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BETWEEN AND WITHIN HABITAT DISTRIBUTION OF THE CANARY COMMON CHAFFINCH *(FRINGILLA COELEBS OMBRIOSA)*: A TEST OF THE FOOD ABUNDANCE HYPOTHESIS

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SUMMARY.—*Between and within habitat distribution of the Canary Common Chaffinch* (Fringilla coelebs ombriosa): *A test of the food abundance hypothesis.* Population density and foraging behaviour of the Canary Common Chaffinch *(Fringilla coelebs ombriosa)* was studied in a pine wood and an evergreen forest at El Hierro island (Canary Islands) to test the influence of food availability on habitat selection during the breeding season. Chaffinch density was significantly lower in the pine wood than in the evergreen forest. In the pine wood chaffinches mainly foraged in the foliage, whereas in the evergreen forest foraging was restricted almost exclusively to the ground. Differences in food intake rate between habitats and substrates were directly associated with differences in population density and use of foraging substrates. These patterns of density variation and foraging behaviour in chaffinches were consistent with food availability (arthropod abundance and prey size). Our results support the hypothesis that food availability is very important in selection of habitat by passerines during the breeding season. The resource abundance hypothesis may represent an alternative view to the previously accepted hypothesis which supports that there has been competitive exclusion with the Blue Chaffinch *(Fringilla teydea)*, to explain the between habitat distribution of the Common Chaffinch among islands.

Key words: Canarian Common Chaffinch, density food availability, habitat distribution, habitat use.

RESUMEN.—*Distribución inter e intrahábitat del Pinzón Vulgar Canario* (Fringilla coelebs ombriosa): *test de la hipótesis de abundancia de alimento.* La densidad y uso del espacio del Pinzón Vulgar *(Fringilla coelebs ombriosa)* se estudió en un bosque de pinos y en un fayal-brezal de la isla de El Hierro (Islas Canarias), para testar la influencia de la disponibilidad del alimento en la selección de hábitat durante el período reproductor. La densidad de pinzones fue significativamente menor en el pinar que en el fayal-brezal. En el pinar los pinzones buscaron principalmente el alimento en el follaje, mientras que en el fayal-berzal lo obtenían fundamentalmente en el suelo. Las diferencias en las tasas de ingestión de alimento entre hábitats y sustratos estuvieron directamente asociadas con las diferencias en la disponibilidad de alimento y tamaño de presas. Estos resultados apoyan la hipótesis de que el alimento es muy importante determinando la selección del hábitat de paseriformes durante la estación reproductora. La hipótesis de abundancia de recursos representa una visión alternativa a la hipótesis previamente aceptada de la exclusión competitiva por el Pinzón Azul *(Fringilla teydea)*, para explicar la distribución entre hábitats del Pinzón Vulgar entre las Islas Canarias.

Palabras clave: Canarias, densidad, disponibilidad de alimento, Pinzón Vulgar, selección de hábitat, uso del espacio.

INTRODUCTION

Studies of habitat selection by birds have been usually centered on the relationship between bird abundance and vegetation structure using correlational analyses (Cody, 1985; Wiens, 1989). However, little attention has been given to the processes implied in the observed patterns (Wiens, 1989). For instance, food availability has received little attention despite of the fact that an individual's ability to obtain food has been recognized as an important proximal factor in determinig habitat preferences (Newton, 1980; Goss-Custard, 1984; Wiens, 1989). A greater abundance of food resources would reduce the amount of

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time required for searching, and/or increase the rate of food ingestion which will in turn influence reproduction and body condition. Therefore, food abundance could be an important factor determining population density and habitat selection through foraging efficiency. To understand the interaction between habitat selection and food availability, a foraging approach can be employed for studying the proximal mechanisms involved in resource use (i.e. patch choice; Pyke, 1984).

In this paper we employ the above mentioned foraging approach to the study of habitat selection by the endemic subspecies of the Canarian Common Chaffinch inhabiting the El Hierro island *(Fringilla coelebs ombriosa* Hartert). The Canarian subspecies of the Common Chaffinch (*tintillon, ombriosa* and *palmae*) inhabit pine woods and monteverde woodlands (evergreen forests composed of several tree species of the Lauraceae, Fagaceae, etc., with tree heath *Erica arborea;* Martín, 1987a and references therein). Its differential pattern of habitat distribution between islands has been formerly interpreted by Lack & Southern (1949) and Grant (1979) as a paradigmatic example of habitat shift due to its exclusion by the dominant Blue Chaffinch *(Fringilla teydea* Moquin-Tandon): the Blue Chaffinch occurs in Gran Canaria and Tenerife islands, where it occupies pine woods, while the Common Chaffinch breeds mainly in evergreen forests in these two islands (Martín, 1987a). Nevertheless, data obtained for Tenerife and El Hierro (Carrascal *et al.*, 1992) have supported the habitat selection hypothesis for differences between islands, while the competitive exclusion hypothesis does not seem to apply, at least in ecological time. In El Hierro only the Common Chaffinch is present, so the between habitat distribution should be independent of the competitive pressure with the Blue Chaffinch. The main objective of this paper is to test the influence of food availability on within habitat distribution and density variation between the main two habitats of the Canarian common chaffinches. The three following specific question will be addressed:

a) If food availability is the main factor affecting the selection of foraging substrata (within habitat distribution), chaffinches should select those substrates in each habitat with the highest food availability.

b) At a larger scale, between habitat distribution of chaffinch abundance at El Hierro island should also track food availability, chaffinches being denser in the habitat with the highest abundance of food resources.

c) If within- and between-habitat use are food mediated, then food intake rate should be higher in those habitats or substrates selected.

STUDY AREA AND METHODS

The study was carried out during April 1991 in El Hierro island (Canary Islands: 28° N, 18° W). El Hierro is the smallest of the principal islands (278 km^2), reaching a maximun altitude of 1,500 m a.s.l. The two study areas were two nearby forest (less than 1 km apart) located at Hoya del Morcillo (pine wood; 1,100-1,200 m a.s.l.) and at Degollada Bailadero de Las Brujas (evergreen forest; 1,300 m a.s.l.). The pine wood was characterized by the presence of sparse old trees of *Pinus canariensis* of an average height of 16 m (50 % of canopy cover), a shrub cover of 3 % (approx. 0.8 m in height), and a herbaceous cover *(Trifolium campestre, Vicia disperma, Micromeria hissopifolia)* of 38 % (Carrascal *et al.*, 1992). The luxuriant evergreen forest had denser tree cover (higher than 80 %) dominated by *Myrica faya* and *Erica arborea* trees of approx. 10 m in height and an abundant shrub-herb layer of approx. 0.6 m in height and 60 % of cover (*Urtica* spp., Myosotis latifolia, Geranium spp.; see Pérez de Paz, 1981 and Gonzalez *et al.*, 1986 for a more detailed description of vegetation in these two habitats). Average meteorological data for April at 1,000 m a.s.l. is 10.6 °C mean temperature, and 20.8 mm of rainfall (Hernández *et al.*, 1984; Marzol-Jaén, 1988).

Birds were censused early in the morning by the line transect method, with fixed belts of 25 m on both sides of the observer (Järvinen & Väisänen, 1975; Tellería, 1986). A total of 60 ha were censused in the pine wood divided in sampling units of 1,000 m long (5 ha).

Due to the small surface of the evergreen forest, only 10 ha were censused; this census was repeated in two consecutive days, and the average density of chaffinches was estimated. Other bird species in the pine wood were *Parus caeruleus, Serinus canaria* and *Regulus regulus,* being in the evergreen forest *Phylloscopus collybita, Turdus merula, Parus caeruleus, Sylvia atricapilla, Serinus canaria* and *Regulus regulus.* In the pine wood, the Kestrel *(Falco tinnunculus)* and the Sparrow Hawk (*Accipiter nisus;* two diurnal predators on passerines), were commonly seen above and below the canopy at densities of 0.3 birds/10 ha and 0.15 birds/10 ha respectively. Nevertheless, these small raptors were rarely seen flying above the denser evergreen forest, and never within it.

The use of space (foraging substrates) was sampled at 30-s intervals on focal birds that were recorded a maximum of 2 times (Carrascal, 1983; Morrison, 1984). Foraging substrates were divided into five categories: ground, trunk, branches, twigs-foliage (small branches less than 1 cm in diameter, and leaves or needles), and air. We also recorded the number of prey items captured (mainly arthropods and a few pine seeds) in the most commonly used substrates, namely ground and twigs-foliage. Only samples longer than 30 seconds were considered in data analyses. Only chaffinches not reacting to the presence of the observer were monitored.

During the sampling period, chaffinches mainly fed on arthropods (only two out of 43 observations of food ingestions were not arthropods but pine seeds). The relative abundance of arthropods was measurend in the foraging substrates most commonly used by the Common Chaffinch in both the pine wood and the evergreen forest: ground and foliage. Arthropod abundance was evaluated by carefully counting invertebrates larger than 1 mm over 2 min (see Cooper & Whitmore, 1990 and references therein). We also annotated the size of each arthropod counted considering the following length categories: 1-3 mm, 3-7 mm, 7-15 mm and more than 15 mm. Forty-five samples were obtained in the foliage and on the ground in both habitats. The most common taxa in the ground samples (and therefore those more probably consumed by chaffinches) were Arachnida, Diptera, Orthoptera and Hemiptera, and in the foliage Diptera, Arachnida, Coleoptera and Lepidoptera (caterpillars).

Statistical analyses used were *t*-test for comparing an observed mean with an expected one, ANOVAs, and χ^2 tests. Original data were log- (food intake rate and chaffinch density) or square-root transformed (arthropod abundance) prior to ANOVAs in order to attain normality and homoscedasticity (Sokal & Rohlf, 1981).

RESULTS

Arthropod abundance was significantly lower in the foliage than in the ground in the

TABLE 1

Food availability (no. arthropods counted/2 min) in the two main substrates used by chaffinches in evergreen forest and pinewood. *F* y *P* refer to ANOVAs comparing arthropod abundance between the two forests. All sample sizes were $n = 45$. $\bar{x}$: average; sd: standard deviation.
[Abundancia relativa de artrópodos (no./2 min) en los dos sustratos principalmente utilizados por los pinzones en el fayal (evergreen forest) y en el pinar (pinewood forest). F y P hacen referencia a las comparaciones entre formaciones vegetales utilizando ANOVAs. Todos los tamaños muestrales son n = 45. $\bar{x}$: media; sd: desviación típica.]

	Evergreen forest		*Pinewood forest*			
	$\bar{x}$	*sd*	$\bar{x}$	*sd*	*F*	*P*
Twigs and foliage	0.66	0.90	0.87	1.10	1.01	0.318
Ground	4.76	4.42	0.76	0.93	44.72	< 0.001

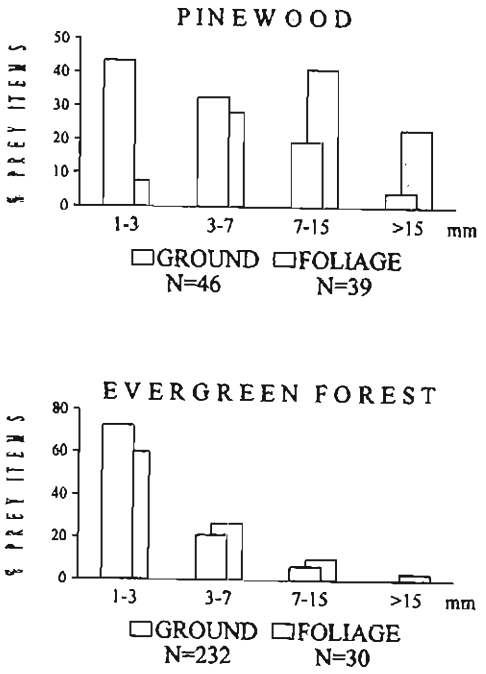

FIG. 1.—Size distribution of prey lenghts in the two mainly used subtrates by chaffinches in the pinewood and evergreen forest. N: sample size.
[Distribución de tamaños de presa en los dos sustratos principalmente utilizados por los pinzones en el pinar y fayal. N: tamaño de muestra.]

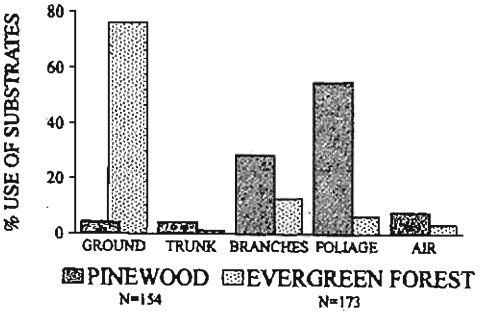

FIG. 2.—Percentage use of foraging sustrates by the Common Chaffinch in the two habitats. N: sample size.
[Porcentaje de uso por el Pinzón Vulgar de los sustratos de alimentación en los dos hábitats. N: tamaño de muestra.]

evergreen forest ($F_{1,88} = 44.73$, $P < 0.001$), but was similar in these two substrates in the pinewood ($F_{1,88} = 0.304$, $P = 0.590$; Table 1). The size distribution of arthropods was significantly different between ground and foliage in the pinewood ($\chi^2 = 19.15$, 3 df, $P < 0.001$), although there was no significant difference in the evergreen forest ($\chi^2 = 2.68$, 2 df, $P = 0.262$; Fig. 1). Prey availability in foliage did not significantly differ between pinewood and evergreen forest ($P = 0.318$), although in the ground it was significantly higher in the evergreen forest ($P < 0.001$).

Chaffinch density in the pinewood was significantly lower than in the evergreen forest (pinewood: $\bar{X} = 1.6$ birds/5 ha, sd = 1.5, $n = 12$; evergreen forest: 9 birds/5 ha; $t_{11} = 17.07$, $P = 0.001$). Chaffinches mainly foraged in the foliage (needles) of the pinewood, while in the evergreen forest foraging was almost restricted to the ground (Fig. 2). Both frequency distributions significantly differed ($\chi^2 = 182.88$, 4 df, $P = 0.001$).

Food intake rate was significantly higher in the evergreen forest than in the pinewood ($F_{1,45} = 6.42$, $P = 0.015$; Fig. 3). This difference was mainly due to the predominant use of ground in the evergreen forest, where food intake was higher than in the foliage ($F_{1,19} = 5.65$, $P = 0.028$). Food intake did not significantly differ between the pinewood and the evergreen forest when comparing records

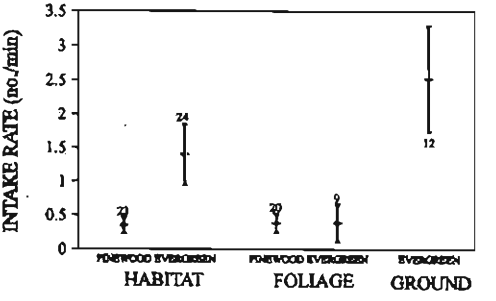

FIG. 3.—Intake rate ($\bar{x} \pm$ sd) of the Common Chaffinch in the two habitats, and in the most commonly used foraging subtrates. Numbers indicate sample sizes.
[Tasa de ingestión de presas ($\bar{x} \pm sd$) del Pinzón Vulgar en los dos hábitats y en los sustratos más frecuentemente utilizados para obtener alimento. Los números indican tamaños muestrales.]

of chaffinches foraging in the foliage ($F_{1,27}=0.0001$, $P=0.996$). These results are consistent with those obtained for food availability, as the higher the arthropod abundance, the higher the food intake rate.

Discussion

The Chaffinch population of El Hierro tracked food availability during the breeding period: chaffinches actively selected the habitat and substrates in which intake rates were higher. This result seems to support the hypothesized role of food availability as a prominent process determining the pattern of abundance and distribution of species in a given region, even during the breeding period (see nevertheless Díaz & Pulido, 1993 for a similar study with *Parus caeruleus*). Contrary to generalization by Fretwell (1972) and Wiens (1977 and 1989), on the limitation of temperate bird populations during winter (see also Nilsson, 1979; Blake & Hoppes, 1986; Dunning & Brown, 1982), recent evidence supports the limiting role of food availabity during the breeding season (Martin, 1987b). Some studies have indicated that food becomes abundant only during insect outbursts (which occur sporadically and infrequently), and that birds in temperate forests depend heavily on non-irrupting prey, which are depressed along the breeding period an may involve prolonged periods of food limitation (Holmes *et al.*, 1986; Holmes, 1990). In a region of tropical climate such as the Canary Islands, in which the seasonal flush of productivity and the related arthropods outbursts may be less marked than in other more seasonal northern regions, the potential food shortages could play an important role in determining between-habitat bird distribution.

Although food abundance does not explain the unbalanced use of substrates in the pinewood, prey size differences between the two mainly used substrates can explain the most frequent use of pine foliage. The effect of prey size on habitat use has been aslo demonstrated with other bird species (e.g. Alonso *et al.*, 1991), and can be explained considering the higher energy intake per prey unit provided by larger prey which allow search time to be reduced (Pyke, 1984). Nevertheless, predation risk may be another factor determining the habitat use of chaffinches in the pinewood (see review by Lima & Dill, 1990; Suhonen *et al.*, 1992, 1993). In this habitat, the frequent presence of kestrels and sparrow hawks, as well as the relative openness of this habitat and the long distance between the ground and the lower branches of the pines (3-5 m on average; pers. obs.), could determine a high perceived predation risk on the ground, and therefore a lower use of this substrate.

The importance of food availability in explaining the habitat distribution of the Common Chaffinch may also support the species-specific habitat selection hypothesis as the main determinant of between-habitat distribution of Canary chaffinches among islands (Carrascal *et al.*, 1992). This hypothesis may represent an alternative view to the previously accepted competitive exclusion hypothesis with the Blue Chaffinch (Lack & Southern, 1949; Grant, 1979). The Blue Chaffinch occurs in Gran Canaria and Tenerife, where it only occupies pinewoods. In the two islands where the Blue Chaffinch occurs, the Common Chaffinch breeds mainly in evergreen forests (Bannerman, 1963; Martín, 1987a). At these latitudes, precipitation is considered to be the main determinant of primary productivity, and consequently of invertebrate abundance (Lieth & Whittaker, 1975; Mooney & Kumerow, 1981). Rainfall has often been linked to the distribution of species on gradients of xericity in woodlands (e.g. Kendeigh & Fawyer, 1981; Smith, 1977; Tellería & Santos, 1993). The role of precipitation on food abundance could explain the high densities of chaffinches in the mesic evergreen forests, in comparison to the more xeric pinewoods, and also could explain the presence or absence of chaffinches in some Canarian pinewoods. Thus, 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 Common Chaffinch is only marginally present (Tenerife and Gran Canaria; 300-600 mm; Anonymous, 1980). Therefore, precipitation, through its influence upon food availability, could be a prime factor determining the higher abundance of

Common Chaffinch in evergreen forests of the whole archipelago, and the presence in some pine woods.

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BIBLIOGRAPHY

ALONSO, J. C., ALONSO, J. A. & CARRASCAL, L. M. 1991. Habitat selection by foraging White Storks, *Ciconia ciconia*, during the breeding season. *Canadian Journal of Zoology*, 69: 1957-1962.

ANONYMOUS. 1980. *Atlas Básico de Canarias*. Ed. Interinsular Canaria. Santa Cruz de Tenerife.

BANNERMAN, D. A. 1963. *Birds of the Atlantic Islands*. Oliver & Boyd. Edinburgh.

BLAKE, F. G. & HOPPES, W. G. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk*, 103: 328-340.

CARRASCAL, L. M. 1983. Análisis comparativo de cinco sistemas de muestreo del uso del espacio en aves forestales. *Ardeola*, 30: 45-53.

——, TELLERÍA, J. L. & VALIDO, A. 1992. Habitat distribution of Canary chaffinches among islands: competitive exclusion or species-specific habitat preferences? *Journal of Biogeography*, 19: 383-390.

CODY, M. L. 1985. *Habitat selection in birds*. Academic Press. New York.

COOPER, R. J. & WHITMORE, R. C. 1990. Arthropod sampling methods in Ornithology. *Studies in Avian Biology*, 13: 29-37.

DÍAZ, M. & PULIDO, F. J. P. 1993. Relaciones entre la abundancia de artrópodos y la densidad del Herrerillo Común *Parus caeruleus* en dehesas durante el período prerreproductor. *Ardeola*, 40: 33-38.

DUNNING, J. B. & BROWN, J. H. 1982. Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. *Auk*, 99: 123-129.

FRETWELL, S. D. 1972. *Populations in a seasonal environment*. Princeton Univ. Press. Princeton, New York.

GONZÁLEZ, M., RODRIGO, J. & SUÁREZ, C. 1986. *Flora y Vegetación del Archipiélago Canario*. Edirca. Santa Cruz de Tenerife.

GOSS-CUSTARD, J. D. 1984. Intake rates and food supply in migranting and wintering shorebirds. In J. Burger & B. L. Olla (Eds.): *Shorebirds: migration and foraging behaviour*, pp. 233-270. Plenum Press. New York.

GRANT, P. R. 1979. Evolution of the chaffinch, *Fringilla coelebs*, on the Atlantic islands. *Biological Journal of Linnean Society*, 11: 301-332.

HERNÁNDEZ, C. E., PÉREZ, P. L. & WILDPRET, W. 1984. Contribución al estudio bioclimático de El Hierro (Islas Canarias). *Vieraea*, 14: 77-111.

HOLMES, R. T. 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. *Studies in Avian Biology*, 13: 6-13.

——, SHERRY, T. W. & STURGES, F. W. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brooks. *Ecological Monographs*, 56: 201-220.

JÄRVINEN, O. & VÄISÄNEN, R. A. 1975. Estimating relative densities of breeding birds by the line transect method. *Oikos*, 26: 316-322.

KENDEIGH, S. C. & FAWYER, B. J. 1981. Breeding bird populations in the Great Smoky Mountains, Tennesse and North Carolina. *Wilson Bulletin*, 93: 218-242.

LACK, D. & SOUTHERN, H. N. 1949. Birds of Tenerife. *Ibis*, 91: 607-626.

LIETH, H. & WHITTAKER, R. H. 1975. Primary productivity of the biosphere. *Ecological Studies*, n.º 14. Springer. New Yor.

LIMA, S. L. & DILL, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68: 619-640.

MARTÍN, A. 1987 a. *Atlas de las aves nidificantes de Tenerife*. Instituto de Estudios Canarios. CSIC. Tenerife.

MARTIN, T. E. 1987b. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematic*, 18: 453-487.

MARZOL-JAÉN, M. V. 1988. *La Lluvia: un recurso natural para Canarias*. Servicio de Publicaciones de la Caja General de Ahorros de Canarias.

MOONEY, H. A. & KUMEROW, J. 1981. Phenological development of plants in Mediterranean-climate regions. In D. Castri, D. W. Goodall & R. L. Specht (Eds.): *Ecosystems of the World II. Mediterranean type shrublands*, pp. 303-307. Elsevier. Amsterdam.

MORRISON, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. *Condor*, 86: 146-150.

NEWTON, I. 1980. The role of food in limiting bird numbers. *Ardea*, 68: 11-30.

NILSSON, S. G. 1979. Seed density, cover, predation and the distribution of birds in a beech wood in southern Sweden. *Ibis*, 121: 177-185.

PÉREZ DE PAZ, P. L., DEL ARCO, M. & WILDPRET, W. 1981. Contribución al conocimiento de la flora y vegetación de El Hierro (Islas Canarias). *Lagascalia*, 10: 25-57.

PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematic*, 15: 523-575.

SMITH, K. G. 1977. Distribution of summer bird along a forest moisture gradient in an Ozark watershed. *Ecology*, 58: 810-819.

SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry*. W. H. Freeman. New York.

SUHONEN, J., ALATALO R. V., CARLSON, A. & HÖGLUND, J. 1992. Food resource distribution and the organization of the *Parus* guild in a spruce forest. Ornis Scandinavica, 23: 467-474.

——, HALONEN, M. & MAPPES, T. 1993. Predation risk and the organization of the *Parus* guild. *Oikos*, 66: 94-100.

TELLERÍA, J. L. 1986. *Manual para el censo de los vertebrados terrestres*. Ed. Raíces. Madrid.

—— & SANTOS, T. 1993. Distributional patterns of insectivorous passerines in the Iberian forests: does abundante decrease near the border? *Journal of Biogeography*, 20: 235-240.

WIENS, J. A. 1977. On competition and variable environments. *American Science*, 65: 590-597.

—— 1989. *The ecology of bird communities*. 2 Vol. Cambridge Univ. Press. Cambridge.

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