# Does interspecific competition affect territorial distribution of birds? A long-term study on Siberian *Phylloscopus* warblers

Oleg V. Bourski and Wolfgang Forstmeier

Bourski, O. V. and Forstmeier, W. 2000. Does interspecific competition affect territorial distribution of birds? A long-term study on Siberian *Phylloscopus* warblers. – Oikos 88: 341–350.

Seven species of *Phylloscopus* warblers breed in the middle taiga subzone of Central Siberia. We studied their territorial distribution over 18 breeding seasons between 1978 and 1996.
*Phylloscopus inornatus*, the most abundant breeding bird species in the study area, breeds in dense clusters of territories. In some habitats, these clusters are very unstable from year to year, providing an excellent opportunity to study the influence of *P. inornatus* on the territorial distribution of other species. We present a method for quantifying decreases in a species' breeding density caused by the presence of a competing congener. Analysing all possible combinations of species, we found reciprocal territorial avoidance between *P. inornatus* and *P. proregulus* as well as between *P. inornatus* and *P. collybita*. This is consistent with the hypothesis that territorial avoidance occurs between the species of greatest morphological similarity. The occurrence of territorial avoidance is not explained by habitat characteristics such as vegetation cover and productivity. However low productivity may be necessary for territorial avoidance to occur.
An alternative explanation for the observed territorial separation of some species, derived from the Fretwell-Lucas model of habitat occupancy, is examined and rejected. Causes and implications of clustering behaviour of *P. inornatus* are also discussed.

*O. V. Bourski, Inst. of Ecological and Evolutionary Problems, Russian Academy of Sciences, Leninski prosp., 33, Moscow 117071, Russia. – W. Forstmeier (correspondence), Inst. for Animal Ecology and Tropical Biology, Würzburg, Univ. (forstmeier@mail.uni-wuerzburg.de) and Research Centre for Ornithology of the Max Planck Society, Vogelwarte Radolfzell, Am Obstberg, D-78315 Radolfzell, Germany.*

Bird communities containing a large number of closely related and morphologically similar species are a favourite subject for studies on interspecific competition. Several studies have focused on the influence of such competition on the spatial distribution of birds. Interspecific territorialism has been studied in two different ways: (1) cases where species show obvious interspecific aggressive behaviour have been investigated using playback experiments (Catchpole 1978, Reed 1982, Alatalo et al. 1985, Leisler 1988), and (2) where aggressive behaviour is less overt, species have been shown to hold more or less exclusive territories in spite similar habitat preferences, using removal experiments (Reed 1982,

Garcia 1983, Sæther 1983), or by mapping territories in consecutive years (Edington and Edington 1972, Hogstad 1975).

Studies of the first type require birds to show interspecific aggression. Studies of the second type are restricted to cases where territories only rarely overlap and where there are no strong differences in habitat preference between species. We ask whether beyond these extreme cases, the presence of one bird species might still have a negative effect on the probability of another species settling in the same area. Therefore we intend to test the following hypothesis: the presence of one species in an area can reduce the habitat quality of

this patch for another species, resulting in a lower breeding density of the latter.

Seven species of *Phylloscopus* warblers breed in the study area. One of them, *P. inornatus*, breeds in dense aggregations of up to 50 territories (Syroechkovski et al. 1991). In habitats which are less suitable for the species, it breeds only in some years and is completely absent in other years. Considering the very high breeding density in these clusters, their formation should influence the presence of other species, if interspecific competition is important. High breeding densities and high instability of *P. inornatus'* distribution, provide an excellent opportunity to study the intensity and consequences of competition with other species.

We developed a method to calculate how the breeding density of a species is influenced by the presence or absence of each of the six other species. A similar method was applied by Slagsvold (1980) to demonstrate association of several passerine species with *Turdus pilaris* colonies, which act as a defence against predators. As far as we know, this is the first study to use a quantitative method to detect cases of partial interspecific territorial avoidance.

We also tested the alternative explanation that cases of apparent territorial avoidance were caused by changes in *intra*specific competition, leading to changes in habitat occupancy, according to the Fretwell-Lucas model (Svärdson 1949, Fretwell and Lucas 1970).

A central aim of this study was to investigate whether interspecific competition is related to morphology of the species concerned and to aspects of the habitats where they coexist. Cody (1974) stated that interspecific territorialism occurs primarily between species of high morphological similarity, reflecting the utilisation of similar food resources. In support of this statement, many studies have shown striking correlations between species morphology and habitat choice, foraging site selection and foraging behaviour (e.g. for *Phylloscopus*: Price 1991). Competition for food resources should therefore be greatest between species of similar morphology. Orians and Willson (1964) reviewed cases of interspecific territorialism and concluded that it is most likely to occur in habitats with low vertical relief, as this makes vertical separation of foraging niches more difficult. We also predict that low habitat productivity precludes the sharing of food resources of a defensible territory by two or more congeneric species.

Accordingly, we conducted an extensive survey of external morphological characters of *Phylloscopus* species (in order to assess their morphological similarity), estimated the vegetation biomasses of the habitats where species coexist and calculated total passerine breeding densities in these habitats to evaluate their productivity.

## Material and methods

### Study area

The study area is situated in the middle taiga subzone of Central Siberia at the Yenisei river (62°N, 89°E). It consists of 15 study plots, which cover an overall area of 450 ha and include nearly all typical habitats of the region: 131 ha of coniferous taiga forests, 176 ha of burned land covered mainly with deciduous woodland or shrub, 101 ha of riparian floodplain forest, 22 ha of open bog and 20 ha of human settlement.

### Territory mapping

We mapped the territories of all passerine species between 1978 and 1996 for at least 9 yr and at most 18 yr per plot (the average for the overall area of 450 ha is 11.6 yr). We used the mapping census technique described in Pinowski and Williamson (1974) and Tomialojc (1980). We determined territory boundaries by observing movements of singing males and recording them for each species on a separate 1:2500 scale map. Since these recordings were made for other purposes than those of the present study, estimation of territory boundaries was not influenced by any intention to prove interspecific relationships.

### Analysis of territorial distribution

We divided the 450 ha of the study area into 1800 squares of 50 m × 50 m. We then estimated the suitability of every square for each of the seven species by the following method. For each year, we calculated the proportion of the total population breeding inside each square (e.g. one half of a territory out of a population of 100 breeding pairs of a species gives an estimate of suitability of: 0.5 territories/100 territories = 0.005). These values were averaged over all years for each square. This mean value reflects the habitat quality of a square for a certain species.

When analysing the effect of a competitor B's distribution on the distribution of species A, we first extracted all those squares out of the total of 1800 that had been occupied by both species at least once, though not necessarily in the same year. For example, there might be 100 such squares over 12 yr, giving a total of 1200 cases. These cases were divided into two groups: (1) competitor B was present (we regarded it as present when its territory covered at least 50% of the square) and (2) competitor B was absent (e.g. 500 and 700 cases).

We then calculated expected values of occupancy by species A for the two groups, using the values of suitability multiplied by the corresponding year population total (e.g. in a year with a total of 50 breeding

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pairs a suitability of 0.005 results in an expected value of occupancy of 0.25 territories). These expected values were summed up over the 500 and 700 cases separately.

Finally, we compared these expected totals with the observed ones. Therefore the real occupancy was summed up, again separately for the cases of competitor presence and absence. The ratio observed/expected number of territories quantifies the magnitude of decrease or increase of breeding density depending on presence or absence of the competitor. To test this statistically we did all the above described calculations for each of the 15 study plots separately and compared the observed/expected ratios at competitor presence with those at competitor absence using a paired $t$-test. Data on plots poorly populated with the species under consideration were pooled with the data of the geographically nearest other plot, to get an expected number at competitor absence of at least one territory.

To test whether the presence of clusters of *P. inornatus* in the habitats of secondary importance is influenced by diffuse competition from other *Phylloscopus* warblers, we used the above methods with the following differences. We extracted all squares which were occupied by both *P. inornatus* and one or more competing species at least once, though not necessarily in the same year (e.g. 200 squares). We then divided the years into those in which (1) the total of all the competitors' populations was above the long-term average (high diffuse competition) and (2) this total was below the long-term average. For example, there may have been 5 yr with high and 7 yr with low diffuse competition for one square. The expected and observed numbers were again summed up separately over these 5 and 7 yr and then over the 200 squares.

Finally, in order to distinguish between main and secondary habitats, squares were divided into two groups, according to whether the long-term average breeding density of *P. inornatus* was above or below 0.9 pairs per ha. To test for statistical significance all calculations were done again for each of the study plots. Decrease or increase of density was tested by paired $t$-tests using plots as independent samples.

## Morphological measurements

To analyse morphological similarity we took the following measurements of birds:

1. We measured 12 morphological characters of 356 Central Siberian bird skins at the Zoological Museum of Moscow University: bill length, bill depth, bill width, rictal bristle length, wing length, distance from wing tip to first primary and to first secondary, notch length of the inner web of the second primary, length of alula, graduation of tail, and length of hind and middle claw.

2. We took weight, wing length and wing formula of 11 196 trapped birds at the Yenisei field station between 1990 and 1994.

3. We measured tail length, tarsus length, footspan with claws and length of hind toe without claw of 491 trapped birds in 1995 and 1996.

Morphological measurements are illustrated in Leisler and Winkler (1991).

## Statistical approach to morphological data

We corrected morphological data for observer error (1), sex (2) and fatness (3) of birds: (1) We used correcting factors to adjust wing length measurements of individual observers, when they did differ significantly. (2) We used the average between sexes as the species mean wherever sexual dimorphism was significant (body size, wing and tail length, pointedness and asymmetry of wing). (3) Visible fat deposition was estimated in seven classes. Using the data of the most numerous species (*P. inornatus*), we calculated the percentile increase of body mass with higher fat classes (fat scores accounted for 23% of the total variation of body masses). Lean body weights were calculated by using regression indices according to the individual fat scores.

We divided all measurements (except wing formula) by the cubic root of lean body weight, to make the data independent of size. To obtain normally distributed values, all absolute measurements were log-transformed. Using the wing formula, we calculated wing pointedness and asymmetry according to Busse (1984) and divided these measures by wing length in order to analyse wing shape independent of wing length.

We studied species distribution in the morphological space using principal component analysis (PCA). Twenty morphological characters were substituted with five principal components. We determined the position of each species in the five-dimensional morphological space and calculated Euclidean distances ($d$) between species pairs, a commonly used approach to study morphological similarity (e.g. Landmann and Winding 1995).

We transformed these distance values to similarity values ($s$) as follows:

$$s_i = 100 \times \left(1 - \frac{d_i}{d_{max}}\right)$$

($i$ = species pair, $d_{max}$ = distance between the least similar species pair).

## Habitat

To examine the influence of habitat on the probability of interspecific territorialism, we extracted 53 areas of different habitat type out of the 15 study plots. Each of the areas is of a size of 4 ha and of more or less uniform habitat.

For each area we estimated the total plant volume (m³ of vegetation per m² of area) that is suitable for foraging of *Phylloscopus* warblers.

As territory maps were made for all passerine species (except Corvidae), we were able to calculate the average breeding density of all passerines for each of the 53 areas. We used the total passerine breeding densities as estimates of habitat productivity, as the two should be highly correlated with each other (von Haartman 1971).

For each pair of coexisting *Phylloscopus* species, we calculated the average values of phytomass and passerine density for the areas in which they coexisted. When calculating these averages we took into account the relative abundance of the two considered species in the habitats.

## Results

Table 1 lists the seven study species and their numbers on the study area summarised over all years of territory mapping work.

Analysis of territory distributions revealed that in only four out of 42 species comparisons was the factor 'presence of the competitor species B' associated with a significant decrease in the breeding density of species A below the expected value (Table 2). In all other cases, we found only a slight (and insignificant) decrease or even a slight increase. The presence of *P. inornatus* reduces the breeding density of *P. proregulus* to 30% of the expected density and that of *P. collybita* to 60%. Vice versa, the presence of *P. proregulus* reduces *P. inornatus* density to 47%, and the presence of *P. collybita* reduces *P. inornatus* density to 41%. Expected and observed numbers of territories are shown in Table 2. To ensure that these results are not simply a spurious effect of the high number of tests conducted, we applied the standard Bonferroni technique (Rice 1989) to control for the type I error of statistical tests. Therefore the significance level of 0.05 was divided by 42 (the number of tests), yielding a threshold of $p < 0.0012$. Using this strict level of significance, there are still two cases satisfying the condition. *P. proregulus* significantly avoids the presence of *P. inornatus* and *P. inornatus* avoids *P. collybita*. The two cases of intermediate prob-

ability of type I error ($0.05 > p > 0.0012$) should not be rejected, as they are just the reciprocal cases of the highly significant ones. In conclusion, there are two species pairs displaying reciprocal spatial avoidance, beyond what would be expected by chance.

Fig. 1 illustrates two extreme cases of spatial separation between *P. inornatus* and *P. proregulus* and between *P. inornatus* and *P. collybita*. For *P. proregulus*, we never observed a territory that overlapped with a *P. inornatus* cluster over more than 30% of its area. Territorial avoidance thus seems to be more or less obligatory, while for *P. collybita*, several cases of complete overlap occurred.

Table 3 illustrates how diffuse competition by other *Phylloscopus* warblers apparently affects the formation of *P. inornatus* clusters in habitats of secondary importance. The main habitat where *P. inornatus* breeds only irregularly (densities below 90 pairs per km² on long-term average) is floodplain forest. In each spring of 18 yr of observation, *P. inornatus* appeared in this habitat, demonstrating territorial behaviour. In 11 of these 18 yr the clusters disappeared completely within two weeks, at the time when *P. borealis* (the most abundant floodplain species) was establishing its territories. In the other 7 yr *P. inornatus* remained in some parts of the central floodplain forest, forming dense settlements of 5 to 35 pairs. The decision of territorial birds to leave the floodplain might be influenced by diffuse competition from other *Phylloscopus* species.

In the following section we test whether cases of negative association may be not the result of interspecific territorial avoidance, but a by-product of year to year changing *intra*specific competition.

According to our data, the species pairs under consideration (*P. inornatus* and *P. proregulus* as well as *P. inornatus* and *P. collybita*) are clearly separated by habitat choice, thus meeting each other only in marginal habitats. To demonstrate this we used the data on *Phylloscopus* distribution over the 53 habitats and calculated whether each habitat holds a larger portion of the *P. inornatus* or the *P. proregulus* population (the same for the other species pair). Following this approach only 4% of the *P. inornatus* population breed in primarily *P. proregulus* habitats. Vice versa, only 8% of *P. proregulus* breed in the habitats of *P. inornatus*. The same applies to *P. collybita* (7%) and *P. inornatus* (6%).

Table 1. The seven studied species, number of mapped territories over the whole study period and average breeding density in the study area.

| Species | | Mapped territories | Territories per km² |
|---|---|---|---|
| Yellow-browed warbler | *Phylloscopus inornatus* (Blyth) | 2049 | 39.2 |
| Arctic warbler | *P. borealis* (Blasius) | 453 | 8.7 |
| Chiffchaff | *P. collybita* (ssp. *tristis*) (Blyth) | 313 | 6.0 |
| Pallas's warbler | *P. proregulus* (Pallas) | 143 | 2.7 |
| Greenish warbler | *P. trochiloides* (ssp. *viridanus)* (Blyth) | 86 | 1.6 |
| Dusky warbler | *P. fuscatus* (Blyth) | 83 | 1.6 |
| Willow warbler | *P. trochilus* (ssp. *acredula*) (Linnaeus) | 21 | 0.4 |

Table 2. Expected (Exp.) and observed (Obs.) territory numbers of *Phylloscopus* species in the presence or absence of a competitor. Species abbreviations: *P. proregulus* (pro), *P. inornatus* (ino), *P. collybita* (col). The ratio observed/expected numbers quantifies the magnitude of decrease or increase of a species by the presence or absence of its competitor. These ratios were tested by a paired *t*-test among study plots.

| Plot | Exp. num. of pro territories | | Obs. num. of pro territories | | Observed/expected | | *t*-test |
|------|------------|------------|------------|------------|------------|------------|---------|
| | ino present | ino absent | ino present | ino absent | ino present | ino absent | *p* |
| 4 | 0.3 | 1.0 | 0.0 | 1.1 | 0.00 | 1.10 | |
| 5 | 1.0 | 1.9 | 0.1 | 2.9 | 0.10 | 1.53 | |
| 6 | 1.4 | 15.7 | 0.3 | 16.9 | 0.21 | 1.08 | |
| 7 | 2.6 | 5.9 | 1.3 | 7.2 | 0.50 | 1.22 | |
| 8 | 1.8 | 3.9 | 0.5 | 5.1 | 0.28 | 1.31 | |
| 19 | 0.3 | 1.8 | 0.0 | 2.1 | 0.00 | 1.17 | |
| Total | 7.4 | 30.2 | 2.2 | 35.3 | 0.30 | 1.17 | <0.0002 |

| Plot | Exp. num. of ino territories | | Obs. num. of ino territories | | Observed/expected | | *t*-test |
|------|------------|------------|------------|------------|------------|------------|---------|
| | pro present | pro absent | pro present | pro absent | pro present | pro absent | *p* |
| 4 | 0.8 | 4.1 | 0.0 | 4.9 | 0.00 | 1.20 | |
| 5 | 5.3 | 16.1 | 0.5 | 21.0 | 0.09 | 1.30 | |
| 6 | 10.8 | 19.7 | 2.9 | 27.6 | 0.27 | 1.40 | |
| 7 | 8.6 | 36.8 | 9.0 | 36.3 | 1.05 | 0.99 | |
| 8 | 9.9 | 25.4 | 4.3 | 31.0 | 0.43 | 1.22 | |
| 13 | 0.6 | 4.8 | 0.3 | 5.1 | 0.55 | 1.06 | |
| 17 | 0.9 | 3.3 | 0.3 | 4.0 | 0.33 | 1.21 | |
| Total | 36.9 | 110.2 | 17.3 | 129.9 | 0.47 | 1.18 | <0.0035 |

| Plot | Exp. num. of col territories | | Obs. num. of col territories | | Observed/expected | | *t*-test |
|------|------------|------------|------------|------------|------------|------------|---------|
| | ino present | ino absent | ino present | ino absent | ino present | ino absent | *p* |
| 2 | 8.2 | 72.1 | 5.0 | 75.3 | 0.61 | 1.04 | |
| 3 | 1.4 | 10.9 | 0.6 | 11.7 | 0.43 | 1.07 | |
| 4 | 1.7 | 8.7 | 2.1 | 8.2 | 1.24 | 0.94 | |
| 8 | 1.6 | 3.0 | 0.1 | 4.5 | 0.06 | 1.50 | |
| 10 | 0.7 | 1.0 | 0.1 | 1.6 | 0.14 | 1.60 | |
| 11 | 0.2 | 1.0 | 0.1 | 1.1 | 0.50 | 1.10 | |
| 14 | 1.4 | 1.5 | 0.5 | 2.4 | 0.34 | 1.60 | |
| 17 | 0.4 | 3.4 | 0.1 | 3.7 | 0.25 | 1.09 | |
| 18 | 1.8 | 3.1 | 1.9 | 3.0 | 1.06 | 0.97 | |
| 19 | 0.9 | 8.1 | 0.5 | 8.5 | 0.56 | 1.05 | |
| Total | 18.3 | 112.8 | 11.0 | 120.0 | 0.60 | 1.06 | <0.0059 |

| Plot | Exp. num. of ino territories | | Obs. num. of ino territories | | Observed/expected | | *t*-test |
|------|------------|------------|------------|------------|------------|------------|---------|
| | col present | col absent | col present | col absent | col present | col absent | *p* |
| 2 | 24.9 | 26.3 | 6.8 | 44.4 | 0.27 | 1.69 | |
| 3 | 2.5 | 3.7 | 1.9 | 4.3 | 0.76 | 1.16 | |
| 4 | 5.8 | 13.8 | 6.9 | 12.7 | 1.19 | 0.92 | |
| 8 | 10.0 | 61.3 | 0.3 | 71.0 | 0.03 | 1.16 | |
| 10 | 1.6 | 10.2 | 0.4 | 11.4 | 0.25 | 1.12 | |
| 14 | 7.8 | 52.8 | 6.1 | 54.5 | 0.78 | 1.03 | |
| 15 | 6.0 | 18.9 | 2.1 | 22.9 | 0.35 | 1.21 | |
| 16 | 0.1 | 1.0 | 0.0 | 1.1 | 0.00 | 1.10 | |
| 17 | 0.8 | 5.3 | 0.3 | 5.8 | 0.38 | 1.09 | |
| 19 | 3.8 | 9.8 | 1.3 | 12.2 | 0.34 | 1.24 | |
| Total | 63.3 | 203.1 | 26.1 | 240.3 | 0.41 | 1.18 | <0.0011 |

In years of low population pressure the reduced intraspecific competition might reduce the range of occupied habitats to those which are optimal according to the 'ideal-free' version of the Fretwell-Lucas model. We analysed whether this change of habitat choice was occurring in the case of *P. inornatus*. We applied the same method used for the calculation of the influence of competitors. Squares were divided into six groups according to their long-term breeding density (habitat quality). Each of these groups was divided into: years when *P. inornatus* population numbers were higher than average, and years when they were lower.

In fact, total numbers showed that in years of low population pressure optimal habitats were populated more densely than expected (increase to 120% of the expected) and habitats of secondary importance were

Table 3. Expected and observed territory numbers of *P. inornatus* where densities of other competing *Phylloscopus* species are above and below their long-term mean (phy above, and below average, respectively). The magnitude of decrease or increase of breeding density (observed/expected) was calculated for each study plot separately (data not shown) to allow testing for significance by a paired *t*-test. The effect of the density of other *Phylloscopus* species on *P. inornatus* density is significant in areas with *P. inornatus* densities below 90 breeding pairs per km².

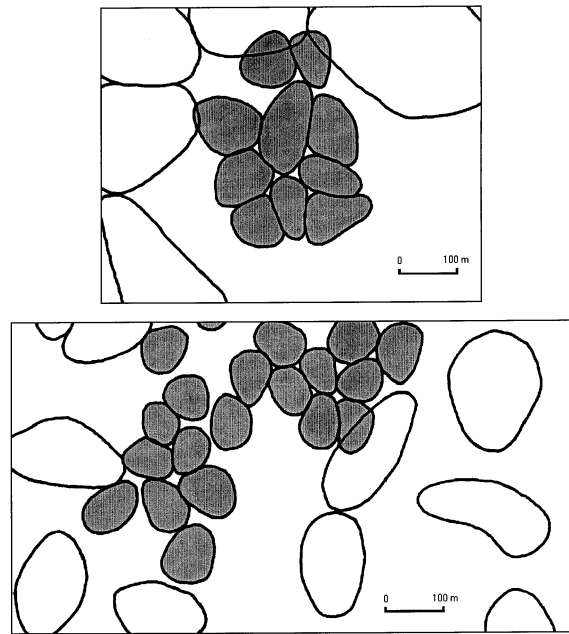| Areas | Expected number of ino territories | | Observed number of ino territories | | Observed/expected | | t-test among plots (data not shown) |
|---|---|---|---|---|---|---|---|
| | phy above average | phy below average | phy above average | phy below average | phy above average | phy below average | |
| ino below 90/km² | 103.2 | 238.1 | 74.1 | 267.2 | 0.72 | 1.12 | $p < 0.011$ |
| ino above 90/km² | 205.9 | 514.3 | 218.1 | 502.1 | 1.06 | 0.98 | $p > 0.5$ |



Fig. 1. Distribution of territories of *P. inornatus* (shaded) and *P. proregulus* (white) on the Taiga plot in 1980 (top). Territories of *P. inornatus* (shaded) and *P. collybita* (white) on the Floodplain plot in 1984 (bottom).

occupied less densely (decrease to 78% of the expected level), confirming the Fretwell-Lucas model. However, when testing for consistency of this pattern among study plots, the effect turned out to be insignificant ($0.1 > p > 0.05$ for the increase in optimal habitats, and $p > 0.5$ for the decrease in marginal habitats).

Still assuming the validity of the Fretwell-Lucas model, only if population densities of two species varied inversely with each other, this pattern could be mistaken as the result of interspecific territorial avoidance. In principle, species of more southern distribution (such as *P. proregulus*) tend to reach high breeding densities in years with benign weather conditions during spring migration, whereas the opposite is true for northern species such as *P. inornatus* (Syroechkovski et al. 1991, Bourski 1994). Assuming such inverse variation, the zone of habitat overlap could be occupied by each species in different years, as a consequence of population dynamics and intraspecific competition. However, our data reveal that population changes in *P. inornatus* show no clear negative correlation with population changes in *P. proregulus* (Pearson correlation, two-tailed, $r = +0.07$; $n = 10$ yr), *P. collybita* ($r = -0.17$, $n = 10$ yr; $p = 0.63$) or all other *Phylloscopus* species combined ($r = -0.21$, $n = 10$ yr; $p = 0.55$).

We conclude that the Fretwell-Lucas model of habitat occupancy provides no alternative explanation for the observed interspecific territorial separation. Primarily because the pattern, that marginal habitats are occupied by *P. inornatus* only in years of high intraspecific competition, is not consistent among study plots

Table 4. Morphological similarity of *Phylloscopus* species, calculated from Euclidean distances in the morphological space. Similarity of 0 indicates the largest observed morphological difference and similarity of 100 indicates no difference. Species pairs where territorial avoidance occurs are indicated using bold print.

| *Phylloscopus* | *proregulus* | *collybita* | *trochiloides* | *borealis* | *fuscatus* | *trochilus* |
|---|---|---|---|---|---|---|
| *inornatus* | **67** | **51** | 56 | 47 | 32 | 44 |
| *proregulus* | | 24 | 40 | 32 | 17 | 16 |
| *collybita* | | | 34 | 14 | 49 | 36 |
| *trochiloides* | | | | 44 | 23 | 45 |
| *borealis* | | | | | 0 | 38 |
| *fuscatus* | | | | | | 15 |

(in contrast to the pattern explained by interspecific competition). In addition, species abundances do not show sufficient negative correlation with each other.

Results of the morphological analysis are summarised in Table 4. The highest morphological similarity is between *P. inornatus* and *P. proregulus*, reflecting their close phylogenetic relatedness (Richmann and Price 1992). *P. inornatus* has a very 'average' morphology, and is also very similar to *P. collybita* and *P. trochiloides*. Looking at individual characters we found that the tarsus, foot and bill measurements of *P. collybita* are closer to those of *P. inornatus* than are those of *P. trochiloides*. On the other hand, *P. trochiloides* is more similar to *P. inornatus* with regard to wing and tail measurements. The species pairs between which territorial avoidance occurs (*P. inornatus* versus *P. proregulus* and *P. collybita*) are a good fit with the pairs between which there is the highest morphological similarity (*P. inornatus* versus *P. proregulus*, *P. trochiloides* and *P. collybita*).

Properties of the habitats where species pairs coexist are shown in Fig. 2. Cases of territorial avoidance occur in habitats where foraging substrate is abundant, unlike the prediction derived from Orians and Willson (1964). Habitat productivity alone (estimated by the total passerine breeding density) cannot explain the occurrence of territorial avoidance. However, in the case of *P. inornatus* versus *P. proregulus*, habitat productivity is very low.

## Discussion

### Factors influencing competition

What is significant about the relationship between the warblers which show interspecific territorial avoidance? Firstly, *P. inornatus* is an extremely abundant species, breeding in dense clusters of small territories. The species may therefore be a superior competitor by virtue of its greater numbers, as in the case of *Agelaius tricolor* (Orians and Collier 1963). If the availability of suitable habitat is not strictly limited by strong intraspecific competition, all other *Phylloscopus* species might profit from avoidance of these exceptionally dense aggregations of possible competitors for food.

Differences in the effect of *P. inornatus* on other *Phylloscopus* species may be explained by morphological similarity between species. The species most similar to *P. inornatus* is *P. proregulus*. *P. collybita* is less similar to *P. inornatus* than *P. trochiloides*, a species whose distribution is clearly not affected by *P. inornatus*. Nevertheless, similarity between *P. collybita* and *P. inornatus* is still very high compared to other species pairs of the genus. In particular the foot and bill morphology of *P. collybita* is closer to that of *P. inornatus* than are those of *P. trochiloides*. It is possible that bill and hind limb morphology is better predictors of competition for food between *Phyllocopus* species than are tail and wing measurements. However the estimates of morphological similarity provided by PCA are arbitrary. We lack quantitative information about how individual morphological characters relate to foraging behaviour and, consequently, to competition for food.

Nevertheless, the ecomorphological approach enabled us to predict cases of strong interspecific competition. In contrast, the analysis of foraging substrate did not help to explain the occurrence of interspecific territorialism. This factor does not appear to have a signifi-
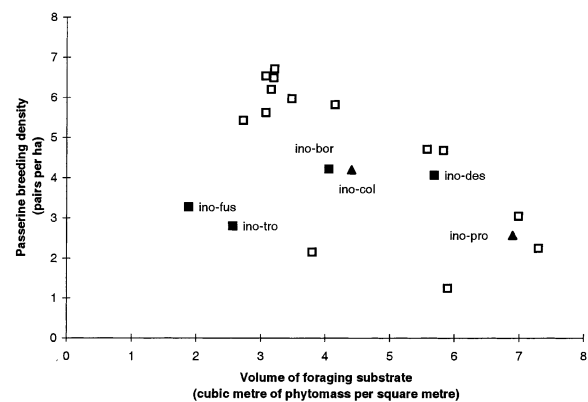


Fig. 2. Amount of foraging substrate and total passerine breeding density in the habitats where *Phylloscopus* species pairs coexist. Each symbol represents the habitat peculiarities of one species pair. Filled symbols indicate pairs including *P. inoratus*. Triangles indicate pairs displaying territorial avoidance. Species abbreviations: *P. borealis* (bor), *P. collybita* (col), *P. trochiloicles* (des), *P. fuscatus* (fus), *P. inornatus* (ino), *P proregulus* (pro), *P. trochilus* (tro).

cant effect on competition in the guild studied. However the possibility that habitat productivity plays an important role in competition cannot be dismissed. We find no evidence of territorial avoidance in the numerous pairs of species that coexist in rich conditions (Fig. 2). One case of partial avoidance occurs in habitats of intermediate productivity (*P. inornatus* versus *P. collybita*) and another case of seemingly obligatory avoidance occurs in very poor conditions (*P. inornatus* versus *P. proregulus*). Habitat productivity alone does not explain the occurrence of territorial avoidance. Nevertheless, low productivity might be necessary for territorial avoidance to occur, as limitation of resources is a premise for competition.

Factors such as site tenacity and intraspecific competition can also affect the incidence of territorial avoidance. Interspecific territorial avoidance will only be found where alternative breeding sites are not completely occupied by conspecific competitors.

## Alternative explanations

Circumstantial evidence is never as strong as that obtained from experiments, and its strength is a function of the degree to which the evidence is incompatible with predictions of other hypotheses (Wiens 1989). The presence or absence of an assumed competitor is a plausible explanation for an observed decrease in the breeding density of another species, but is not, necessarily, the correct one. The presence of the competitor might only covary with the factors responsible for this decrease.

We were able to reject the hypothesis that the observed pattern of territorial separation of species was due to changes in habitat occupancy resulting from different levels of intraspecific competition (Fretwell-Lucas model).

An alternative explanation might be that the pattern reflects different responses to environmental variation in time and space. That such 'unknown' factors are important is impossible to disprove in principle; a general problem of non-experimental studies (Alatalo et al. 1986). We are aware of the importance of factors such as weather and insect distribution, but in most cases these should influence all *Phylloscopus* species in a similar manner, as there is substantial overlap in diet (Glutz von Blotzheim and Bauer 1991) and foraging behaviour (unpubl.) between species.

Our analysis of territorial distributions revealed that the presence of *P. trochilus* has a significantly positive (!) influence on the presence of *P. inornatus* (increased density to 137% of the expected value; paired *t*-test among study plots, $p < 0.05$). These two species both belong to the rather early arriving passerines (*P. trochilus*: mean of first day of arrival: 14.5, $n = 5$ yr, *P. inornatus* 22.5, $n = 7$ yr). In years with a delayed spring there is still a closed snow cover in the forests at this time. These two species are then simultaneously concentrated on places of early snow melting, such as open bogs and south-facing slopes.

To understand more about environmental influences and the possible effects of 'third species' (competitors, predators or parasites sensu Tilman, 1987) on spatial distribution, it seems crucial to discuss the clustering behaviour of *P. inornatus*.

## Clustering of *Phylloscous inornatus*

Territorial clustering is a rare phenomenon in Palaearctic passerines. One notable exception is the wood warbler, *Phylloscopus sibilatrix* (Herremans 1993).

We propose four hypotheses for the clustering of *P. inornatus*. (1) Birds react to locally superabundant insects. (2) Birds are attracted by another species' vigilance or nest defence behaviour, as shown by Slagsvold (1980) for *Turdus pilaris* colonies. (3) Clustering of *P. inornatus* enhances communal defence against predators through increased vigilance (Rogacheva 1992), or by a 'swamping effect' of the local predators (Clark and Robertson 1979). (4) Clustering males profit by attracting females more effectively, as supposed for the wood warbler by Herremans (1993).

To test the first hypothesis, we collected insects by shaking trees, both within and outside a cluster, a few days after its foundation in early June 1996. We observed the foraging behaviour of *P. inornatus* to ensure that we were sampling insects in sites used for foraging. We found no increase in prey abundance inside the cluster (unpubl.). Thus it appears unlikely that insect abundance is the primary cause leading to clustering.

The second hypothesis was tested using the same method we used for calculating the competitive influence of other species on the distribution of *P. inornatus*. Habitat distribution of the black-throated thrush, *Turdus ruficollis*, strongly correlates with that of *P. inornatus* and the species shows a prominent alarming behaviour near its nests. However, the breeding density of *P. inornatus* did not increase significantly in the presence of *Turdus ruficollis*. Density increased to 102% of the expected value, which is clearly non-significant, despite a very large sample size of 1630 territories (paired *t*-test among study plots, $p = 0.70$). We can therefore reject attraction by *Turdus ruficollis* as the principal cause of clustering.

The third and fourth hypotheses remain to be tested, and provide the most likely explanations for clustering, so far.

How do these factors relate to interspecific territorial avoidance? If clustering benefits *P. inornatus* by decreasing nest predation (third hypothesis), then other *Phylloscopus* species should profit in the same way. However, if clustering is caused by another factor (e.g. fourth hypothesis), leading to increased predation due

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to predator attraction, then other warblers should avoid *P. inornatus* clusters for this reason (apparent competition, Holt 1977). Investigating aggregating behaviour in yellow warblers (*Dendroica petechia*), Clark and Robertson (1979) found support for the 'swamping effect' of predators (third hypothesis). We therefore assume that increased predation is a less likely explanation for territorial avoidance than direct interspecific competition between warblers.

## Mechanisms of territorial exclusion

As *P. inornatus* and *P. proregulus* meet infrequently in the same habitat, we have few observational data on their mutual behaviour. Observation on other species breeding in the flood-plain was intensive, but we never observed any aggressive interspecific interaction. Such behaviour can, however, be easily overlooked (Morse 1971). We are therefore of the opinion that 'territorial avoidance' is a more appropriate term than 'territorialism', as we observed no aggressive behaviour which could have resulted in territorial exclusion. Later arriving species might simply avoid areas occupied by earlier arriving congeneric competitors. Our interpretation is strengthened by the outcomes of interspecific interactions we observed. Earlier arriving species have a greater negative influence on the density of later arriving species than vice versa. *P. inornatus* (mean of first day of arrival: 22.5, $n = 7$ yr) is more strongly affected (breeding density decreased to 41%) by the earlier arriving *P. collybita* (9.5, $n = 6$), than *P. collybita* is affected by *P. inornatus* (60%). In the same way, *P. inornatus* is less affected (47%) by the later arriving *P. proregulus* (2.6, $n = 7$), than the breeding density in *P. proregulus* is decreased by *P. inornatus* (30%) (see Table 2).

However, the same pattern is predicted by aggressive interactions, assuming that larger species are dominant over smaller species (Persson 1985, Alatalo and Moreno 1987). *P. collybita* (lean body weight of 6.97 g; $n = 882$) is larger than *P. inornatus* (6.13 g; $n = 1071$), which is larger than *P. proregulus* (5.18 g; $n = 143$).

Finally it is noteworthy that spatial separation of closely related species, such as *P. inornatus* and *P. proregulus*, is unlikely to be solely a consequence of misdirected intraspecific competition (Murray 1971), as songs of all seven species are highly distinct (Glutz von Blotzheim and Bauer 1991).

## Conclusions

Compared to other studies (e.g. on *Arocephalus* warblers, Leisler 1988), this study reveals that both the intensity and the importance of interspecific competition (sensu Welden and Slauson 1986) are relatively insignificant in the studied guild. No aggressive interac-

tions were observed, and the consequences of territorial avoidance for individual fitness seem to be unimportant, due to clear habitat separation of the species involved. To satisfy the definition of interspecific competition, it would have been necessary to demonstrate this impact on fitness. We can only infer that territorial avoidance leads to the occupancy of less preferred habitats, and that differences in use of habitat types should be directly related to the quality of those habitats for reproduction of the species (Schamberger and O'Neil 1986).

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