (Guptill *et al.* 2003). To date, however, we do not know of any evidence indicating WNV occurrence in the South Hills or in South Hills crossbills.

We began the development of age models with the time-dependent Cormack–Jolly–Seber (CJS) model (Lebreton *et al.* 1992), incorporated in Program MARK (Version 5.1, build 2600; White & Burnham 1999). We added a dichotomous parameter identifying two groups, individuals banded as young and individuals banded as adults. Individuals banded as young were constrained to become adults after their first year of life. Models were then developed to test for age and time dependence in survival. Analyses were based on capture histories of 934 juveniles and 983 adults captured between 2000 and 2007. We then assessed the fit of an age model $\{\phi_{\text{year}}, p_{\text{year}}\}$, where ϕ denotes apparent survival and p recapture probability. The starting model allowed survival and capture probability to vary with year, but without age structure. Models testing for age-specific differences in survival were then developed by allowing survival during a juvenile's first year to differ from annual survival in subsequent years (i.e. once they become adults). Additional models were developed to

test for age-specific differences in capture probability or temporal variation in juvenile and adult survival and capture probability. In this case, juvenile capture probability refers to the probability of recapturing an individual banded as a juvenile in t in $t + 1$.

A hypothesis-testing framework was then implemented using information-theoretic approaches that include the use of AIC for selecting among models (i.e. hypotheses). Inference was based on the relative fit of each model to the data (Burnham & Anderson 2004). The variance inflation factor estimated using the median \hat{c} method was 1.12 (SE = 0.02), suggesting little evidence of overdispersion in the data. Models were, however, adjusted accordingly, and QAIC_c values are presented because of the adjustment made to \hat{c} and the use of the small sample size correction (Burnham & Anderson 2004). For these analyses, capture probability (p) was constrained to vary solely as a function of year. Lebreton *et al.* (1992) favour modelling capture probability first while minimizing constraints on survival, rather than the alternative approach of constraining survival before capture probability. We, however, began by constraining capture probabilities because previous analyses of this data set (shorter time series) by Benkman *et al.* (2005) found that capture probabilities were year-dependent and did not differ among individuals owing to mites.

Models were considered well substantiated if their QAIC_c value was < 2 from the most parsimonious model. Models with QAIC_c values between 2 and 4 were considered less well substantiated but nevertheless informative. Akaike weights (w) were computed and used as a measure of relative support in the data for each model. We characterized the impact of environmental covariates on adult survival by calculating the relative importance of focal covariates in generating variation in adult survival (Grosbois *et al.* 2008):

$$R^2_{\text{Dev}} = \frac{\text{Dev}(\phi_{(\cdot)}) - \text{Dev}(\phi_{(\text{cov})})}{\text{Dev}(\phi_{(\cdot)}) - \text{Dev}(\phi_{(\text{year})})}$$

where Dev is the calculated deviance for the model with constant survival, $\phi_{(\cdot)}$, models with a focal environmental covariate, $\phi_{(\text{cov})}$, and the model with year-varying survival, $\phi_{(\text{year})}$. Parameterization of the recapture rate was kept constant among the three models included in the formula. We considered covariates potentially influential if they accounted for more than 20% of temporal variation in survival (i.e. $R^2_{\text{Dev}} > 0.20$; Grosbois *et al.* 2008). Lastly, model averaging was used to derive estimates of annual survival and capture probability based on the relative support for individual models in the model set (i.e. QAIC_c weights; Burnham & Anderson 2004).

Apparent adult survival and potential causes of variation

The CJS model (Lebreton *et al.* 1992), incorporated in Program MARK (Version 5.1, build 2600; White & Burnham 1999), was used to evaluate support for hypotheses concerning the relative influence of multiple climatic variables and two epizootics on annual adult survival. The modelling process was similar as above for the age models, except that we excluded juveniles and included 'sex' as a grouping variable and both epizootics, scaly-leg mites and WNV, as covariates. The influence of scaly-leg mites on survival was assessed by including the presence or absence of mites upon initial capture as an individual covariate. The mite models assumed that individuals initially captured without evidence of mites did not subsequently contract mites. If mites depress adult survival, then violation of this assumption will cause an underestimation of survival rates for adults that never contract mites.

The modelling process began with an evaluation of the goodness-of-fit of a general starting model with capture histories for 849 adults captured between 2000 and 2007. We began developing our candidate model set with a null model, with adult survival and capture

probability constrained to be constant among years, and a 'year' model, with survival and capture probability allowed to vary among years. Adult survival was then constrained to be a linear function of different climate variables and the two epizootics. The general starting model was $\{\phi(\text{sex}*\text{mites}*\text{year}), p(\text{sex}*\text{mites}*\text{year})\}$. The estimate of the variance inflation factor (\hat{c}) derived from the starting model and the median \hat{c} technique was 0.98 (SE = 0.02), suggesting no overdispersion in the data. Results are qualitatively similar when \hat{c} was set equal to 0.98 or 1, so we left \hat{c} equal to 1 for model selection (Burnham & Anderson 2004). We evaluated these adult models as above for the age models but used AIC_c values instead of QAIC_c values. We considered models including at most two of the covariates potentially underlying the interannual variation in survival because we felt it prudent to limit the number of candidate models given the limited number of years and the sample sizes in some years.

RECRUITMENT

Annual variation in crossbill population size may be attributable to demographic variables other than annual survival. For example, population declines could be explained by declines in fecundity. During the course of regular fieldwork, we recorded the number and sex of adults and number of juveniles between 2001 and 2006. Because there was a seasonal peak in the juvenile/female ratios, we estimated annual fecundity as the maximum semimonthly ratio of juveniles to adult females observed during a year. We evaluated evidence for consistent changes in fecundity by fitting a least-squares linear regression through these annual maxima.

PROJECTED POPULATION SIZE

We used a simple life-table analysis to estimate projected changes in density in response to variation in annual adult and juvenile survival. Annual adult survival was set at 0.68 (the mean of annual apparent survival before 2004), juvenile survival at 0.14 and the number of female offspring produced per adult female was set at 2.4 so that the finite rate of population growth (λ) equalled 1 (i.e. the population would be stable). Model-averaged yearly adult and juvenile survival rates were then used to estimate annual λ values to project successive changes in population density while keeping female fecundity constant. The confidence intervals for the projected population densities were based on the 95% confidence intervals associated with each year's annual adult survival (ϕ) estimates. Predicted density at year $t + 1$ is based on observed density at year t to avoid propagating the error from one estimate over subsequent density estimates.

Results

TRENDS IN THE CROSSBILL POPULATION

Crossbill densities declined by 63% from 281 to 104 birds per km² between 2003 and 2008 (Fig. 1; $r = -0.985$, $P = 0.0003$).

SURVIVAL AND ITS CORRELATES

Adults and juveniles

Models with age-class structure for ϕ and p were overwhelmingly favoured over single age-class models ($\Delta\text{QAIC}_c > 258$). Results indicate that recapture rates

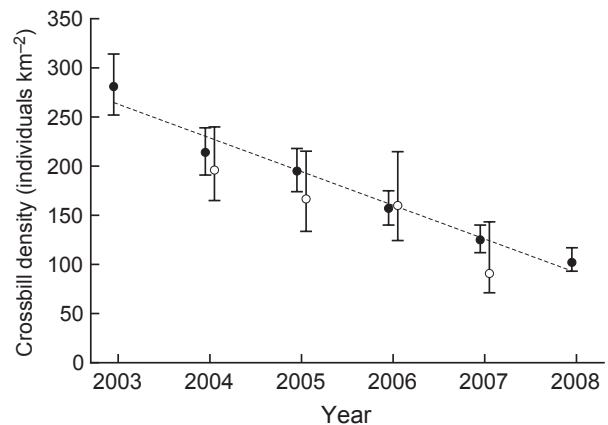


Fig. 1. Post-breeding annual population density of South Hills crossbills has declined between 2003 and 2008 (dashed line, linear regression). Density estimates derived from 10-min point-transect surveys (filled circles) are shown along with 95% confidence intervals, which are based on restricted inference procedures (see text). The annual density estimates predicted from adult and juvenile survivorship (open circles) track the observed decline. Predicted density at year $t + 1$ is based on observed density at year t and was calculated using a simple life-table model (see text).

Table 1. Model-averaged estimates of annual capture probabilities for South Hills crossbills based on mark-recapture efforts between 2000 and 2007

	Year	Estimate	SE	LCI	UCI	
Juveniles	2001	0.182	0.266	0.007	0.881	
	2002	0.359	0.266	0.055	0.843	
	2003	0.467	0.131	0.238	0.712	
	2004	0.497	0.139	0.250	0.746	
	2005	0.195	0.072	0.090	0.373	
	2006	0.342	0.142	0.131	0.641	
	2007	0.775	0.285	0.122	0.988	
Adults	Banded as juveniles	2001	–	–	–	–
		2002	0.622	0.289	0.129	0.948
		2003	0.722	0.153	0.369	0.920
		2004	0.745	0.123	0.450	0.913
		2005	0.418	0.117	0.219	0.648
		2006	0.605	0.119	0.366	0.802
		2007	0.900	0.146	0.271	0.995
	Banded as adults	2001	0.650	0.195	0.257	0.909
		2002	0.814	0.085	0.592	0.929
		2003	0.868	0.056	0.715	0.945
		2004	0.521	0.062	0.400	0.639
		2005	0.487	0.060	0.373	0.603
		2006	0.538	0.070	0.401	0.670
		2007	0.865	0.193	0.202	0.994

Estimates were derived using age models fit to encounter histories from individuals banded as juveniles and adults.

differed between juveniles and adult crossbills and vary year-to-year among individuals banded as adults or as juveniles (Table 1). Three of the top four models receiving the most support ($\Delta\text{QAIC}_c < 2$) indicate that juvenile survival did not vary appreciably among years, while support for one model suggests a linear increase in apparent juvenile survival

Table 2. Top-performing models of apparent annual survival (ϕ) and capture probability (p) for the analysis of mark–recapture data collected from individuals banded as juveniles and adults between 2000 and 2007

Model	QAIC _c	Δ QAIC _c	w	L	K	Deviance
$\{\phi_{(\cdot/\cdot)}, P_{(t/\cdot)} A, M^* T\}$	2339.36	0.00	0.25	1.00	22	120.77
$\{\phi_{(\cdot/C)} \text{ spring temp}, P_{(t/\cdot)} A, M^* T\}$	2340.33	0.96	0.16	0.62	17	131.93
$\{\phi_{(\text{linear}/\cdot)}, P_{(t/\cdot)} A, M^* T\}$	2340.73	1.36	0.13	0.51	23	120.09
$\{\phi_{(\cdot/\cdot)} M + A + T, P_{(t/\cdot)} A, M^* T\}$	2340.90	1.54	0.12	0.46	23	120.26
$\{\phi_{(\cdot/C)} \text{ spring temp}, M, P_{(t/\cdot)} A, M^* T\}$	2342.17	2.80	0.06	0.25	18	131.74
$\{\phi_{(t/\cdot)} M, A^* T, P_{(t/\cdot)} A, M^* T\}$	2342.39	3.02	0.06	0.22	27	113.54
$\{\phi_{(\cdot/C)} \text{ hot, dry day 5-year avg}, P_{(t/\cdot)} A, M^* T\}$	2343.37	4.01	0.03	0.13	17	134.98
$\{\phi_{(\cdot/C)} \text{ annual temp}, P_{(t/\cdot)} A, M^* T\}$	2344.16	4.79	0.02	0.09	17	135.76
$\{\phi_{(\text{WNV}/\text{WNV})}, P_{(t/\cdot)} A, M^* T\}$	2346.08	6.72	0.01	0.03	17	137.69
$\{\phi_{(\cdot/C)} \text{ nonbreeding temp}, P_{(t/\cdot)} A, M^* T\}$	2346.62	7.25	0.01	0.03	17	138.22
$\{\phi_{(\cdot/C)} \text{ hot, dry day 5-year wt. avg}, P_{(t/\cdot)} A, M^* T\}$	2348.02	8.65	0.00	0.01	17	139.62
$\{\phi_{(\cdot/C)} \text{ hot, dry day 3-year avg}, P_{(t/\cdot)} A, M^* T\}$	2348.46	9.10	0.00	0.01	17	140.07
$\{\phi_{(\cdot/C)} \text{ hot, dry day 3-year wt. avg}, P_{(t/\cdot)} A, M^* T\}$	2349.34	9.97	0.00	0.01	17	140.94
$\{\phi_{(C/C)} \text{ spring temp}, P_{(t/\cdot)} A, M^* T\}$	2350.70	11.33	0.00	0.00	17	142.30
$\{\phi_{(C/C)} \text{ annual temp}, P_{(t/\cdot)} A, M^* T\}$	2351.57	12.21	0.00	0.00	17	143.18
$\{\phi_{(\cdot/C)} \text{ hot, dry day}, P_{(t/\cdot)} A, M^* T\}$	2351.74	12.37	0.00	0.00	17	143.34
$\{\phi_{(C/C)} \text{ nonbreeding temp}, P_{(t/\cdot)} A, M^* T\}$	2352.81	13.44	0.00	0.00	17	144.41
$\{\phi_{(\cdot/C)} \text{ cold, wet day}, P_{(t/\cdot)} A, M^* T\}$	2353.26	13.90	0.00	0.00	17	144.87
$\{\phi_{(C/C)} \text{ hot, dry day}, P_{(t/\cdot)} A, M^* T\}$	2353.60	14.24	0.00	0.00	17	145.21
$\{\phi_{(t)}, P_{(t)}\}$	2598.17	258.80	0.00	0.00	13	397.89
$\{\phi_{(\cdot/\cdot)}, P_{(\cdot/\cdot)}\}$	2608.75	269.39	0.00	0.00	4	426.64
$\{\phi_{(\cdot)}, P_{(\cdot)}\}$	2624.92	285.55	0.00	0.00	2	446.82

Columns represent Akaike Information Criterion with small sample correction (QAIC_c), QAIC_c differences (Δ QAIC_c), normalized QAIC_c weights (w), model likelihoods (L), numbers of parameters (K) and model deviance. Subscript terms denote parameterizations of ϕ and p using models with two age-classes: (\cdot/\cdot), constant over group and year variables; (\cdot/t), constant for juveniles but year-variant for adults; (\cdot/C), inclusion of a climatic variable for adults but not juveniles; (linear/ t), linear change for juveniles but year-variant for adults; A, age of the individual; M, age at marking; T, year; ‘*’, an interaction allowing for differing slopes and intercepts; ‘+’, additive relationship between parameters. All models with a Δ QAIC_c < 5 are presented, in addition to top models that include each climatic variable considered.

from 0.10 (0.04 SE; 95% CI: 0.04–0.21) to 0.19 (0.08 SE; 95% CI: 0.07–0.42) between 2000 and 2007 (Table 2). The estimate of apparent juvenile survival (i.e. first-year survival) from the most parsimonious model $\{\phi_{(\cdot/\cdot)}, P_{(t/\cdot)} A, M^* T\}$ was 0.14 (0.02 SE; 95% CI: 0.10–0.19). There was essentially no support for models including an association between juvenile survival and any climatic variable (Table 2; Δ QAIC_c > 11). In contrast, there was a strong support for models allowing for either temporal variation or climatic effects on adult survival with model-averaged estimates of apparent annual adult survival declining over the study (Table 2; Fig. 2a). All models with Δ QAIC_c < 10 included parameters for temporal variation or climatic variables (Table 2). Increasing spring mean temperature was most closely associated with declines in adult survival rates (Table 2; Fig. 2b). The second climatic variable to receive support was the 5-year unweighted average number of hot, dry days ≥ 32 °C (Δ QAIC_c = 4.01). Remaining climatic variables (e.g. cold, wet days, mean annual temperature, nonbreeding temperature) received considerably less or essentially no support (Table 2). Table 3 shows that spring temperature and the 5-year average number of hot, dry days (≥ 32 °C) accounted for the highest proportion (32–41%) of the variation in adult survival based on the analysis of deviation, although annual and nonbreeding temperatures, and WNV exceeded our 20% threshold to be considered potentially influential.

Adults

Analysis of adult crossbill capture histories provides strong evidence of temporal variation in survival (Table 4). The seven most strongly supported models (Δ AIC_c < 2) included spring and annual temperatures, and the number of hot (≥ 32 °C), dry days as a correlate of adult survival. The two most strongly supported models included sex as a factor (Table 4), with female survival declining more rapidly than male survival as temperatures increased. The next best model included annual temperatures (Table 4; Δ AIC_c = 1.70), and the next two models in the set ($1.81 \leq \Delta$ AIC_c ≤ 2.25) provided support for an influence of an increasing number of hot, dry days over the preceding three and 5 years. There was support for relationships between adult survival and the occurrence of scaly-leg mites acting in concert with spring temperature (Δ AIC_c = 1.68) and the 3-year average number of hot, dry days (Δ AIC_c = 1.81), but minimal support for a primary effect of mites (Δ AIC_c = 12.26). There was also minimal support for WNV cases in the region (Δ AIC_c = 13.13) and the duration of consecutive cold and wet days (Δ AIC_c = 13.37). We tested the fit of mites and WNV as additive factors to the reduced spring temperature model $\{\phi_{(\text{spring temp})}, P_{(\text{year})}\}$. The addition of mites or WNV did not result in statistically significant improvement of model fit ($P > 0.05$), leading to selection of the reduced model including only spring temperature as a correlate of

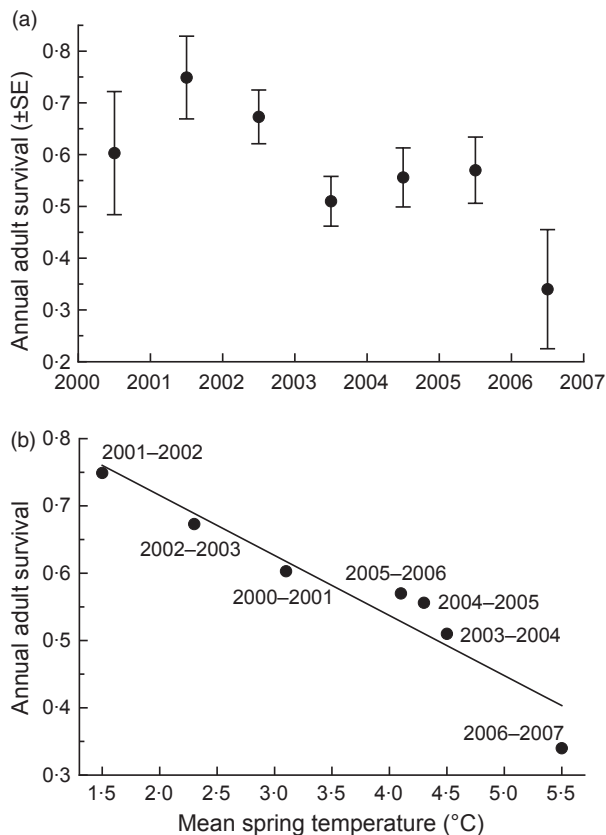


Fig. 2. Model-averaged estimates of annual survival for adult South Hills crossbills (Table 1) have declined in (a) recent years, and in relationship to (b) mean spring temperature. The line represents a linear best-fit line for illustration; R^2 Dev = 0.41 for adult survival in relation to spring temperature (Table 2).

Table 3. Analysis of deviance estimates of the fraction of temporal variation in adult and juvenile South Hills crossbill apparent annual survival accounted for by candidate covariates

Covariate	R^2 Dev
Spring temperature	0.41
Annual temperature	0.29
Nonbreeding temperature	0.22
Number of hot, dry day ($\geq 32^\circ\text{C}$) – 5-year unweighted average	0.32
Number of hot, dry day ($\geq 32^\circ\text{C}$) – 3-year unweighted average	0.17
Number of cold, wet day	0.03
West Nile virus	0.24

adult survival. The model allowing for an interaction between spring temperature and mites ($\Delta\text{AIC}_c = 3.21$) indicated that the depressing effect of mites on survival decreased by an order of magnitude over the study (during the last year 2006–2007, apparent annual survival for crossbills with mites was only 0.01 less than for crossbills without mites). Given that the overall incidence of mites has not changed consistently between 2000 and 2007 (linear regression: $F_{1,6} = 0.96$,

$P = 0.37$), the apparent decrease in the virulence of mites indicates that they have not contributed to the large decline in adult annual survival.

The R^2 Dev values for each of the focal covariates further corroborated these results (Table 5). The three temperature variables and 3- and 5-year average number of hot, dry days accounted for the majority ($\geq 79\%$) of variation in adult survival and were the only covariates to exceed our 20% threshold to be considered potentially influential.

FECUNDITY

Fecundity (maximum number of juveniles per female across the population each year) averaged 1.82 (± 0.51 SE, $n = 6$ years) and did not change consistently between 2001 and 2006 (linear regression: $F_{1,4} = 0.38$, $P = 0.57$). Fecundity peaked during the last half of July in 5 of the 6 years and was lowest in 2003 (0.92) and highest in 2002 (4.31). Excluding 2002, fecundity ranged from only 0.92 to 1.67 and did not change consistently with time ($P = 0.48$).

CAN DECLINES IN ADULT SURVIVAL ACCOUNT FOR THE POPULATION DECLINE?

The projected population densities beginning in 2003 are shown relative to the observed decline in Fig. 1. Given the large overlap in the confidence intervals for the observed and projected estimates of crossbill densities (Fig. 1), the decline in annual adult survival alone is sufficient to cause the observed decline in crossbill population density. Based on the higher survival rates prior to 2003 (Fig. 2a) and relatively stable density estimates during earlier surveys (2000–2002) using a different method (Benkman, Fetz & Talluto, in press), we suspect that the population decline began after the summer of 2003 (Fig. 1).

Discussion

Previous research on the South Hills crossbill identified a significant decrease in adult survival owing to scaly-leg mites (Benkman *et al.* 2005). Current evidence, however, indicates that the impact of scaly-leg mites on annual adult survival rates has decreased over time rather than increased as expected if they had caused the decline both in annual adult survival and in the crossbill population. Similarly, the number of reported WNV cases in the region does not appear to be related to variation in annual adult survival rates, although the dip in survival between 2006 and 2007 (Fig. 2a) could be, in part, a response to a spike in the incidence of WNV in the summer of 2006. However, this decrease in annual survival also coincides with an increase in temperature (Figs 2b and 3b). Moreover, the decline in survival from 2003 to 2006 likely occurred in the absence of WNV. We suspect that WNV is not a great threat for South Hills crossbills because the mosquito vectors for WNV are uncommon in the South Hills (CWB, pers. obs.). Nevertheless, data on the prevalence of WNV in the South Hills are required to fully

Table 4. Top-performing models of apparent annual adult survival (ϕ) and capture probability (p) for the analysis of mark–recapture data collected from 2000 to 2007

Model	AIC _c	Δ AIC _c	w	L	K	Deviance
{ $\phi_{\text{spring temp}} * \text{sex}, P_{\text{year}}$ }	1673.57	0	0.13	1.00	11	207.47
{ $\phi_{\text{spring temp}} + \text{sex}, P_{\text{year}}$ }	1673.63	0.07	0.12	0.97	10	209.59
{ $\phi_{\text{spring temp}}, P_{\text{year}}$ }	1674.67	1.10	0.07	0.58	9	212.66
{ $\phi_{\text{spring temp}} + \text{mites}, P_{\text{year}}$ }	1675.25	1.68	0.05	0.43	10	211.20
{ $\phi_{\text{annual temp}} + \text{sex}, P_{\text{year}}$ }	1675.26	1.70	0.05	0.43	10	211.22
{ $\phi_{\text{annual temp}} * \text{sex}, P_{\text{year}}$ }	1675.35	1.78	0.05	0.41	11	209.26
{ $\phi_{\text{hot, dry day 3-year avg}} * \text{mites}, P_{\text{year}}$ }	1675.38	1.81	0.05	0.40	11	209.29
{ $\phi_{\text{hot, dry day 5-year avg}}, P_{\text{year}}$ }	1675.82	2.25	0.04	0.32	9	213.81
{ $\phi_{\text{annual temp}}, P_{\text{year}}$ }	1676.21	2.64	0.03	0.27	9	214.20
{ $\phi_{\text{hot, dry day 3-year avg}}, P_{\text{year}}$ }	1676.45	2.88	0.03	0.24	9	214.44
{ $\phi_{\text{hot, dry day 5-year avg}} + \text{mites}, P_{\text{year}}$ }	1676.64	3.08	0.03	0.21	10	212.60
{ $\phi_{\text{spring temp}} * \text{WNv}, P_{\text{year}}$ }	1676.67	3.10	0.03	0.21	10	212.62
{ $\phi_{\text{spring temp}} + \text{WNv}, P_{\text{year}}$ }	1676.71	3.14	0.03	0.21	10	212.66
{ $\phi_{\text{spring temp}} * \text{mites}, P_{\text{year}}$ }	1676.77	3.21	0.03	0.20	11	210.68
{ $\phi_{\text{annual temp}} + \text{mites}, P_{\text{year}}$ }	1676.96	3.39	0.02	0.18	10	212.91
{ $\phi_{\text{nonbreeding temp}} + \text{sex}, P_{\text{year}}$ }	1677.04	3.47	0.02	0.18	10	212.99
{ $\phi_{\text{annual temp}} * \text{mites}, P_{\text{year}}$ }	1677.17	3.60	0.02	0.17	11	211.08
{ $\phi_{\text{nonbreeding temp}}, P_{\text{year}}$ }	1677.36	3.79	0.02	0.15	9	215.35
{ $\phi_{\text{hot, dry day 5-year avg}} * \text{mites}, P_{\text{year}}$ }	1677.47	3.90	0.02	0.14	11	211.38
{ $\phi_{\text{annual temp}} + \text{WNv}, P_{\text{year}}$ }	1677.56	3.99	0.02	0.14	10	213.51
{ $\phi_{\text{sex}} * \text{year}, P_{\text{year}}$ }	1681.28	7.72	0.00	0.02	20	196.61
{ $\phi_{\text{year}}, P_{\text{year}}$ }	1682.76	9.19	0.00	0.01	13	212.56
{ $\phi_{\text{mites}} * \text{year}, P_{\text{year}}$ }	1683.35	9.78	0.00	0.01	20	198.67
{ $\phi_{(\cdot)}, P_{\text{year}}$ }	1685.76	12.19	0.00	0.00	8	225.79
{ $\phi_{\text{WNv}}, P_{\text{year}}$ }	1686.70	13.13	0.00	0.00	9	224.69
{ $\phi_{\text{cold, wet day}}, P_{\text{year}}$ }	1686.94	13.37	0.00	0.00	9	224.93
{ $\phi_{\text{group}} * \text{year}, P_{\text{group}} * \text{year}}$ }	1718.68	45.12	0.00	0.00	56	156.16
{ $\phi_{(\cdot)}, P_{(\cdot)}$ }	1727.97	54.41	0.00	0.00	2	280.13

Columns represent Akaike Information Criterion with small sample correction (AIC_c), AIC_c differences (Δ AIC_c), normalized AIC_c weights (w), model likelihoods (L), numbers of parameters (K) and model deviance. Subscript terms denote parameterizations for ϕ and p : (·), constant over group and year variables; sex, male and female; mites, presence or absence of scaly-leg mites; WNv, West Nile virus cases; *, an interaction allowing for differing slopes and intercepts; +, additive relationship between parameters. All models with a Δ AIC_c < 4 are presented, in addition to the general starting model and top models that include other parameters considered (e.g. scaly-leg mites).

Table 5. Analysis of deviance estimates of the fraction of temporal variation in adult South Hills crossbill apparent annual survival accounted for by candidate covariates

Covariate	R^2 Dev
Spring temperature	0.99
Annual temperature	0.88
Nonbreeding temperature	0.79
Number of hot, dry day ($\geq 32^\circ\text{C}$) – 5-year unweighted average	0.91
Number of hot, dry day ($\geq 32^\circ\text{C}$) – 3-year unweighted average	0.86
Number of cold, wet day	0.06
Scaly-leg mites	0.15
West Nile virus	0.08

address the significance of this biotic factor for local bird populations.

The population projection model indicates that observed changes in annual adult survival (Fig. 2a) can account for the observed declines in crossbill density between 2003 and 2007 (Fig. 1). However, observed declines in density tended to be less severe than predicted based on adult and juvenile survival

rates, suggesting possible compensatory changes in other demographic variables, including immigration and increased fecundity (Stearns 1992; Newton 1998). Substantial net immigration is unlikely because the lodgepole pine habitat is restricted and uniform (other than stand age differences) across the South Hills and Albion Mountains. The observation that adult female South Hills crossbills captured in June and July nearly always show evidence of breeding (i.e. brood patches) indicates that there has not been a shift in the age of first reproduction (i.e. all or nearly all females start breeding their first year). Finally, our measure of local production of offspring (peak number of fledged juveniles per adult female) has not increased between 2001 and 2006. However, during the 3 years (2004–2006) for which we have fecundity data and both estimated and projected densities, the extent to which the estimated density exceeded the projected density (ln-transformed) increased with increases in our measures of fecundity ($r = 1.00$, d.f. = 1, $P = 0.01$). This suggests that the extent to which the projected densities differed from the estimated densities was related to annual variation in fecundity. Such a result is not surprising given that our surveys occurred during and soon after most of the young were fledged. Thus, in a year of low fecundity (2006), our projected

density closely approximated the estimated density (Fig. 1), whereas years of higher fecundity (e.g. 2005) led to higher densities than projected based on survival alone (Fig. 1). In sum, these results indicate that the decline in adult survival alone has caused crossbills to decline in abundance. Below, we address the potential mechanisms by which adult survival has declined.

CROSSBILLS AND CLIMATE CHANGE

Decreases in population density in response to declining adult survival rates are not surprising (e.g. Thomson, Baillie & Peach 1997; Barbraud & Weimerskirch 2001) because asymptotic population growth rates in birds are typically most sensitive to changes in adult survival (Sæther & Bakke 2000). However, a decline in survival rather than in fecundity indicates that the phenology mismatch hypothesis, which has the most support for declines in migratory bird species (e.g. Both *et al.* 2006, 2010; Møller, Rubolini & Lehikoinen 2008; Jones & Cresswell 2010), is unlikely to apply to South Hills crossbills. Mismatch mechanisms that pertain to the mistiming of breeding relative to resource availability are unlikely because South Hills crossbills are resident and appear to use feeding rates to time their breeding (Smith & Benkman 2007). Crossbills are among the most flexible of birds in their timing of breeding, with breeding recorded in every month of the year, and shifts in their timing of breeding correspond to shifts in the availability of seeds and their ability to nest successfully (Benkman 1990).

The factor most closely associated with declines in annual adult survival was increasing temperature, both spring and annual (Tables 2–5). Over the study (2000–2007) period, mean spring temperature increased by 0.39 (± 0.15 SE) degrees/year and mean annual temperature increased by 0.37 (± 0.06 SE) degrees/year (Fig. 3a). The increase in mean annual temperature in the South Hills mirrors the trend documented throughout the Western United States (Thompson *et al.* 1998; Schwartz & Reiter 2000; Folland *et al.* 2001) and, more generally, the Northern Hemisphere (e.g. Schwartz, Ahas & Aasa 2006b; Christensen *et al.* 2007).

We can envision three mechanisms by which increases in temperature could negatively impact adult survival. First, increasing spring temperatures may lead to more precipitation falling as rain rather than snow (Mysterud *et al.* 2000; Cheng *et al.* 2007), which is then susceptible to freezing. Because it is extremely difficult for crossbills to access seeds in frozen cones (CWB and LS, personal observations), an increase in the amount of time cones remain frozen could negatively impact crossbill survival. We examined various measures during the spring (March–May), including cumulative rainfall (not shown) and the maximum duration of consecutive cold and wet days (mean temperature $< 5^\circ\text{C}$ and > 1 mm precipitation; and other combinations). However, we did not find consistent correlations between changes in climate that would be associated with cone freezing and variation in annual survival (Tables 2–5).

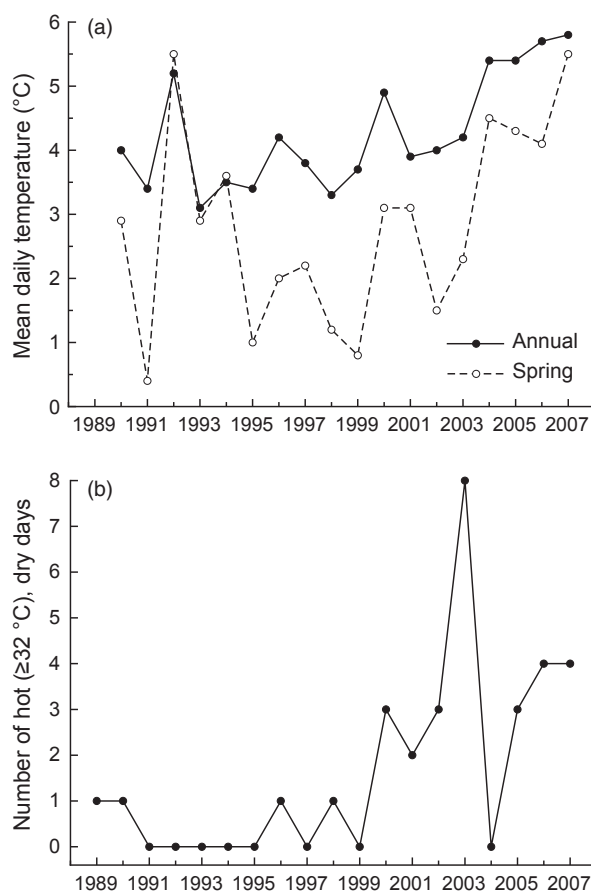


Fig. 3. (a) Average daily mean temperature during spring (March–May) and annually (July–June; year on abscissa corresponds to last half of year), and (b) the incidence of hot, dry days with < 5.1 mm of precipitation each year have increased over time in the South Hills. Spring temperatures increased from 2000 to 2007 (linear regression: $F_{1,6} = 7.09$, $P = 0.04$), but not between 1990 and 2007 (linear regression: $F_{1,16} = 2.39$, $P = 0.14$; Fig. 3a), whereas annual temperature increased both between 2000 and 2007 (linear regression: $F_{1,6} = 9.01$, $P = 0.02$) and between 1990 and 2007 (linear regression: $F_{1,16} = 11.99$, $P = 0.003$).

Second, increasing temperatures could stress trees by increasing water deficits and thus cause a decline in seed production. Many trees including pines have suffered increasing mortality rates in the Western United States since the 1970s apparently because of increasing regional temperatures causing increasing water deficits (Van Mantgem *et al.* 2009). As might be expected, annual cone production by lodgepole pine has declined in the South Hills by 27% between 1991 and 2007 (Fig. 4). Cone production was negatively correlated with annual temperature ($r = -0.64$, $P = 0.005$), but not with spring temperature ($r = -0.35$, $P = 0.16$). Lodgepole pine cones require 2 years from bud initiation to cone maturation, although most of the cone growth occurs during the last summer. Thus, conditions during the previous year or two might also have an effect on cone production. Cone production was negatively correlated with annual temperature 1 year earlier ($r = -0.60$, $P = 0.01$) but not 2 years earlier ($r = -0.32$, $P = 0.23$); cone production was not correlated with either measure of spring temperature.

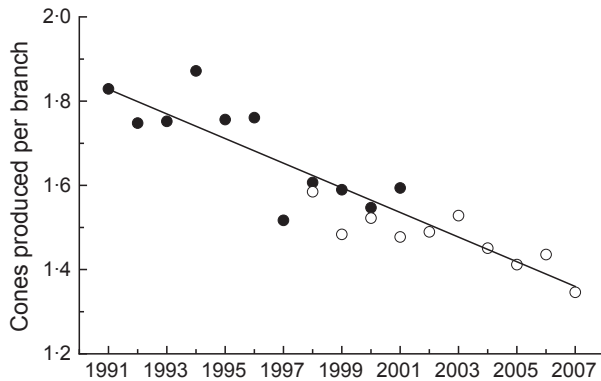


Fig. 4. Mean annual cone production on the main stem of three lateral branches in the upper canopy of fallen trees (mean of three branches per tree) between 1991 and 2007. The different symbol types represent data from different observers and different sample sizes (filled circles: T. Fetz, 78 trees per year; empty circles: J. Smith, 67 trees per year). The line represents a best-fit linear regression ($r^2 = 0.86$, $F_{1,15} = 91.8$, $P < 0.0001$; for the 4 years of data overlap [1998–2001], we used the means of the two samples).

Although increasing annual temperatures likely account for the decline in annual cone production, this does not explain why spring or annual temperatures would be predictive of annual survival during the same year because South Hills crossbills forage relatively rarely on current cone crops and instead rely mostly on seeds in older (> 5 year old) cones (see Benkman *et al.* 2003). Thus, temperatures > 5 years earlier should be more critical in determining current seed availability and annual survival than temperatures during this year. Indeed, the large decrease in cone production beginning in 1997 (Fig. 4) may have contributed to the decline in survival rates 6–7 years later in 2003–2004 (Fig. 2a). Over the long term, past and ongoing declines in cone production and increasing tree mortality will cause further declines in crossbills.

A third mechanism by which climate change might alter seed availability to crossbills is an increase in hot, dry days causing cones to open and prematurely shed their seeds (i.e. xeriscence). Models testing for a relationship between numbers of hot, dry days and adult survival received support, especially models where survival is affected by the number of hot, dry days during the previous 3–5 years (Tables 2–5). The largest decline in annual adult survival followed the summer of 2003 (Fig. 2), coinciding with a sharp increase in hot, dry days (Fig. 3b). Presumably as a result, the frequency of open cones on trees appears to be increasing in the South Hills (CWB, pers. obs.). The consequences of hot, dry conditions are likely to extend beyond the subsequent year because crossbills rely on the gradual weathering of cones that in past years (e.g. 2000–2002) nearly constantly replenished the number of accessible seeds (Benkman, Fetz & Talluto, in press). High temperatures in the summer are likely to cause a large fraction of the most weathered cones to open and shed their seeds and thus reduce the availability of seeds for the next several years. Such a mechanism could account both for the large decline in survival following the summer of 2003 with

extreme hot and dry conditions and for survival remaining low in subsequent years. Perhaps warmer temperatures during spring might further contribute to cone opening. This could help account for the strong support for models that included spring temperatures (Tables 2–5).

We expected juvenile survival to decrease as found in adults; however, the one model with strong support for a trend (Table 2: the third-ranked model, $\Delta\text{QAIC}_c = 1.36$) showed an increase in juvenile survival between 2000 and 2007. Although this may seem counterintuitive, a large fraction of the mortality of independent juveniles (we captured and banded both dependent and independent juveniles) likely occurs during the first several weeks after the juveniles become independent from their parents as found in yellow-eyed juncos (*Junco phaeotus* Wagler, Sullivan 1989; see also Sillett & Holmes 2002). Recently, independent juncos have a high mortality rate because they are inefficient at foraging (Sullivan 1989). Young crossbills are also relatively inefficient at foraging, especially on more closed cones (CWB, personal observation), and once independent likely require several months to approach the foraging proficiency of adults (Fig. 5b). Figure 5 shows seed intake rate data from 2001 when there were and had been relatively few hot, dry days (Fig. 3b) and thus relatively few cones opening during summer. In addition to juveniles having relatively low feeding rates compared to adults (Fig. 5b), seed availability, when few cones open, decreases over summer as reflected by the decline in adult seed intake rates (Fig. 5a; see Smith & Benkman 2007; Benkman, Fetz & Talluto, in review). If mortality is exceptionally high because of inefficient foraging during their first few weeks of independence when seed availability may have historically been declining over summer (Fig. 5), then the large increase in easily accessible seeds in opening cones following hot, dry days may have especially enhanced juvenile crossbill survival during their most vulnerable post-fledging stage. An increase in post-fledging survival during the first several months would compensate in part for the expected decrease in winter survival, with the net effect being no change or even an increase in annual juvenile survival in their first year. This increase in juvenile survival, however, has been negated by the decrease in annual adult survival, and South Hills crossbills have declined.

Unfortunately, the occurrence of warmer spring temperatures, higher average annual temperatures, and hot days (> 32 °C) in the South Hills is likely to increase substantially by the end of this century (Karl, Melillo & Peterson 2009) causing further declines in the carrying capacity for the South Hills crossbill. The increase in climatic variation, in particular extreme high temperatures associated with climate change (Karl, Melillo & Peterson 2009), has the potential to further reduce the carrying capacity for crossbills as well as alter forest recruitment dynamics and subsequent stand structure (Nathan *et al.* 1999; Nathan & Ne'eman 2004). Research is needed to test the mechanisms proposed here linking warming trends and crossbill demographic rates (Grosbois *et al.* 2008). In addition, the risk of locally catastrophic events will likely increase with increasing temperatures and subsequent

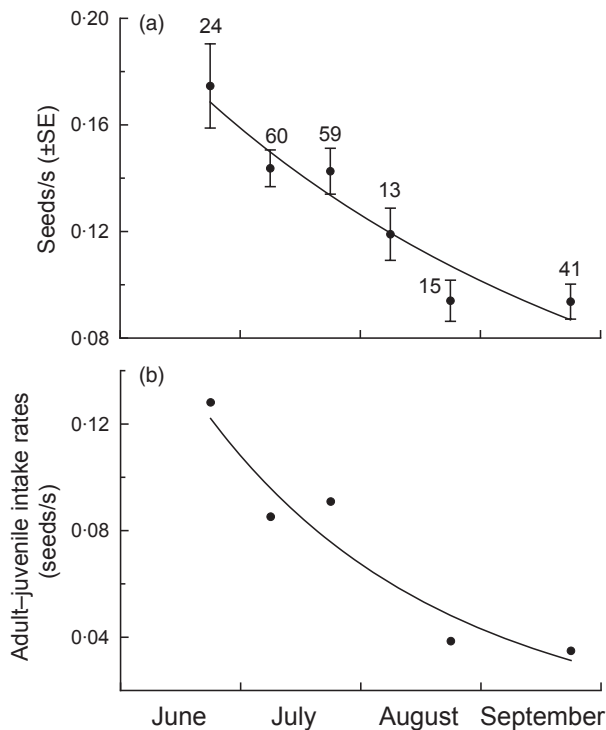


Fig. 5. (a) Seed intake rates of adult South Hills crossbills declined during the period when juveniles were fledged and became independent in 2001. Intake rates represent the means for semimonthly periods when data were gathered (numbers above each mean represent the number of foraging bouts, with a mean of 10 seeds eaten per bout). Curve represents a least-squares regression of mean intake rates in relation to semimonthly categories (ln-transformed: $r^2 = 0.90$, $F_{1,4} = 38.0$, $P = 0.004$; see Smith & Benkman 2007 for details on foraging data). (b) The differences between the mean seed intake rates of adults and juveniles decreased during late summer in 2001. Curve represents a least-squares regression of the differences between the mean intake rates of adults and juveniles in relation to semimonthly categories (ln transformed: $r^2 = 0.91$, $F_{1,3} = 32.2$, $P = 0.01$). The sample sizes (number of foraging bouts) for juvenile seed intake rates were 6, 18, 15, 16 and 9 over the five semimonthly periods.

drought conditions, including increases in the severity and extent of both pine beetle outbreaks (Logan, Regniere & Powell 2003) and forest fires (Westerling *et al.* 2006). Moreover, regional climate change models predict the complete disappearance of lodgepole pine populations from southern Idaho by the end of the 21st century (Thompson *et al.* 1998). Because the seedling stage of conifers is often the most vulnerable to higher temperatures and drought (Kolb & Robberecht 1996), management efforts should consider reforestation methods to maintain lodgepole pine forests in the South Hills and the adjacent Albion Mountains. Effort should also be devoted to ensuring reliable canopy seed banks.

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