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RESEARCH ARTICLE

Habitat associations and abundance of a range-restricted specialist, the Cassia Crossbill (*Loxia sinesciuris*)

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ABSTRACT

The recently discovered Cassia Crossbill (*Loxia sinesciuris*) occurs only in 2 small, isolated mountain ranges in southern Idaho, USA: the South Hills and the Albion Mountains. The species faces 2 major threats from climate change related to its reliance on seeds of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*). First, increased numbers of hot summer days ($\geq 32^{\circ}$C) since 2003 apparently caused premature cone opening and seed shedding, leading to reduced seed availability and an 80% decline in Cassia Crossbill densities between 2003 and 2011. Second, climate change is predicted to prevent recruitment and could potentially cause the extirpation of lodgepole pine from the South Hills and Albion Mountains by 2080. This extirpation would cause the extinction of Cassia Crossbills, because they are unable to compete for lodgepole pine seeds elsewhere. Although recent summers with fewer hot days have allowed Cassia Crossbills to recover, determining their status will require using density across habitat types to estimate population size. We estimated the density of Cassia Crossbills at 137 locations and used conditional modeling to evaluate the influence of 12 habitat metrics on the species' habitat use. Cassia Crossbills more commonly used larger, mature lodgepole pine stands, and north-facing slopes where cones experience less insolation and more likely retain seeds despite hot summer days. Their estimated range was 67 km^2 of lodgepole pine forest, with a population of $\sim$5,800 individuals (95% confidence interval: 3,100–11,000). Given their restricted distribution, small population, and reliance on mature lodgepole pine, the threats posed to Cassia Crossbills by climate change represent a considerable conservation challenge.

Keywords: climate change, endangered species, Idaho, *Loxia sinesciuris*, *Pinus contorta*

Asociaciones de hábitat y abundancia de una especie especialista de rango restringido, *Loxia sinesciuris*

RESUMEN

La especie recientemente descubierta, *Loxia sinesciuris*, se distribuye en solo dos pequeños sectores montañosos aislados en el sur de Idaho, EEUU, South Hills y Albion Mountains, donde enfrenta dos amenazas importantes derivadas del cambio climático relacionadas a su dependencia de las semillas de *Pinus contorta latifolia* de las Montañas Rocallosas. Primero, el aumento del número de días de verano calientes ($\geq$32 °C) desde 2003 aparentemente causó la apertura de los conos y la caída de las semillas de modo prematuro, llevando a una reducción en la disponibilidad de semillas y a una disminución del 80% de las densidades de *L. sinesciuris* entre 2003 y 2011. Segundo, se predice que el cambio climático impide el reclutamiento y podría potencialmente causar la extirpación del pino de South Hills y Albion Mountains para el año 2080. Esta extirpación podría causar la extinción de *L. sinesciuris*, debido a que no es capaz de competir por las semillas de este pino en otra parte. Aunque los veranos recientes con menos días calientes han permitido la recuperación de *L. sinesciuris*, la determinación de su estatus requerirá usar densidades en los distintos tipos de hábitat para estimar el tamaño poblacional. Estimamos la densidad de *L. sinesciuris* en 137 ubicaciones. Usamos modelos condicionales para evaluar la influencia de 12 métricas del hábitat en el uso de hábitat por parte de *L. sinesciuris*. *L. sinesciuris* usó más comúnmente rodales de pino más grandes y maduros, y pendientes con orientación norte donde los conos están expuestos a menos insolación y tienen más probabilidad de retener las semillas a pesar de los días de verano calientes. El rango estimado de uso de bosque de *P. c. latifolia* fue de 67 km^2, con una población de $\sim$5,800 individuos (95% NC: 3,100–11,000). Dada su distribución restringida, pequeña población y dependencia de individuos maduros de *P. c. latifolia*, las amenazas generadas por el cambio climático representan un desafío de conservación considerable para *L. sinesciuris*.

Palabras clave: cambio climático, especie en peligro, Idaho, *Loxia sinesciuris*, *Pinus contorta*

INTRODUCTION

Biodiversity is declining at a pace unprecedented in human history (Leakey and Lewin 1995, Glavin 2007, Kolbert 2014). Numerous drivers are causing this decline, including habitat loss and land-use change (Wilcove et al. 1998), invasive species (Lambertini et al. 2011), the spread of pathogens (Rohr et al. 2008, Wake and Vredenburg 2008),

climate change (Thomas et al. 2004), and interactions between these factors (Jetz et al. 2007, Mantyka-Pringle et al. 2012). Of these threats, climate change alone is predicted to put over a million species at risk of extinction by 2050 (Thomas et al. 2004) and threatens 30–60% of all land bird species in the Western Hemisphere (Sekercioglu et al. 2008). The avian species most threatened by climate change are nonmigratory, range-restricted, and highly specialized (Parmesan 2006, Jiguet et al. 2007, Harris and Pimm 2008, Sekercioglu et al. 2008, Pearce-Higgins et al. 2015). One such species is the Cassia Crossbill (*Loxia sinesciuris*; Santisteban et al. 2012, Benkman 2016), a cardueline finch recently split from the Red Crossbill (*L. curvirostra* complex; Chesser et al. 2017).

Cassia Crossbills (hereafter "crossbills") are confined to higher-elevation forest present in 2 small mountain ranges in southern Idaho, USA: the South Hills and the Albion Mountains (hereafter "Albions"). They rely almost entirely on seeds held within older serotinous cones of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*; Benkman et al. 2009, 2012). Serotinous cones generally remain closed for years or even decades until exposed to high temperatures (e.g., fire), during which time they gradually weather and the scales begin to separate, eventually providing access to seeds for crossbills (Benkman et al. 2012). Serotinous cones are particularly abundant in the South Hills and the Albions, because red squirrels (*Tamiasciurus hudsonicus*), which are usually the primary predispersal seed predator of lodgepole pine and select strongly against serotiny (Talluto and Benkman 2013, 2014), are absent (Benkman 1999). In response to relaxed selection from red squirrels, 90% of the lodgepole pine in the South Hills and Albions have serotinous cones, compared with just 30% in mountains where red squirrels are present (Benkman and Siepielski 2004). As a result, a much greater number of cones with seeds can accumulate in the canopy than in areas where squirrels harvest them. The accumulation of a large canopy seed bank and the gradual weathering of serotinous cones provide crossbills an extraordinarily stable food resource (Benkman et al. 2012). This has allowed crossbills to become resident and replace red squirrels as the primary selective agent on lodgepole pine cone structure (Benkman et al. 2013). Here, crossbills are engaged in a coevolutionary arms race with lodgepole pine, favoring local adaptation (Benkman 1999, 2016, Benkman et al. 2001, 2003, 2013) and resulting in reproductive isolation and speciation (Smith and Benkman 2007, Benkman et al. 2009, Parchman et al. 2016, Benkman 2017). Because of this evolutionary history, Cassia Crossbills are much less efficient than Red Crossbills (in particular, call type or ecotype 5) at foraging on lodgepole pine cones in areas where red squirrels are present, and are therefore restricted to the South Hills and Albions (Benkman et al. 2001).

This combination of range-restriction and specialization on serotinous lodgepole pine cones makes crossbills especially vulnerable to the negative impacts of climate change (Santisteban et al. 2012, Benkman 2016). An 80% decline in their population density between 2003 and 2011 appears to have been caused by an increase in the number of hot summer days ($\geq 32°C$; Benkman 2016). Apparently, 4 hot days are sufficient to weaken the resinous bonds holding serotinous cones closed, causing many seeds to be released in a pulse in late summer rather than becoming available more continuously throughout the year (Benkman 2016). Seeds were therefore less available to crossbills in the months and years following such summers, which led to reduced apparent annual survival and population declines (Santisteban et al. 2012, Benkman 2016).

Although crossbill populations have recovered in recent years, following a series of summers with few or no hot days (Benkman 2016), hotter temperatures are predicted for the region with climate change (Duffy and Tebaldi 2012, Christidis et al. 2014). The result will likely be more frequent and more severe crossbill declines. Moreover, climate change is predicted to prevent recruitment if not cause the extirpation of lodgepole pine from the South Hills and Albions before the end of this century (Coops and Waring 2011). Such an extirpation would lead to the extinction of the crossbill. The species' continued existence may therefore require management that furthers the persistence of suitable pine forest and closed cones (e.g., planting seedlings arising from trees with higher cone-opening temperatures in cooler microhabitats; Benkman 2016).

Despite this dire outlook, knowledge about habitat use and population size can be valuable for conserving imperiled species. For example, population estimates for Kirtland's Warbler (*Setophaga kirtlandii*) indicated a small and declining population in 1971 (Mayfield 1972), which contributed to its listing under the Endangered Species Act in 1973. Additional study identified key aspects of Kirtland's Warbler habitat that supported higher breeding success and led to the development of a habitat management plan (Byelich et al. 1976). This plan, with subsequent revision, led to the ongoing recovery of Kirtland's Warbler (Bocetti et al. 2012). Similar efforts to characterize habitat use and estimate population size have proved useful for the management of many other species, including Golden-cheeked Warbler (*Setophaga chrysoparia*; USFS 1992), Black-capped Vireo (*Vireo atricapilla*; USFS 1991), Southwestern Willow Flycatcher (*Empidonax traillii extimus*; USFS 2002), and Northern Spotted Owl (*Strix occidentalis caurina*; USFS 2011).

Given the apparent vulnerability of crossbills to climate change and their restricted range, our goals were to examine their habitat use and provide an estimate of their population size. First, we characterized the relationship
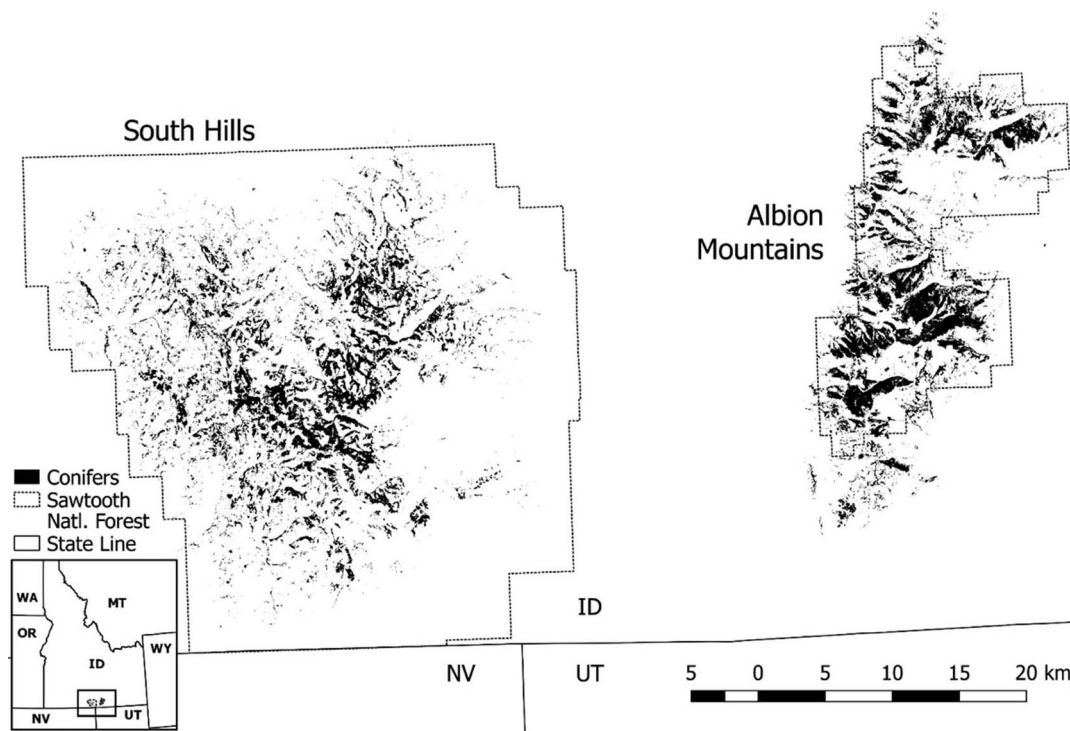
FIGURE 1. Predicted distribution of coniferous forests in the South Hills and Albion Mountains, Idaho, USA. Lodgepole pine is present in 59% and 13% of the coniferous forests in the South Hills and Albions, respectively. Pine occurs mostly between 1,850 and 2,600 m, and it can be found approximately from 42.05°N latitude on the south side of the South Hills to 42.21°N on the north side of the Albions, and from 114.24°W longitude on the west side of the South Hills to 113.36°W on the east side of the Albions.

between the densities of crossbills and 12 landscape, topographic, and forest features. Of particular interest was whether we would detect a preference for sites where cones are less susceptible to opening during hot days (e.g., north-facing slopes). These relationships could provide clear guidance for management; nearly all the lodgepole pines on which the crossbill rely occur within the Sawtooth National Forest (Figure 1). Second, we used our habitat-specific density estimates to estimate global population size.

METHODS

Study Area

The South Hills and Albions are characterized by isolated forest patches in a matrix of sagebrush steppe (Figure 2). Dominant tree species include lodgepole pine (hereafter "pine"), subalpine fir (*Abies lasiocarpa*), and quaking aspen (*Populus tremuloides*), with Utah juniper (*Juniperus osteosperma*) present at lower elevations. We have not observed crossbills feeding on subalpine fir seeds. Douglas-fir (*Pseudotsuga menziesii*) and Engelmann spruce (*Picea engelmannii*) occur in the Albions but are not native to the South Hills. We have conducted much less fieldwork in the

Albions than in the South Hills and suspect that Cassia Crossbills, like Red Crossbills, feed on the occasional large seed crop of Douglas-fir and Engelmann spruce. However, during most years when few or no Douglas-fir or spruce seeds are produced, Cassia Crossbills will be limited by the availability of lodgepole pine seeds (Benkman et al. 2012). Douglas-fir and Engelmann spruce produced few if any seed during fieldwork in 2016.

Rocky Mountain lodgepole pine forests are characterized by stand-replacing fires. Based on the frequency of serotiny (Benkman and Siepielski 2004, Parchman et al. 2011) and the model in Talluto and Benkman (2014), the historical mean fire interval for a pine stand in the South Hills and Albions is predicted to be just over 100 yr. Fire intervals are decreasing in the region (Westerling et al. 2006) and are projected to decrease dramatically in this century (Westerling et al. 2011). This decrease will limit the development of the canopy seed bank relied upon by crossbills (see Enright et al. 2015) and increasingly favor vegetation other than pine (Westerling et al. 2011). The projection of a pine decline, if not disappearance, is consistent with predictions for the region from other modeling approaches (Coops and Waring 2011).
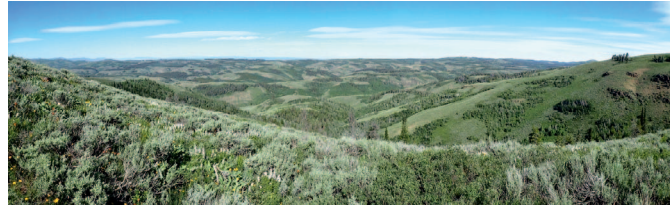
FIGURE 2. Forest patches interspersed within a matrix of sagebrush steppe in the South Hills, Idaho, USA. Photo credit: N. Behl

Pine Coverage and Survey Plots

We estimated the amount of area containing pine from predicted distributions of cover types generated from random-forest (RF) modeling based on Landsat 8 satellite imagery and digital elevation model (DEM) derived layers, combined with measurements of classification accuracy obtained during field surveys. RF modeling is a machine learning method often used in remote sensing for vegetation mapping (Cutler et al. 2007). This approach uses the characteristics of areas with known coverage to predict habitat classification over wide areas of unknown coverage by bootstrapping multiple classification trees. It has many advantages over other classification methods, including high classification accuracy, the ability to determine the relative importance of predictor variables, and the capacity to model complex interactions among predictors (Cutler et al. 2007).

While pine is the dominant conifer in these mountain ranges, we were unable to accurately distinguish it from other conifer taxa in preliminary analyses. We therefore estimated the total area of pine by first estimating the area of coniferous forest, and then determined the proportion of coniferous forest containing pine. Four main cover types were classified by the RF model: coniferous forest, deciduous forest (primarily aspen; hereafter "aspen"), bare ground/rock, and sagebrush (*Artemisia* spp.). Based on previous knowledge of the study area and high-resolution imagery obtained from Google Earth, we established 150 plots (30 m radius) in coniferous forests and 50 such plots for each non-conifer cover type to train RF models. We established 150 plots for coniferous forest rather than 50 because there was greater variability in their underlying predictor variables (Landsat 8 imagery and DEM derived raster layers) than for the other cover types.

To identify which spectral and topographic variables were predictive of each cover type, Landsat 8 satellite images and raster layers derived from DEMs were overlaid on the plots, and Landsat 8 and DEM layer values were determined for a randomly selected point within each plot. Layers were then ranked by their relative importance for predicting cover type. We used the variable selection algorithm in the R package "rfUtilities" (Murphy et al. 2010, Evans et al. 2011) to test for and eliminate predictor layers showing strong multicollinearity. Eleven layers were

retained and used in the final RF models. We ran 10 RF models, each consisting of 999 trees using the "random-Forest" package in R (Liaw and Wiener 2002). These models were averaged to create a final composite RF model used to predict the distribution of each cover type.

To ground-truth the final composite RF model and determine how accurately the model predicted coniferous forest, we visited sites separated by >300 m that were randomly selected from the predicted distribution of conifers. Sites were classified as containing conifers if ≥1 tree within 20 m of the point was a conifer (pine, subalpine fir, Engelmann spruce, Douglas-fir, or Utah juniper). Locations were randomly selected until 150 sites (130 in South Hills, 20 in Albions) were identified as coniferous forest with pine, where crossbill density and environmental variables were later assessed; these sites were separate from those used to train RF models.

To estimate the area of pine in areas mapped as sagebrush, bare ground/rock, and aspen, 30 sites were visited in each of these cover types and evaluated for pine presence. Areas mapped as sagebrush or bare ground/rock never had conifers within 20 m of the survey point, nor did areas predicted to be aspen in the Albions. However, areas predicted to be aspen in the South Hills occasionally had conifers, including pine. Furthermore, while the presence of coniferous forest was predicted with similar accuracy in both mountain ranges (Table 1), the proportion of coniferous forest containing pine was much lower in the Albions than in the South Hills (Table 2). Consequently, classification accuracy and estimated area of pine were assessed separately for each mountain range.

Crossbill Densities and Habitat Use

Each of 3 observers conducted point-count surveys between September 18 and November 4, 2016, at the 150 points that had been selected randomly from within the estimated distribution of pine as described above. Point-count surveys were conducted between sunrise and 1100 hours MST, when crossbills are most active, and during autumn, when crossbill densities are relatively stable (Benkman et al. 2012). Surveys followed methods outlined in Buckland et al. (2001) and lasted 10 min following a 5 min rest period. Because of the upward biases inherent in most density estimates obtained using data

TABLE 1. Predicted and observed cover types in our study area in Idaho, USA, based on the RF model. Sites were classified as "conifer" if lodgepole pine, subalpine fir, Douglas-fir, Engelmann spruce, or Utah juniper was present within 20 m of the survey center.

Observed cover type	Predicted cover type				Total
	Conifer	Aspen	Sagebrush	Rock	
South Hills					
Conifer	165	4	0	0	169
Aspen	28	19	0	0	47
Sagebrush	17	0	19	0	36
Rock	0	0	0	24	24
Total	210	23	19	24	276
Albion Mountains					
Conifer	125	0	0	0	125
Aspen	11	7	0	0	18
Sagebrush	14	0	11	0	25
Rock	0	0	0	6	6
Total	150	7	11	6	174

from full 10 min surveys (Buckland et al. 2001; for Cassia Crossbills, see Santisteban et al. 2012), an instantaneous count was made by recording the number and distance of crossbills present at the end of the survey for estimating the total abundance of crossbills. All perched crossbills were recorded and the distance to the center of each flock from the survey point was measured with a range-finder (Buckland et al. 2001, Matsuoka et al. 2014); Cassia Crossbills were distinguished from the much less common Red Crossbills by vocalizations (Benkman et al. 2009). Flyovers were not included in the analyses (see Santisteban et al. 2012). Local wind conditions, cloud cover (0%, 1–50%, and 51–100%), and occurrence of raptors during surveys were recorded to account for their effects on crossbill detection. Surveys were not conducted during periods of precipitation or dense fog or if wind speeds exceeded about 12–20 km hr^{-1}. Thirteen of the points in the South Hills were within recent (past 10 yr) stand-

replacing fires with few live trees. Because crossbills were not detected at these sites and were unlikely to be of use to crossbills for at least several decades, we excluded these 13 sites from estimates of crossbill density and pine coverage.

As a measure of crossbill habitat use, we estimated point-specific crossbill densities using the full 10 min survey period in Program DISTANCE (Thomas et al. 2010). Note that although 10 min point counts result in inflated densities, they still provide estimates of relative density for comparisons among points, and their larger samples of individuals should provide better estimates of habitat use. We used 4 models to estimate detection probabilities with distance: uniform key function with cosine adjustment, half-normal with cosine, half-normal with hermite polynomial, and hazard-rate with simple polynomial (Thomas et al. 2010). Based on recommendations in Buckland et al. (2001), observations were truncated where detection dropped to 0.10 (85 m), and distances were assigned to 3 variable-sized bins (0–17.5 m, 17.5–35 m, and 35–85 m). Detection of individual crossbills rather than of flocks was modeled because Program DISTANCE does not generate point-specific density estimates when flock size is included in the model. Observer, flock size, wind, cloud cover, and presence of predators were considered as potential covariates in the models (except uniform with cosine adjustment, which is not compatible with using covariates). Variance was estimated by bootstrapping (999 iterations), and model performance was evaluated using Akaike's Information Criterion corrected for small sample size (AIC$_c$). The top-ranked model was used to estimate densities.

Average crossbill density of all survey points was estimated using Program DISTANCE as above, except that data from the instantaneous counts were used and detection of flocks rather than individuals was modeled. Detection dropped to 0.10 at 82 m from the point, and

TABLE 2. Classification accuracies, predicted area of each cover type, estimated area of coniferous forest in each type, estimated proportion of coniferous forest that contained pine, and adjusted estimates for the area of pine present in each cover type in our study area in Idaho, USA. Sites were classified as "conifer" if lodgepole pine, subalpine fir, Douglas-fir, Engelmann spruce, or Utah juniper was present within 20 m of the survey center.

Cover type	Classification accuracy	Predicted area (km^2)	Conifer area (km^2)	Proportion conifer with pine	Pine area (km^2)
South Hills					
Conifer	0.79	102.10	80.22	0.59	47.65
Aspen	0.57	120.96	52.59	0.20	10.52
Sagebrush	1.00	713.60	0	0	0
Rock	1.00	51.90	0	0	0
Albions Mountains					
Conifer	0.83	87.3	72.35	0.13	9.16
Aspen	0.86	69.59	9.94	0	0
Sagebrush	1.00	301.60	0	0	0
Rock	1.00	17.00	0	0	0

distances were assigned to 3 equal-sized bins. The top-ranked model was used to estimate average density.

Landscape, Topographic, and Forest Variables

Crossbill habitat was characterized at each point-count location by 12 landscape, topographic, and forest variables. These same variables were also measured at all points classified as aspen but having pine to account for any differences in the environmental variables between these points and those classified as pine. The 3 landscape variables account for variation in the amount of pine at different spatial scales. These include mountain range (South Hills or Albions; the South Hills contain ~85% of the total pine area; Figure 1), contiguous coniferous forest stand area predicted by the RF model, and predicted amount of coniferous forest area within 85 m of the point (area within which crossbill detections were included in point-count analyses; hereafter "proportion forest"). Crossbill density increased logarithmically with lodgepole pine area at the scale of mountain ranges in the northern Rocky Mountain region (Siepielski and Benkman 2005; South Hills and Albions were considered a single mountain range in the study). The amount of pine at the local scale could also positively influence crossbill abundance.

Topographic variables included slope, a local measure of relative elevation (hereafter "slope position"), and aspect (cosine-transformed so that northerly aspects have positive values). These metrics were extracted from DEM-derived raster layers created with the Geomorphometry and Gradient Metrics toolbox for ArcGIS (Evans et al. 2014). Slope can influence runoff and soil moisture, thereby influencing tree density and primary productivity (Qui et al. 2001, Turner et al. 2004). Slope position may be influential, given that crossbills appear to prefer ridgetops (Nethersole-Thompson 1975). Aspect is potentially important to crossbills because the higher insolation on south-facing slopes could cause cones to open and shed their seeds in the summer, resulting in fewer seeds being available during the rest of the year (Benkman 2016). Thus, north-facing slopes could provide crossbills with more resources and support more crossbills. Heat-load index was estimated but not included in the analyses, because it was correlated with aspect ($r = 0.61$) and was less predictive of crossbill occurrence than aspect.

Six metrics were used to characterize the pine forests within 20 m fixed-radius circular plots centered on each point, based on measurements of the diameter at breast height (DBH) and species identity of all trees with DBH >5 cm. Five of the metrics were as follows: mean DBH for live pines with DBH >15 cm, density of small pines (DBH <15 cm, individuals m^{-2}), density of large pines (DBH >15 cm, individuals m^{-2}), density of non-pines (DBH >15 cm, individuals m^{-2}), and proportion of pines (DBH >15 cm) that were dead. We used DBH = 15 cm as a size threshold

because relatively few cones are predicted to be damaged by foraging crossbills for pines smaller than 15 cm (see Figure 3). Overall, 16% of pines with DBH >15 cm were dead, including many killed by mountain pine beetle (*Dendroctonus ponderosae*) in the 10 yr prior to our study (Benkman 2016). Although the death of lodgepole pines might initially benefit crossbills because the cones weather and open more readily once needles are lost from the canopy (Teste et al. 2011), this benefit is short term because the canopy seed bank is not renewed.

The sixth metric of the pine forests was the estimated number of cones damaged by foraging crossbills at each plot. We used the relationship between the number of cones damaged by foraging crossbills and DBH (Figure 3), in combination with the number and size of pines on each plot, to estimate the total number of cones damaged by foraging crossbills (i.e. the sum of the estimates for each pine within the 20 m radius plot). Cone production and the estimated number of cones foraged on by crossbills come from 726 trees in 74 locations dispersed throughout much of the South Hills, sampled in 2002 (T. Fetz personal communication). Fetz used binoculars to count the number of cones on one side of each tree and then estimated the total number on the tree (LaMontagne et al. 2005). To estimate the proportion of cones damaged by foraging crossbills on each tree, 10 cones on each of 2 randomly selected branches were examined using 10× binoculars or a 20–60× telescope. The proportion of a cone damaged by foraging crossbills was estimated categorically with values of 0, 0.2, 0.4, 0.6, 0.8, or 1.0, depending on the proportion of the scales bent back by foraging crossbills, which spread scales apart to expose underlying seeds (for a photograph of such a cone, see Benkman et al. 2013). The total number of cones damaged by foraging crossbills was estimated by the product of the mean proportion damaged and the total number of cones on the tree. Crossbills damaged an increasing proportion of the cones as tree size increased (Figure 3), presumably because larger (older) trees have an increasing proportion of old, weathered cones whose seeds are more accessible to crossbills (Benkman et al. 2012, Benkman 2016). The large variation among trees in the proportion of cones damaged by foraging crossbills is related, in part, to the variation in seed defenses among trees (see Benkman et al. 2013).

Habitat Use by Crossbills

While landscape and topographic metrics could be assessed over the same spatial scale as crossbill densities (85 m radius around each point), it was not feasible to assess the pine forest variables over such a large area (i.e. beyond a 20 m radius). Because of this mismatch in scale and because most crossbills were detected outside the 20 m radius during point counts, crossbill–habitat analyses were limited to points where the proportions classified as
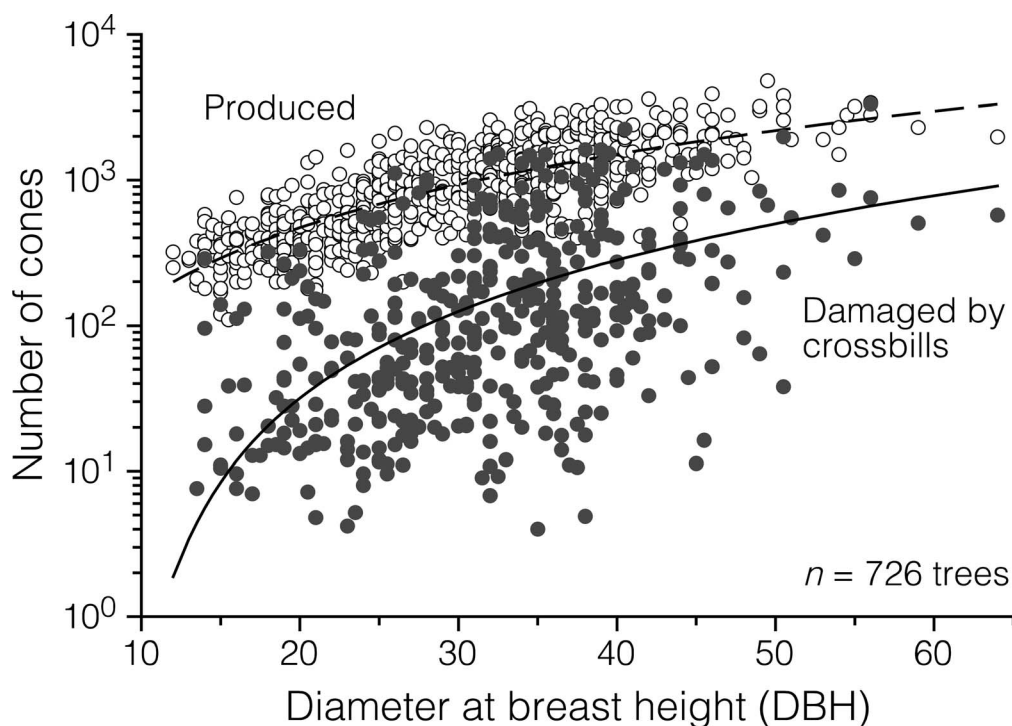
FIGURE 3. The number of cones retained on a tree increased with diameter at breast height (DBH, cm) of lodgepole pine (open circles, dashed curve: ln number of cones = 1.120 + 1.680[ln DBH], $F_{1,724}$ = 1,158, r^2 = 0.62, P < 0.0001) in our study area in Idaho, USA. The number of cones damaged by foraging Cassia Crossbills also increased with DBH (filled circles, solid curve: number of cones = −246.084 + 12.381[DBH] + 0.313[DBH − 29.822]^2, $F_{2,723}$ = 62.9, r^2 = 0.15, P < 0.0001) and represented an increasing proportion of the tree's cone crop with increasing DBH.

coniferous forest by the RF model within the 2 radii at each point (20 m and 85 m) did not differ by >0.15 (results using 0.10 and 0.20 are presented in Appendix Tables 4 and 5, respectively). To further ensure that forest structure was comparable at each scale, Google Earth satellite images were visually inspected. Changes in forest structure within the South Hills and Albions often occur abruptly and are clearly identifiable (Figure 2). Sites where forest structure differed obviously between the 2 scales (20 m and 85 m radii) were also excluded from all crossbill–habitat modeling. Excluding these points left 68 survey sites to assess crossbill–habitat relationships.

Because crossbills were not detected at over half of the survey sites (35 of 68), the conditional model of Fletcher et al. (2005) was used to evaluate environmental influences on crossbill habitat use (i.e. point-specific crossbill density estimates). This modeling approach combines both logistic regression, predicting the probability that crossbills were present, and ordinary regression, predicting the relative density of crossbills among sites where crossbills were present. The logistic regression used the data from the above 68 survey sites, whereas the ordinary regression was limited to the 33 survey sites where crossbills were detected. Variables included in the regressions were selected using a best subsets analysis (package "leaps" in

R; Lumley 2017). For both datasets, model fit (based on R^2 values) stopped improving after ~6 predictor variables were included. Thus, we ran all possible combinations containing up to the 6 top predictor variables, eliminating all models containing highly correlated variables (r > 0.35). Final models were ranked by AIC_c, and all models with AIC_c values ≤2 were presented. The top-ranked logistic and ordinary regression models were selected for generating final estimates of crossbill density at misclassified points.

Population Estimates
Population size was estimated as the product of average crossbill density and the estimated area of pine, plus the product of the adjusted crossbill density and estimated area originally classified as aspen but having pine. Because point counts were not conducted in areas misclassified as aspen (i.e. aspen containing pine), density estimates for aspen were based on the habitat's characteristics using the conditional model. Initially, pine was considered to be present at the site if at least one living, canopy-level, cone-bearing pine with a diameter at breast height (DBH) >5 cm was present. However, crossbills rely on old weathered cones characteristic of large old pines and use small, scattered pines only sparingly (Benkman et al. 2012,

TABLE 3. Parameter estimates for top-ranked ($\Delta AIC_c \leq 2$) logistic regression models predicting Cassia Crossbill presence (A; $n = 68$ survey points) and ordinary regression models predicting Cassia Crossbill abundance (B; $n = 33$ survey points) in our study area in Idaho, USA, with associated ΔAIC_c, w_i (model weight), and R^2 values. The similarity in conifer cover between the 20 m and 85 m radii around survey points was 0.15. All predictor variables were standardized to mean = 0 and SD = 1, except slope position, which was not compatible with transformation. "Proportion forest" refers to the amount of coniferous forest within an 85 m radius plot, and "forest stand area" represents the size of the largest contiguous conifer stand overlapping the plot. "Mean DBH" refers to pines with diameter at breast height (DBH) >15 cm.

(A) Logistic regression models

Parameters [a]							
Proportion forest	Mean DBH	Pine density (DBH <15 cm)	Aspect	Slope position	ΔAIC_c [b]	w_i	R^2
0.22***	0.11[+]	–	–	–	0.00	0.25	0.19
0.21***	–	−0.12	–	–	0.23	0.22	0.19
0.21***	–	–	–	–	1.00	0.15	0.15
0.20**	–	−0.12	0.10	–	1.10	0.14	0.20
0.22***	0.10	–	–	0.06	1.20	0.14	0.20
0.21***	–	–	–	0.07	1.78	0.10	0.17

(B) Ordinary regression models

Parameters [c]							
Forest stand area	Aspect	Range	Pine density (DBH <15 cm)	Proportion forest	ΔAIC_c [d]	w_i	R^2
0.28*	0.39*	0.35	–	–	0.00	0.36	0.28
0.22[+]	0.32[+]	–	–	–	0.78	0.24	0.22
0.28*	0.41*	0.41[+]	−0.39	–	0.82	0.24	0.30
0.28*	0.39*	0.38	–	0.10	1.58	0.16	0.29

[a] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[b] Lowest value of AIC_c 93.71.
[c] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[d] Lowest value of AIC_c −42.35.

Benkman 2016). We excluded sites (both pine and aspen) where the predicted number of cones damaged by foraging crossbills was <500. Crossbills were not detected during surveys at sites with an estimated <650 cones damaged by foraging crossbills, and 500 is many fewer cones than had been damaged in individual trees (Figure 3).

RESULTS

Pine Distribution and RF Model Accuracy

The presence of coniferous forest was predicted with similar accuracy in both the South Hills and Albions (∼80%; Table 2). However, the percentage of coniferous forests containing pine differed considerably between mountain ranges: 59% of coniferous forests in the South Hills and only 13% in the Albions (Table 2). This difference was mostly due to more Douglas-fir and Utah juniper in the Albions: 68% of coniferous forests in the Albions had Douglas-fir or Utah juniper, compared with just 6% in the South Hills. Forty-three percent of aspen in the South Hills had conifers, though only 20% of aspen areas with conifer also had pine (Table 2). By contrast, only 14% of aspen in

the Albions had conifers, and none included pine. Areas predicted to be rock or sagebrush were never misclassified (Table 2). The total area of pine habitat for crossbills was 67 km² (Table 2), which is similar to the previous estimate of 70 km² (Siepielski and Benkman 2005).

Crossbill–Habitat Relationships

The top-ranked model for estimating point-specific densities included a half-normal key with cosine adjustment and a negative effect of increasing cloud cover on detection. Nearly all top models included the same respective core predictor variables and similar parameter estimates (Table 3), suggesting few substantive differences among top models within each set. Only proportion forest was consistently included in all competing logistic models, indicating that crossbills were more likely to be detected where more of the area surveyed for crossbills (within 85 m radius) was forested with conifers (proportion forest in Table 3A). The top logistic model also suggested that crossbills were more likely to be present at sites with larger pines. Mean DBH of pine was also consistently included, and was always significant or nearly so, when restricting

the analyses to sites where the proportion of pine within 20 m and 85 m differed by 0.10 or 0.20 (Appendix Tables 4A and 5A, respectively), further supporting higher crossbill occurrence at sites with larger pines.

All 4 top-ranked ordinary regression models provided evidence for crossbills occurring in relatively higher densities in larger coniferous forest stands and on north-facing slopes (Table 3B). Three of the 4 models provided evidence for higher crossbill densities in the South Hills than in the Albions. Similar results were found when the analyses were restricted to sites where the difference between the proportion of coniferous forest within the 20 m radius forest survey plot and the larger 85 m radius bird survey plot was limited to 0.10 or 0.20 (Appendix Tables 4B and 5B, respectively).

Population Size

The top-ranked DISTANCE model for estimating crossbill density from instantaneous counts used a half-normal key with cosine adjustment and did not include covariates. It produced an average density of 87.5 individuals km^{-2} (95% confidence interval [CI]: 46.7–164.1 individuals km^{-2}). Based on results from the conditional model (Table 3) and habitat characteristics, average crossbill density was 7.7% lower in misclassified aspen sites (80.8 individuals km^{-2}) than in those classified as pine. These density estimates combined with the estimated areas of each cover type (Table 2) yielded an estimate of 5,820 crossbills (95% CI: 3,144–11,049).

DISCUSSION

Cassia Crossbills were restricted to ~67 km^2 of pine forest in the South Hills and the Albions and numbered ~5,800 individuals in fall 2016. Given its restricted range, small population size, and apparent vulnerability to climate change (Santisteban et al. 2012, Benkman 2016), the Cassia Crossbill appears to be one of North America's more imperiled bird species. Below, we discuss patterns of crossbill habitat use, how the latter may be related to climate, and implications of these results for crossbill conservation.

Crossbill Habitat Use

We treat our results as preliminary because of the problematic nature of associating site use with habitat features. Crossbills are not territorial and usually wander in flocks; thus, three 10 min surveys provide only a rough assessment of local density. Moreover, foraging crossbills can be difficult to detect aurally because they often remain quiet. By contrast, crossbills that momentarily land on, for example, a lone tree may be more vocal and detectable. Yet proper assessment of foraging was most important for assessing habitat value to crossbills. Consequently, additional study is warranted. For example, radio-tagged birds could show habitat use. The number and proportion of

older cones damaged by foraging crossbills would also be valuable to estimate (Figure 3). The latter, in particular, provides an integrated estimate of habitat or resource use over multiple years, which would be very useful for characterizing crossbill–habitat relationships. Finally, additional study of nest-site characteristics and the surrounding habitat would be useful to complement our findings for the nonbreeding season. Nest sites, however, are likely not limiting, especially given that major nest predators (e.g., red squirrels and jays) are absent from both the South Hills and the Albions, and that crossbills are not limited to feeding near their nest.

Crossbills were more likely to be detected at sites where more of the survey area was coniferous forest and where forest stands were large. Most top ordinary regression models also suggested that crossbills occurred at higher densities in the South Hills than in the Albions. These findings are not surprising, given crossbills' reliance on pine seeds, and are in keeping with the area–density relationship previously observed in crossbills, whereby crossbill densities increase with increasing total area of lodgepole pine in separate mountain ranges (Siepielski and Benkman 2005).

Although neither slope nor slope position influenced our estimate of habitat use by crossbills, crossbills were detected more often on north-facing slopes. This finding is notable because cones on more northerly facing slopes receive less insolation and presumably experience lower temperatures. Consequently, these cones should be less likely to open and shed seeds in late summer following occasional hot days ($\geq 32°C$), thereby retaining more seeds for crossbills during subsequent months and even years (Benkman 2016). Thus, north-facing slopes may be particularly important for crossbills, especially with the projected increase in hot summer days (Duffy and Tebaldi 2012, Christidis et al. 2014).

No metric of the pine forests was consistently included in either the logistic or ordinary regressions, though mean pine DBH was nearly significant in the top logistic model (Table 3A). The importance of increasing mean pine DBH was found using other thresholds for similarity in the proportion of coniferous forest within 20 m and 85 m radii of measurements (Appendix Tables 4A and 5A), which suggests that crossbills were more likely to be present at sites with larger pines. This result is in keeping with what we would expect given crossbills' reliance on large canopy seed banks and their disproportionate foraging on larger trees (Figure 3) and provides evidence that older stands are critical for maintaining large crossbill populations (Benkman 1993).

Conservation Implications

Many of our results were consistent with those of previous work on the crossbill's reliance on a large canopy seed bank (Benkman et al. 2012, Benkman 2016), underscoring the importance of large stands of mature pine for crossbill

populations (Benkman 1993, Holimon et al. 1998, Summers and Proctor 1999). Crossbills were also more prevalent on north-facing slopes, which would not experience temperatures as high as on other slopes. Previous research has documented how an increase in hot summer days ($\geq 32°C$) resulted in an 80% decline in the crossbill population (Benkman 2016). While crossbills have since rebounded (their density in 2015 was $\sim$90% of that prior to the decline; Benkman 2016), such population declines will likely become more frequent and more severe as climate change progresses and extreme high temperatures become more prevalent (Duffy and Tebaldi 2012, Christidis et al. 2014). Furthermore, long-term projections for the region predict the absence of recruitment of pine in the South Hills and Albions by 2080 (Coops and Waring 2011), which, along with increasing fire frequency (Westerling et al. 2006, 2011), would ensure the extinction of the crossbill.

Although the long-term persistence of crossbills likely depends on halting and reversing climate change (Santisteban et al. 2012, Benkman 2016), our research suggests that several other immediate actions can be taken to improve their chance of persistence. Maximizing the continued presence of large stands of mature pine will be essential, especially given the additional threats from increasing fire frequency and intensity (Westerling et al. 2011). Over the short term, this goal likely requires maintaining multiple, large, mature pine stands, separated by sufficient areas of less flammable sagebrush with little or no cheatgrass (*Bromus tectorum*; for the effect of cheatgrass in increasing fire frequency and size in sagebrush, see Balch et al. 2013). This would reduce the likelihood that a large portion of crossbill habitat is burned in a single fire. Because pine in the Albions and, especially, in the South Hills is patchily distributed in a sagebrush matrix (Figure 2), preventing cheatgrass establishment and expansion could be critical for maintaining large amounts of mature pine for the crossbills. Additional measures to reduce the potential for intense and more rapidly spreading wildfires include thinning younger stands, which would further aid in the rapid development of the more open forests dominated by larger trees with larger canopy seed banks (Verkaik and Espelta 2006) relied on by crossbills (Figure 3). Although the Albions appear to have lower densities of crossbills than the South Hills, the value of the Albions is enhanced by their isolation from the South Hills and thus their lower risk of pine forest loss from a single fire.

Mitigation of the negative impacts of climate change should also be considered. One possible solution is to identify local trees with higher cone-opening temperatures, harvest their seeds, and plant seeds or seedlings on cooler north-facing slopes (Benkman 2016). Assuming that cone-opening temperatures are heritable, such plantings would ensure that the trees most likely to retain seeds following hot summers are present in the areas most insulated from heat, creating a refuge for crossbills. Planting pine seedlings, and perhaps even watering them for one or more summers to enhance their survivorship, might be needed on a large scale, especially in areas of forest disturbance (e.g., fire, logging, or even grazing; Stevens-Rumann et al. 2018).

While crossbill populations have recovered partially from recent declines (Benkman 2016), their total population numbered only $\sim$5,800 individuals in 2016 (95% CI: 3,100–11,000). This population estimate is similar to, or less than, those for many other North American avian species currently listed as threatened or endangered: Golden-cheeked Warbler (95% CI: 4,822–16,016 individuals; Wahl 1990), Marbled Murrelet (*Brachyramphus marmoratus*; 17,800 $\pm$ 3,200 individuals; USFWS 2009), Gunnison Sage-Grouse (*Centrocercus minimus*; 4,554 individuals; USFWS 2014), and Kirtland's Warbler ($\sim$4,000 individuals; Bocetti et al. 2014). While no official assessment of the Cassia Crossbill's conservation status has been conducted, its limited geographic range (Figure 1; Benkman et al. 2009) as well as its recent and probable future habitat and population declines (Coops and Waring 2011, Benkman 2016) qualify it for listing as critically endangered under criteria A and B of the IUCN Red List (IUCN 2012). These considerations, plus its value as a textbook example of coevolution and diversification (Zimmer and Emlen 2017), make the Cassia Crossbill a species of significant conservation concern.

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APPENDIX

APPENDIX TABLE 4. Parameter estimates and associated ΔAIC_c, w_i (model weight), and R^2 values for the top-ranked ($\Delta AIC_c \leq 2$) logistic regression models predicting Cassia Crossbill presence (A; $n = 61$ survey points) and ordinary regression models predicting Cassia Crossbill abundance (B; $n = 29$ survey points) in our study area in Idaho, USA. The similarity in conifer cover between the 20 m and 85 m radii around survey points was 0.10. All predictor variables were standardized to mean = 0 and SD = 1, except slope position, which was not compatible with transformation. "Proportion forest" refers to the amount of coniferous forest within an 85 m radius plot, and "forest stand area" represents the size of largest contiguous conifer stand overlapping the plot. "Mean DBH" refers to pines with diameter at breast height (DBH) >15 cm.

(A) Logistic regression models

		Parameters [a]						
Proportion forest	Mean DBH	Pine density (DBH <15 cm)	Slope position	Proportion dead	Non-pine density	ΔAIC_c [b]	w_i	R^2
0.19**	0.14**	–	–	–	–	0.00	0.28	0.21
0.18**	–	−0.12*	–	–	–	0.41	0.23	0.20
0.19**	0.12[+]	–	0.07	–	–	0.60	0.21	0.23
0.18**	0.13*	–	–	0.07	–	1.08	0.16	0.23
0.21***	0.14*	–	0.08	–	−0.06	1.64	0.12	0.22

(B) Ordinary regression models

		Parameters [c]					
Forest stand area	Aspect	Range	Pine density (DBH <15 cm)	Proportion forest	ΔAIC_c [d]	w_i	R^2
0.27*	0.39[+]	0.45[+]	−0.64	–	0.00	0.23	0.31
0.27*	0.37[+]	0.38	–	–	0.13	0.21	0.26
0.21[+]	0.29	–	–	–	1.00	0.14	0.18
0.22[+]	–	–	–	–	1.29	0.12	0.12
0.27*	0.38[+]	0.49[+]	−0.66	0.13	1.43	0.12	0.32
0.27*	0.36[+]	0.41	–	0.10	1.77	0.09	0.26
0.27*	–	0.27	–	–	1.84	0.09	0.16

[a] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[b] Lowest value of AIC_c 102.91.
[c] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[d] Lowest value of AIC_c −34.13.

APPENDIX TABLE 5. Parameter estimates and associated ΔAIC_c, w_i (model weight), and R^2 values for the top-ranked ($\Delta AIC_c \leq 2$) logistic regression models predicting Cassia Crossbill presence (A; $n = 74$ survey points) and ordinary regression models predicting Cassia Crossbill abundance (B; $n = 36$ survey points) in our study area in Idaho, USA. The similarity in conifer cover between the 20 m and 85 m radii around survey points was 0.20. All predictor variables were standardized to mean = 0 and SD = 1, except slope position, which was not compatible with transformation. "Proportion forest" refers to the amount of coniferous forest within an 85 m radius plot, and "forest stand area" represents the size of largest contiguous conifer stand overlapping the plot. "Mean DBH" refers to pines with diameter at breast height (DBH) >15 cm. Sample sizes for the logistic and ordinary regression models were 74 and 36 survey points, respectively.

(A) Logistic regression models

Proportion forest	Mean DBH	Pine density (DBH <15 cm)	Slope position	Slope	ΔAIC_c [b]	w_i	R^2
		Parameters [a]					
0.21**	0.14*	–	–	–	0.00	0.38	0.17
0.21**	–	−0.13[+]	–	–	1.01	0.23	0.17
0.21***	0.13[+]	–	0.07	–	1.02	0.22	0.19
0.21**	0.13[+]	–	–	0.04	1.58	0.17	0.17

(B) Ordinary regression models

Forest stand area	Aspect	Range	Pine density (DBH <15 cm)	Slope position	ΔAIC_c [d]	w_i	R^2
		Parameters [c]					
0.27*	0.31[+]	0.37	–	–	0.00	0.25	0.22
0.27*	0.35[+]	0.43[+]	−0.46	–	0.35	0.21	0.25
0.20[+]	0.24	–	–	–	0.93	0.16	0.15
0.22[+]	–	–	–	–	1.15	0.14	0.10
0.28*	0.34[+]	0.42[+]	–	0.07	1.45	0.12	0.23
0.27*	–	0.26	–	–	1.66	0.11	0.14

[a] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[b] Lowest value of AIC_c 83.01.
[c] *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [+] $P < 0.10$.
[d] Lowest value of AIC_c −43.98.