

A hierarchical analysis of nesting and foraging habitat for the conservation of the Hispaniolan White-winged crossbill (*Loxia leucoptera megaplaga*)

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Abstract

Little is known about habitat use by the endemic Hispaniolan White-winged crossbill (*Loxia leucoptera megaplaga*), in part because of its small population size and wandering tendencies; before this study only a single nest had been described for the species. From 1996 to 1999 we studied crossbill abundance, and foraging and nesting habitat at three scales (individual tree, local patch, and landscape), in the Sierra de Bahoruco, Dominican Republic. Point-count estimates of the number of crossbills encountered in the 3 study sites varied significantly among years and sites (range = 0.00–2.95 birds/ha), but we estimate that there may be as many as 3000 crossbills in the Sierra de Bahoruco and 3375 island-wide. Annual means of crossbill abundance were highly correlated with mean scores of pine cone abundance. Fifteen nests found in pine trees had a mean nest height of 14.2 m. Two nests were found at heights of 1.0 m and 1.5 m in understory shrubs of *Lyonia* sp. (Ericaceae). The mean age of 15 trees used for foraging or nesting by the crossbill was 96 years. The height of trees used for foraging was significantly greater, and bore significantly more cones, than randomly chosen cone-bearing trees from across the study sites. Results from our multivariate analyses of nesting and foraging habitat at the patch level suggest that crossbills favor sites that have taller, more densely spaced pine trees, and foraging sites contain more cones than are generally available. At the landscape level, both nesting and foraging results suggest that crossbills may respond negatively to fragmentation of the pine forest. Uncontrolled fires are the most important threat to pine forests and the persistence of the crossbill; our models suggest that at current burning regimes pine forest will be nearly eliminated within 100–150 years. Changes in the fire regime are probably human-caused and have altered the nature of fire in this system. Our study supports previous findings that expanses of mature pine are required by this species, but we also suggest protection of unfragmented areas with higher rates of canopy closure. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The endemic Hispaniolan White-winged crossbill (*Loxia leucoptera megaplaga*; American Ornithologists' Union, 1957), which has been recommended for full-species status [Hispaniolan crossbill, (*L. megaplaga*); Benkman, 1994; Smith, 1997], is restricted to pine forests

of the Dominican Republic and Haiti, where it is dependent on pine seeds for food (Benkman, 1994). In the Dominican Republic the crossbill is known primarily from the Sierra de Bahoruco and the Cordillera Central (Keith et al., in prep.). In Haiti, crossbills have been recorded from the westward extension of the Sierra de Bahoruco, known as the Massif de la Selle, and farther west in the Massif de la Hotte (Woods and Ottenwalder, 1986; Raffaele et al., 1998). Whether much forest remains, however, is unknown (Paryski et al., 1989). Although pine forests occurred as low as 200 m in elevation within the last century (Darrow and Zanoni, 1991; Farjon and Styles, 1997), they are now

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restricted to 760–2350 m in the Sierra de Bahoruco and to 450–3100 m in the Cordillera Central.

The Hispaniolan crossbill was first reported to science in 1916, and was known to Wetmore and Swales (1931), but was not reported by ornithologists until 1970 (see Smith, 1997 for a history of this species). The only nest found was described in 1975 (Kepler et al., 1975). The crossbill has been considered an occasional or local wanderer (Wetmore and Swales, 1931), but Dod (1978) speculated that the species had declined in numbers as a result of deforestation through timber cutting. Following a reduction in logging of pine forests after 1967, however, populations of the species may have rebounded (Dod, 1978). Estimates of the number of individual crossbills remaining have ranged from 600 (Benkman, 1992) to “less than 1000” (Benkman, 1994; Smith, 1997) but total numbers of crossbills probably fluctuate depending on food availability. The species has been recently proposed as endangered by the Globally Threatened Species Programme of BirdLife International (BirdLife International, in prep.) because of the small and declining size of the population and the severe fragmentation of subpopulations. Nevertheless, little published literature concerning the Hispaniolan crossbill exists and its habitat has not been quantitatively described.

We constructed a hierarchical habitat model (sensu Johnson, 1980) and examined crossbill habitat characteristics on three scales: tree, patch and landscape. We used measurements of vegetation structure and other habitat variables to create a multivariate statistical model of crossbill habitat. Our specific objectives were to (1) determine abundance of Hispaniolan crossbills in the Sierra de Bahoruco, (2) quantify Hispaniolan crossbill foraging behavior, (3) determine differences between available areas and those used by Hispaniolan crossbills for foraging and nesting at the scale of the individual tree, the local patch and the landscape, (4) determine the relationship between cone production and conifer use by crossbills, and (5) use these data, as well as data quantifying frequency of forest fires and habitat loss, to assess long-term conservation concerns for the Hispaniolan crossbill.

2. Methods

2.1. Description of study area

We studied Hispaniolan crossbills from October 1996 to April 1997, October 1997 to April 1998, and January–February 1999 at three sites in the Sierra de Bahoruco, Pedernales Province, Dominican Republic (Fig. 1). These sites, P1, P2 and P3, were all in mature pine forest at 1100, 1375, and 1470 m elevation, respectively. Foraging and abundance observations were made

at all three sites and all three time periods, but P1 was selected for more intensive studies in 1997–1998 because of the abundance of crossbills at this site. Nesting observations were made in all three sites in 1997–1998 only. P2 and P3 were approximately 15 ha, but P1 was 18.4 ha.

Based on climate and other factors, pine forest in the Sierra de Bahoruco can be classified as lower montane moist forest, lower montane wet forest, and montane wet forest (Holdridge, 1964). The pine forest is relatively homogeneous, however, because fire and soil conditions are most important in determining vegetation at this site (Fisher-Meerow and Judd, 1989). Mean annual temperature is about 15°C, and mean rainfall is about 1700 mm per year (Fisher-Meerow and Judd, 1989) with normally two dry seasons annually (December–March and July–August).

A foliage height profile constructed using data from these same sites (Latta and Sondreal, 1999) shows a fairly open canopy, a sparse intermediate layer, and a denser mixed-broadleaf understory. Canopy cover averaged 51% (S.D. = 26.4) with greatest cover in the 6–15 m height categories and a maximum pine height of

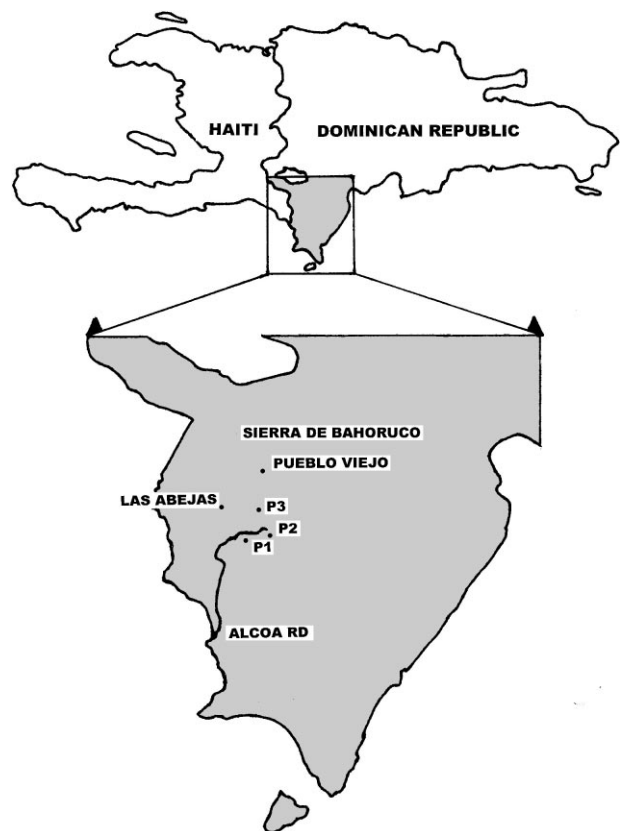


Fig. 1. Map showing locations of three study sites (P1, P2, P3) in the Aceitillar Sector of Sierra de Bahoruco National Park, Pedernales Province, Dominican Republic. The principle study sites, P1, P2 and P3, are at 1100, 1375 and 1470 m elevation, respectively. Surveys were also made from the principle study sites to Las Abejas (1285 m) and Pueblo Viejo (1695 m).

23 m. Mean and median pine heights were 17.7 m (S.D.=4.9 m) and 19.0 m, respectively. The intermediate layer also consisted solely of pine. Broadleaf trees and shrubs formed a dense ground cover and understory, with broadleaf trees extending to heights of 2.5 m. Young pines were also present in the understory.

Pine forest in the Sierra de Bahoruco is characterized as pine savanna and has been studied by Fisher-Meerow and Judd (1989), who found 48% of the plant species to be endemic. These pine savannas are dominated by Hispaniolan pine (*Pinus occidentalis*), and the only other common tree is the palm *Coccothrinax scoparia*. A well-developed shrub layer is present, and common broadleaf species include *Cestrum brevifolium*, *Chamaecrista glandulosa*, *Coreopsis buchii*, *Eupatorium illitum*, *Hypericum hypericoides*, *Lyonia truncata*, *L. microcarpa*, *Myrica picardae*, *Senecio picardae* and *Sophora albopetiolulata*, as well as the succulent *Agave antillana*. The ground is covered by a thick layer of grasses including *Andropogon glomeratus*, *A. urbanianus*, *Schizachyrium gracile*, *Triodia eragrostoides*, *Tripsacum dactyloides* and *Panicum aciculare*, as well as the sedge *Bulbostylis subaphylla*.

Confusion exists as to the nature of the pine savanna typical of these sites (summarized by Fisher-Meerow and Judd, 1989), especially as to whether the savanna is a true climax and whether fire is natural or human induced in the system. However, Sarmiento and Monasterio (1975) and Fisher-Meerow and Judd (1989) argue that since only about 2% of the savanna plant species are non-native and the area supports a large number of endemics, the pine savannas of the Sierra de Bahoruco are natural and have been historically maintained by natural fires that eliminate hardwood trees and encourage pine regeneration. In addition, fire has been shown to be a ubiquitous element of pre-human and post-human landscapes in other pine forests of Hispaniola (Horn et al., in press).

2.2. Data collection

2.2.1. Abundance

We conducted 10-min, 25-m radius point counts at 6 points in each of the three pine forest sites in October, January, and March 1996–1998 and January 1999. Points were situated in a grid pattern with each point 150 m from the closest point. All point counts were conducted by the same observer (SCL), begun at sunrise, and completed by 0930. No point counts were conducted in inclement weather. We calculated the mean number of detections of crossbills within 25 m at each site during each month sampled and the mean number of detections across all sites in each year. A second measure of abundance was made by counting the number of crossbills encountered in 10 min within 50 m of 32 randomly located vegetation plots across the

Sierra de Bahoruco (see Vegetation structure for how these plots were selected).

To assess the relationship between crossbill abundance and pine cone abundance 10 trees at the P1 site were chosen at random, marked, and pine cone presence scored on a scale of 0–4, with 0 representing no cones and 4 representing abundant cones in all portions of the canopy. Trees were scored monthly and a mean score for cone abundance was calculated for each year of the study. Age of cones was not quantified.

2.2.2. Foraging behavior

We recorded a single foraging event for each Hispaniolan crossbill encountered. We used the methods of Remsen and Robinson (1990) and recorded location of the food item or foraging substrate, height of the bird above the ground, canopy height (estimated height of the tallest tree within 15 m), horizontal position of the bird (1=inner 1/3 of tree, 2=middle 1/3 of tree, 3=outer 1/3 of tree), and foliage density at the foraging site. Foliage density was estimated as the amount of light passing through an imaginary 2.0 m diameter sphere surrounding the foraging site (1=75–100% of light passes through, 2=25–74%, 3=0–24%). We identified the food item taken as often as possible.

2.2.3. Nesting behavior

Nests were found in all three study sites, but only P1 was regularly searched intensively for all crossbill nests. Once located, nest placement was measured in terms of nest height, nest height relative to tree height, and distance of the nest from the trunk. Nest locations from the intensively searched P1 were plotted on a map. Area of the polygon defined by nest locations was determined by computer from a digitized image using ARC INFO software.

2.2.4. Vegetation structure

Vegetation was characterized using methods based on Schemske and Brokaw (1981). Vegetation structure was measured at 149 20-m radius circular plots. These plots were centered on (1) trees where crossbills were observed foraging (“foraging plots”), (2) trees with crossbill nests (“nesting plots”), (3) randomly located trees within the P1 study site (“local random plots”), and (4) randomly located trees across the Sierra de Bahoruco (“Bahoruco random plots”). Random trees in the P1 study site were selected by covering the study site in a 6 × 6 m grid, selecting grid coordinates at random, and then locating the tree large enough to be cone-bearing nearest to the center of the randomly selected point. Random trees in the Sierra de Bahoruco transects were located by driving two transects along mostly undeveloped roads (4WD accessible only) principally on the south side of the mountains. One transect (10 points) ran essentially east–west from the end of the

paved Alcoa road to the site known locally as Las Abejas. The second transect (22 points) ran essentially north–south from the lower margins of pine habitat (760 m elevation) in the Aceitillar sector of the park to Pueblo Viejo on the north side of the mountains. We stopped every 1.0 km, randomly determined which side of the road to work, then located a focal tree as the nearest tree to the point 100 m from the road and perpendicular to it. Deforested sites were noted but avoided in vegetation plots; in the event of deforestation on one side of the road the other side was selected.

Within each plot we (1) measured all pine stems > 3 cm diameter at breast height (dbh) and placed these into one of five size classes: 3–8, 8–15, 15–23, 23–38 and > 38 cm, (2) counted all broadleaf stems \geq 3 cm dbh, (3) determined canopy height by measuring the heights of the 10 tallest trees, (4) measured maximum canopy height as the height of the tallest tree in the plot, (5) counted the number of cones on the 10 tallest trees, (6) recorded maximum cone number from these same 10 trees, (7) calculated canopy cover as the mean of 16 spherical densiometer readings from one reading in each cardinal direction at the midpoint of each cardinal radius, (8) measured broadleaf shrub density as the number of woody or herbaceous stems < 3.0 cm dbh present within 1 m of transects along each cardinal radii, (9) measured pine shrub density as the number of pine stems < 3.0 cm dbh present within 1 m of each transect, and (10) counted the number of dead trees (snags). A measure of pine forest continuity on a larger landscape scale was made by recording the presence or absence of contiguous pine forest at 250 m from the focal tree in each cardinal direction. We also recorded plot elevation, slope, and aspect. For circles based on focal foraging trees or nesting trees, and the local random plots, we also recorded the dbh, height, and number of cones of the focal tree, height of the focal tree relative to the mean canopy height in the plot, and number of cones of the focal tree relative to the mean number of cones in the plot. Shrub density was not measured in the Bahuco random plots because it was not expected to be biologically informative on a landscape scale. We used these measurements to create 29 vegetation and site variables (Table 1).

Twenty focal trees at the P1 site were sampled with a core sampler to determine age of the tree. Fifteen trees were selected randomly from those used for foraging or nesting; five additional trees were selected non-randomly to represent the range of dbh sizes of cone-bearing trees present on the site.

2.2.5. Fire history

Fire frequency data for the period 1978–1997 (except 1989) were gathered from records provided by the Dirección Nacional Forestal (DNF). For each fire recorded in Pedernales, Barahona or Independencia

Province we noted year of the fire, hectares burned, and cause of the fire. We believe that most of these fires were in pine forest because precise locations of fires are often given in the records, large portions of each of these provinces lie in the mountains, and more than 75% of all forest fires in the country are in pine forests (Martínez, 1990).

We modeled the effect of fire on habitat availability using the assumptions that: (1) 47,412 ha of pine forest are present in the Sierra de Bahuco (E. Marcano, in lit.); (2) all burns are stand replacement fires leaving few trees suitable for crossbill habitat (SCL, pers. observ.); (3) forests are not used by crossbills until trees reach 71 years of age (the age of the youngest tree used for foraging); and (4) regenerating forest < 71 years old is not susceptible to fire. Two models were generated using different estimates of annual rate of pine forest burned: Model A used the mean amount of forest burned in the last 20 years (1112 ha) expressed as a percentage (1.4%) of the amount of forest originally available (80,000 ha); Model B used a conservative modification of the mean amount of forest burned in the last 20 years (607 ha or 0.8%) by assuming that large fires are eliminated; thus,

Table 1
Twenty-nine vegetation and site variables originally measured or calculated and the code used to describe them

Variable code	Variable description
DBH1	Number of pine trees 3–8 cm dbh
DBH2	Number of pine trees 8–15 cm dbh
DBH3	Number of pine trees 15–23 cm dbh
DBH4	Number of pine trees 23–38 cm dbh
DBH5	Number of pine trees > 38 cm dbh
DBHT	Total number of pine trees \geq 3 cm dbh
D1PC	Percent of total pine trees 3–8 cm dbh
D2PC	Percent of total pine trees 8–15 cm dbh
D3PC	Percent of total pine trees 15–23 cm dbh
D4PC	Percent of total pine trees 23–38 cm dbh
D5PC	Percent of total pine trees > 38 cm dbh
BRLF	Total number of broadleaf trees \geq 3 cm dbh
XCHT	Mean canopy height
MXHT	Maximum canopy height
XCON	Mean number of pine cones
MXCN	Maximum number of pine cones
XCCV	Mean canopy cover
BLSB	Number of woody stems (other than pine) < 3 cm dbh
PNSB	Number of pine stems < 3 cm dbh
SNAG	Total number of dead trees (snags) \geq 3 cm dbh
BRDR	Number of borders to the plot which are deforested
FDBH	DBH (cm) of focal tree
FTHT	Height of focal tree
FCON	Number of pine cones on focal tree
RLHT	Height of focal tree relative to mean tree height in plot
RLCN	Number of pine cones on focal tree relative to mean number in plot.
ELEV	Elevation (m) at center of plot
SLOP	Percent slope of the plot
ASPC	Aspect of the plot

three fires >2000 ha that occurred in 1978 (4088 ha), 1993 (3239 ha), and 1994 (2264 ha) were excluded from fire statistics before a mean was calculated.

2.2.6. Statistical analyses

The software package SYSTAT Version 5.2 (Wilkinson, 1992) was used to perform statistical tests described by Sokal and Rohlf (1995). Data presented are means±S.E. values unless otherwise stated. Data were tested for normality using normal probability plots and tests of skewness and kurtosis. When data were not normally distributed and transformations to normalize the data were unsuccessful, equivalent non-parametric tests were used.

Pearson product-moment correlation coefficients were calculated for all pairwise comparisons of vegetation variables. We then eliminated from subsequent analyses 10 variables which were found to be highly correlated ($r > 0.65$) with other measures of vegetation: DBH1, DBH2, DBH3, DBH4, and DBH5, (correlated with D1PC, D2PC, D3PC, D4PC, and D5PC, respectively), MXHT (correlated with XCHT), MXCN (correlated with XCON), RLHT (correlated with FTHT), RLCN (correlated with FCON), and FDBH (correlated with FTHT and RLHT). Three additional variables were eliminated as being biologically uninformative in this study (ELEV, ASPC, SLOP) since most measurements were from a single intensively studied site or from an array of sites which were predominately on the south slope of the Sierra de Bahoruco.

The 16 remaining vegetation variables were then analyzed using a Mann–Whitney U -test with a Bonferroni correction for multiple comparisons (Dunn–Sidak method; Sokal and Rohlf, 1995) to test the equality of means of each vegetation variable grouped by (1) nesting plot vs. local random plot, (2) nesting plot vs. Bahoruco random plot, (3) foraging plot vs. local random plot, and (4) foraging plot vs. Bahoruco random plot. Vegetation variables that did not differ significantly in these comparisons were then eliminated from further analyses.

Multivariate analyses of the remaining vegetation variables were performed to determine the relative contribution of each variable to nesting or foraging activity. We used a discriminate function analysis (DFA) to compare the vegetation characteristics surrounding foraging trees or nesting trees and randomly placed plots at local and landscape scales. The DFA calculates a linear combination of the vegetation variables such that the difference between random and non-random plots is maximized. The linear discriminant function is: $z = \alpha_1 x_1 + \alpha_2 x_2 + \dots + \alpha_p x_p$, where z is the discriminant score for P vegetation variables normalized with a mean of 0 and a standard deviation of 1, α is the weight for the vegetation variable I , and x is the value of vegetation variable I ($I = 1, \dots, P$). The Wilks' Lambda F -statistic was used to test the equality of discriminant scores.

3. Results

3.1. Abundance

Point-count estimates of the number of crossbills encountered in the 3 study sites varied significantly among years and sites ($G = 556.0$, $P < 0.000$; Table 2) and ranged from 0.00 to 2.95 birds/ha. The abundance of crossbills in 32 randomly located plots across the Sierra de Bahoruco was 0.12 birds/ha (12 birds/km²).

Mean scores for abundance of pine cones varied annually from 1.56 in 1996–1997 to 2.07 in 1997–1998 and 1.40 in 1999. Annual means of crossbill abundance were highly correlated with mean scores of pine cone abundance (Spearman rank = 1.000).

3.2. Foraging behavior and foraging trees

We made 122 observations of feeding crossbills. Nearly all (98%) were of birds feeding on seeds in pine cones; single observations were made of crossbills foraging on palm (*Coccothrinax scoparia*) fruit, pine mistletoe (*Arceuthobium bicarinatum*) fruit, and an unidentified food item taken off a pine branch. The mean height of trees used for foraging was 17.5 ± 0.5 m (range = 10.0–29.0) and these trees contained a mean of 211.5 ± 25.4 cones (range = 3–1000). Birds foraged in the middle to outer third (mean horizontal position = 2.4 ± 0.07) of the upper reaches of the pines (relative height = 0.68 ± 0.02) where foliage density was moderate (mean = 2.27 ± 0.07). Foraging trees tended to be in groups of similar sized trees (relative height 1.02 ± 0.02) but contained more cones (relative cones = 1.51 ± 0.17) than immediate neighbors. In comparison to randomly chosen cone-bearing trees from across the study site, the height of trees used for foraging was significantly greater ($U = 615.5$, $P = 0.008$), and these trees bore significantly more cones ($U = 684.0$, $P = 0.036$). The mean age of 15 trees used for foraging or nesting by the crossbill was 96.4 ± 8.4 years (range = 55–159).

Table 2

Number of Hispaniolan crossbills estimated per hectare at three sites in 3 years in the Sierra de Bahoruco, Dominican Republic^a

Site	1996–1997	1997–1998	1999
P1	2.85	2.95	1.68
P2	0.00	0.20	0.87
P3	0.56	1.13	0.00
Mean	1.13	1.47	0.85

^a Estimates from 1996 to 1998 are the means of six fixed-radius point counts made at each site in November, January and March each year; estimates from 1999 are from six counts per site made in January.

3.3. Nesting behavior and nesting trees

Seventeen nests were found in the three study sites, though most (13 or 77%) were found in the intensively studied P1 site. Fifteen nests (88%) were found high in pine trees with a mean nest height of 14.20 ± 0.81 m (range = 8.0–19.0) and a mean relative height of 0.83 ± 0.03 . Nests were placed near the trunk of the tree (mean distance from trunk = 1.27 ± 0.29 m; range = 0–4.5). Two nests were found at heights of 1.0 and 1.5 m in understory shrubs of *Lyonia* sp. (Ericaceae). At the P1 site, all thirteen nests were found in an area of 2.31 ha, although some of these were not active simultaneously and two were re-nesting attempts by a single pair. Excluding the two shrub nests, heights of trees selected for nesting averaged 17.5 ± 0.9 m tall (range = 11.0–23.0), and these contained a mean 121.9 ± 31.4 cones (range = 0–400). Nest trees tended to be within groups of similar sized trees (relative height 0.96 ± 0.04), but nest trees contained more cones (relative cones 1.53 ± 0.56).

Nesting was confirmed from early January 1998 to April 1998 when incubating adults were observed, but adults feeding juveniles were observed on 30 January 1998, and four birds in juvenal plumage with crossed bills were mist-netted on 3 November 1997.

3.4. Foraging sites — local patch and landscape levels

Fisher's linear discriminant function equation for foraging plots at the local patch level is: $z = 0.286(\text{SNAG}) - 0.081(\text{XCCV}) - 0.002(\text{PNSB}) + 3.373$. The normalized scores from the discriminant function analysis for foraging plots (-1.258) and randomly selected plots (1.304) from P1 differed significantly (F -statistic, $P < 0.0001$). Using this model, counts of snags, mean canopy cover, and pine stems < 3 cm dbh successfully distinguished 69% of the plots used by foraging crossbills in P1 (Table 3).

At the landscape level, Fisher's linear discriminant function equation for foraging plots is: $z = -0.058(\text{D2PC}) - 0.086(\text{BRLF}) - 2.076(\text{BRDR}) - 0.268(\text{XCHT}) - 0.011(\text{XCON}) - 0.019(\text{XCCV}) + 15.327$. The normalized scores from the discriminant function analysis for foraging plots (-2.144) and randomly selected plots (2.193) across the Sierra de Bahoruco differed significantly (F -statistic, $P < 0.0001$). Using this model, the percent of trees in the 8–15 cm dbh size class, number of broadleaf trees > 3 cm dbh, number of borders of the plots which contained contiguous forest, mean canopy height, mean number of cones, and mean canopy cover, successfully distinguished 85% of the sites used by foraging crossbills (Table 3).

The absolute value of the linear correlation of each vegetation variable with the discriminant function was calculated for foraging plots at the local patch level (SNAG, $r = 0.72$; XCCV, $r = 0.89$; PNSB, $r = 0.44$), and

at the landscape level (D2PC, $r = 0.27$; BRLF, $r = 0.38$; BRDR, $r = 0.52$; XCHT, $r = 0.48$; XCON, $r = 0.59$; XCCV, $r = 0.40$). These correlations are a relative indication of the strength of the specific vegetation variable to discriminate between foraging and non-foraging sites in the discriminant function equations.

3.5. Nesting sites — local patch and landscape levels

Fisher's linear discriminant function equation for nesting trees at the local patch level is: $z = -0.0110(\text{DBHT}) + 0.1070(\text{XCCV}) - 4.756$. The normalized scores from the discriminant function analysis for nesting plots (0.934) and randomly selected plots (-1.035) from P1 differed significantly (F -statistic, $P < 0.0001$). Using this model, total number of stems > 3 cm dbh and mean canopy cover, successfully distinguished 78% of the sites used by nesting crossbills in P1 (Table 3).

At the landscape level, Fisher's linear discriminant function equation for nesting plots is: $z = 0.2980(\text{BRLF}) + 1.738(\text{BRDR}) + 0.213(\text{XCHT}) + 0.024(\text{XCCV}) - 12.248$. The normalized scores from the discriminant function analysis for nesting plots (2.576) and randomly selected plots (-2.550) from across the Sierra de Bahoruco differed significantly (F -statistic, $P < 0.0001$). Using this model, number of broadleaf trees > 3 cm dbh, number of borders of the plots which contain contiguous forest, mean canopy height, and mean canopy cover, successfully distinguished 90% of the sites used by nesting crossbills (Table 3).

The absolute value of the linear correlation of each vegetation variable with the discriminant function for nesting plots at the local patch level (DBHT, $r = 0.55$; XCCV, $r = 0.98$), and at the landscape level (BRLF, $r = 0.68$; BRDR, $r = 0.45$; XCHT, $r = 0.43$; XCCV, $r = 0.41$) indicates the relative strength of the specific vegetation variable to discriminate between nesting and non-nesting sites.

3.6. Fire history

Wildfires are a frequent occurrence in the Sierra de Bahoruco and other pine forests of the Dominican Republic (Table 4). Across the Sierra de Bahoruco, 4 of 32 (13%) sites randomly selected for vegetation surveys were deforested by wild fire. From 1978 to 1997, at least 80 wildfires (mean = 4.2 ± 0.6 fires annually) were reported in the Sierra de Bahoruco. Fires burned an average of 1112 ± 308 ha per year. Most fires (54%) were not attributed to a particular cause, but 26% were attributed to farmers, 10% to illegal hunters, 6% to other "criminal elements," and 4% to passing immigrants. The data suggest an increasing trend in the number of fires reported ($F_{1,17} = 3.75$, $P = 0.70$), although variability is high ($r^2 = 0.19$); there is no trend in the mean number of hectares burned per year ($F_{1,17} = 0.23$, $P = 0.64$).

Table 3

Comparison of mean (S.E.) vegetation measurements collected in 20-m radius circles in foraging plots, nesting plots, random plots in the P1 study site, and random plots across the Sierra de Bahoruco

Vegetation variable ^a	Mean vegetation measurements				<i>P</i> values ^b			
	Foraging plot (FP)	Nest plot (NP)	P1 random (PIR)	Bahoruco random (SBR)	FP×PIR	FP×SBR	NP×PIR	NP×SBR
N	76	17	25	32				
DBHT	45.4(6.8)	58.1(14.1)	28.4(4.1)	41.8(7.8)	0.018	0.549	0.016*	0.258
D1PC	31.1(2.6)	32.6(7.0)	26.5(3.5)	39.8(6.1)	0.474	0.417	0.502	0.623
D2PC	30.1(2.2)	30.3(4.1)	34.9(2.9)	19.1(3.8)	0.159	0.002*	0.301	0.028
D3PC	20.3(1.3)	21.6(3.0)	23.8(2.8)	17.5(3.4)	0.359	0.054	0.665	0.160
D4PC	16.3(1.6)	13.7(3.8)	13.4(2.3)	22.3(4.3)	0.426	0.628	0.737	0.599
D5PC	2.1(0.4)	1.8(0.6)	1.5(0.8)	2.6(1.1)	0.157	0.374	0.195	0.387
SNAG	1.4(0.3)	1.9(0.7)	3.5(0.8)	1.4(0.4)	0.001*	0.656	0.147	0.438
BRLF	6.6(1.0)	8.7(2.3)	2.6(0.9)	0.5(0.2)	0.086	0.000*	0.062	0.000*
BRDR	3.9(0.1)	4.0(0.0)	4.0(0.0)	3.3(0.1)	0.073	0.000*	1.000	0.001*
XCHT	17.1(0.3)	18.1(0.6)	16.5(0.6)	13.4(1.0)	0.402	0.001*	0.076	0.002*
XCON	136.5(6.2)	114.3(16.4)	152.1(14.0)	70.6(9.3)	0.455	0.000*	0.135	0.022
XCCV	53.3(1.6)	59.2(3.6)	37.7(3.2)	38.5(4.4)	0.000*	0.001*	0.001*	0.005*
PNSB	5.3(0.9)	13.7(6.3)	10.6(1.4)		0.005*		0.119	
BLSB	30.2(1.7)	44.2(8.4)	58.7(8.3)		0.011		0.187	
FTHT	17.5(0.5)	17.5(0.9)	14.0(1.1)		0.008		0.052	
FCON	211.5(25.4)	121.9(31.4)	138.3(32.1)		0.036		0.812	

^a Vegetation variables described in Table 1.

^b *P* values from Mann–Whitney *U*-test; (*) = statistically significant after a Bonferroni correction for multiple comparisons.

Table 4

Forest fires reported in the Sierra de Bahoruco by the Dirección Nacional Forestal for 1978–1997

Year	Number of fires	Hectares burned
1978	2	4686.1
1979	5	1286.3
1980	0	0.0
1981	4	1541.1
1982	3	679.3
1983	3	272.0
1984	6	241.5
1985	0	0.0
1986	4	103.8
1987	7	1678.2
1988	1	56.6
1989 ^a		
1990	6	1635.4
1991	7	1361.8
1992	4	832.8
1993	8	3933.5
1994	5	2389.1
1995	1	37.7
1996	4	181.8
1997	10	207.3
Sum	80	21124.1
Mean	4.2	1111.8
S.E.	0.6	307.8

^a No data available.

Our models of the effects of fire on pine habitat available for crossbills suggest that the expanse of pine forest quickly decreases to less than one half its original

size in the first 50 years of burning at the current fire frequency, and two-thirds its original size under the less intense fire regime (Fig. 2). Regardless of the burn scenario, pine forest is nearly eliminated within 100–150 years.

4. Discussion

4.1. Abundance

Our estimate of 85–147 birds/km² across our study sites is more than two orders of magnitude greater than the 1 crossbill/5 km² that Benkman calculated in strip transects (Benkman, 1994). Whereas P1 was chosen for intensive studies because of its abundance of crossbills, none of the three sites was originally selected based on crossbill abundance. Evidence that our abundance estimates are not entirely unrealistic is provided by our estimate of a crossbill density of 12 birds/km² in randomly selected sites across the Sierra de Bahoruco. Extrapolated across the 253 km² of pine forest remaining in the Sierra de Bahoruco (E. Marcano, in lit.), population estimates may be as high as 3036 individuals, in contrast to the 1000 individuals estimated for the entire island by Benkman (1994). This higher population estimate may reflect, (1) the effects of a large cone crop or other resource, or (2) an estimate skewed by local concentrations of birds.

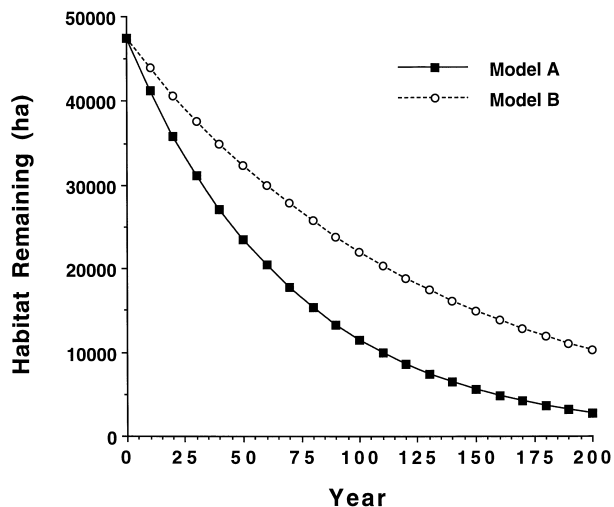


Fig. 2. Two models of the effect of fire on pine habitat used by the Hispaniolan crossbill. Models were generated using different estimates of annual rate of pine forest burned: model A uses the mean amount of forest burned in the last 20 years expressed as a percentage of the amount of forest available at any given time; model B uses a conservative modification of the mean amount of forest burned in the last 20 years by assuming that large fires are controlled or eliminated. See text for full descriptions of model assumptions.

The availability of pine seed may explain the presence of relatively large numbers of crossbills (Benkman, 1987, 1990). Crossbill abundance among years in this study was highly correlated with pine cone abundance at our intensively studied site. Although we did not make systematic estimates of temporal changes in pine cone crops across the Bahoruco, results from our vegetation circles suggest that crossbills were responding positively to pine cone abundance at the landscape level in their choice of foraging (but not nesting) sites. Interestingly, crossbill abundance was relatively high throughout the three years of this study, indicating that the Hispaniolan population of crossbills does not wander as much as other White-winged crossbills (Benkman, 1987, 1992), probably because pine seeds were continuously available. This suggests that *P. occidentalis* holds seeds for extended periods of time in partially open cones (C. Benkman, pers. commun.). Although this has not been reported before for this little-studied pine species (Farjon and Styles, 1997), several other fire-adapted pines hold their seeds, including the Torrey pine (*P. torreana*) and the Table Mountain pine (*P. pungens*; Burns and Honkala, 1990; Richardson, 1998). While we did not quantify age of cones, large numbers of green cones were only observed in 1999, suggesting that the crossbills were utilizing a large cone crop produced in one good year.

An alternative explanation of crossbill abundance based on resource availability may be the presence of water. Surface water is extremely rare in the Sierra de

Bahoruco. The presence of a small, artificial reservoir near the P1 site, which is frequently used by crossbills and other species (Klein et al., 1998), may influence bird distributions and may explain why so much nesting occurred at P1 in particular. This hypothesis is reinforced by the observation that Red crossbills (*L. curvirostris*) drink 22% of their body mass daily when given unlimited access to water in captivity (Dawson et al., 1965).

Finally, our high population estimates may be the result of counts in local areas containing unusually large concentrations of birds. Benkman (1994) speculated that large concentrations of crossbills are unlikely on Hispaniola because of the restricted geographic area from which to draw birds, and the apparent absence of extensive areas of cones produced simultaneously. However, “large” is relative and any concentration of birds will skew population estimates when the true population size is small. Our abundance estimates may reflect the concentration of crossbills on several scales; individuals may gather around scarce resources, but birds also may be concentrated in the Sierra de Bahoruco. Several observers have commented that the species is more common in the Sierra de Bahoruco than in the Cordillera Central (Benkman, op. cit.; Smith, 1997; SCL, pers. observ.), and Benkman (unpubl. data) found that cones were significantly more prevalent along a 3-mile transect on the north side of the Sierra de Bahoruco than they were along a similar transect in the Cordillera Central in March 1988 ($U = 1198.0$, $P = 0.004$). Beyond habitat differences, lower crossbill populations in the Cordillera Central may be the result of historical biogeography or the phenology of cone development, but the possibility of a crowding effect (Lovejoy et al., 1983; 1984), resulting from the packing of more individuals into less habitat as fragmentation and habitat loss proceed, should not be ruled out.

Given these possible explanations for high population densities in our study area, we suggest that our estimate of 3000 birds in the Sierra de Bahoruco is realistic. We have no reason to question Benkman’s (1994) estimate of 0.2 birds per km² in the Cordillera Central (1693 km² of habitat in 1996; Tolentino and Peña, 1998) and we expect few crossbills persist in Haiti (Woods and Ottenwalder, 1986; Benkman, 1994). Thus a total population size might be around 3375 birds.

Finally, simple presence of a species, even the presence of the species in relatively high densities or the presence of breeding individuals, is not a reliable indicator of habitat of sufficient quality and quantity to sustain a population (Van Horne, 1983). In the future we must evaluate reproductive success and determine the habitat variables most significantly correlated with successful reproduction in order to better understand the population dynamics and conservation of this species.

4.2. Nesting behavior

Crossbills breed whenever conifer seeds are abundant and available (Newton, 1972; Benkman, 1990). Benkman (1994) suggested that Hispaniolan crossbills breed from January to May when the cones of *P. occidentalis* are beginning to open. Kepler et al. (1975) reported nest building in early April and summarized museum collection data on gonad size and other morphological characteristics to conclude that breeding likely occurs from mid-winter (January) through early spring (May) but concludes by June. Our data confirm that breeding takes place in the late winter and early spring. However, our mist-netting of birds in juvenal plumage with crossed bills in November suggests breeding probably took place as early as August or September since incubation and fledging take 18–26 days and birds <2 weeks old tend to have uncrossed bills (Benkman, 1992). This extension of the potential breeding season of the Hispaniolan crossbill to nearly year-round is not surprising if, as suggested, *P. occidentalis* retains its cones and seeds over an extended period of time.

The apparent clumping of crossbill nests at our sites is not unusual. Benkman (1992) reports that White-winged crossbill nests in North America are usually clustered, perhaps because of favorable microclimates, distribution of food, or defense against predators. Nest predators in this area are not known, but both jays and squirrels, which are important predators of other crossbill populations (Benkman, 1992), are absent. The clumping of nests in the Bahoruco in the same area in which birds are foraging suggests crossbills may be responding to the distribution of food or water, although other factors cannot be ruled out. For example, clumping as a result of shortages of suitable nesting habitat, forcing birds to nest more densely than expected, should be considered. However, DFA scores show that several plots at the site level (6 of 41 plots in P1 = 14.6%) and the landscape level (4 of 48 plots across the Sierra de Bahoruco = 8.3%) which fell within the range of vegetation characteristics for nest sites were not used for nesting, suggesting that apparently suitable nesting habitat is un-used.

4.3. Foraging and nesting habitat

Results from our multivariate analyses of foraging habitat suggest that crossbills favor foraging sites that have taller, more densely spaced pine trees containing more cones than are generally available. At the local patch level, mean canopy cover was the strongest variable distinguishing sites used for foraging from randomly chosen plots. Foraging sites were also characterized by fewer snags and fewer pine trees <3 cm dbh than found in local random plots. This general pattern was seen at the landscape level as well where a

suite of characters distinguished foraging habitat from the Bahoruco random plots. Here crossbills again preferred plots containing larger trees with higher canopy closure which also resulted in more cones on average than the random plots. Foraging plots also contained more broadleaf trees with stems >3 cm dbh. Since fire would be expected to eliminate these broadleaf trees, snags and small pines (Fisher-Meerow and Judd, 1989), and we believe that recent changes in fire regimes have resulted in fires that eliminate mature pines as well (see Fires and habitat loss below), our results may indicate that crossbills are simply selecting more mature pine sites at both the local patch and landscape levels that have not burned, and in so doing are also encountering vegetation normally excluded by fire.

Sites with taller trees and a more closed canopy were also important in distinguishing nesting habitat. At the local patch level, canopy cover and total number of trees in the plot were both positively correlated with use areas in comparison to randomly selected plots. And at the landscape level, nest sites were distinguished by higher canopy cover and canopy height, and a greater number of broadleaf trees ≥ 3 cm dbh. This again suggests that these are sites dominated by older trees with a more closed canopy where fire may have been recently excluded.

The importance of taller trees and closed canopies at crossbill foraging and nesting sites supports the idea that mature forests are important for crossbill populations (Benkman, 1993, 1994). Although more intensive coring of trees and analysis of growth rates is warranted, our data suggest that forests must be at least 75–100 years old before they will be used by crossbills. These forests are more likely to produce a cone crop during a given year and older trees produce more cones than younger trees (Benkman, 1993). The larger cone crop results in higher intake rates for crossbills (Benkman, 1987), and the larger the cone crop the more crossbills breed (Benkman, 1990).

At the landscape level, both the foraging and nesting results suggest that crossbills may respond negatively to fragmentation of the pine forest. The number of study plot borders where deforestation was recorded was a significant factor in distinguishing between used and random plots for both foraging and nesting birds. In both cases the absolute value of the correlation of this variable (BRDR) with the discriminant function was relatively strong. This negative response to fragmentation is not surprising since Helle (1985) also found that crossbills declined as forests were fragmented in Finland. But these declines were attributed to simultaneous declines in forest age resulting from logging rather than to habitat fragmentation (Helle and Järvinen, 1986). Benkman (1993), however, utilized a metapopulation model to suggest that fragmentation that results in smaller and more isolated patches of appropriate crossbill

habitat with good cone crops will be colonized by crossbills at a decreased rate making crossbills more vulnerable to extinction. In fact, studies have shown that crossbill populations decline disproportionately to the rate of decrease in forest habitat (Väisänen et al., 1986; Benkman, 1993).

4.4. Fires and habitat loss

Uncontrolled fires are the most important threat to pine forests (Martínez, 1990; Ottenwalder, 1999) and the persistence of the Hispaniolan crossbill. In randomly located points across the Sierra de Bahoruco, 13% of the points fell in areas deforested by fire, and LANDSAT images from May 1998 indicate that 47% of 474 km² of pine in the Sierra de Bahoruco are in early seral stages (E. Marcano, in lit.). Analyses presented here suggest that if fires continue to burn at the rate they have in the past 20 years, in the near future little habitat will be available for crossbills or other species dependent upon mature pine. Although pine savannas of the Sierra de Bahoruco are thought to be fire-maintained (Sarmiento and Monasterio, 1975; Fisher-Meerow and Judd, 1989) recent fires tend to be overwhelmingly stand replacement fires. At best, perhaps 30% of the vegetation is skipped over by the flames and may recover (Martínez, 1990; SCL, pers. observ.). This is in contrast to the characteristic surface fires of savannas which burn the grass and understory with return times of 1–10 yr depending on natural moisture levels (Bourlière and Hadley, 1970; Casagrandi and Rinaldi, 1999).

Changes in the fire regime are probably human-caused and have altered the nature of fire in this system. Darrow and Zanoni (1990) reported that frequent and intense fires through Hispaniolan forests disturbed by local farming practices were killing trees before they acquired fire tolerance, especially in Haiti, and that human modification of disturbance regimes had allowed the introduced broadleaf tree (*Syzygium jambos*) to form dense thickets beneath some pines thereby excluding fire and natural regeneration of the pine. We suggest that stand replacement fires may have become the norm because of one or more of the following factors: (1) more frequent ignitions, particularly from escaped fires from slash-and-burn agriculture and fires used to promote growth of forage for cattle; although little agriculture takes place within the pine zone, agriculture is prevalent in the former broadleaf forest at elevations immediately below the pine and these garden plots are frequently burned; more frequent fires may also be associated with changes in the patterns of immigration by Haitians moving through the high mountains and sparking fires through unattended cooking fires; (2) the effects of timber harvest in the decades before 1967 when timber cutting was outlawed may be seen today in that fires, once started, burn more quickly and hotter; Casagrandi

and Rinaldi (1999) and Hoffmann (1999) recently showed how changes in forest morphology will change forest fire regimes in savanna systems like this; (3) changes in the time of burning; agricultural plots in particular are most often burned in February or March at the height of the dry season; if fires burned through pine during these months they may be expected to burn hotter than they would if natural fires were historically lightning-caused and more prevalent in the wet season, resulting in cooler, slower burning fires.

4.5. Conservation measures

Various measures have been proposed to help protect the Hispaniolan crossbill. But, until now, few data have been available to evaluate habitat requirements of this species. Ottenwalder (1992) and Woods et al. (1992) presented a generalized recovery plan for the species in Haiti which recommended surveys to determine the status and distribution of the species, description of habitat requirements, and protection and restoration of habitat accompanied by environmental education and awareness-raising. Benkman (1994) recommended that a basic conservation strategy for protecting the Hispaniolan crossbill should be centered on reducing the probability of the simultaneous failure of the cone crop island-wide by protecting large tracts of mature pine over a wide geographic and elevational range.

Our study supports Benkman's (1994) conclusion that expanses of mature pine are required by this species, but goes further in suggesting that higher rates of canopy closure are preferred over more open sites, and that fragmented sites may be avoided. Whereas crossbills are more prone to wandering than other species, our observation that the endemic pine on which the species depends may retain its cones over an extended period of time is positive in that it offers the promise that local concentrations of large pine seed crops, as we apparently experienced at our study sites, may support concentrations of birds for an extended period of time.

Previous discussions of the conservation of the Hispaniolan crossbill have emphasized the threat to the species posed by the destruction of the pine forests which have been reduced from 16% of original forest cover to only 6% (Tolentino and Peña, 1998; Ottenwalder, 1999), principally through illegal logging (Benkman, 1994; Smith, 1997) and the clearing of land for agriculture (J. Wiley, in lit.). Although these activities are often blamed on illegal Haitians in the border region, Dominican interests frequently encourage the land-clearing (SCL, pers. observ.; J. Wiley, in lit.). Other perceived threats to crossbills have included the cutting of trees for charcoal (Smith, 1997) and the effects of brood parasitism by the Shiny cowbird (*Molothrus bonariensis*; Raffaele et al., 1998). However, we believe these threats are erroneous as pine is not used

for charcoal production (Ottenwalder, 1999), and cowbirds are seldom seen except at low elevations in the Dominican Republic (SCL, pers. observ.; Keith et al., in prep.). This study suggests that the principle threat now is not logging but uncontrolled stand replacement fires which burn far too much of the remaining habitat than can be replaced through regeneration. Immediate steps to reduce and control fires, perhaps including controlled burns during the wet season in areas prone to fire ingress, should be considered. Of course, the relative importance of wildfires will change if industrialized logging is once again permitted on the island, or if timber cutting is not as well controlled as it is now through the vigilance of DNF and national park guards.

We have no reason to believe that our estimates of habitat loss are unique to the Sierra de Bahoruco. Data suggest that on average 4700–6250 ha of forest are lost each year in the Dominican Republic and most of this pine forest (Martínez, 1990; Ottenwalder, 1999). Even were the situation with respect to fire less grim elsewhere, the Sierra de Bahoruco has been recognized as the population center for the Hispaniolan crossbill (Benkman, 1994; Smith, 1997; SCL, pers. observ.) and likely still represents the last best chance to save the species from extinction.

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