

Habitat distribution of canary chaffinches among islands: competitive exclusion or species-specific habitat preferences?

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Abstract. The habitat distribution between islands of the Common Chaffinch (*Fringilla coelebs* L.), viewed in relation to the presence of its potential competitor species, the Blue Chaffinch (*Fringilla teydea* Moquin-Tandon), has been studied for the Canary Islands (Tenerife and El Hierro). The Common Chaffinch was significantly denser in the pine woods of El Hierro than in Tenerife, while the Blue Chaffinch was only present in Tenerife. The vegetation structure was very different in the pine woods of the two islands. In the pine woods of El Hierro, the Common Chaffinch selected more grassy places, and foraged mainly in the foliage.

The habitat selection pattern observed in Hierro was congruent with that obtained for the continental subspecies in the North of the Iberian Peninsula. An empirical model was thus developed to predict density variations of the Common Chaffinch in the continental pine woods of Northern Spain. This continental model (not subject to the influence of the potential competitive effect of the Blue Chaffinch) was then used to predict the abundance of the Common Chaffinch in

the pine woods of El Hierro and Tenerife. The similarity between the densities predicted by the non-competitive continental model and those actually observed in the pine woods of El Hierro and Tenerife indicates that the presence of the Blue Chaffinch is not relevant in explaining the differences in Common Chaffinch density between islands. The habitat preferences of the Common Chaffinch quantitatively explain density differences observed between El Hierro and Tenerife. These results show clearly the relevance of habitat structure in determining the patterns of presence and density of the Common Chaffinch between islands. Data obtained thus supports the species-specific habitat preference hypothesis, with the competitive exclusion hypothesis not being justified at least in ecological time.

Key words. Canary Islands, Chaffinches (*Fringilla* spp.), habitat preferences, competitive exclusion, island-continental model.

INTRODUCTION

Competitive theory predicts that birds tend to utilize a wider range of habitats in the absence of close competitors (e.g. congeneric species) than when other ecologically related species are present (niche expansion; MacArthur, 1972; Cody 1975). Some studies on this subject, dealing with insular avifaunas and considering the habitat and the altitudinal range of the species involved, have been carried out (e.g. Diamond, 1975; Schluter & Grant, 1982; review by Wiens, 1989). Moreover, if for any reason, such as chance or history, the number of ecologically related species is impoverished in an area, the remaining species will tend to use part of the vacated resource, and will increase their densities. This process has been called density compensation (MacArthur, Diamond & Karr, 1972), and it

has been demonstrated for several bird species (e.g. Cody, 1975; Wright, 1980; Faeth, 1984; Wiens, 1989). Although habitat expansion and density compensation at a geographical scale may be understood in terms of competition between species (Brown, 1975; Schoener, 1988), several authors have pointed out the necessity of not assuming this *ceteris paribus* in geographical and ecological comparisons, particularly if other environmental factors and selective pressures remain unmeasured (e.g. review by Wiens, 1989).

The Canary Islands are inhabited by two Chaffinch species, namely the Blue Chaffinch (*Fringilla teydea* Moquin-Tandon) and the Common Chaffinch (*Fringilla coelebs* L.) (Fig. 1), which probably reached the islands in two different invasion waves coming from Southwestern Europe or Northern Africa (Stresemann, 1927–34; Moreau,

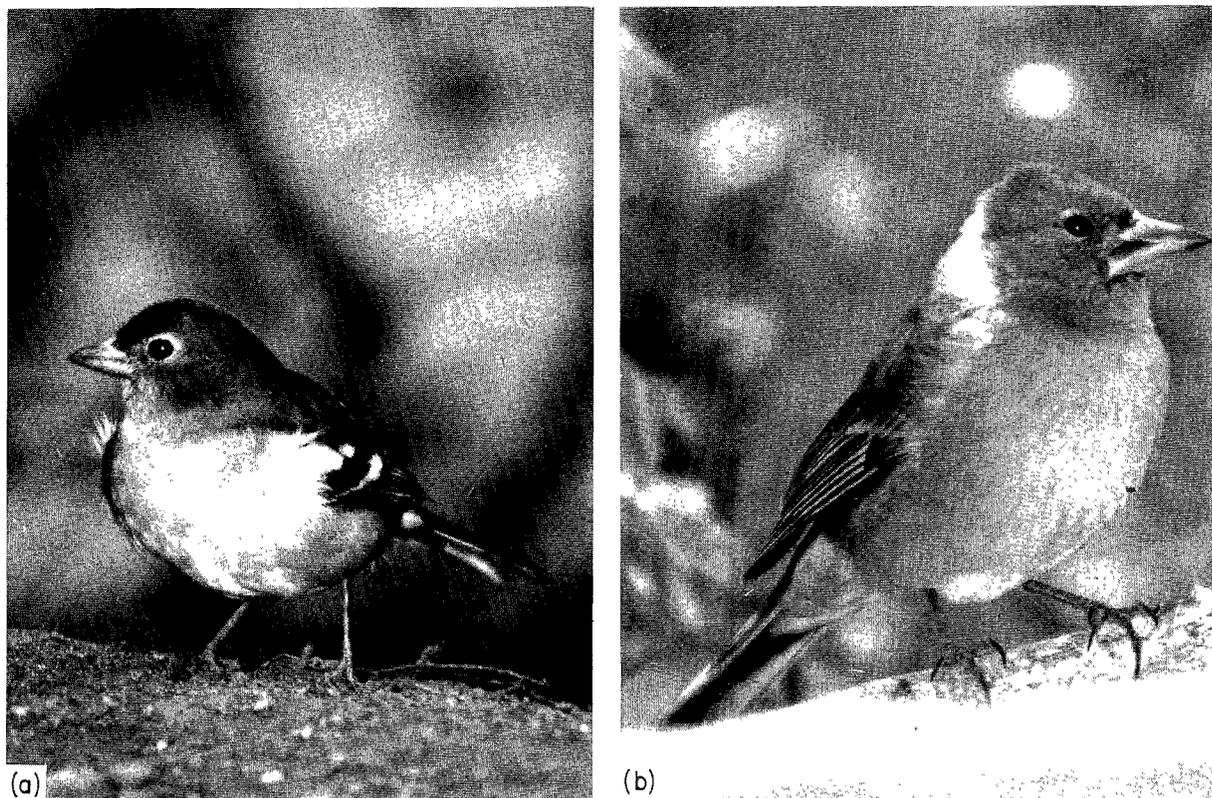


FIG. 1. (a) The Common Chaffinch (*Fringilla coelebs*) and (b) the Blue Chaffinch (*Fringilla teydea*) from Tenerife Island (photos: V. Quilis).

1966). The earlier invader, the Blue Chaffinch, is an endemic species from Gran Canaria and Tenerife, where it occupies pinewoods of *Pinus canariensis* Sweet ex Sprengel. The later invader, the Common Chaffinch (which probably reached the Canary Islands less than one million years ago; see Grant, 1979, 1980; Baker *et al.*, 1990), is more broadly distributed in the archipelago, occupying the islands of La Palma, El Hierro, La Gomera, Gran Canaria and Tenerife (Bannerman, 1963). In the two islands where the Blue Chaffinch occurs, the Common Chaffinch breeds mainly in *Monteverde* woodlands (evergreen forests composed of several tree species of the Lauraceae, Fagaceae, etc., with the tree heath *Erica arborea*), while its habitat distribution is wider in the other islands where it inhabits pine woods (Lack & Southern, 1949; Grant, 1979, for a review). These differential patterns of habitat preferences between islands have been interpreted as a paradigmatic example of habitat shift due to interspecific competitive exclusion between conspecific species: that is, the Common Chaffinch is excluded from the pine woods by the larger Blue Chaffinch in the islands where this species occurs (Lack & Southern 1949). Although this competitive exclusion hypothesis has been largely accepted, empirical data supporting it is rather scarce and qualitative, and other alternative hypotheses have never been considered and tested.

In this paper, we test the above-mentioned competitive exclusion hypothesis and the alternative hypothesis of species-specific habitat preferences. If Common Chaffinch density, all other things being equal, is lower in the pine

woods of the islands where the Blue Chaffinch is present, then competitive exclusion between these two finch species could be argued to explain their patterns of distribution and abundance. However, if environmental features are different between islands and fit the habitat and food requirements of the Common Chaffinch, then the classical interpretation of the 'finches problem' of the Canary Islands is not justifiable in terms of competitive exclusion, at least in ecological time. In this case, the absence of the Common Chaffinch from the pine woods in the islands where the Blue Chaffinch is present should be due to the unsuitability of these pine woods for the former species, a situation largely independent of the presence of Blue Chaffinches.

We study these two alternative hypothesis by measuring the densities of the two finch species and the vegetation structure and food availability in representative pineforests (*Pinus canariensis*) of Tenerife and El Hierro. We also analyse the use of space and the habitat selection of the Common Chaffinch in a pine wood of El Hierro. Considering the vegetation attributes selected in this last island, we compare their availability between Tenerife and El Hierro in order to test if the absence of Common Chaffinches in the pine woods of Tenerife is a result of their low suitability for this species. In order to document the consistence of Common Chaffinch habitat preference patterns at a broad geographical scale (continent versus island), we develop an empirical model to predict density variations in continental pine woods (Northern Spain). The variables entering the



FIG. 2. Pinewoods of *Pinus canariensis* from (a) El Hierro and (b) Tenerife islands.

continental model are compared with the variables selected in El Hierro. The continental model (not subjected to the influence of the potential competitive effect of the Blue Chaffinch) is also used to predict the abundance of Common Chaffinches in the pine woods of El Hierro and Tenerife. If difference in Common Chaffinch density between El Hierro and Tenerife is accurately predicted by this model, then it could be concluded that the presence or absence of the Blue Chaffinch has no relevance in explaining the habitat distribution pattern of the Common Chaffinch between islands.

MATERIAL AND METHODS

The study was carried out in Tenerife and El Hierro (Canary Islands: 28°N, 17°W). Tenerife is the largest and highest island of the archipelago, covering an area of 2057 km² and reaching 3717 m a.s.l. in the Pico Teide. El Hierro is the smallest of the principal islands (278 km²), reaching its maximum altitude in the Pico Malpaso (1500 m a.s.l.) (for details on climate and vegetation of these islands see Anonymous (1980), González, Rodrigo & Suárez (1986) and Marzol Jaen (1984)). In April 1991, we studied a large *Pinus canariensis* woodland in El Hierro, located at 1100–

1200 m a.s.l. on the south slope of the island, at 'Hoya del Morcillo' (Taibique-Bailadero de las Brujas; Fig. 2a). The pine forests of Tenerife were studied during April 1986 (vegetation structure and bird species density) and April 1991 (food availability samples) at 1400–1700 m a.s.l. in the extensive reforestations which spread over the top part of the Orotava valley; these reforestations (Fig. 2b; mainly *Pinus canariensis*, and some plantations of *Pinus radiata* D. Don) were made between 1940 and 1950. Mean annual precipitation at the two study sites is very similar (500–600 mm yr⁻¹). Other more mature forests in the south of Tenerife (e.g. Vilaflor) were not studied because the geographical distribution of the Common Chaffinch is restricted to the north of the island (Martín, 1987).

The relative density of breeding chaffinches (*F. coelebs* and *F. teydea*) was estimated by means of line transect method, with fixed belts of 25 m on both sides of the researcher (Tellería, 1986). Census samples were 500 m long (2.5 ha), and were divided into five units, each 100 m long. At the centre of each of these units we estimated, by eye, the structural features of the forest in a circular plot of 50 m diameter: rock, grass and shrub cover, mean tree height, and the number of trunks 10–30 cm, and >30 cm in diameter. These variables were then averaged across the five

sampling units of each census sample of 2.5 ha. Results were used to compare finch density and habitat features between the pine woods of El Hierro and Tenerife. In both pine woods, additional information on the pine profile was gathered by measuring the length of branches perpendicular to the trunk axis at 4, 8, 12, 16 and 20 m intervals.

Data on the physiognomy of the habitat were also used to study the habitat selection of Common Chaffinches in the pine woods of El Hierro island by comparing the environmental features of those sampling units of 100×50 m in which the species was observed with a random sample obtained from all sample units (one unit per census sample).

The foraging substrates used by the Common Chaffinch were also sampled on El Hierro. They were divided into ground, trunk, branches (>1 cm in diameter), foliage (twigs and needles), and cones. Data were taken at 30-s intervals, with no more than six records for each individual bird, at most three of which were in the same tree (Carrascal, 1983; see however Helj, Verner & Bell, 1990). When possible, the type of prey captured was also recorded.

We also measured the relative abundance of arthropods in the foraging substrates most commonly used by the Common Chaffinch in the pine woods of El Hierro and Tenerife, namely the ground (with and without grass) and foliage. Arthropod abundance was evaluated by counting invertebrates larger than 1 mm over 2 min (Cooper & Whitmore, 1990).

In order to develop an empirical model of Common Chaffinch habitat selection pattern not subjected to the potential competitive influence of the congeneric Blue Chaffinch, we studied the relationship between Common Chaffinch density and habitat features in some plantations of *Pinus radiata* in the North of the Iberian Peninsula (Basque Country, 43°10'N 02°45'W). Common Chaffinch density and habitat features were obtained by the same methods used in Tenerife and El Hierro. Twenty samples of 5 ha (obtained by grouping two contiguous samples of 2.5 ha) were censused during May 1985. The relationships between Common Chaffinch density and habitat features in these twenty samples were analysed by means of stepwise multiple regression analysis.

Statistical tests employed were *t*-test for means and stepwise multiple regression analysis (Sokal & Rohlf 1981). When required, original data were log-transformed prior to analysis in order to attain normality and homoscedasticity.

RESULTS

The combined density of the two *Fringilla* spp. in the pine woods of the two islands did not differ significantly ($t_{40}=0.132$, $P=0.895$; Fig. 3). However, the Common Chaffinch was significantly denser in El Hierro than in Tenerife ($t_4=2.949$, $P=0.005$). In fact, it reached the same density in the pine woods of El Hierro (where the Blue Chaffinch is not present) as the two finch species in the pine woods of Tenerife.

In the pine woods of El Hierro, the Common Chaffinch selected more grassy places (grass cover was higher in the samples where the Common Chaffinch was observed than

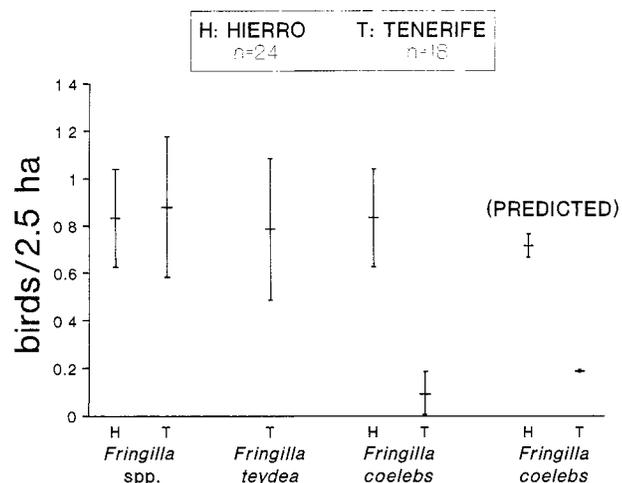


FIG. 3. Observed and predicted densities of Blue and Common Chaffinches in Tenerife (T; $n=18$) and El Hierro (H; $n=24$) (mean \pm one standard error). Predicted densities have been obtained from a non-competitive continental model (see text for details), n : number of transects of 2.5 ha.

in a random sample). Significant differences were not found in the remaining structural variables measured (Table 1). While searching for food, 53.8% of the foraging records were among needles, 28% on branches, 9.8% on pine cones, 4.2% searching on the ground, and 4.2% foraging on trunks (143 records obtained from fifty-two different individuals). Regarding prey capture data (twenty-three observations), 65.2% were arthropods (mainly caterpillars and beetles, 4–40 mm long), and 34.8% pine-seeds; 60.9% of the captures were in the pine foliage, 21.7% on pine cones, 13% in ground, and 4.3% on branches.

The structure of the vegetation was different between the pine woods of the two islands (Table 2). Rock cover, height and cover of shrubs, and tree density were significantly higher in Tenerife than in El Hierro, while grass cover, pine height and foliage cover over 8 m were significantly higher in El Hierro than in Tenerife.

Arthropod abundance in the pine foliage did not differ significantly between Tenerife and El Hierro pine woods. The same result was obtained when comparing the results for ground only covered by dry needles (Table 3). Arthropod abundance was significantly higher in the ground covered by grasses than in the ground covered only by needles in the pine woods of El Hierro ($t_{88}=5.415$, $P<<0.001$); the same result was obtained when comparing these two substrates in the pine woods of El Hierro and Tenerife ($t_{83}=3.367$, $P=0.002$).

Common Chaffinch density in the plantations of *Pinus radiata* of Northern Spain was significantly, and positively, correlated with grass cover ($P=0.008$), with tree height ($P=0.046$), and with density of pines with 10–30 cm of trunk diameter ($P=0.004$; stepwise multiple regression model with twenty samples). These three variables accounted for 72.5% of the variance in finch density ($F_{3,16}=14.041$, $P=0.0001$; see Fig. 4). Of these three variables explaining density variations in the Common Chaffinch in the continent, only one is selected in the island of El Hierro (grass

TABLE 1. Mean (\bar{x}) and standard deviation (s) of vegetation structure variables in plots (0.2 ha) of the pine wood of El Hierro where *F. coelebs* was present and in a random sample, with the results of *t*-test comparisons for each variable (see Material and Methods for more details). Sample sizes: Observed $n=26$, Random $n=24$. Trunk density is expressed as no./0.2 ha.

	Random		Observed		<i>t</i>	<i>P</i>
	\bar{x}	<i>s</i>	\bar{x}	<i>s</i>		
Rock cover (%)	4.2	13.1	0.3	0.8	1.27	0.210
Grass cover (%)	37.8	20.0	57.5	23.0	2.30	0.026
Shrub cover (%)	2.6	4.5	6.2	10.5	1.31	0.195
Shrub height (m)	0.83	1.18	0.85	1.02	0.23	0.579
Tree height (m)	16.6	2.7	16.2	2.3	0.56	0.579
No. trunks 10–30 cm	1.7	3.0	3.3	9.9	0.59	0.561
No. trunks >30 cm	16.9	9.5	20.5	9.0	1.61	0.114

TABLE 2. Mean (\bar{x}) and standard deviation (s) of vegetation structure variables in the pine woods of Tenerife and El Hierro, and results of *t*-test comparisons for each variable between the two islands. Sample sizes: Structural variables: Hierro $n=24$, Tenerife $n=18$; Vegetation profile: Hierro $n=13$, Tenerife $n=16$, *** $P<0.001$. Trunk density is expressed as no./0.2 ha.

	Hierro		Tenerife		<i>t</i>	<i>P</i>
	\bar{x}	<i>s</i>	\bar{x}	<i>s</i>		
Structural variables						
Rock cover (%)	4.1	10.4	18.9	8.8	7.86	***
Grass cover (%)	38.2	15.9	0.0	0.0	24.52	***
Shrub cover (%)	3.0	3.4	13.7	11.4	4.46	***
Shrub height (m)	0.79	0.73	1.86	0.57	5.10	***
Tree height (m)	16.3	2.1	13.1	1.6	5.58	***
No. trunks 10–30 cm	3.0	3.2	94.1	30.0	17.06	***
No. trunks >30 cm	16.8	8.6	45.6	17.1	29.13	***
Tree profile (length of branches with needles)						
20 m	1.0	1.6	0	0	2.46	0.05
16 m	3.5	2.1	0	0	6.85	***
12 m	3.8	1.6	0.6	0.2	7.89	***
8 m	1.0	1.5	1.2	0.6	0.30	0.80
4 m	0.6	0.9	0.6	0.7	0.02	0.98

TABLE 3. Mean (\bar{x}) and standard deviation (s) of arthropod availability (no. arthropods counted per 2 min) in the pine woods of Tenerife and El Hierro, and results of *t*-test comparisons for each variable between the two islands. Sample sizes: Hierro $n=45$, Tenerife $n=40$.

	Tenerife		Hierro		<i>t</i>	<i>P</i>
	\bar{x}	<i>s</i>	\bar{x}	<i>s</i>		
Ground without grass	0.70	1.04	0.36	0.68	1.69	0.095
Pine foliage	0.58	0.84	0.87	1.10	1.54	0.127
Ground with grass	—	—	1.64	1.54		

cover). However, the other two vegetation structure variables were not selected in El Hierro probably due to the small range of variation (tree height: Northern Spain= 3–19.1 m, El Hierro= 13.4–21.2 m; tree density (10–30 cm in trunk diameter: Northern Spain= 1–73.5 trees/0.2 ha, El Hierro= 0–11.6 trees/0.2 ha).

The equation obtained for Northern Spain pine plantations was employed to predict the density of the Common Chaffinch in the pine woods of Tenerife and El Hierro (pre-

diction of bird numbers for each sample of 2.5 ha). Predicted density for the Common Chaffinch in El Hierro was significantly higher than in Tenerife (Fig. 3; $t_{40}=9.259$, $P<0.001$), so the 'continental' pattern of habitat preference of the Common Chaffinch qualitatively explains the density differences observed in the two islands. When considering the pooled sample of the two islands, predicted and observed abundances were significantly correlated ($r=0.384$, $n=42$, $P=0.012$; $a=-0.003$ (SE=0.234), $b=1.058$

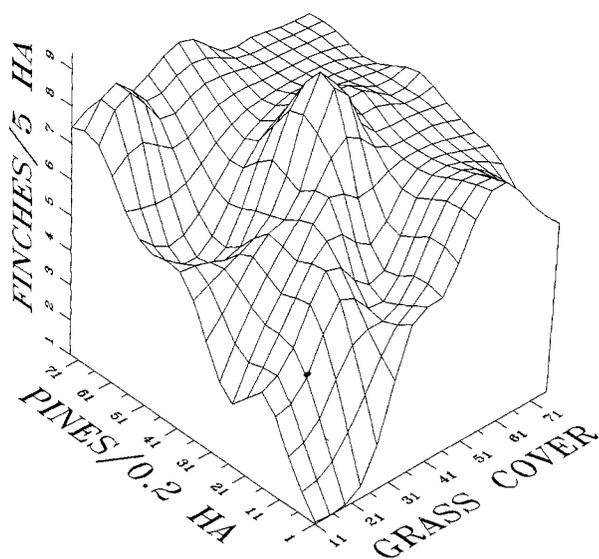


FIG. 4. Relationship among grass cover (%), tree density (no. pines 10–30 cm in diameter/0.2 ha), and Common Chaffinch density (birds/5 ha) in pine woods of the Northern Iberian Peninsula.

($SE=0.402$). The regression parameters a and b did not significantly differ from 0 and 1 respectively ($a: t=0.014, P=0.989$; $b: t=0.144, P=0.886$). The residuals of the regression of observed versus predicted densities for the two islands did not differ significantly ($t_{40}=0.726, P=0.472$). Differences between predicted and observed abundances did not differ significantly from zero, neither in Tenerife ($t_{17}=1.051, P=0.308$) nor in El Hierro ($t_{23}=0.564, P=0.578$). Therefore, the habitat preferences of the Common Chaffinch quantitatively explain the density differences observed between El Hierro and Tenerife. Moreover, Common Chaffinch density and vegetation structure followed the same pattern of covariation in the two pine woods of Tenerife and El Hierro, and in the pine plantations of Northern Spain.

DISCUSSION

The results described above apparently support the existence of a phenomenon of density compensation in the two finch species of the Canary Islands (Fig. 3). Finch density in Tenerife and El Hierro was nearly equal, but attained by different finch species. According to the density compensation hypothesis (Cody, 1975), the increase of Common Chaffinch density in El Hierro would be due to the additional resources it could exploit in the absence of the Blue Chaffinch. Related to this density compensation is the fact that when both species coincide in islands within their geographical range, they occupy different habitats. The Blue Chaffinch, probably the dominant species because of its larger body size (Alatalo & Moreno, 1987), might exclude the Common Chaffinch in pine forests. Nevertheless, a detailed inspection of data in Table 2 shows that this interpretation is not justified, because habitat features are very different between the pine forests of the two islands.

Hence, vegetation structure must be considered in order to avoid its confounding effects on habitat shifts and density compensation.

Considering the habitat preferences of the Common Chaffinch, and the differences in vegetation features between the pine woods of El Hierro and Tenerife, data obtained in this study support the species-specific habitat preference hypothesis. The dominant use of the tree canopy while foraging, and the higher foliage volume in the pine woods of El Hierro than in Tenerife, explain the absence or scarcity of the Common Chaffinch in Tenerife, and its presence, and higher abundance, in El Hierro. Although relative abundances of invertebrates in El Hierro and Tenerife pine woods were similar, the higher canopy development of the El Hierro pine woods may result in a higher absolute arthropod abundance than in the Tenerife pine woods. This difference will be further magnified because of the higher grass cover in the El Hierro pine woods, a ground substrate richer in invertebrates than the needle litter.

The habitat selection pattern observed in El Hierro was in agreement with that obtained for the continental subspecies in the north of the Iberian Peninsula (selection of places with high grass cover and intense use of pine foliage; see also Prodon & Lebreton, 1981). Similarly, the use of foliage observed in the pine woods of El Hierro agreed with the data available for other continental habitats (Herrera, 1980; Saether, 1982; Carrascal, Potti & Sánchez-Aguado, 1987). Therefore, our results indicate that Common Chaffinch habitat preference, and use of space while foraging, are fairly constant geographically (see Noon *et al.*, 1980, and Carrascal & Tellería, 1985, for a similar result; but see Collins, 1983, James *et al.*, 1984, and Shy, 1984). Although the Common Chaffinch in the Canary Islands has evolved several distinguishing features (song, plumage colour and biometry of bill, tarsus and wing; Bannerman, 1963; Grant, 1979; Lynch & Baker, 1986; Baker *et al.*, 1990), these subspecific differences have not resulted in changes in general habitat selection patterns.

The similarity between the densities predicted by the non-competitive continental model and the observed densities in the pine woods of El Hierro and Tenerife indicates that the presence of the Blue Chaffinch is not relevant in explaining the differences in Common Chaffinch density between islands (see T. L. George in Wiens, 1989, for a similar approach). If competition with the Blue Chaffinch in ecological time actually constrains the population level of Common Chaffinch in the pine woods of Tenerife, the observed density should be lower than expected if vegetation features are considered. This prediction was not supported. These results show clearly the relevance of habitat structure in determining the patterns of presence and density of the Common Chaffinch between islands.

The density compensation hypothesis implies that both finch species should overlap in resource use in pine forests (Cody, 1975), a necessary, but not a sufficient, condition for competition (Wiens, 1989). Nevertheless, habitat selection patterns of the two Canary chaffinches are very different. The Blue Chaffinch is a generalist of pine forests not influenced by grass cover and foliage volume, and only constrained by tree density: the higher the pine density, the

lower the Blue Chaffinch abundance (Carrascal, 1987; the opposite trend was obtained for the Common Chaffinch). On the other hand, the differences in bill morphology between the two chaffinch species seem to be related to differences in food requirements, the heavy bill of the Blue Chaffinch being adapted to crack the seeds of Canary pine (Grant, 1979; Martín, 1987; Martín *et al.*, 1986). In addition, as Slater & Catchpole (1990) have shown by means of play-back experiments, both chaffinch species are not usually interspecifically territorial, as their data demonstrated a lack of active exclusion of the Common Chaffinch by the Blue Chaffinch from the areas where the latter species breeds (see nevertheless Slater & Sellar, 1986). These ecological and behavioural differences should diminish the overlap and the probability of interference between the Common and Blue Chaffinches.

However, these results do not exclude the possibility that the between-habitat distribution of both Chaffinch species is the result of past competitive interactions (the 'ghost of competitive past'; Connell, 1980; Wiens, 1983). Nevertheless, the congruence of habitat selection patterns between the Canary Islands and the continent does not support the hypothesis that competitive pressure with the Blue Chaffinch would have shifted the habitat preferences of the Common Chaffinch in the past (see above). Besides, differences in bill morphology of the Common Chaffinch between islands within the Canary archipelago are not consistent with the predictions derived from the character displacement hypothesis (Grant, 1972). Differences in bill morphology are stronger between islands without the potential competitor than between these islands and those in which the Blue Chaffinch occurs (see Table 5 in Grant, 1979, and critical comments on his results by Wiens, 1989). Therefore, competitive pressures in the past do not appear to have played any role in determining morphological differences *between* islands, and density and presence/absence of the Common Chaffinch in the islands where the Blue Chaffinch is present can be explained by other factors, like species-specific habitat preferences. Carrascal (1987) has proposed a similar non-competitive explanation for the absence of the Blackcap, *Sylvia atricapilla obscura* Tschusi, in the pine forests of Tenerife, where other congeneric and potential competitor species are not present.

Finally, the present-day distribution of the Common Chaffinch in the Canary pine woods may be explained by considering some other large-scale factors determining the described local patterns. At these latitudes, precipitation is the main determinant of primary productivity (Lieth & Whittaker, 1975; and consequently of invertebrate availability). Interestingly, the mean annual precipitation of the pine forest belts in the islands where the Common Chaffinch inhabits pine woods (La Palma and El Hierro, 600–800 mm) is higher than in those where the species is absent from pine woods (Tenerife and Gran Canaria, 300–600 mm; Anonymous, 1980). Climatological differences between islands may therefore be the ultimate cause for the presence of the Common Chaffinch in Canary pine forests through mechanisms related to species-specific habitat selection and foraging behaviour.

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