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Introduction of exotic tree species as a threat to the Azores bullfinch population

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Summary

1. The Azores bullfinch (or Priolo), *Pyrrhula murina*, is largely confined to native forest in the east of the island of S. Miguel (Azores). This paper assesses the impact of a recent large-scale invasion of the native forest by exotic flora on the population and distribution of this species. It examines the population size and importance of vegetation characteristics to explain the seasonal distribution of this bird. The conservation of this population, including the planning of forest management practices is addressed.

2. Point-counts and capture–recapture indicate a population of 60–200 pairs. The bird occurred all year round in the largest fragment of native vegetation to the east of the range and was recorded in a smaller patch to the west only in autumn.

3. The Azores bullfinch's monthly density was much higher in laurel forest than in exotic forests (*Cryptomeria japonica* and *Pittosporum undulatum*). There were peaks in the density of birds in exotic forests in summer and autumn. The edge of the native forest was important from May to December and the interior from January to April. The degree and intensity of the selection of habitat structure varied seasonally. More habitats were selected over summer than over winter. Native forest and *Clethra arborea* were highly preferred at all seasons. Bare ground and short vegetation were selected in summer and avoided in winter.

4. The Azores bullfinch was sedentary but ranged widely locally. They appeared more mobile over summer than over winter. Larger-scale altitudinal movements were carried out in May.

5. Monthly habitat selection may be interpreted as preference for habitats where feeding resources are more abundant. A large home range is needed in summer because birds feed in openings that are separated by unsuitable tall vegetation.

6. Both demographic and environmental stochasticity are important factors in the conservation of the small population of Azores bulfinch. The first factor may not be the major one because the population may have increased recently due to the introduction of *C. arborea* and also because recruitment seems to compensate annual adult mortality. The invasion of the native forest by aggressive exotic flora seems to be the most important environmental stochasticity factor affecting this population. Present exotic forests are too dense but they could be valuable habitats in summer if they were more scattered. Improvement of the habitat quality of the existing native forest and expansion of its area are important nature conservation strategies for this population.

Key-words: bullfinch, Azores, distribution, habitat selection, mobility, conservation.

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Introduction

The Azores (or São Miguel) bullfinch or Priolo, *Pyrrhula murina* Godman, is only known in the east of the island of S. Miguel. It seemed locally abundant in the second half of the last century and early this century; it was regarded a pest because it ate the flower buds of orange trees and was easily collected for museums at mid altitudes (Hartert & Ogilvie-Grant 1905; Bannerman & Bannerman 1966). Early this century it became rare in mid altitude areas where it was

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easily collected and observed (around Furnas, Fig. 1; Bannerman & Bannerman 1966), which coincided with an apparent increase in the felling and use of the native forest (Ramos 1993). More recently the population was estimated at 30–40 pairs in the late 1970s (Le Grand 1983) and 100 pairs in 1989 (Bibby & Charlton 1991; Bibby, Charlton & Ramos 1992b). Observations in 1990 found the Azores bullfinch largely confined to native vegetation (Bibby & Charlton 1991) but did not attempt a quantitative description of the habitat or of seasonal variations in habitat selection. This species living in small numbers in a restricted area may be affected by demographic and environmental stochasticity and is of considerable conservation interest.

Native vegetation in the east of S. Miguel has been cleared for pasture and afforested mainly with *Cryptomeria japonica*. In addition, recently introduced aggressive exotic plants, *Pittosporum undulatum*, *Hedychium gardneranum* and *Clethra arborea* are causing major changes to the remaining fragments (Sjogren 1973; Haggar, Westgarth-Smith & Penman 1989; personal observations). Birds were observed near the edges of *C. japonica* plantations or in areas where trees were young or scattered but were not recorded in extensive plantations (Bibby & Charlton 1991).

This study evaluates the influence of the recent large-scale invasion of the native forest by exotic flora on the population and distribution of the Azores bullfinch. It provides data on numbers, distribution, movements and seasonal variations in the selection of forestry areas, as a way to: (i) establish seasonal vegetation characteristics selected by the birds, (ii) attempt to explain its range contraction over this century, and (iii) plan forest management practices for this population.

Methods

STUDY AREA

The Azores (36–39°N, 25–31°W), are subject to a temperate oceanic climate (Medeiros 1987). The Azorean laurel cloud forests are, together with those of Madeira and the Canaries, considered remnants of the old Tertiary forests that once covered Southern Europe (Tutin 1953). Altogether 56 taxa are endemic, of which 35 are restricted to the cloud forests (Palhinha 1966; Sjogren 1984). For plant taxonomy see Palhinha (1966). For a general description of most species see Sjogren (1984).

The study area (in S. Miguel), is densely vegetated with steep ground. Surveys were made in 1991–92 and 1993. Sampling in and around the entire area of native forest was important to ascertain its range but most other observations were concentrated on the area around Pico da Vara summit (Figs 1 & 2). The observations ranged from 100 to about 870 m of altitude; native forests being present above 400–500 m. Areas below are dominated by exotic vegetation; *P. undulatum* around streams, *C. japonica* on slopes and *H. gardneranum* on recently formed openings. *C. arborea* is widely scattered amongst the native forest. A vegetation map of the range of the Azores bullfinch (Fig. 1) was prepared at 1: 25 000 scale from aerial

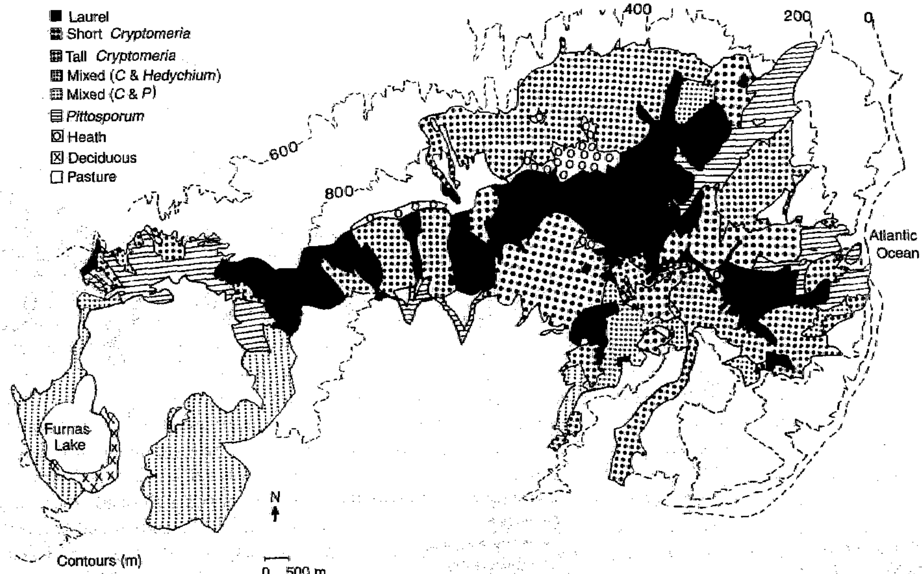

Fig. 1. General vegetation types across the entire range of the Azores bullfinch. Pasture land with small hedges predominates between sea-level and the general vegetation types indicated on the map.

photographs (from 1: 9000–1: 15 000 scale) and verification of vegetation types in the ground.

POINT COUNTS

Random transects were not possible as the habitat was inaccessible. Instead, 22 routes were established along walkable tracks covering all vegetation types in the historical range of the Azores bullfinch (Fig. 2). Points were marked every 200 m along these routes. To ascertain distribution and population size birds were counted during 8 min at these points, starting 2 min after arrival at the point (1 min rest and 1 min imitating the piping call). Imitating the piping call may lead to density overestimates as some birds approached the stations (Bibby, Burgess & Hill 1992a) but, because vegetation was dense and bullfinches are inobtrusive, this was necessary to ensure that birds were dectected. Birds were counted as within, on or beyond 30 m (in order to compare estimates with a previous study) of station at first detection. Most routes were walked in April/May, August/September and December/January (Table 1). To estimate population size only May counts (prior to the start of the breeding season) on routes 3–9 and 11, 12 (the main distribution area of the bird) were used.

A small variation of this counting method was developed to study habitats along routes 3–9 and 11, 12 (Fig. 2), in a total of 125 points covering all vegetation types in the area. Each route was walked three times a month (in August, September, January and April routes 4, 5 and 7 were walked only twice); two mornings between 07.30 and 12.00 h and one afternoon between 15.30 and 19.00 h to score the presence or absence of birds at stations in a 3-min watch (so a suitable sample size for each month could be obtained). Watches started with 15 s imitating the bullfinches piping call. Birds were located within on or beyond 50 m of the station and assigned to the habitat type (see below) in which they were first detected. Three minutes were used instead of 8 min to provide a suitable sample size for each month. A 50-m detection distance was used rather than 30 m because: (i) about 70% of these records were estimated to be within 50 m, and (ii) the evaluation of habitat types and habitat structure in a larger area was not praticable in this ground.

MIST-NETTING

Mist-netting was carried out at feeding sites on up to 4 days a week. Three sites (A, B and C) were used quite regularly. Site A (valley site) was a large P. *capitatum* patch in Ribeira do Guilherme, 550 and 450 m away from sites B and C, respectively. Sites B and C (road sites) comprised two patches of *Polygonum capitatum*, one patch of *Leontodon filii* and a gap between *C. japonica* and laurel forest mixed with pines. The two sites were 200 m apart. Netted birds were colour-ringed. All captures and sightings were recorded and 1:25 000 maps were made of the occurrence of individual birds.

POPULATION ESTIMATES

The variable circular plot and the capture–mark–recapture methods were used. In the first, given some

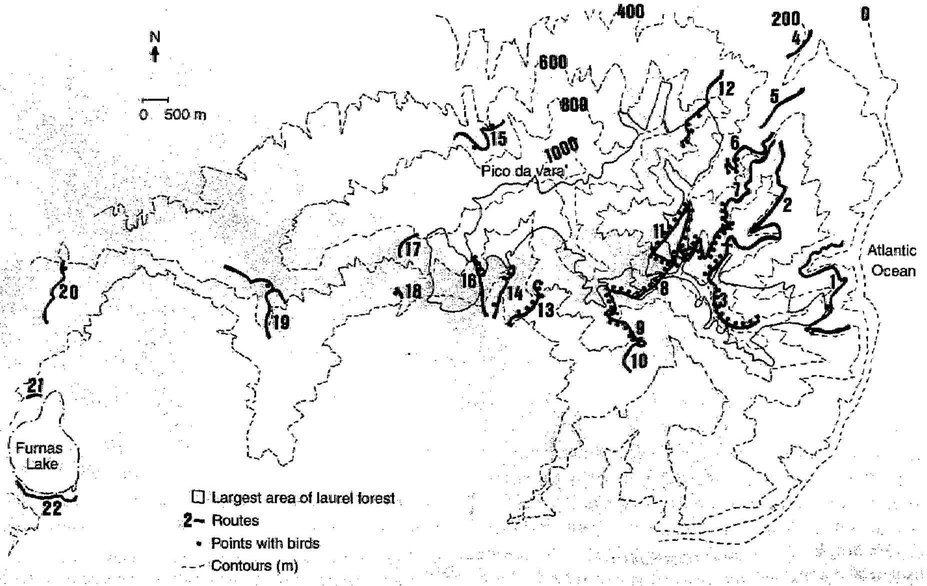

Fig. 2. Distribution of the Azores bullfinch and location of routes in eastern S. Miguel. Stations were marked every 200 m along routes.

Table 1. Details of survey routes and records of Azores bullfinches during 8-min point counts. Route numbers correspond to those shown in Fig. 2

			No. birds during surveys						
Route	No. points	Main habitats	Apr/ May 1991	Apr/ May 1992	Apr/ May 1993	Aug/ Sep 1991	Oct 1992	Dec 1992	Jan 1992
1	20	*Pittosporum*/*Cryptomeria*	0			2			0
2	18	*Cryptomeria*	0			0			
3*	15	Laurel	2	5	5	3		3	
4*	9	*Pittosporum*	0	0	0	0			
5*	9	*Pittosporum*/Pasture	0	0	0	0			
6*	12	*Cryptomeria*/*Pittosporum*	3	1	2	3		0	
7*	19	*Cryptomeria*	0	0	1	1		0	
8*	23	*Cryptomeria*/Laurel	12	8	6	5			
9*	6	*Cryptomeria*/Pasture	2	0	0	3		0	
10	5	Pasture/Hedges	0			0			
11*	17	Laurel	11	9	7	6			
12*	15	Laurel/*Cryptomeria*	8	2	2				
13	12	*Cryptomeria*/Laurel				6			2
14	10	*Cryptomeria*/*Clethra*				4			3
15	11	*Cryptomeria*	0			2			
16	8	Laurel				3			2
17	3	Laurel/*Cryptomeria*	0			0			
18	2	Laurel	0			1			
19	13	Laurel	0	0	0	1	0	0	0
20	8	Laurel/*Cryptomeria*	0		0	1	2	1	0
21	3	Deciduous/*Cryptomeria*	0			0			0
22	8	Deciduous	0			0	0		

* Routes where presence or absence of birds per habitat type were recorded three times a month and where habitat types and habitat structure were recorded within a 50-m radius.

assumptions (Buckland 1987), knowledge of the numbers of birds detected inside and beyond 30 m allows relative density estimates (D) by assuming an exponential relationship between detectability and distance: $D = \ln (n/n_1)\, n/m\pi r^2$ where n = total number of birds detected, n_1 = number of birds outside the pre-selected radius r, and m = number of points. A crude estimation of population size was obtained multiplying the number birds ha^{-1} by the area of the native forest (mean = 580 ha, range = 557–585, calculated using a planimeter) where they occurred throughout the year.

The second method was computed using sightings (net recaptures were too few) along marked routes, walked in the morning at a slow pace. Estimates were obtained for: (a) routes 6, 8, 9, 11, used as the most accurate estimate of summer population sizes and year to year differences; and (b) routes 8, 9, used to examine seasonal differences. Population size was estimated for areas (a) and (b) averaging 6–11 different estimates, in which sample sizes between 3 and 37 ringed birds were used. This minimizes the effect of chance variation (Stamm, Davis & Robins 1960). Standard errors were calculated according to Bailey (1951). The visible area covered by the routes fitted ≈ 2·8 (routes 6, 8, 9, 11) and 4·8 (routes 8, 9) times into the main range of the bird, enabling a crude estimate of total population size. Several assumptions underline the use of the Lincoln index (see Nichols *et al.* 1981). Movement data showed that caution about two basic assumptions, that animals should mix freely and that no animals should move in and out of the area being sampled during the recapture period, would be necessary (see mobility).

MEASURING AND ANALYSING HABITAT TYPES

In order to establish seasonal variations in the use of forestry areas by Azores bullfinches the following habitat types were identified: (i) laurel forest (Laurel); (ii) laurel edge (L.edge); (iii) short *C. japonica* within 200 m of the laurel forest (Sc < 200 m L); (iv) short *C. japonica* (< 6 m) beyond 200 m of the laurel forest (Sc > 200 m L); (v) tall *C. japonica* (> 6 m) within 200 m of the laurel forest (Tc < 200 m L); (6) tall *C. japonica* beyond 200 m of the laurel forest (Tc > 200 m L); (vii) *P. undulatum*; and (viii) other habitats and birds in flight (other habitats). Laurel edge was considered to be 10–20% of the 50 m radius at each point, where laurel had adjoined with other vegetation types. *C. japonica* within or beyond 200 m of the laurel forest was differentiated because areas within 200 m had more openings and landslides and were within easy reach of birds from the laurel forest.

The proportion of each habitat type in a 50 m radius of each station was estimated visually. Maps and aerial photographs helped to record habitats within and beyond 200 m of the laurel forest. This was converted to area (Table 4) and an index of population density per habitat type (number of sightings per ha) was determined at each visit as: number of positive records in habitat A/area of habitat A. The average of three visits provided a monthly index of bird density per habitat type. Values are presented as mean ± SE. Statistical differences in bird density amongst habitat types were examined within summer, autumn and winter, as defined before, by one way ANOVA followed by the Tukey test (Sokal & Rolf 1969)

MEASURING AND ANALYSING HABITAT STRUCTURE

Vegetation structure and composition were measured to establish vegetation characteristics that determine the selection of forestry areas by Azores bullfinches. These were recorded by visual estimation (Bibby, Aston & Bellamy 1989) within a radius of 50 m. I estimated percentage coverage of grass (GRAS) and bare ground (GROUND); % volume of foliage between 0 and 0·5 m (FOLA), 1–2 m (FOLB), 2–4 m (FOLC) and > 4 m (FOLD); % volume of foliage of the following vegetation types: Native 0–4 m (LAUA) and > 4 m (LAUB), *C. arborea* 0–4 m (CLEA) and > 4 m (CLEB), *P. undulatum* 0–4 m (PITA) and > 4 m (PITB), *C. japonica* 0–4 m (CRYA) and > 4 m (CRYB). The canopy height (CANOPY) of the dominant plant species was estimated and the altitude (ALT) was measured with an altimeter.

Stations used more often are expected to be more important for birds; so the number of times a bird recorded within 50 m radius of each station was used as the dependent variable (occurrence). The contribution of composition and structural habitat variables in explaining the variance of occurrence was assessed using logistic regression with the denominator being equal to the number of times a station was surveyed. Three different time periods were considered: summer (May–August), autumn (September–December) and winter (January–April). This multivariate approach enables one to remove the effects of correlations between variables and makes no assumption about the form of the frequency distribution of the habitat structure values (Manly, McDonald & Thomas 1993).

The logistic modelling was fitted as stated by Bowden (1990) using the statistical package GLIM (Payne 1987). First, the effects of all habitat variables were examined. Secondly, the effect of omitting each variable in turn was examined by recalculating the model and comparing the deviances between the two models including and excluding the focal variable. The model of best fit was identified when removal of any of the remaining variables would increase ($P < 0.05$) the deviance significantly.

Results

DISTRIBUTION

Two main aspects were found: (i) the bird was encountered on routes largely confined to native vegetation and its margins (Figs 1 & 2); (ii) the bird was present throughout the year in the largest area of laurel forest (Fig. 2, Table 1) but on a smaller area to the west (Fig. 1; routes 20, 19 of Fig. 2) it was found only in autumn (Table 1). The birds seen in the west were only juveniles (with brown caps; see Newton 1964); routes 19 and 20 provided very good views of the native forest. The Azores bullfinch is the only species in S. Miguel that feeds on fern fronds in spring, leaving conspicuous beak marks (Ramos 1994a). These were not found on west routes which indicates that in spring birds were no longer present there.

POPULATION ESTIMATES

Population estimates are given in Tables 2 and 3. Estimated values using the variable circular plot method were not significantly different between 1991, 1992 and 1993 ($\chi^2 = 3.73$, d.f. = 2). Table 3a presents the Lincoln index for routes 6, 8, 9, 11 and Table 3b for routes 8, 9. The larger sample (a) represents the most accurate estimate of summer population sizes and of year-to-year differences whereas (b) is used to examine seasonal differences. A significant decrease (all χ^2, d.f. = 1 with Yates correction) occurred in (a) between 1991 and 1992 ($\chi^2 = 26.47$, $P < 0.001$). Seasonal differences (b) were significant between 1991 and 1992 ($\chi^2 = 13.5$, $P < 0.001$), and 1992 and 1993 ($\chi^2 = 5.16$, $P < 0.05$).

HABITAT SELECTION

Table 4 shows the area of each habitat type measured within 50 m radius of each point ($n = 125$ points). Figure 3 shows monthly densities of Azores bullfinches per habitat type. Four features arise from this figure. (i) Laurel forest was the only habitat consistently used throughout the year; in winter and early spring it accounted for up to 90% of the records. (ii) The edge of the Laurel forest and areas in its vicinity were heavily used in summer and autumn. (iii) Stands of tall *C. japonica* and *P. undulatum* were of marginal importance. (iv) Other habitats, mixed copses of *P. undulatum* and *Acacia meloxylon*, small areas of deciduous trees, pasture with hedges and fields of *H. gardneranum* and heath were pratically not used. During the study only four birds were seen in hedges, situated very close to short stands of *C. japonica* with openings. There were small peaks in the density of the Azores bullfinch in exotic forest habitat types: (i) *P. undulatum* in June and October; (ii) tall *C. japonica* within 200 m of the laurel forest in August (direct observations of colour-ringed birds showed this peak

Table 2. Population estimates: variable circular plot method. Eight minutes point counts were made in May (early June for 1993) within laurel forest and margins, including exotic vegetation, where birds were recorded more regularly. Bird density was multiplied by the area of native forest where birds occurred throughout the year (580 ha) enabling a crude estimation of population size

Year	No. birds in 99 point counts	Density (birds ha^{-1})	Total N (birds ha^{-1} × 580 ha)
1991	36	0·58	336
1992	25	0·46	267
1993	22	0·48	278

Table 3. Population estimates (N): Lincoln index. (a) is used as an estimate of summer population sizes and year to year differences and (b) is used to examine seasonal differences. The visible area covered by the routes fits ≈ 2·8 (routes 6, 8, 9, 11) and 4·8 (routes 8, 9) times into the main range of the bird, enabling a crude estimation of total population size (total N = average × 2·8 for routes 6, 8, 9, 11 or 4·8 for routes 8, 9)

	No. estimates	No. birds ringed	Estimated pop. size N	SE
(a) Routes 6, 8, 9, 11				
1991	11			
Range		14–37	76–420	24·8–402·1
Average		28	151	86·4
Total N			423	
1992	10			
Range		10–33	26–99	9·1–93·3
Average		24	73	32·6
Total N			204	
(b) Routes 8, 9				
Summer				
1991	6			
Range		8–22	45–140	15·2–74·8
Average		16	73	30·8
Total N			350	
1992	7			
Range		7–23	36–59	8·0–63·6
Average		13	45	21·6
Total N			216	
Winter				
1992	8			
Range		10–21	26–40	2·7–20·8
Average		15	34	12·1
Total N			163	
1993	7			
Range		3–14	5–66	1·8–60·3
Average		8	25	15·6
Total N			120	

Table 4. Area of each habitat measured within 50 m radius of the 125 marked stations. Distribution of areas is indicated as the number of points (No. points) which main habitat type is indicated. Apart from laurel edge all other points were largely within the referred habitat type

Habitat code	Habitat type	No. points	Area (ha)
Laurel	Laurel (native) forest	24	19·6
L. edge	Laurel edge	15	3·2
Sc < 200 m L	Short (< 6 m) *Cryptomeria japonica* within 200 m of the laurel forest	15	15
Sc > 200 m L	Short *C. japonica* beyond 200 m of the laurel forest	7	5·5
Tc < 200 m L	Tall (> 6 m) *C. japonica* within 200 m of the laurel forest	11	6·5
Tc > 200 m L	Tall *C. japonica* beyond 200 m of the laurel edge	27	21·6
Pitt.	*Pittosporum undulatum*	21	17·9
Other habitats	Other habitats	5	8·1

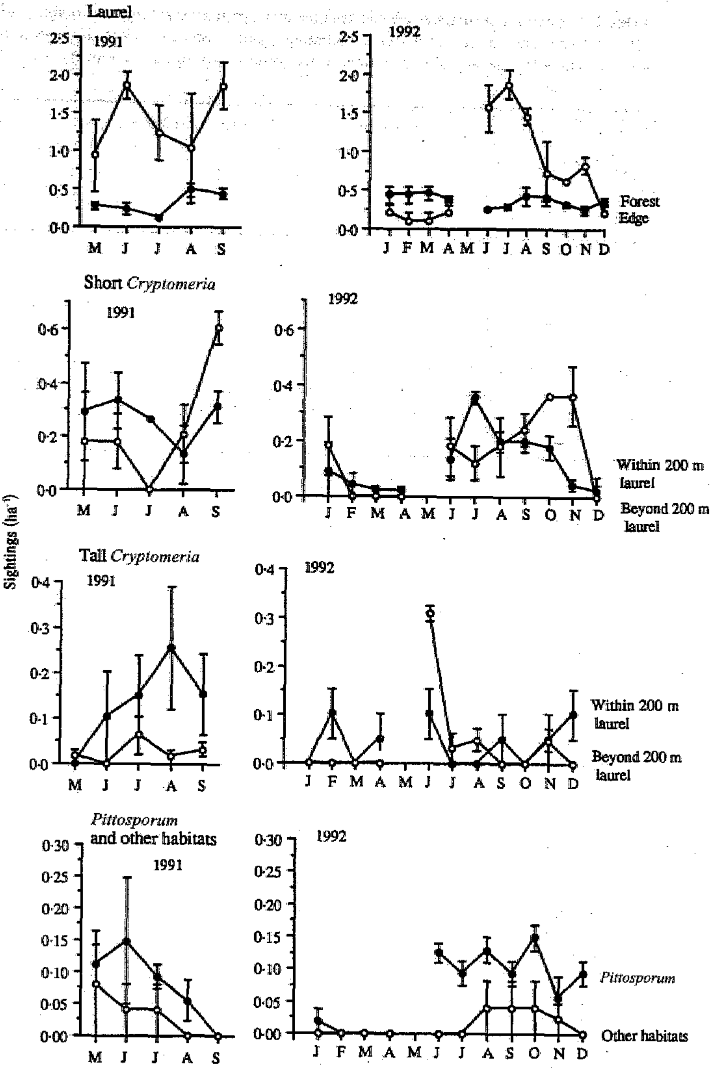

Fig. 3. Azores bullfinch density as sightings ha^{-1} in different habitat types present within 50 m radius of sampled stations. Values are mean and SE of three visits per month (see Methods). Note the different scale for different habitats.

to be due to no more than 6–8 birds); (iii) tall *C. japonica* beyond 200 m of the laurel forest in June; and (iv) short *C. japonica* beyond 200 m of the laurel forest in November (Fig. 3).

The Azores bullfinch densities were highly significantly different between habitats in summer ($F = 43{\cdot}60$), autumn ($F = 20{\cdot}54$) and winter ($F = 31{\cdot}58$; all one way ANOVA $P < 0{\cdot}001$, d.f. = 7,88). Tukey tests were performed on these analyses. The summer ANOVA was accounted for by a higher mean density in L.edge when compared with Laurel ($q = 15{\cdot}8$) and with all exotic forest habitats ($16{\cdot}2 < q < 19{\cdot}9$). The autumn ANOVA was explained by a difference in mean density between L. edge–Laurel ($q = 7{\cdot}4$), L. edge–exotic forest habitats ($8{\cdot}5 < q < 13{\cdot}7$) and Laurel–exotic forest habitats ($4{\cdot}9 < q < 6{\cdot}2$) except short *C. japonica*. The density in short *C. japonica* beyond 200 m of laurel was also higher than the one in tall *C. japonica* beyond 200 m of laurel ($q = 5{\cdot}1$). This suggests that as *C. japonica* plantations get older they became more unsuitable for birds. In the winter ANOVA the mean density in Laurel was higher than the density in L. edge ($q = 10{\cdot}6$) and that in all other habitat types ($14{\cdot}8 < q < 16{\cdot}3$).

HABITAT STRUCTURE

The habitat parameters that accounted for habitat selection showed seasonal variation. LAUA and CLEB were highly preferred ($P < 0\cdot001$) during all seasons, which implies that they are very important criteria for habitat occupancy. Small stands and individual *C.arborea* trees were scattered within the endemic forest, which makes it difficult to assess its sole influence on Azores bullfinch occurrence. Ground was preferred in summer and autumn. PITB and CANOPY were avoided. (Table 5). All exotic species presented taller canopy (usually > 6 m) than native species (usually < 5 m). A surprising finding was the fact that CRYB and PITA were highlighted as preferred ($P < 0\cdot05$ or $P < 0\cdot01$) in summer and autumn and, summer and winter, respectively.

Examining the important variables in the logistic models (Table 5) suggests that, to a large extent, LAUA, LAUB, CLEB and CANOPY can be used to characterize the Azores bullfinch's habitat selection during all seasons. Changes in the degree of significance of these parameters were uncommon and most significant habitat parameters were usually preferred or avoided. A seasonal difference in preference for foliage profiles was detected. Tall vegetation (> 2 m) was avoided in summer whereas short vegetation (< 2 m) was avoided in autumn and winter.

The difference in deviance between models provides a chi-square test of goodness-of-fit with degrees of freedom equal to the difference in the number of parameters estimated for the two models being compared (Bowden 1990; Manly, McDonald & Thomas 1993). The winter model gave a much better fit than the summer ($\chi^2 = 121\cdot1$, $P < 0\cdot001$, d.f. = 4) and autumn models ($\chi^2 = 97\cdot8$, $P < 0\cdot001$, d.f. = 7). The difference in deviance between the autumn and summer models was less but still highly significant ($\chi^2 = 23\cdot2$, $P < 0\cdot001$, d.f. = 5). Therefore, this exploratory analysis suggests that precision of habitat selectivity may increase in the following direction: summer < autumn < winter.

MOBILITY

Most sightings of breeding birds overlapped extensively. Figure 4 shows the cumulative number of Azores bullfinches caught in each netting session in relation to cumulative netting effort. In the summer of 1991 the capture rate of new birds at all sites approached zero, but only in site C was the cumulative curve better described by logarithmic regression ($r^2 = 0\cdot87$) than by linear regression ($r^2 = 0\cdot78$). In the other sites the cumulative curve was better described by linear regression (r^2(A and B) $= 0\cdot93$) than by logarithmic regression ($r^2 = 0\cdot75$ and $0\cdot85$). In 1992 the effort was increased and the cumulative curves were closely fitted by a logarithmic relationship for both summer ($r^2(A) = 0\cdot95$ and $r^2(C) = 0\cdot93$) and winter ($r^2(A) = 0\cdot84$). These cumulative curves conform to the patterns expected of a resident population (MacArthur & MacArthur 1974; Greig-Smith 1980). In all sets of data, except for site A in 1991, the effort accumulated was sufficient to show that the capture rate of new birds approached zero. The total capture rate also decreased throughout. This implies that birds, after a while, became infrequent visitors to the sites because sightings of colour-ringed birds showed that they had not left the area. Also, birds ringed at road sites (1991: $n = 11$, 1992: $n = 14$) were sighted more often in the road (1991: 96%, number of sightings = 57, 1992: 100%, number of sightings = 26) than in the valley.

Table 5. Logistic models: the coefficient of the logistic regression is compared between seasons

Variable code	Habitat variable	Summer	Autumn	Winter
LAUA	% volume of laurel foliage 0–4 m	0·74***	NS	1·74***
LAUB	% volume of laurel foliage > 4 m	0·98***	1·09***	1·62***
CLEA	% volume of *Clethra arborea* foliage 0–4 m	NS	NS	NS
CLEB	% volume of *C. arborea* foliage > 4 m	0·80***	2·23***	1·04**
CRYA	% volume of *Cryptomeria japonica* 0–4 m	NS	NS	NS
CRYB	% volume of *C. japonica* > 4 m	0·60**	0·85**	NS
PITA	% volume of *Pittosporum undulatum* 0–4 m	0·68*	NS	0·79*
PITB	% volume of *P. undulatum* > 4 m	–1·69***	NS	–2·13**
GRAS	% coverage of grass	NS	NS	NS
GROUND	% coverage of bare ground	0·68**	0·65*	NS
FOLA	% volume of all foliage 0–0·5 m	NS	–0·81*	NS
FOLB	% volume of all foliage 1–2 m	–0·69**	NS	–1·41**
FOLC	% volume of all foliage 2–4 m	–0·59**	NS	NS
FOLD	% volume of all foliage > 4 m	NS	NS	NS
CANOPY	Canopy height (m)	–0·13***	–0·29***	–0·31***
ALT	Altitude (m)	–0·002*	NS	NS
Final deviance		235·19	211·95	114·12

***$P < 0\cdot001$, **$P < 0\cdot01$, *$P < 0\cdot05$, NS, not significant.

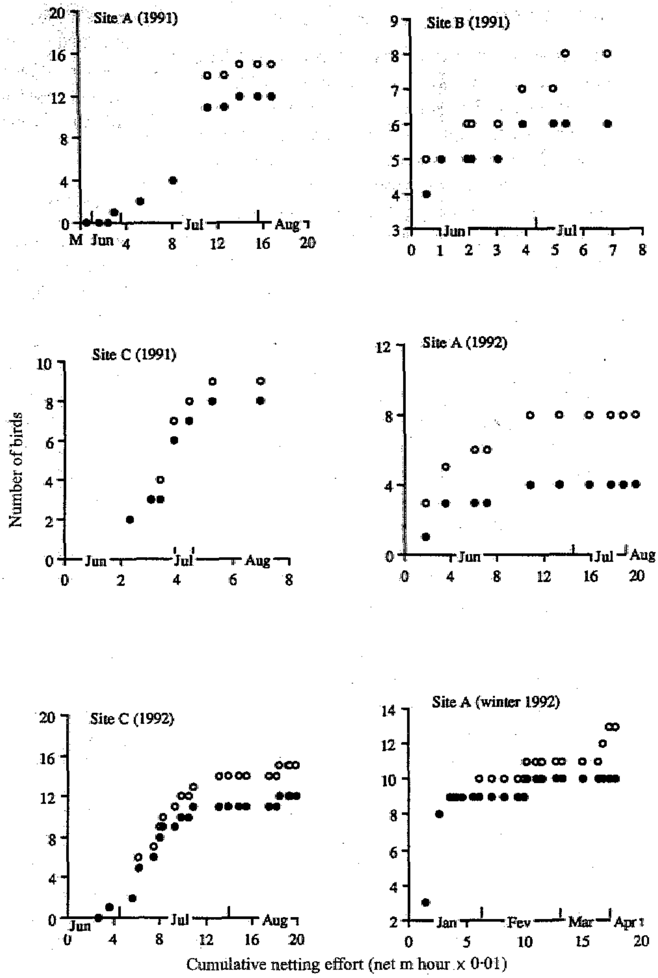

Fig. 4. Numbers of Azores bullfinches captured at three sites in relation to cumulative netting effort. Unfilled symbols indicate the cumulative totals for all captures, and filled symbols indicate previously uncaught birds, for each netting session.

Movement data of individual birds were divided into Summer (Jun–Sep) and Winter (Jan–Apr). Sightings of colour-ringed birds in May and autumn (Oct–Dec) were too few to use in further analysis. A Mann–Whitney test and a Wilcoxon's test for matched-pairs were used to test the null hypothesis that the median of the mean distance moved between consecutive locations of individual birds was equal in both seasons. Home ranges were calculated using the formula R (radius) = $(\sqrt{\Sigma x_i^2/n})$, where x_i is intercatch distance and n the number of recaptures (Taylor 1966; Fery, Frochot & Leruth 1981); values are given in Table 6 and are simply meant to convey an idea of home ranges. More preferable methods are available (White & Garrott 1990) but larger sample sizes would be required.

The median of the mean distance moved between consecutive locations by individual birds in summer was significantly greater than that moved by birds in the winter (Mann–Whitney test = 9, $P < 0{\cdot}01$, $n_1 = 14$ and $n_2 = 10$; Table 6). It was possible to calculate the mean distance between successive sightings for six individuals in summer and in the following winter. Their medians were significantly different (Wilcoxon's test for matched pairs: $t = 0$, $P < 0{\cdot}05$, $N = 6$). The longest movements were recorded in May (Table 6). Three birds, commonly seen (throughout the summer and from February to April) around 700 m, were located feeding on herbaceous seeds at about 300 m. One bird ringed by C. J. Bibby in July 1990 at 730 m was also observed at 300 m in late May of 1992. Nevertheless, of the 26 birds that were seen at least during 8 months, 24 (92%) were seen again near their netted site. From three birds ringed by C. J. Bibby in July 1990, two were again recaught in the same place in June 1991 and the third one was recaught in the same place in July 1992.

Table 6. Comparison between summer and winter mobility of colour-ringed birds. Summer home ranges were calculated using sightings from early June to mid September, and winter home ranges sightings from early January to late April

Bird	Sex	Mean distance between successive sightings (m)	Number of records	Time span (days)	Longest movements (m)	Home range (ha)
Summer						
White-red	f	88	12	60	Sep-1450	4·69
Red-blue	f	200	15	62	Jul-350; Aug-750, 425	31·72
Red-yellow 91	f	165	13	53	Jun-500, 530	4·07
Red-yellow 92	f	79	17	49	Aug-188	9·40
Green-green 91	m	75	7	24	May-2275; August-375	12·59
Green-green 92	m	150	11	84	Jun-425	38·86
Green-red	f	213	18	50	Jul-603, 550, 425; August-800	18·09
Pink-orange	m	163	18	82	Jun-425, 525; Jul-300; Aug-375	18·09
Orange-blue	f	106	20	96	Jun-550; Sep-500, 775; Nov-425	26·59
Blue-white	m	168	9	72	Jul-475	16·80
Red-red	f	100	9	64	May-2450; Jun-500	14·34
Red-green	m	138	10	59	Jun-575; Jul-375, 350; Aug-775	43·27
Red-white	f	90	8	67	Aug-300	9·18
White-green	m	128	4	32	Aug-150	5·38
Average		133·1	12	61		18·33
Winter						
Pink-red	?*	65	12	90	Mar-163	2·72
Pink-blue	?*	70	8	62	Mar-175	3·01
Pink-orange 92	m	61	16	85	Apr-178	2·25
Pink-orange 93	m	88	12	15	Mar-164	2·99
Green-green	m	89	7	32	Mar-363	9·74
White-green	m	29	7	36	Apr-53	0·38
Red-yellow	f	95	6	48	Mar-178	3·98
Red-red	f	103	6	32	Apr-153	6·48
Orange-blue	f	69	5	54	Mar-115	2·79
Blue-blue	f	83	6	19	Apr-200	4·49
Average		75·2	9	47		3·88

* Azores bullfinches can be sexed by slight differences in plumage, but some individuals are impossible to sex (see Ramos 1994b).

Discussion

DISTRIBUTION AND POPULATION ESTIMATES

Population estimates found in this study are in the order of magnitude of the 100 pairs found by Bibby & Charlton (1991). Overall range coincided also but this study defined an area of higher density towards the east of the bird's range (which might coincide with the breeding area) and an area of lower density towards the west (which is occupied only in autumn). Only juveniles were located in the west, which suggests the possibility of juvenile dispersal. This area must have been occupied all year round when the bird was reported feeding on buds of orange trees in the end of the last century and early this century (Hartert & Ogilvie-Grant 1905; Bannerman & Bannerman 1966).

It must be noted that the areas that were accessible (covered by the routes) were more on the edge of the native forest. Consequently, the density values obtained may not be representative of the whole range (see Bibby *et al.* 1992b for a full discussion of this problem). Both methods may lead to over-estimates. Capture–recapture estimates over summer are biased because birds were then highly mobile. In winter, population estimates are more reliable since large-scale movements were not recorded. These showed a slight decline from 1992 to 1993, but note that sample sizes were smaller in 1993. Population size appeared stable using the variable circular plot method.

HABITAT SELECTION

The degree and intensity of habitat selection varied seasonally but bird density was significantly higher in laurel than in exotic forets at all seasons. The summer and autumn logistic models gave a poorer fit than the winter model and, in summer, five more variables were selected as habitat selection discriminators than in winter. This suggests less specialization or more complex habitat selection in summer and autumn than in winter. The inclusion of *C. japonica* and *P. undulatum* in the summer and autumn models gave further support to this idea.

A wider range of habitats were used in summer than in winter. Alatalo (1981) and Bilcke (1982) reported the opposite for woodland birds in Finland and Holland. Reduced habitat heterogeneity and, therefore, foraging opportunities mean that oceanic island birds may have to use a relatively wider range of habitats during the breeding season. British bullfinches studied by Crocker (1987) commuted between several separated activity centres, but these were never more than 500 m apart. In this study distances between successive sightings as far apart as 700 or 800 m were quite common over summer. Locally, Azores bullfinches appear more mobile than bullfinches in Britain. In winter both seem to remain faithful to small areas.

In evergreen (the native) forests foliage density measures show little seasonal variation. Variation in vegetation composition was obvious as most herbaceous plants, shrubs and ferns growing in openings were absent in winter. Scattered exotic forests or areas that are bare or have short vegetation (forest edge) due to natural or human disturbance are occupied by Azores bullfinches from early summer to autumn. The avoidance of tall *P. undulatum* and *C. japonica* is likely to be due to changes in food resources within this forests than to growth of trees. Azores bulfinches stop using these forests when high density of tall trees shade the ground area and herbaceous plants providing seeds exploited by the birds over summer (Ramos 1995) cease to exist. Preference for native forest seems to reflect the superiority of this habitat in terms of food resources: seeds of *Leontodon filli* and *Vaccinium cylindraceum* in summer and autumn, seeds of *C. arborea* and sori of *Woodwardia radicans* and *Culcita macrocarpa* in autumn and winter, and flower buds of *Ilex perado* and other vegetable material in spring (Ramos 1995). High preference for native forest from January to April reflects the fact that feeding resources exploited at this time (seeds of *C. arborea*, flower buds of *I. perado* and sori of large ferns) were present only in this forest (Ramos 1995). The area of native forest to the east, occupied only in autumn, is less mature and has smaller populations of large ferns and *I. perado* than the area to the west (Ramos 1995).

In terms of mobility three annual time periods can be devised: summer, autumn/winter and late winter. Wider ranging behaviour in summer than in winter may be explained by the heterogeneous habitat use of birds over summer: openings, streams, and landslides that are separated by plantations of *C. japonica*, copses of *P. undulatum* and areas of mature laurel forest that are unsuitable for foraging. In late winter, the movements of Azores bullfinches were more pronounced; like those of birds in western Europe (Greig-Smith & Wilson 1984; Newton 1967; Noval 1971). This occurs when natural food in the woodlands becomes scarce (Newton 1964; Ramos 1995). It is likely that, in late winter, Azores bullfinches face food shortage (Ramos 1995). They were then seen feeding at about 300 m of altitude feeding on the first coming seeds of herbaceous plants.

CONSERVATION CONSIDERATIONS

Mainland bullfinches have colonized open areas and suburban habitats (Maheo 1965; Yeatman 1965; Newton 1967; Summers 1979). Conversely, the Azores bullfinch has been gradually contracting its range since the middle of the last century (Bannerman & Bannerman 1966; Bibby & Charlton 1991). The area of laurel has been reduced and present exotic forests are marginal habitats. The present distribution pattern suggests a relict population. It is important that a mosaic of vegetation types, from openings to areas of mature laurel forest, be provided for the Azores bullfinch to complete its annual cycle.

Such a small population may be affected by demographic and environmental stochasticity. A concept of minimum viable population as 50 breeding pairs (Gilpin & Soulé 1986) is now being questioned (Walter 1990). It seems that the Azores bullfinch overcome a demographic bottleneck early this century; isolation and lower predation levels may have provided buffers against extinction. The effect of inbreeding is unknown. Demographic stochasticity is certainly an important factor but it may not be the major one because: (i) the population may have increased due to the introduction of *C. arborea* in the 1950s, which now provides a superabundance of food in the winter (Ramos 1995), and (ii) mortality figures (about 50%) and recruitment (45% to 59%) suggest a stable population, though sample sizes were small (Ramos 1994b).

The recent large-scale invasion of the native forest by exotic flora seems to be the most important environmental stochasticity factor affecting this population. The area of native forest that is needed for a minimum viable population is an important but difficult question. If 580 ha of existing forest can support about 200 birds, it is necessary to improve the quality of the existing native forest (controlling the expansion of *P. undulatum*, *C. japonica* and *H. gardneranum*) and expand its area (planting native species). Exotic forests are marginal habitats but they may be important in summer if ground vegetation is allowed to grow. Plantations of *C. japonica* should be more scattered. Trees have also been knocked down in some areas due to exposure to strong winds. These areas are now densely carpeted by *H. gardneranum* and should be converted to their primitive vegetation. Research on the control of this and other exotics is urgently needed. The margins of the forests at lower altitudes seem to be important habitats in late spring and should be considered in the conservation of this species.

C. arborea is an important food supply in winter, but it grows taller and is now present in higher densities than native species; therefore, it is outcompeting native plants that are important foods at other times, especially *I. perado* (Ramos 1995). In 50-m transects the mean number of flower buds of *I. perado* per first branch encountered was 212 (SE = 29·9) in an area without *C. arborea* and 47 (SE = 13·6) in an area with *C. arborea* (Ramos 1993). *C. arborea* dry seeds are available in spring but other fresh foods are preferred (Ramos, 1996). On the whole, *C. arborea* may now begin to have a negative impact on this population and it must be controlled to avoid turning into monospecific copses.

In conclusion, the survival of this unique bird depends on the appropriate managment of the last remaining natural areas, the clear definition of areas that are ecologically suitable for the plantation of exotic trees and on a monitoring scheme of the population.

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