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Increased Response of the Short-Toed Treecreeper *Certhia brachydactyla* in Sympatry to the Playback of the Song of the Common Treecreeper *C. familiaris*

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Abstract

The two European species of treecreepers, the short-toed treecreeper *Certhia brachydactyla* and the common treecreeper *C. familiaris*, occupy different habitats, but are sympatric to a certain extent. The response to specific and heterospecific song was studied both in a sympatric and in an allopatric population of short-toed treecreeper in the Iberian Mountains (Burgos, Castilla-León, Spain). Short-toed treecreepers in sympatry showed a more aggressive response towards the song of the common treecreeper than those in allopatry. Although strict interspecific territoriality was not found, the experimental data suggest that the altitudinal distribution pattern of the two species may be a consequence of the increased aggression. This interspecific aggression may be advantageous for the short-toed treecreeper, as it may achieve a loose interspecific territoriality resulting in some spacing. However, a non-adaptive hypothesis for this behaviour cannot be rejected.

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Introduction

In the Iberian Peninsula, the short-toed treecreeper, *Certhia brachydactyla*, is widely distributed, whereas the common treecreeper, *C. familiaris*, is restricted to some areas in the Pyrenees, the Cantabrian and the Iberian Mountains. Interchange between these populations of common treecreeper is unlikely to occur, as the species is thought to be almost sedentary (DE JUANA 1980; MUNTANER et al. 1983).

The most southern population of the common treecreeper is in the Iberian Mountains. Here it exclusively inhabits beech forests, *Fagus sylvatica*, a habitat in which no short-toed treecreeper was found in 1977 (DE JUANA 1980). Nevertheless, a survey in 1982 showed

a high degree of sympatry (DE JUANA, pers. comm.), and it is evident that the short-toed treecreeper has now succeeded in colonizing formerly allopatric areas, to such an extent that its density is the higher of the two species (GIL, unpubl. data).

The populations of common treecreeper in the Iberian Peninsula are extremely isolated because of the felling of many beech forests in recent decades. Pine plantations have also mushroomed in the area, facilitating colonization by the short-toed treecreeper (PURROY 1973). Previous research conducted at these sympatric sites has shown that the two species differ in altitudinal distribution (Fig. 1). The common treecreeper is restricted to the higher part of the forest, and the short-toed treecreeper occupies the lower range, though a great deal of overlap occurs. Several instances of interspecific aggression and countersinging have been observed, but the species do not defend proper interspecific territories (GIL, unpubl. data).

Sibling species with partially overlapping distributions have often been examined for interspecific territoriality. ORIANS & WILLSON (1964) predicted interspecific aggression when two closely related species of birds come into contact for the first time, particularly where there is simple vegetation structure, stratified food sources or niche overlap. The literature suggests two patterns. In some pairs of species of the same genus, such as *Dendroica* warblers (MURRAY & GILL 1976; MORRISON 1982), *Vermivora* warblers (CROOK 1984) or *Fringilla* finches (LYNCH & BAKER 1990; SLATER & CATCHPOLE 1990), there is a greater discrimination of song in sympatry, resulting in less aggression than in allopatry. On the other hand, other pairs of closely related species show higher levels of aggression in sympatry, and this is the case for some species of *Passerina* buntings (EMLEN et al. 1975), *Acrocephalus* warblers (CATCHPOLE 1978; CATCHPOLE & LEISLER 1986), *Empidonax* flycatchers (PRESCOTT 1987) and *Luscinia* nightingales (LILLE 1988). A similar pattern of

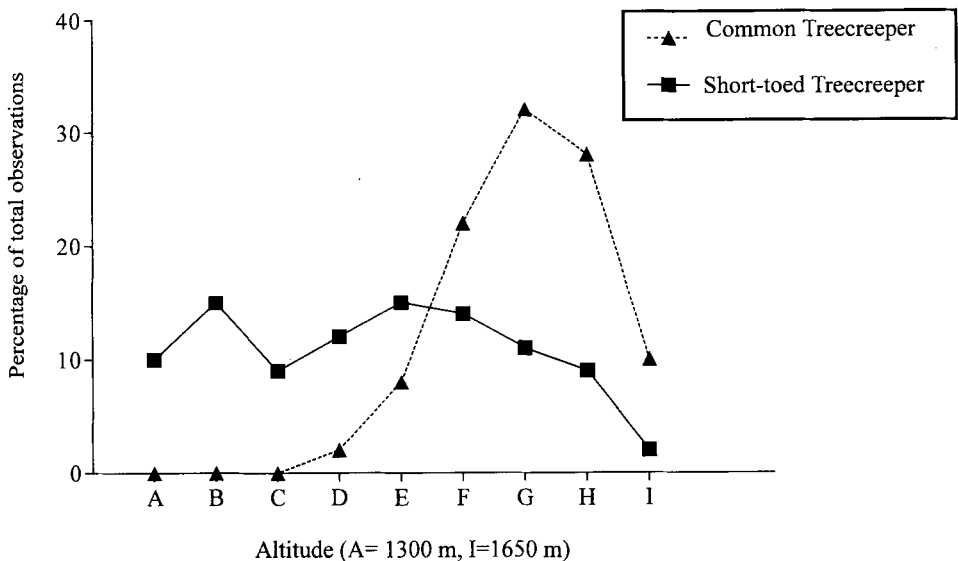


Fig. 1: Altitudinal distribution of both species of treecreepers, as shown by percentage of observations within different altitude bands in the study site

aggressiveness may be found between less closely related species in structurally simple habitats, as between the great tit, *Parus major*, and chaffinch, *Fringilla coelebs*, on some Scottish islands (REED 1982); or in competition for nest sites between the pied flycatcher, *Ficedula hypoleuca*, and great tit (JÄRVI et al. 1978). The crucial factor seems to be the existence of competition for the use of a limiting resource. Different populations of the same species show varied responses depending on local conditions.

The overlapping populations of common and short-toed treecreeper in the Iberian Mountains are ideal for the study of this issue. The original objective of this study was to test for both species the null hypothesis that there is no difference in the interspecific response to playback between the sympatric and allopatric populations. The allopatric tests for the common treecreeper could not be carried out, so this paper considers only the experiments on the short-toed treecreeper. There are two alternative hypotheses to the null one.

1. There is higher aggression in sympatry. This might occur because it is adaptive to respond to the sibling species song if the species are competitors; the interspecific response may facilitate interspecific spacing and territoriality (e.g. REED 1982). Alternatively, this behaviour may be maladaptive (MURRAY 1981).

2. There is lower aggression in sympatry. This is expected if the songs of the two species are very similar and it is not adaptive to respond to the sibling species song. Some niche or habitat partitioning may be working, or perhaps the niche is wide enough to be shared (e.g. SLATER & CATCHPOLE 1990).

Material and Methods

Study Sites and Subjects

The experiment involved playback in both an allopatric and a sympatric area of short-toed treecreeper. The sympatric site was a beech forest in the slope of Monte Mencilla, near Pineda de la Sierra (Iberian Mountains, N Spain) between 1400 and 1650 m; and the allopatric area comprised several oak *Quercus pyrenaica* forests in the outskirts of Burgos, at an average of 900 m. The study sites were 40 km apart.

The degree of sympatry (Table 1) was measured by presence/absence recordings of each species in 10 min periods (BLONDEL 1977). 'Allopatry' here means 'breeding allopatry', as a certain degree of winter movement may result in an overlapping winter distribution (DE JUANA 1980), and all records were made in the breeding season.

The sample was of 9 birds in the allopatric and 10 in the sympatric area. The territories of these birds were mapped in May, and the experiments were carried out in Jun.–Jul. 1993, in the first 4 h after dawn.

Table 1: Degree of sympatry as shown by the number of recording periods of 10 min (BLONDEL 1977) in which any species was heard; 40 recording periods were performed for each site. Fisher's exact test, $p = 0.0248$

Site	Species	
	<i>Certhia brachydactyla</i>	<i>Certhia familiaris</i>
Outskirts of Burgos (allopatry)	18	0
Pineda de la Sierra (sympatry)	22	7

Experimental Tapes

A single playback tape was used for each species. They were prepared from recordings of French birds supplied by the British Library of Wildlife Sounds (BLOWS). In these tapes, artificial bouts were built from a single stimulus song, at a delivery rate of 6 songs per min. Songs were recorded from a Marantz CP430 to a Sony WMD6C through a Marantz EQ551 Graphic Equaliser, filtering frequencies below 500 Hz by -10 dB and boosting the range 1 kHz to 16 kHz by $+7$ dB.

Although the use of a single tape for each species is not the ideal experimental design (KROODSMA 1989), there are reasons to justify it. Firstly, the songs of these species are very distinct (e.g. BERGMANN & HELB 1982), and it is likely that the specific traits outweigh other local or individual features that might affect the response. Secondly, the stimulus songs used came from distant populations, minimizing sensitization or habituation effects. Thirdly, as the original project involved the study of the response of both species, it was expected that the responses to the species-specific song would produce a baseline measure, allowing inter- and intraspecific comparisons. Though the data for common treecreeper are not suitable for inter-site comparisons, the results on this species indicated that the tape that was used for this species was recognized by all the birds as species-specific.

Experimental Procedure

Each bird was tested twice, the control test being the playback of conspecific song and the treatment-test the heterospecific one. The order of the trials was random, and a day at least was allowed between the two tests for the same bird. A Sony WMD6C and two Sony SRS-38 loudspeakers were used for the playback. The volume setting was decided by testing three people familiar with the species separately in the field at a distance of 10 m from the speaker. All agreed on roughly the same volume.

The experiment was carried out by waiting in the centre of each territory until the male was heard singing. The territories had been mapped in advance, and this made possible the individual identification of each bird. The tape was switched on at a distance of 40 m from the bird. The playback experiment consisted of a 3 min test period, during which the tape was broadcast, followed by a silent 3 min post-test period. The observed response of the bird was dictated into a Walkman 10 m away from the speaker and the following variables were measured for each of the two periods: 1. number of songs; 2. number of 'srii' calls; 3. number of 'tut' calls; 4. number of aggressive calls; 5. time spent within a 10 m diameter circle around the speaker; and 6. number of chasing flights within that circle. This led to a total of 12 variables across the two 3-min periods.

Statistical Analysis

The use of a large number of variables for the analysis of the playback response yields a better picture of the different aspects of the response, although it makes the interpretation of the results more difficult (MCGREGOR 1992). To avoid this the 'multivariate-measure approach' proposed by MCGREGOR (1992) was followed and a PCA (principal components analysis) was performed to reduce the 12 original variables to the first two uncorrelated components. The scores of the birds' responses for these new variables were tested using two-tailed non-parametric tests: for the paired comparisons, those used were Wilcoxon matched-pairs signed-ranks tests and for the unpaired comparisons, Mann-Whitney U-tests.

All the statistical tasks were performed using the Statgraphics package, 5.0 release (STATISTICAL GRAPHICS CORP. 1991).

Results

A principal components analysis was performed for 11 variables, after discarding the variable AGGR_POST (number of aggressive calls in the post-experimental period) as no bird scored on it. Two principal components were extracted, and these explain 70% of the variance (Table 2).

The first component (PC_1) accounts for 43% of the variance. The variables that most contribute to it are time near the speaker, number of chasing flights (for both test and post-test periods), number of aggressive calls in the test period and number of songs in

Table 2: Eigenvalues and variance explained by the two first principal components extracted from the original variables of the response to the playback

Principal component	Eigenvalue	Per cent variance	Cumulative variance
PC ₁	3.25464	42.9	42.9
PC ₂	2.06673	27.2	70.1

the post-test period (Table 3). The signs of the main variables are all positive, and this indicates that PC₁ is a general component (FREY & PIMENTEL 1978), or in other words, a common factor that is measured by all the variables in the same direction. The nature of this common factor is revealed by the analysis of the leading variables accounting for PC₁, suggesting that it reflects agonistic behaviour. Thus, PC₁ can be considered as a measure of the strength of response to playback, although some vocal variables fail to load heavily on it (MCGREGOR 1992). An analysis of the internal heterogeneity for the scores of PC₁ showed no difference between months (Mann-Whitney U-test, $n_1 = 27$, $n_2 = 11$, ns).

Comparisons of the PC₁ scores (Fig. 2) show that both groups responded strongly to their own species' song, this response being significantly higher than that to common treecreeper song (Wilcoxon matched-pairs signed-rank; $n_1 = 9$, $n_2 = 9$, $p < 0.01$ for allopatry; $n_1 = 10$, $n_2 = 10$, $p < 0.005$ for sympatry). There was no difference between the groups in their response to conspecific song (Mann-Whitney U-test, $n_1 = 9$, $n_2 = 10$, ns).

There was a significant difference between the groups in their response to hetero-specific song as measured by PC₁ (Fig. 2). Birds in sympatry with the common treecreeper responded significantly more to common treecreeper song than those in allopatry (Mann-Whitney U-test, $n_1 = 9$, $n_2 = 10$, $p < 0.05$).

The second component (PC₂) is a bipolar component (FREY & PIMENTEL 1978),

Table 3: Weightings of the original variables in the first principal component

Variables	Weights in PC ₁
TIME_TEST	0.92183
TIME_POST	0.84506
CHAS_TEST	0.78614
CHAS_POST	0.77312
SONG_POST	0.42944
AGGR_TEST	0.37240
SRII_POST	0.30103
SONG_TEST	0.18383
SRII_TEST	0.15898
TUT_TEST	0.04245
TUT_POST	-0.02054

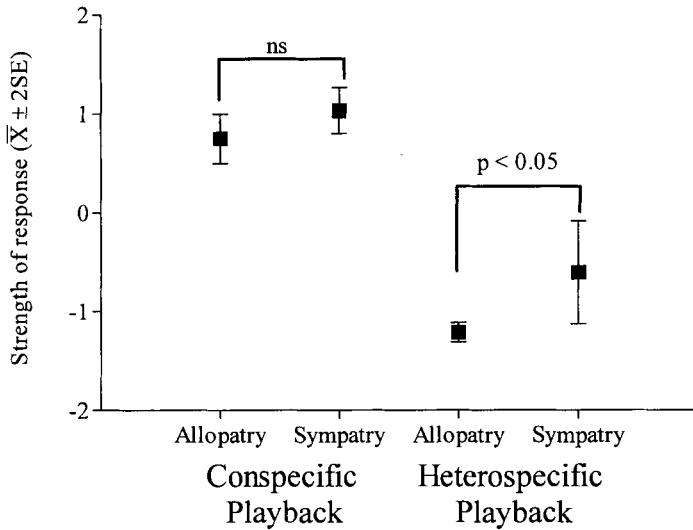


Fig. 2: Responses ($\bar{x} \pm 2SE$) of the short-toed treecreeper to the playback of conspecific and heterospecific song in allopatric and sympatric populations with the common treecreeper. Response is measured by the first principal component drawn from eleven variables of response. Statistical significances are for Mann–Whitney U-tests

with positive and negative loading of variables. It is clear from the examination of these variables that it shows a particularly strong dichotomy between singing response and ‘srii’ calling response (Table 4). Analysis of the internal consistency across months shows that this dichotomy is likely to be due to differences in these measures with the different stage in the breeding season. Birds in Jul. called more and sang less in response to playback than

Table 4: Weightings of the original variables in the second principal component

Variables	Weights in PC ₂
SONG__POST	0.57162
SONG__TEST	0.53502
CHAS__TEST	0.18088
AGGR__TEST	0.08163
TIME__POST	-0.00755
TIME__TEST	-0.01697
CHAS__POST	-0.16543
TUT__TEST	-0.26213
TUT__POST	-0.32203
SRII__TEST	-0.75218
SRII__POST	-0.80527

in Jun. (Mann–Whitney U-test, $n_1 = 27$, $n_2 = 11$, $p < 0.001$). Any further analysis of PC_2 was rejected because of this seasonal bias.

Discussion

The results show that the short-toed treecreeper is more aggressive towards the song of common treecreeper in sympatry than in allopatry. This means that the null hypothesis, which predicted no difference between groups, must be discarded, as well as the second alternative hypothesis, which predicted a decrease of aggression in sympatry.

The results support the hypothesis that the amount of aggression rises in sympatry due to adaptive interspecific territoriality, but does not rule out the possible maladaptivity of this behaviour, as MURRAY (1981) invokes. However, it seems likely that this higher aggression is responsible for the partitioning of the habitat in relation to the altitudinal gradient (Fig. 1), but experimental data would be necessary to test whether there is a causal relationship between aggression and partitioning. The distribution might simply be due to the different habitat selection of the two species.

A comparison with other populations in sites of overlap will contribute to understanding these findings. The pattern of habitat selection of *Certhia* treecreepers seems to be mainly a product of the different ecological conditions in which the two species evolved (STRESEMANN 1919; MOREAU 1954; SCHNEBEL 1972). Basically, in the area of overlap in Central Europe, the short-toed treecreeper shows a preference for open, oak-dominated areas, whereas the common treecreeper seems to be the euryoecious species, with less specialization and higher tolerance for a wide range of forests (SCHNEBEL 1972; MILDENBERGER 1984; KUITUNEN 1985). Nevertheless, there is no strict habitat segregation, and a high degree of sympatry is the rule. The picture is not the same in more southern areas. In France and Spain the common treecreeper is the stenoecious species, restricted to mountainous, high-altitude areas, whereas the short-toed treecreeper occupies any kind of forest or altitude (PURROY 1973; SPITZ 1976; DE JUANA 1980; MUNTANER et al. 1983; ELOSEGUI 1985; LAURENT 1987).

With regard to the use of space within the habitat, both species attain resource partitioning with other bark-foraging species by feeding on prey of different sizes (CSORBA & TÖRÖK 1988) and by using different searching movements, foraging techniques and substrates (VANICSEK 1988). Only two studies have tried to find any niche partitioning within the genus *Certhia*. SCHÖNFELD (1983) reports a possible horizontal division in tree use, with the common treecreeper foraging more often on trunks and the short-toed treecreeper in the branches. Unfortunately, his evidence is very weak: he only suggests this partitioning on the basis of the differences in territory size and morphology of the bill and hind claw. A more detailed study by FRÜHAUF (1993) failed to find any substantial difference in the niche of the two species in sympatry. Also, no differences between species were found in the musculature of the pelvic appendages, which includes several myological adaptations for tail-supported climbing (MORENO 1991). THIELCKE (1972) reported the existence of common treecreepers with mixed songs (composed of the two species' species-specific elements) which defended interspecific territories. However, the percentage of mixed songsters did not increase during a time span of 20 yr (THIELCKE 1986). This suggests that either this behaviour is not advantageous, or birds with mixed song incur

other costs that cause them to be selected against. For instance, potential mates are unlikely to recognize these birds as conspecific.

Thus, it seems that the habitat selection found in the population of the Iberian Mountains (Fig. 1) does follow the expected pattern in the common treecreeper, with a preference for higher altitude. It seems unlikely; however, that the restricted use of the altitudinal range made by the common treecreeper is the same as that before the arrival of the short-toed treecreeper, as habitat selection is expected to be more strict when two similar species share the same habitat (BLONDEL 1979). As has been said before, the lack of previous data from the area does not allow one to rule out the possibility that the division of habitat may be unrelated to the arrival of short-toed treecreeper. FRÜHAUF (1993) found no interspecific aggression between the two species in a sympatric area in Austria, nor any mechanism that would help to share the niche, and this led the author to conclude that the niche was wide enough to be shared and that the principle of competitive exclusion was not universally applicable. The striking differences with the findings in this study could be related to the following.

1. The habitat of the common treecreeper in the Iberian Mountains has been recently colonized by the short-toed treecreeper, and it is located right on the edge of the sympatric range of the common treecreeper, whereas the area studied by FRÜHAUF (1993) has been an area of sympatry for a long time. This would agree with MURRAY's (1981) hypothesis on the maintenance of non-adaptive or even maladaptive interspecific aggression when only a small fraction of one species interacts with the other.

2. The differences might also be due to intrinsic characteristics of the different habitats. The wood where this study was conducted is a homogeneous, simple habitat, so it may not provide enough niche diversity for two species. The beech forest in the Iberian Mountains could also be considered as a biogeographical island, having thus less structural diversity and less capacity to resist a colonization (BLONDEL 1979).

3. Alternatively, the methodology used by FRÜHAUF (1993) in his playback experiments may not be fine enough to pick up an interspecific response, as he did not use a whole range of variables of response.

The non-adaptive hypothesis proposed by MURRAY (1971, 1981) implies that the increased aggression in sympatry is due to birds misidentifying the signal used in species-specific recognition. However, from this, one might expect a similar level of mistakes in sympatry and allopatry, instead of the increase of aggression in sympatry that was found (CATCHPOLE & LEISLER 1986). We know that song learning takes place in this species (THIELCKE 1972, 1973). It is possible to imagine a mechanism, based on this ability to learn song, which allows the bird to recognize and respond to the song of those heterospecific birds it encounters foraging in its niche.

It is not possible to prove a functional link between the higher aggression and the habitat partitioning that has been found in this area of sympatry. Though both species are able to share habitat and niche in Central Europe (FRÜHAUF 1993), it is unclear whether the ecological conditions are similar enough in the Iberian Mountains for the data to be extrapolated. The fact that 'mistaken identity' (MURRAY 1981) may have a role in the origin of this process does not rule out an advantage that the males of the short-toed treecreeper may obtain by 'being mistaken' and behaving aggressively towards the common treecreeper males. MURRAY (1981) clearly confuses ontogenetic, causal and functional

levels of explanation in his analysis. Interspecific territoriality is not an all-or-none phenomenon (CODY 1974; HILL & LEIN 1989) and a restricted form of it may increase the fitness of the individuals that show it, whatever its origin may be.

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Literature Cited

- BERGMANN, H.-H. & HELB, H.-W. 1982: Stimmen der Vögel Europas. BLV Verlag, München.
- BLONDEL, J. 1977: The diagnosis of bird communities by means of frequential sampling (E.F.P.). *Pol. Ecol. Stud.* **3**, 19—26.
- 1979: *Biogeografía y Ecología*. Ed. Academia, León.
- CATCHPOLE, C.K. 1978: Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. *Anim. Behav.* **26**, 1072—1080.
- & LEISLER, B. 1986: Interspecific territorialism in reed warblers: a local effect revealed by playback experiments. *Anim. Behav.* **34**, 299—300.
- CODY, M.L. 1974: *Competition and the Structure of Bird Communities*. Princeton Univ. Press, Princeton.
- CROOK, J.R. 1984: Song variation and species discrimination in blue-winged warblers. *Wilson Bull.* **96**, 91—99.
- CSORBA, G. & TÖRÖK, J. 1988: Fatörzson táplálkozó madárfajok táplálékszegregációja. *Aquila* **95**, 78—82.
- ELOSEGUI, J. 1985: Navarra: Atlas de Aves Nidificantes. Caja de Ahorros de Navarra, Pamplona.
- EMLEN, S.T., RISING, J.D. & THOMPSON, W.L. 1975: A behavioral and morphological study of sympatry in the Indigo and Lazuli Buntings of the Great Plains. *Wilson Bull.* **87**, 145—302.
- FREY, D.F. & PIMENTEL, R.A. 1978: Principal component analysis and factor analysis. In: *Quantitative Ethology* (COLGAN, P.W., ed.). Wiley, New York. pp. 219—246.
- FRÜHAUF, J. 1993: Treecreeper species with highly overlapping niches do not show interference competition. *Abstracts XXII Intern. Ethol. Conf.*: 245.
- HILL, B.G. & LEIN, M.R. 1989: Natural and simulated encounters between sympatric black-capped chickadees and mountain chickadees. *Auk* **106**, 645—652.
- JÄRVI, T., RADESÄTER, T. & JAKOBSSON, S. 1978: Aggressive responses of two hole-nesting passerines, *Parus major* and *Ficedula hypoleuca*, to the playback of sympatric species song. *Ornis Fennica* **55**, 45—74.
- DE JUANA, E. 1980: Atlas Ornitológico de la Rioja. Instituto de Estudios Riojanos, Logroño.
- KROODSMA, D.E. 1989: Suggested experimental designs for song playbacks. *Anim. Behav.* **37**, 600—609.
- KUITUNEN, M. 1985: Is the Common Treecreeper (*Certhia familiaris* L.) more widespread in Hungary than has been previously believed? *Aquila* **92**, 255—261.
- LAURENT, J.-L. 1987: Utilisation de l'espace par deux espèces jumelles, *Certhia brachydactyla* et *familiaris* en zone de sympatrie. *Rev. Ecol. Terre et Vie* **42**, 297—310.
- LILLE, R. 1988: Art- und Mischgesang von Nachtigall und Sprosser (*Luscinia megarhynchos*, *L. luscinia*). *J. Orn.* **129**, 133—159.
- LYNCH, A. & BAKER, A.J. 1990: Increased vocal discrimination by learning in two species of chaffinches. *Behaviour* **116**, 109—126.
- MCGREGOR, P.K. 1992: Quantifying responses to playback: one, many, or composite multivariate measures? In: *Playback and Studies of Animal Communication* (McGregor, P.K., ed.). Plenum, New York. pp. 79—96.
- MILDENBERGER, H. 1984: Die Vögel des Rheinlandes. Gesellschaft Rheinischer Ornithologen, Düsseldorf.
- MOREAU, R.E. 1954: The main vicissitudes of the European avifauna since the Pliocene. *Ibis* **96**, 411—431.
- MORENO, E. 1991: Musculature of the pelvic appendages of the Treecreeper (*Passeriformes: Certhiidae*): myological adaptations for rail-supported climbing. *Can. J. Zool.* **69**, 2456—2460.

- MORRISON, M.L. 1982: The structure of western warbler assemblages: ecomorphological analysis of the black-throated gray and hermit warblers. *Auk* **99**, 503—513.
- MUNTANER, J., FERRER, X. & MARTINEZ-VILALTA, A. 1983: Atlas dels Ocells Nidificants de Catalunya i Andorra. Ketres, Barcelona.
- MURRAY, B.G. 1971: The ecological consequences of interspecific territorial behaviour in birds. *Ecology* **52**, 414—423.
- 1981: The origins of adaptive interspecific territorialism. *Biol. Rev.* **50**, 1—22.
- & GILL, F.B. 1976: Behavioral interactions of blue-winged and golden-winged warblers. *Wilson Bull.* **88**, 231—253.
- ORIAN, G.H. & WILLSON, M.F. 1964: Interspecific territories of birds. *Ecology* **45**, 736—745.
- PRESCOTT, D.R.C. 1987: Territorial responses to song playback in allopatric and sympatric populations of alder (*Empidonax alnorum*) and willow (*E. traillii*) flycatchers. *Wilson Bull.* **99**, 611—619.
- PURROY, F.J. 1973: La répartition des deux grimpeaux dans les Pyrénées. *L'Oiseau et R.F.O.* **43**, 205—211.
- REED, T.M. 1982: Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: playback and removal experiments. *Anim. Behav.* **30**, 171—181.
- SCHNEBEL, G. 1972: Die Ökologie der Baumläufer (*Certhia brachydactyla* und *Certhia familiaris*) in Ostniedersachsen. *Vogelwelt* **93**, 201—215.
- SCHÖNFELD, M. 1983: Beiträge zur Ökologie und zum intraspezifischen Verhalten der Baumläufer *Certhia familiaris* und *C. brachydactyla* in Eichen-Hainbuchen-Lindenwäldern unter dem Aspekt der erhöhten Siedlungsdichte durch eingebrachte Nisthöhlen. *Hercynia*, N.F., Leipzig **20**, 290—311.
- SLATER, P.J.B. & CATCHPOLE, C.K. 1990: Responses of the two chaffinch species on Tenerife (*Fringilla teydea* and *F. coelebs tintillon*) to playback of the song of their own and the other species. *Behaviour* **115**, 143—152.
- SPITZ, F. 1976: Problèmes de répartition des deux grimpeaux (*Certhia familiaris* et *brachydactyla*) en France. *L'Oiseau et R.F.O.* **46**, 187—193.
- STATISTICAL GRAPHICS CORPORATION 1991: Statgraphics, 5.0 release.
- STRESEMANN, E. 1919: Über die europäischen Baumläufer. *Verh. Orn. Ges. Bayern* **13**, 245—288.
- THIELCKE, G. 1972: Waldbaumläufer (*Certhia familiaris*) ahmen artfremdes Signal nach und reagieren darauf. *J. Orn.* **113**, 287—296.
- 1973: On the origin of divergence of learned signals (songs) in isolated populations. *Ibis* **115**, 511—516.
- 1986: Constant proportions of mixed singers in tree creeper populations (*Certhia familiaris*). *Ethology* **72**, 154—164.
- VANICSEK, L. 1988: The study of bird species foraging on the bark. *Aquila* **95**, 83—96.

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