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Habitat and territory segregation within Sylviine warblers of the Flemish coastal dunes

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ABSTRACT. Sylviine warblers are abundant breeding birds in the Flemish coastal dunes. Although their habitat preferences are clearly different, habitat overlap can occur. Their habitat preferences can largely be explained by the overall territory-specific vegetation structure (all components included in the discriminant analysis). The transition from woodland to scrubs and from scrubland to short grasslands explains 92% of the total variance within the species' habitat characteristics. Species of the different genera (*Sylvia, Phylloscopus, Acrocephalus, Locustella*) show a large amount of habitat overlap. Within the *Phylloscopus* and *Sylvia*-genus, only the Lesser Whitethroat *S. curruca* and the Whitethroat *S. communis* use the same breeding habitat. Although the other congeneric species show distinct habitat characteristics, a priori classification cannot predict territory occupancy without errors: only 78.3% of the two *Phylloscopus*-territories and 58.3% of the *Sylvia*-territories were correctly classified. This indicates a certain amount of territory settlement in non-typical habitats, where competition can occur between sister species.

All possible interactions between congenerics were studied by comparing the expected (based on the total of wrong classifications in the typical habitat of the other) and the observed coexistence. The number of wrong classifications could only be explained by real coexistence in the species pair *S. borin-S. curruca*. Interactions between all other congeneric species pairs were asymmetrical, resulting in distinct territory occupancy with one dominant species. *S. borin* was always the dominant species, whereas *S. communis* was never dominant within the possible interactions. In general, species typical for higher vegetation were dominant (with the exception of the species pair *S. atricapilla-S. borin*). Direct and song aggressiveness are probably the driving forces for the observed territory segregation. Our results confirm and supplement the findings of CODY (1978), who studied similar habitat and territory segregation in Sylviine Warblers in England, Southern Sweden and Sardinia.

KEY WORDS: *Acrocephalus*, *Locustella*, *Phylloscopus*, *Sylvia*, interspecific interactions, habitat characteristics, vegetation, discriminant function analysis, Geographic Information System.

INTRODUCTION

During 1998, breeding birds were inventoried in the Flemish coastal dunes within the framework of a monitoring project, financed by the Flemish government, Nature Division AMINAL (Life-project – ICCI Integral Coastal Conservation Initiative). The aim of this project was to describe the breeding bird species composition and their landscape ecological relationships as a tool for the evaluation of the applied nature management (BONTE et al. 1998).

The inventory yielded a total of 78 species with a total of 4455 territories. The most common species were Dunnock *Prunella modularis*, Wood Pigeon *Columbo palumbus*, Whitethroat *Sylvia communis*, Blackbird *Turdus merula* and Willow Warbler *Phylloscopus trochilus*. Also nine Flemish Red List species were noted as breeding birds.

Sylviine-warblers (Marsh Warbler *Acrocephalus palustris,* Grasshopper Warbler *Locustella naevia,* Chiffchaff *Phylloscopus collybita,*Willow Warbler *P. trochilus,* Blackcap *Sylvia atricapilla,* Garden Warbler *S. borin,* Whitethroat *S. communis and* Lesser Whitethroat *S. curruca*) were particularly abundant, and their territories could be easily mapped by applying common bird census

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techniques. An initial analysis (Bonte et al., 2001) indicated that all Sylviine warblers are restricted to half open or closed dune scrub landscapes. Their presence in a common environment is very interesting because it enables us to study their specific habitat preferences and the potential niche overlap or coexistence based on the detailed vegetation description of their territories.

Of the mentioned Sylviine warblers, only *L. naevia* is a rather rare species in Flanders (200-500 pairs, with more than 10% of the total population along the Flemish coastal dunes: Devos & Anselin, 1999). All other species are common and occur in a variety of woody habitats (including gardens and woodlands). They are all insectivorous birds and typical summer guests in North-Western Europe. Chiffchaffs *P. collybita* and Blackcaps *S. atricapilla* are partial migrants with part of the population annually hibernating in our temperate regions. In the south of Europe they are year-round residents. The other species winter in northern or sub-Saharan Africa . Many of the Sylviine warblers are characterised by similar habitats and food preferences in the winter-grounds and tend to segregate their winter habitats in a similar way as in the breeding quarters (Cody, 1985).

Sylviine warblers are territorially aggressive during the breeding season, and most of them seem to be opportunistically polygynous. Many authors have reported interspecific territoriality in Sylviine warblers (Cramp & Brooks, 1992). Cody (1978) documented this phenomenon between Willow Warblers *P. trochilus* and Chiffchaffs *P. collybita* in England; *Hippolais* species are interspecifically territorial when their home ranges overlap in France (Ferry & Deschaintre, 1976 in: Cramp & Brooks, 1992). Cody (1985) recorded interspecific territoriality in congeneric species of the genus *Sylvia* in Southern Sweden, England and Sardinia. The latter also states that interspecific territoriality is a rare phenomenon between *Sylviine* warblers of different genera, although some evidence exists of interactions between *Hippolais sibilatrix* and *Sylvia atricapilla* (Crivelli & Blandin, 1977). Cody (1978) stated further that these interspecific interactions are presumably effected through interspecific reactions to territorial songs (song convergence).

Cody (1985) gives a detailed overview of his results on habitat segregation and interspecific interactions within *Sylviine* warblers in Sweden, England and Sardinia. In this contribution we firstly studied whether habitat segregation of *Sylviine* warblers is similar to that in other regions in Europe. Secondly we investigated whether interspecific interactions occur in the Flemish coastal dunes as well and if so, in what way they differ from those mentioned in other studies.

STUDY AREA

The study was undertaken in the coastal dunes between Dunkerque (North of France) and Nieuwpoort (Belgium). Eight dune sites were selected in order to cover a substantial portion of the landscape-ecological range within young dunes. The sites are situated in the Perroquet (Bray Dunes, France; 225 ha), the Westhoek (340 ha), Houtsaegerduinen (80 ha) (De Panne, Belgium), the Noordduinen (45 ha), Doornpanne (160 ha) and parts of the Ter Yde dune complex (110 ha) (Koksijde, Belgium).

These aeolian dunes are characterised by large dune slacks and distinct parabola-shaped ridges. Some mobile dunes are almost without vegetation. The wandering dunes in the Westhoek, for example, consist of nearly 100 ha of drifting sand, leaving large dune slacks on the lee side. Front dunes and smaller mobile dunes are covered with *Ammophila arenaria* (Marram grass). Fixed dune ridges primarily develop into grey dunes, mainly dominated by *Tortula ruralis* var. *ruraliformis* or *Hypnum cupressiforme* var. *lacunosum. Hippophae rhamnoides* scrub (Sea-buckthorn) dominates the next successional stage, and climax vegetation in dry dunes consists of woodland with *Quercus robur, Fraxinus excelsior* and *Acer pseudoplatanus*.

In dune slacks succession occurs significantly faster. Within a decade bare sand can turn into scrub or even woodland. Large dune slacks can be covered with various types of scrubland depending on elevation and successional stage. Dominant species are mainly *Hippophae rhamnoides, Salix repens* and *Ligustrum vulgare* but *Sambucus nigra, Crataegus monogyna* and *Rosa* spp. can be abundant as well. These species contribute to the structural diversity of the scrub. Besides trends towards woodland development, scrub can degenerate and be replaced by species-poor *Calamagrostis epigejos* stands.

Former livestock grazing or actual nature management can keep vegetation in a grassland or marshland stage. Botanically these vegetations can be very rich with species such as *Thesium humifusum, Helianthemum nummularium* and *Potentilla neumanniana* in dry grassland and *Epipactis palustris, Centaurium littorale* and *Parnassia palustris* in wet dune slacks.

MATERIAL AND METHODS

Field methods

In 1998, we carried out a census of Sylviine warblers in the Flemish coastal dunes (Bonte et al., 2001), using the territory mapping method (common bird census, CBC) as described by Hustings et al. (1985). Common bird census is the only reliable method to obtain detailed information about absolute breeding bird densities and territory distribution in a particular area. A total of ten mapping visits were made during the breeding season (March to July).

Detailed vegetation maps of the larger, non-urbanised dune areas, which were not available (Westhoek and Perroquet), were produced by a stereoscopical interpretation of aerial photographs with scale 1:2000. The resulting contour maps were digitised with the GIS package Genamap 6.2, checked in the field and coded for vegetation composition with the units proposed and used by Provoost & Hoffmann (1996). Detailed digital vegetation maps of the Doornpanne (Kuijken et al., 1993), Ter Yde (Hoffmann et al., 1998) and Lombardsijde (Hoffmann et al., 1996) were available at the Institute of Nature Conservation (Brussels). The following vegetation types were lumped into structurally similar units: dune woodland, mixed shrubs (*Hippophae rhamnoides* with *Rosa* species and *Crataegus monogyna*). *Ligustrum vulgare* dominated shrub, *Salix repens* dominated shrubs, *Hippophae rhamnoides-Sambucus nigra* shrubs, tall grasslands dominated by *Calamagrostis epigejos*, short rabbit grazed pastures, grey dunes and blond dunes with Marram grass (*Ammophila arenaria*).

Data Analyses

We used the interpretation criteria of Hustings et al. (1985) to construct the specific territory maps. These maps were digitised within a GIS (Genamap 6.2). The simplified vegetation and territory maps were imported in Arcview 5.1, by means of which overlays were made. In this way, specific vegetation descriptions were obtained for each territory.

Differentiation in habitat structure (i.e. vegetation composition) was studied by a forward discriminant analysis (Statistica 5.1) for all Sylviine warblers, and specifically for the congeneric *Sylvia* and *Phylloscopus* species, for all species together, and for the different studied species pairs.

The discriminant analyses were used to determine which vegetation types were the best predictors for the habitat segregation. Habitat segregation was studied by canonical plots of the discriminant functions, with 95% confidence ellipses around the species' means and Mahalanobis distances. The significance levels of the Pearson correlation were calculated following Jerrold (1996). For each species combination, *a priori* classifications revealed the number of correctly classified territories and the amount of occupied territories, in the typical habitat for the congeneric species. The wrongly classified territories should be in reality be the result of common habitat use because of coexistence in the field or from common habitat use without territory overlap as a result of direct interspecific interactions, where one species excludes the other.

The percentage of predicted common habitat use (predicted coexistence) was compared with the observed percentage of coexistence (we assumed coexistence when the territories overlapped) by the application of a χ^2-test (Jerrold, 1996). When the observed proportion of coexistence does not differ from the expected, common habitat use is the result of real coexistence. If the observed proportion of territory overlap is significantly lower than the expected, common habitat use is accompanied by interspecific territorial interactions and thus by territory segregation. These interactions are either symmetrical when the two species equally occupy the typical territory of each other, or asymmetrical in the case when one dominant species occupies more territories in the sister species typical habitat. These differences were again tested by χ^2-tests for deviations from equal proportions .

RESULTS

Habitat overlap between *Sylviine* warblers

In the study area, a total of 1296 territories of the eight Sylviine species were recorded (Table 1): *Sylvia communis* and *Phylloscopus trochilus* were the most abundant species (resp. 331 and 324 territories); *Acrocephalus palustris* was the rarest included Warbler (22 territories).

TABLE 1

Total number of territories in the study area per species

Species	**Total number of territories**
Acrocephalus palustris Bechstein, 1798	22
Locustella naevia Boddaert, 1783	55
Phylloscopus collybita Vieillot, 1817	254
Phylloscopus trochilus Linnaeus 1758	324
Sylvia atricapilla Linnaeus 1758	176
Sylvia borin Boddaert, 1783	65
Sylvia communis Latham, 1787	331
Sylvia curruca Linnaeus 1758	69
Total	1296

All variables were included in the forward discriminant function analysis (Table 2). Although the overall discriminating power is low (36.88 % correctly classified), the

TABLE 2

Vegetation components included in the discriminant function analysis (Wilks' Lambda= 0.654, F (77,7665)=7.293, $p<0.0001$), based on all species. Bold: significant contribution to the overall discrimination.

Vegetation type	**Wilks' Lambda**	**p-level**	**R^2**
Grey dunes	0.662	0.063	0.045
Ligustrum vulgare shrub	0.659	0.324	0.009
Marram dunes	0.659	0.326	0.099
Mixed shrub	0.660	0.141	0.511
Salix repens-shrub	0.657	0.589	0.051
Sambus nigra-shrub	0.657	0.612	0.279
Sandy dune slack	0.656	0.826	0.046
Short grassland	**0.664**	**0.013**	**0.327**
Tall grassland	0.659	0.366	0.077
Woodland	**0.817**	**0.000**	**0.397**
Young dune slack	0.657	0.631	0.051

analysis was highly significant, indicating that the species' territories can be discriminated on the basis of their vegetation composition. Of all included vegetation types, only two contributed significantly to the overall discrimination: the proportions of woodland and short grassland within the territories.

Of the seven calculated canonical axes, only the first two contribute significantly to the total amount of variation (Table 3). Although the first axis contributes 86.4 % and the second another 5.6 %, the eigenvalue of the second axis is very low. The first canonical axis correlates significantly (Table 3) with the proportion of woodland (negatively) and different types of scrub (positively) within the territories. This axis is also positively, but less significantly, correlated with open sandy dunes and short vegetation. The second axis correlates negatively (Table 3) with the amount of different types of scrubland, and positively with short vegetation and open dune (particularly with short grasslands).

The plot of the discriminant functions with species' habitat means surrounded with 95% confidence ellipses (Fig. 1) visualises the habitat segregation: congeneric *Sylvia* and *Phylloscopus* species segregate completely. A certain habitat overlap exists between the species pair *P. collybita* and *S. atricapilla*. *Acrocephalus palustris* and *S. curruca* are characterised by a certain amount of habitat overlap, while the latter shares a common habitat with both *Locustella naevia* and *Phylloscopus trochilus*. Territories of the latter species pair overlap consistently.

Taking into account the canonical correlation, *P. collybita* and *S. atricapilla* can be categorised as dune woodland-preferring species and *S. borin* as an intermediate species between scrubs and woodland. All other *Sylviine* warblers prefer scrub. Of these, *S. communis* and *L. naevia* are associated with grassland-shrub mosaics, while *S. curruca* and *A. palustris* apparently prefer homogeneous scrub.

In contrast to the results of the canonical ordination, the Mahalanobis distances (Table 4) indicate significant habitat segregation only between woodland associated species (*P. collybita* and *S. atricapilla*) and the other *Sylviine* warblers. *S. borin* shows no habitat segregation with *A. palustris* and a low one with *S. atricapilla*.

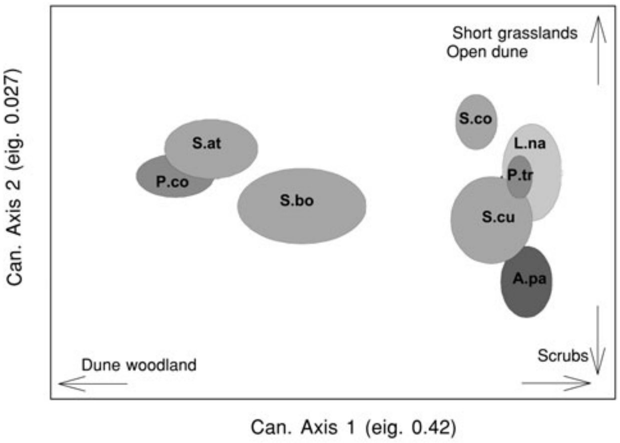

Fig. 1. – Discriminant ordination plot of the species' territories (means and 95% confidence ellipses) with eigenvalues (eig.) based on the vegetation composition within the territories. Species abbreviations: A.pa: *Acrocephalus palustris*, L. na: *Locustella naevia*; P. tr: *Phylloscopus trochilus*; P. co: *Phyllsocopus collybita*; S. at: *Sylvia atricapilla*; S. bo: *Sylvia borin*; S.co: *Sylvia communis*; S. cu: *Sylvia curruca.*

TABLE 3

Correlation coefficients and canonical analysis results of the vegetation characteristics with the seven calculated canonical roots (Spearman correlations, n=1296; **bold: p<0.001**; underlined: p<0.01).

Vegetation type	**Root 1**	**Root 2**	Root 3	Root 4	Root 5	Root 6	Root 7
Grey dunes	0.037	**0.146**	0.627	0.035	0.092	-0.221	0.407
Ligustrum vulgare shrub	-0.004	**-0.146**	0.418	-0.075	0.336	0.321	0.274
Marram dunes	0.096	**0.222**	0.388	-0.137	-0.436	0.097	-0.144
Mixed shrubs	**0.247**	**-0.600**	0.112	0.501	-0.110	0.106	-0.335
Salix repens-shrub	**0.140**	0.059	-0.060	-0.568	0.054	0.060	0.143
Sambucus nigra-shrub	**0.233**	**-0.146**	0.042	-0.436	-0.255	-0.625	0.077
Sandy dune slack	**0.116**	0.088	-0.139	-0.537	-0.009	0.108	-0.215
Short grasslands	0.095	**0.817**	-0.011	0.242	0.228	-0.118	-0.272
Tall grassland	-0.005	0.021	-0.440	0.294	-0.022	-0.307	0.534
Woodland	**-0.973**	0.002	-0.006	-0.208	0.000	-0.036	0.013
Young dune slack	0.037	**0.164**	-0.102	0.014	-0.682	0.431	0.377
Eigenvalue	0.429	0.028	0.023	0.009	0.004	0.002	0.001
Cum.Prop	0.864	0.920	0.966	0.984	0.992	0.997	1.000
Canonical R	0.548	0.165	0.150	0.094	0.063	0.049	0.037
Wilks' Lambda	0.655	0.935	0.961	0.983	0.992	0.996	0.999
Chi-Sqr	544.647	86.168	50.604	21.413	9.907	4.812	1.750
df	77.000	60.000	45.000	32.000	21.000	12.000	5.000
p-level	0.000	0.015	0.262	0.922	0.980	0.964	0.883

The species associated with scrub and ordinated at the right of the diagram, do not show any significant interspecific Mahalanobis distances, indicating a certain amount of habitat overlap. The high proportion of wrong a priori classifications and the overall low percentage correct classification (Table 5) confirm the common habitat use and the high degree of habitat overlap.

TABLE 4

Squared Mahalanobis distances (shaded) and F-values for the discrimant function between all species pairs. Significant different distances at the 0.01-level in bold, significant distances at the 0.05 level underlined.

Squared Mahalanobis Distances F-values; df = 11,1278	*A. palustris*	*L. naevia*	*P. collybita*	*P. trochilus*	*S. atricapilla*	*S. borin*	*S. communis*	*S. curruca*
A. palustris	——	1.003	**5.226**	0.961	**4.553**	2.179	1.594	0.541
L. naevia	0.735	——	**10.865**	0.557	**8.429**	**4.092**	1.276	1.075
P. collybita	**2.988**	**2.707**	——	**30.323**	1.214	**3.980**	**24.346**	**9.968**
P. trochilus	0.540	0.133	**2.369**	——	**20.348**	**6.410**	2.092	0.834
S. atricapilla	**2.692**	**2.265**	0.130	**1.987**	——	2.360	**14.884**	**7.896**
S. borin	1.528	**1.549**	**0.864**	**1.330**	0.558	——	**5.227**	**3.780**
S. communis	0.895	0.305	**1.885**	0.142	**1.443**	**1.081**	——	1.489
S. curruca	0.374	0.396	**2.062**	0.165	**1.788**	**1.271**	0.293	——

TABLE 5

A priori classification matrix of all Sylviid-warblers

Species	**Percentage correctly classified**	**A.pa**	**L.na**	**P.co**	**P.tr**	**S.at**	**S.bo**	**S.co**	**S.cu**
A. palustris	0.000	0	0	0	21	0	0	1	0
L. naevia	0.000	0	0	2	35	0	0	18	0
P. collybita	53.541	0	0	136	78	3	0	37	0
P. trochilus	69.135	0	0	13	224	2	2	83	0
S. atricapilla	1.136	0	0	77	54	2	4	39	0
S. borin	3.076	0	0	24	27	0	2	12	0
S. communis	34.441	0	0	31	181	3	2	114	0
S. curruca	0.000	0	0	5	52	0	0	12	0
Total	36.882	0	0	288	672	10	10	316	0

Territory overlap and interspecific interactions within the genera *Phylloscopus & Sylvia*

P. collybita and *P. trochilus* discriminate significantly by the amount of tall grassland and woodland within the territories (Wilks' Lambda: 0.632; approx. F (11,566)=29.915; p<0.0001: Table 6). 78.03% of the territories were well classified. 52 territories of both species overlapped in the field, while 127 were expected based on the a priori classification (χ^2=111.58, p<0.001; Table 7). This indicates that the observed territory overlap is significantly lower than can be expected based on the common habitat occupancy. Within the common habitat, *P. collybita* is the dominant species, as a result of an asymmetrical interaction in which the latter occupies more territories typical for *P. trochilus* without tolerating its presence.

All Sylvia-warblers can be discriminated based on the included vegetation variables (Wilks' Lambda: 0.738; approx. F (33,1847)=6.081; p< 0.001 (proportion of woodland and short grasslands contribute significantly: Table 8)), resulting in an overall correct classification score of 58.35% (Table 9). Especially the territories of *S. communis* (90.93% correctly classified) can be well discriminated. All territories of *S. curruca* were classified as other Sylvia-habitats, indicating a high interaction between this species and the congeneric warblers.

With the exception of the species pair *S. communis-S. curruca*, all territories of the congeneric pairs could be discriminated by the included vegetation variables (Table 6). Of these, only the observed coexistence of the species pair S. *borin-S. curruca* matched the expected coexistence based on the a priori classification of the territories (Table 7), indicating a common habitat with territory overlap and without interspecific interactions.

Of all other species pairs (Table 7), *S. borin* was significantly dominant in potential territories of *S. atricapilla* and *S. communis*, *S. atricapilla* in potential territories of *S. curruca* and *S. communis*, while *S. curruca* was dominant only in the territories of *S. communis*. Although the latter is capable of occupying territories of the other congeneric species, it is never dominant in the interaction.

TABLE 6

Results of the discriminant analysis between congeneric Sylviid warbler pairs, with indication of the significant differentiating vegetation components.

Species-pair	**Wilks' Lamda**	**F**	**p**	**sign. Components**
P. trochilus- P. collybita	0.632	29.915	<0.001	Tall grassland, woodland
S. communis - S. curruca	0.967	1.167	0.307	
S. communis - S. borin	0.862	5.552	<0.001	woodland, *L. vulgare* shrub
S. communis - S. atricapilla	0.768	13.54	<0.001	woodland
S. borin - S. atricapilla	0.883	2.733	<0.01	*S. repens* shrub, short grassland
S. borin - S. curruca	0.7	4.756	<0.001	woodland, grey dunes
S. curruca - S. atricapilla	0.773	6.199	<0.001	short grassland, woodland

TABLE 7

Overview of the observed and expected territory overlap within congeneric Sylviid warbler pairs, with indication of the dominant species in the interaction. Total possible interactions are calculated as the sum of both species' numbers of territories; observed coexistence is derived from field data; expected coexistence is based on the discriminant analysis classification. The χ^2-coexistence is the result of frequency testing between expected and observed coexistence; χ^2-dominance is the result of frequency testing between the dominant species' and equal occupancies.

Species-pair	**total possible combinations**	**obs. coexistence**	**exp. coexistence**	**χ^2-coexistence**	**p**	**dominant species in interaction**	**χ^2-dominance**	**p**
P. trochilus- P. collybita	578	52	127	111.58	< 0.001	*P. collybita*	124.74	< 0.001
S. communis - S. curruca	400	47	69	4.89	0.027	*S. curruca*	138.00	< 0.001
S. communis - S. borin	396	41	74	11.08	< 0.001	*S. borin*	18.27	0.011
S. communis - S. atricapilla	507	42	129	28.34	< 0.001	*S. atricapilla*	87.21	< 0.001
S. borin - S. atricapilla	205	18	64	26.41	< 0.001	*S. borin*	78.13	< 0.001
S. borin - S. curruca	134	22	31	1.91	> 0.05			
S. curruca - S. atricapilla	245	18	63	29.95	< 0.001	*S. atricapilla*	26.71	< 0.001

TABLE 8

Summary of the discriminant analysis of the Sylvia-warblers, based on the vegetation composition within the species' territories (Wilks' Lambda= 0.738; F_{approx} (33,1847) = 6.0812, p<0.001).

Vegetation type	Wilks' Lambda	Partial Lambda	p-level	R^2
Grey dunes	0.743	0.993	0.207	0.051
L. vulgare shrub	0.745	0.991	0.138	0.016
Marram dunes	0.742	0.995	0.364	0.131
Mixed shrub	0.744	0.992	0.174	0.528
S. nigra-shrub	0.739	0.998	0.791	0.283
S. repens-shrub	0.740	0.998	0.713	0.058
Sandy dune slack	0.740	0.997	0.614	0.066
Short grassland	0.746	0.989	0.078	0.371
Tall grassland	0.741	0.995	0.409	0.080
Woodland	0.864	0.854	0.000	0.423
Young dune slack	0.741	0.996	0.510	0.059

TABLE 9

A priori classification matrix of the Sylvia-warblers

Species	**% correctly classified**	**S.at**	**S.bo**	**S.co**	**S.cu**
S. atricapilla	40.340	71	4	101	0
S. borin	3.0763	20	2	43	0
S. communis	90.936	28	2	301	0
S. curruca	0.000	4	0	65	0
Total	58.346	123	8	510	0

DISCUSSION

Habitat selection

Cramp (1992) gives a general habitat description of the discussed species, based on numerous studies in Britain, Continental Europe and Northern Africa. The Chiffchaff *P. collybita* is basically a bird of mature lowland woodland without a dense canopy and with a fairly copious variety of medium or tallish undergrowth. *P. trochilus* prefers scrub, second growth and transitions to more open woodland. An analogous habitat segregation between both species was observed by Fuller et al. (1989) in a mixed coppiced woodland in Kent, England. Saether (1983) studied habitat selection and foraging niches in an area of sympatry in Norway. There the species were characterised by a considerable overlap in their foraging niches but were found to occupy almost mutually exclusive territories. Especially the Willow warbler selected a greater variety of habitats (but was mainly found in the early stages of woodland succession) than did the Chiffchaff.

Of the Sylvia species, *S. curruca* flourishes in habitats intermediate between extensive closed forest and open country, restoring to well-spaced often tall bushes, scrubs, taller than those preferred by the Whitethroat *S. communis.* The latter's basic requirement is a patchy, low, fairly dense cover, natural or planted. In contrast to the former species, S. *borin* and *S. atricapilla* are primarily woodland species, but in comparison to *S. atricapilla*, *S. borin* prefers a more even open canopy accompanied by much fairly dense and tall scrub or a shrub layer. Fuller et al., 1989 confirm these results in their study from Kent, England. With the exception of *A. palustris*, the other Sylviine species are characteristic for low, herbaceous vegetation. As a result of his findings, Cody (1978) states that vegetation above 1.5 m. in height supports both *Phylloscopus* and *Sylvia* representatives, below 1.5 m in height just *Sylvia* but with *Acrocephalus* and *Locustella* in combination with the short vegetation patches. In the Flemish coastal dunes, however, *Phylloscopus* may be present in lower *Salix repens* or *Hippophae rhamnoides* shrubs, where it shows a habitat preference analogous to that of *L. naevia*. The latter, however, has a somewhat larger territory size (Cramp & Brooks, 1992; Bonte, personal data).

Our results confirm these general findings. According to the discriminant function analysis of the species' territories, Sylviine Warblers in the Flemish coastal dunes have distinctive habitat preferences, based on the territory-specific vegetation composition. The plot with confidence intervals characterises *P. collybita* and *S. atricapilla* as two species of tall dune woodlands and higher scrubs. The other Sylviine species are more or less typical for scrubland. Only *S. borin* is positioned between dune woodlands and scrubs, confirming Cramp's classification. *A. palustris* and *S. curruca* are typical for homogeneous mixed scrub, while especially *S. communis* is typical for scrub-grassland mosaics. The presence of low vegetation in the species' territory is, however, of minor importance for the overall ordination (low eigenvalue) and probably only important for the settlement of *S. communis*.

Although the discriminant-plot does not show any habitat overlap between congeneric species, mahalanobis distances and a priori classifications indicate a certain amount of habitat overlap between *S. curruca* and *S. communis*, and a low but significant distance between *S. borin* and *S. atricapilla*. For the other species pairs, mahalanobis distances indicate a substantial habitat overlap between the typical scrub species. The habitat segregation between *S. borin* and *A. palustris* is also non-significant, indicating a similar habitat preference.

Cody (1978) showed in English habitats (Yorkshire) that the species pairs *Phylloscopus trochilus-P. collybita* (intermediate scrubland), *Sylvia atricapilla-S. borin* (tall woodland) and *S. communis-S.curruca* (low shrub) considerably overlap in preferred habitat type. Only a minor segregation was present between *S. atricapilla* and *S. borin* in higher vegetation, where *S. atricapilla* was more abundant in habitats with both dense canopy and dense middle layers and *S. borin* was alone present in habitats with dense but lower canopy that inhibits a bush layer but encourages thick ground cover lower than 1 m. Similarly as in our study area*, S. communis* shows an extensive habitat overlap with *S. curruca* in scrub with taller emergent shrubbery. In England, *S. communis* overlaps in more open bushy habitats with *S. undata*; a species which was absent in our study area.

In the Flemish coastal dunes, only the habitat segregation between the two *Phylloscopus* species is very clear, probably because of the high proportion of woodland in our study area, whereas Cody only studied habitat segregation in scrubland, with only a minor proportion of woody vegetation.

Despite these significant habitat differences, shrub- and canopy-inhabiting warblers have a broad habitat choice, which accounts for the low success of habitat occupancy predictions, based on discriminant analysis with the vegetation characteristics. Cody (1978) did use vegetation height measures instead of vegetation typology. These height-classes are also represented in our distinguished vegetation types ordered from the tallest to the shortest vegetation: woodland, mixed scrubs, *Sambucus nigra* scrubs, *Hippophae*-scrubs, *Ligustrum* scrubs, *Salix repens* scrubs, high dense grasslands, short grasslands and grey dunes and blond dunes.

The a priori classification of *Phylloscopus trochilus, P. collybita* and *P. sibilatrix* in Sweden (Cody, 1978) resulted in a correctness of 67 %. In the Flemish coastal dunes, this classification is better, probably because of the absence of *P. sibilatrix*. In the same study, interspecific classifications were a priori obtained for our discussed *Sylvia* species supplemented with *S. undata* in Britain and supplemented with *S. nisoria* in Sweden. In both cases, the correct rate of classification was 54%, slightly lower than in our study (58.3 %). In both studies of CODY (1978), especially *S. curruca-S. communis* and *S. atricapilla-S. borin* displayed considerable habitat overlap, a similar result to that obtained by MASON (1976).

Interspecific territoriality

Although habitats of the congeneric Sylviine Warblers overlap, only a minor proportion of territories overlap, probably as a result of interspecific territoriality. In this contribution, only interspecific territoriality was studied between congenerics, because of their similar morphology (same body and wing size, same weight), territory size and feeding preference.

In the Flemish coastal dunes, territory overlap occurs between all *Phylloscopus* and *Sylvia* species pairs. Only in the case of the species pair *S. borin* and *S. curruca* does the expected coexistence (territory overlap) match the observed coexistence based on the a priori classifications. In all other species pairs, one species is dominant in the other's potential territory. Apparently, *S. borin* is a strong competitor since it coexists with *S. curruca* and dominates *S. atricapilla* and *S. communis* in their potential habitat. *S. atricapilla* is dominant over *S. curruca* and *S. communis*. The latter will never dominate other congenerics. *P. collybita* is dominant when *P. trochilus* habitats are occupied.

Our results confirm and supplement the data of CODY (1978; 1985) who also studied interspecific territoriality based on observed and expected common habitat use in scrubland of the Beyershamn reserve (Öland, Sweden). He also found that *S. borin* excluded *S. communis* and *S. nissoria*, but not *S. curruca*. In Krapperup Wood (Hörby, mainland, Sweden), however, *S. borin* excluded *S. curruca* weakly, with the existence of territory overlap. This interaction was, however, variable and certainly far weaker than could be expected on the basis of other species pairs (CODY, 1978). The other possible interactions *curruca - atricapilla* and all *S. communis* combinations could not be studied because of their rarity. In this study site, *S. borin* excluded *S. atricapilla* via song competition. This contrasted to the Yorkshire site, where both species occupied territories in a symmetrical way, as if they were members of the same species.

The time of arrival in the breeding areas does not guarantee dominance of the first arrival since *S. borin* is the last *Sylvia*-species returning from the winter quarters. With the exception of the species pair *S. borin-atricapilla*, congeneric species typical for higher scrub-types dominate sister species of lower scrubland. The dominance of *S. borin* over the other congenerics explains its potential settlement in both woodlands and scrubs. Besides song competition (song convergence: when a song of a neighbouring species is incorporated into the repertoire and the neighbour is thereby discouraged from interspecific territory overlap) as investigated by CODY (1987), direct aggression may be the basis of the interspecific territoriality. Both Cody's and our results contradict this hypothesis since BERTHOLD (1978) reported a higher amount of direct agression in *S. atricapilla* over *S. borin*. However, the observed territory interactions in the species pairs involving *S. borin, S. curruca* and S. *communis* can be explained by direct aggressiveness (discussed per species in CRAMP & BROOKS, 1992), especially in the case of *S. curruca* and *S. communis*, which have broadly overlapping habitat preferences. CODY (1978) observed effective aggressive interactions between both species, resulting in non-overlapping, often contiguous territories. Direct aggression and song convergence between *S. borin* and *S. curruca* (which has an aberrant song in comparison to the other Sylvia-members) has never been observed and possibly explains the species' coexistence.

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