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TESTING FOR THE RELATIONSHIP BETWEEN CONIFEROUS CROP STABILITY AND COMMON CROSSBILL RESIDENCE

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Abstract.—Variability in the cone crop of coniferous trees is thought to be the most important cause of the nomadic nature of Common Crossbills (*Loxia curvirostra*). Exploitation of conifers with stable cone crops should therefore enable crossbills to be sedentary. In this study, capture-recapture analysis and comparative analysis of survival data were used to demonstrate that Common Crossbills foraging on Pyrenean mountain pine (*Pinus uncinata*), which produces a stable cone crop, were sedentary from year to year.

PONIENDO A PRUEBAS LA RELACIÓN ENTRE LA RESIDENCIA DE INDIVIDUOS DE *LOXIA CURVIROSTRA* Y LA ESTABILIDAD EN LA PRODUCTIVIDAD DE CONIFEROS

Sinopsis.—Se ha sugerido que la variabilidad en el grado de fructificación y producción de conos de las coníferas es la causa más importante de la naturaleza nómada del Piquituerto común (*Loxia curvirostra*). En consecuencia, la explotación de coníferas con una productividad estable debería permitir a los piquituertos ser sedentarios. En el presente estudio, se utilizan análisis de captura-recaptura y análisis comparativos de la tasa de supervivencia para demostrar que los piquituertos que explotan el pino negro de los Pirineos (*Pinus uncinata*), con fructificaciones estables, desarrollan hábitos sedentarios de año a año.

Common Crossbills (*Loxia curvirostra*) are characterized as nomadic finches with large yearly fluctuations in both breeding and wintering numbers (Haapanen 1965, Newton 1972). Variability in the cone crop of coniferous trees, their main food source, has been regarded as the most important cause of this fluctuation, with birds shifting from area to area in response to food availability (Benkman 1987, Haapanen 1965, Knox 1987, Newton 1970). If such movements are solely to locate food, however, the stability of crossbill populations should increase as the annual variability in fruiting of different, exploited coniferous species decreases (Haapanen 1965, Reinikainen 1937). Thus crossbills exploiting coniferous trees with a regular fruiting, which hold seeds in their cones for extended periods, should have the potential to become resident (Benkman 1989; Génard and Lescourret 1987a; Knox 1987, 1990; Massa 1987; Senar and Borras 1983). Whether such populations are locally resident is unknown, however. Crossbill surveys carried out in a few areas where the birds rely mainly on stable cone supplies have suggested that crossbills are continuously present (e.g., Benkman 1989; Génard and Lescourret 1986, 1987a). Nevertheless, although a given area may contain crossbills for several years in succession, the birds may not be resident, because the population may consist of transients. Capture-recapture studies are therefore the only method of testing for the existence of resident individuals that use the area from year to year. The aim of this study is to use capture-recapture data to determine if Common Crossbills in the Pyrenees are resident. Here the birds mainly rely on the seeds of Pyrenean mountain pine (*Pinus uncinata*) (Génard and Lescourret 1987a, Senar and Borras 1983), a conifer with a remarkable regularity in the production of cones from year to year (Ceballos and Ruiz de la Torre 1971; Génard and Lescourret 1986, 1987a).

METHODS

Crossbills were trapped from June to October 1987–1991 at a permanent banding station in Port del Compte (Pre-Pyrenees, north-east Spain). Birds were caught using mist nets at a drinking bowl. Trapping effort was similar within each trapping session (a whole day from dawn to night), but number of trapping days varied between years (Table 1). The area is a typical subalpine woodland of mountain pine at an altitude of 2000 m (see Vives 1964 for more details). The inter-year stability of the cone crop of this pine and its role as a reservoir of seeds have been studied in detail by Génard and Lescourret (1984, 1986, 1987a) at two Pyrenean stands very close to our study area. According to their 5 yr of data, mountain pines produced a relatively stable cone crop, unproductive years never being recorded (Génard and Lescourret 1986, p. 34, 1987a, p. 59). The vertebrate communities inhabiting these woods have also been described by Génard and Lescourret (1986, 1987b).

Our approach to the study of site fidelity has been the comparison of survival rates of crossbills to those of two sorts of other similar sized passerine species: (1) those known to be resident, and (2) those known to be nomadic. If the survival estimate is based solely on recapture data from the original banding location (i.e., capture-recapture methodology), as is the case here, then the parameter (1-Survival) will include both death and failure to return to the banding location. Therefore, a comparison of crossbill survival rates with those of resident and nomadic species will indicate whether these birds are site faithful (i.e., survival rates similar to other resident species and higher than those of nomadic birds) or highly mobile (i.e., rates much lower than those predicted from resident species) (see Hepp et al. 1987, Hestbeck et al. 1991 for similar rationales). We have used, for comparison, only studies based on the capture-recapture methodology, with recapture data from the original ringing station.

Survival rates were estimated using the Jolly-Seber (J-S) capture-recapture model for open populations (Seber 1982). We used the program JOLLY (Pollock et al. 1990) to compute the different survival and recapture parameters, goodness-of-fit tests and likelihood ratio tests between pairs of models described in the JOLLY handbook. Survival rates were compared using program CONTRAST (Hines and Sauer 1989), which allows for the multiple comparison (as in ANOVA) of rate estimates. Although we present for comparison survival data on several species, contrast analysis was only carried out for species with SE available.

TABLE 1. Capture-recapture data on Common Crossbills on Port del Compte (Pre-Pyrenees, NE Spain) summarized using the Leslie Method of tabulation (Leslie and Chitty 1951, cited in Pollock et al. 1990), and trapping effort in days for each of the years of the study.

Initial capture year	Year of recapture 1987	1988	1989	1990	1991
1987	—	4	1	0	0
1988	—	—	9	1	2
1989	—	—	—	4	3
1990	—	—	—	—	4
1991	—	—	—	—	—
Marked	0	4	10	5	10
Unmarked	32	199	181	87	150
Caught	32	203	191	92	160
Trapping effort	9	7	10	19	17

RESULTS AND DISCUSSION

Over the course of the study, 649 Common Crossbills were trapped and banded, and 27 were recaptured in subsequent years. Tables 1 and 2 summarize the capture-recapture data. Crossbill recapture rates remained quite low, but Table 1 shows that some individuals were recaptured over several years, one of them even in the first, second and fifth year of the study (i.e., they showed site fidelity). The important point, however, is to know if this residency is shown only by a few birds or is characteristic of the whole population. Hence the reason of our probabilistic approach using survival rates.

Crossbill recapture and survival rates can be estimated according to various models and assumptions (Pollock et al. 1990). Model A (the J-S model) calculates survival assuming that recapture and survival rates can vary between the years of the study. Model B assumes that, although recapture rates can vary between years, survival is constant (Model D,

TABLE 2. Capture history for the different individual Crossbills recaptured. 0: not captured in sample, 1: captured and released in sample, n = number of animals with that capture history (see Pollock et al. 1990).

1987	1988	1989	1990	1991	n
1	1	0	0	0	3
1	1	0	0	1	1
1	0	1	0	0	1
0	1	1	0	0	9
0	1	0	1	0	1
0	1	0	0	1	1
0	0	1	1	0	4
0	0	1	0	1	3
0	0	0	1	1	4

TABLE 3. Survival rate and associated SE for several passerine species for which survival rates were calculated from capture-recapture studies. The method of computation of the survival rate is given (CJS: Cormack-Jolly-Seber; JS: Jolly-Seber; Brownie: Brownie et al. 1985).

Species	S	SE	Method	Author
Erithacus rubecula[1]	0.50	—	% alive	Adriaensen and Dhondt 1990
Parus major[1]	0.43[2]	—	CJS	Clobert et al. 1988
	0.40[3]	—	CJS	Clobert et al. 1988
Parus caeruleus	0.68[2]	0.05	CJS	Blondel et al. 1992
	0.47[3]	0.05	CJS	Blondel et al. 1992
	0.49	—	CJS	Dhondt et al. 1989
Parus atricapillus[1]	0.59	0.01	JS	Loery and Nichols 1985
Parus bicolor	0.40	—	Life table	Elder 1985
Serinus serinus	0.60	0.08	Brownie	Senar and Copete 1990
Carduelis spinus	0.22	0.05	JS	J. C. Senar and J. L. Copete (unpubl. data)
Loxia curvirostra	0.46	0.15	JS	This paper
Cyanocitta cristata[1]	0.54	0.09	JS	Hickey and Brittingham 1991

[1] Resident subpopulations.
[2] Males.
[3] Females.

which assumes that both recovery rate and survival are constant between years, could not be used due to insufficient data). Survival results for model A were: S = 0.449 (SE = 0.188) and for model B: S = 0.463 (SE = 0.154). Goodness-of-fit tests could not be computed for either of the models due to insufficient data. The test comparing model A vs. B indicated model B to be the one with the most realistic assumptions concerning recovery rates and survival, however (i.e., it had a comparatively better fit) ($\chi^2 = 0.081$, df = 1, NS) (see Pollock et al. 1990).

Table 3 shows survival rates obtained for several passerine species from other capture-recapture studies. All the included species, except the Eurasian Siskin (*Carduelis spinus*), are typically sedentary species, or resident subpopulations from those species. The siskin is a typically nomadic bird with high mobility between seasons (Newton 1972), and so it is used for comparison. A multiple comparison contrast test among all the species for which SE were available (Hines and Sauer 1989) showed that their survival rates were not homogeneous ($\chi^2 = 62.32$, df = 6, $P = 0.001$). If we excluded the siskin from the comparison test, however, survival rates became homogeneous ($\chi^2 = 10.03$, df = 5, NS), indicating that the difference in survival rates lay between the nomadic siskin and the other species (contrast between the siskin and the other species: $\chi^2 = 30.89$, df = 1, $P < 0.001$), and that the recapture rate of crossbills in this area was equivalent to that of resident species, and was not simply due to a small minority of birds remaining in or returning to the area (survival rate contrast between the crossbills and the other resident species: $\chi^2 = 0.58$, df = 1, NS). This result confirms the suggestion made by several authors that Common Crossbills exploiting coniferous trees with stable crops are able to become resident (see Benkman 1989; Génard and Lescourret 1987a; Knox 1987, 1990; Massa 1987; Senar and Borras 1983), and stresses the fact that crossbill movements mainly result from the need to locate alternative food supplies.

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