Ornis Fennica 71:55–60. 1994

Does competition with residents affect the distribution of migrant territories?

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Received 28 December 1993, accepted 14 April 1994

Herrera (1978) found an inverse relationship between relative densities of resident and migrant passerines in European breeding bird assemblages. He hypothesized that the decreasing proportion of migrants to the south would be due to interspecific competition with residents. The putative competition between resident titmice (*Parus montanus* and *P. major*) and migrant conguilders (*Fringilla coelebs* and *Phylloscopus trochilus*) was tested by a playback experiment in northern Finland. If competition was important between individual birds, it could reduce overlap between territories. The spatial configuration of the two migrant species was studied in relation to the nests of the two residents during the breeding season in late May – early June, in 1989 and 1990. The experiment was carried out at 13 (year 1989) and 17 (year 1990) tit-nest plots. To control habitat effects, the tape was also played at control plots where the tit pair had bred in the previous year and at randomly chosen plots. The data were analysed using log-linear models, which test for dependencies between categorical variables. In 1990, there were far fewer positive responses at the study points than in 1989, possibly due to changes in the population densities of the migrants. We found that migrants did not avoid settlement near or in resident territories. There was a tendency that migrants aggregated more at the vicinity of tit-nests compared with the random- and control plots. This result is consistent with the 'heterospecific attraction' hypothesis generated by Mönkkönen et al. (1990).

1. Introduction

In the 1960's and 1970's interspecific competition was considered to be the main process affecting animal communities. During the last decade ecologists have emphasized also the role of various other processes (e.g. predation, individual responses), but the relative importance of competition has remained controversial (Wiens 1989b).

Interspecific competition is commonly viewed as a process acting on populations, but actually it occurs between individuals (Martin 1986). Depending on its intensity and importance between individuals (Welden & Slausson 1986), interspecific competition can affect patterns of populations, communities, and even larger geographical areas. Herrera (1978) observed an inverse relationship between the proportions of migrant and resident passerines in European breeding bird communities. He suggested that the decreasing proportion of migrants towards the south is due to the intensification of interspecific competition by resident birds. Herrera's suggestion is in line with the commonly held assumption that residents are superior competitors over migrants and thus have a prior access to resources.

Studies on interspecific competition have usually focused on population level phenomena such as niche metrics and morphological patterns (Ulfstrand 1977, Mönkkönen et al. 1990, Herrera 1981). At the level of individuals, however, birds can avoid competition by reducing encounters with potential competitors, which may lead to a spatially non-overlapping distribution (Reed 1982, Garcia 1983, Sherry & Holmes 1988).

This study focuses on the four most numerous species in the area. These species belong to the same insectivorous foliage gleaning 'guild': the Willow Tit *Parus montanus* and the Great Tit *Parus major* are residents, and the Chaffinch *Fringilla coelebs* and the Willow Warbler *Phylloscopus trochilus* are migrants. The aim of this paper was to study the distribution of the territories of individual pairs: if competition occurs between migrants and residents, their territories overlap less than expected by chance.

2. Study area, material and methods

The study was conducted in Haukipudas, near Oulu, in northern Finland (about 65°N, 25°30′E). The area covers about 75 ha birch (*Betula pubescens*) dominated forest mixed with spruce (*Picea abies*) (see Orell & Ojanen 1983 for a more detailed description of the habitat). There were 90 nest-boxes in the study area.

The study was carried out during two-week periods in late May – early June, in 1989 and 1990. Three different study plots were assigned in the study area. *Tit-nest plots* (T) were comprised of active nests of tits during the study periods. *Control plots* (C) consisted of sites where tits had bred a year before, or sites where a nest of a tit was destroyed before the 15th of May during the study year. To select the *random plots* (R), a grid of 50×50 m was superimposed on the study area. Of the 120 grid plots, some of the plots were randomly assigned, in order to equal the number of tit-nest plots each year. The minimum distance between the plots was 100 meters. The total number of all different plot categories was as follows: 1989: T = 13, C = 10, R = 13 and 1990: T = 17, C = 13, R = 18.

The locations of Chaffinch and Willow Warbler territory boundaries in relation to these plots was studied by a playback experiment. Nine playback sites were assigned to all plots, and a two-minute bout of Chaffinch's and Willow Warbler's song was played at each of them. First, songs were played at the center of the plot, and subsequently at two sites located 20m and 40m from the center at four cardinal points. During the playing of the tape, the observer moved to a distance of 20 meters and watched the responses of birds. The response was considered to be positive when a male bird came closer than 5 meters to the loudspeaker and acted like a territory owner (wing vibrations, eager singing).

To analyse the results, we compared the distributions of playback responses between different categories. If migrants avoided settlement close to the residents, we would find fewer positive responses at tit-nest plots than at other plot categories. If the habitat preferences of the tits and the migrants were similar and the migrants did not avoid the residents, there would be more positive responses at nest and control plots than at random plots. Otherwise, if both the habitat effects and competition were of minor importance, then the distribution of positive responses between the different plots would be similar. The information from all nine playback sites was reduced to a single score to avoid redundancy of the data. This score was the total number of positive responses at a plot. It varied from 0 (no positive responses) to 9 (all playback sites yielded a positive response). Prior to the statistical analysis the scores were further classified into three categories to avoid inadequately small samples in the analysis of cross-classified data (see below). Score 9 alone comprised the "high occupancy" category, scores from 8–2 formed the "middle occupancy" category, and scores 1 and 0 the "low occupancy" category. The use of this categorizing resulted from our *a priori* logic to make the overall number of observations equal in each category. Since the results might be affected by the way the observations are categorized in different classes, we also analysed the data using another category, where response was either positive (scores 1–9) or negative (score 0).

As the results were similar in the two analyses, only the first one is reported here.

The results were presented with four-dimensional contingency tables and the dimensions were: *the plot category* (P), *the bird species* (S), *the study year* (Y) and *the occupancy category* (O). The data were analysed with log-linear models and a logit-model (using SPSS-X statistical package, see Norusis 1988), which are used to identify dependencies between categorical variables (Fienberg 1980). The best models were the most parsimonious ones still in agreement with the data. Our small sample size allowed us to analyse only three variables at a time. In both log-linear- and logit-models we use a comma (,) to mean independence between variables and a star (*) to mean dependence. A more detailed examination of the cell frequencies was made by examining adjusted residuals (Everitt 1977), which reveal the deviations between the observed and expected frequencies in each cell.

3. Results

The distributions of responses to different occupancy- and plot categories on both species are shown in Table 1.

First, we pooled the data of both years and tested the differences between the two migrant species. The selected log-linear model indicated total independence between plot, species and occupancy categories (P, S, O; $G^2 = 4.08$, df = 12, P = 0.982). In other words, there was no difference in the distribution of Chaffinches' and Willow Warblers' responses in relation to the plot or occupancy categories. Therefore, we pooled the species-specific data and tested for dependencies between plot category, study year and occupancy. In the selected log-linear model, there was a dependence between occupancy and study year, but plot category was independent of both plot occupancy and year (Y*O, P; $G^2 = 4.80$, df = 8, P = 0.905). This independency between plot and occupancy categories applied to both study years separately as indicated by a logit-model (Y(P,O), $G^2 = 4.75$, df = 8, P = 0.783).

To analyse further the dependency between year and occupancy we calculated adjusted residuals for each cell in a two-way contingency table, where these variables were classifying variables (Table 2). Positive responses were far more common in 1989 than in 1990. Next we examined the distribution of responses in each occupancy- and plot category in both years separately (Table 3). The categorizing of observations into occupancy classes differed between the years and from the pooled data of both years.

Table 1. The distributions of responses in migrants to different occupancy- and plot categories in the pooled data of both study years.

	Plot	Occupancy		
		high	middle	low
Chaffinch	Tit-nest	12	9	9
	Random	9	11	11
	Control	5	10	7
Willow Warbler	Tit-nest	11	9	10
	Random	12	10	9
	Control	9	8	6

Table 2. Adjusted residual values for high-, middle- and low occupancy categories in both years. Adjusted residuals measure the deviation between the observed and expected cell frequencies. Negative values denote an observed frequency less, and positive higher than expected. As the adjusted residuals follow the standard normal distribution, the values over absolute value 1.96 are statisticallly significant (P < 0.05).

	Occupancy		
	high	middle	low
1989	3.326	2.014	–5.493
1990	–3.326	–2.014	5.493

Table 3. The distribution of responses to different plot- and occupancy categories in 1989 and 1990. Expected frequences are in parentheses.

	Plot	Occupancy		
		high	middle	low
1989	Tit-nest	14 (12.6)	9 (5.8)	3 (7.6)
	Random	12 (12.6)	3 (5.8)	11 (7.6)
	Control	9 (9.7)	4 (4.4)	7 (5.8)
1990	Tit-nest	10 (9.8)	8 (9.6)	16 (14.9)
	Random	10 (9.2)	12 (10.1)	14 (15.8)
	Control	6 (7.0)	8 (7.3)	12 (11.4)

We followed the same *a priori* basis in categorizing, as with the pooled data, to achieve equal marginal totals.

In 1989, the overall distribution differed slightly from the random distribution ($\chi^2 = 7.94$, df = 4, $0.05 < P < 0.1$); whereas, in 1990, the distribution was random ($\chi^2 = 1.13$, df = 4, NS). The adjusted residuals for the 1989 data revealed that positive responses were significantly fewer than expected only in the low-occupancy category at tit-nest plots (adjusted residual value 2.481). At random and control plots, the values were in the opposite direction, but the values were not significant.

4. Discussion

Spatial avoidance between the migrants and residents was not observed; this was indicated by the independency between the plot category and the occupancy category. However, there was a between-year difference in the overall occupancy; in 1990, there were far fewer positive responses by the Chaffinch and Willow Warbler to the song playback than in 1989. In addition, in contrast to the competition hypothesis, there was a tendency that migrants could actually prefer the vicinity of tit-nests, as observed in 1989. The difference in the overall occupancy level most probably reflects changes in population densities of the Chaffinch and Willow Warbler. In 1990, number of Chaffinches and Willow Warblers, in the study area, was low. The result confirms evidence from the data of the Finnish line-transect censuses, which showed a decrease in the abundance of the Willow Warbler between 1989 and 1990 (Väisänen & Routasuo 1991).

Previous studies in breeding habitats and foraging niches of the species presented here have not provided consistent results concerning interspecific competition. Some have found no evidence of competition (Alatalo 1981, 1982, Virkkala 1988, Mönkkönen et al. 1990), whereas others have shown it to be possible (Hogstad 1975, Ulfstrand 1977). The importance and intensity of competition certainly do vary, depending on the environmental conditions, as emphasized by Martin (1986). According to our study, competition between residents and migrants did not affect the spatial configuration of territories. Also, the study conducted by Haila & Hanski (1987) at the Åland archipelago found no between-species avoidance in the territory overlaps.

Herrera's hypothesis that competition with residents would actually determine the relative abundance of migrants in breeding communities, is an example of inference of a local process from a geographical pattern. This sort of extrapolation across scales is considered to be ambiguous (Wiens 1989a, b).

Our result does not provide any support for Herrera's idea of competition between residents and migrants. However, Herrera's hypothesis implicitly indicates where competition should occur: as the relative abundance of residents is highest in the south, competitive effects should also be strongest there. A study of the spatial relationship between residents and migrants in a southern or central European bird community might provide interesting results.

We found that in 1989, the territories of migrant birds overlapped with the territories of resident tits more than we expected. Since it was only the tit-nest plots that tended to differ from the control- and random plots, it seems that this co-occurrence was not due to similar habitat preferences. A similar result was documented in Scotland, where the territories of the Chaffinches and Great Tits were found to co-occur more than expected by chance alone (Reed 1982). Mönkkönen et al. (1990) executed an experiment with resident and migrant birds in Central Finland and found that migrant birds seemed to be more numerous on islands where the abundance of tits was experimentally increased. They hypothesized that migrants could use residents as cues for 'good' breeding sites. In this study, this attraction could have been more common during the year of high population density when there was a surplus of young, "naive" birds (Baillie & Peach 1992) on the breeding grounds. The "heterospecific attraction" hypothesis should be examined more thoroughly to provide direct experimental evidence.

Acknowledgements. This study was financially supported by the Emil Aaltonen Foundation and the Academy of Finland. We also thank Kari Koivula and Seppo Rytkönen for their help and advice throughout the study. Raimo Virkkala, Jari Kouki, Hannu Pietiäinen and an anonymous referee made fruitful comments on the manuscript.

Selostus: Vaikuttaako muutto- ja paikkalintujen välinen kilpailu niiden reviirien sijoittumiseen toisiinsa nähden?

Yksi vähän selvitetty lajienvälisen kilpailun seuraus on muutokset yksilöiden välisissä tilasuhteissa. Tässä tutkimuksessa selvitettiin mahdollisen lajienvälisen kilpailun vaikutusta kahden muuttolinnun (peippo ja pajulintu) ja kahden paikkalinnun (tali- ja hömötiainen) reviirien sijaintiin. Lajit käyttävät samankaltaista ravintoa pesimäaikaan, jolloin kilpailu voisi olla mahdollista. Lisätaustana selvitykselle oli Herreran (1978) esittämä hypoteesi, jonka mukaan eurooppalaisissa varpuslintuyhteisöissä esiintyvä käänteinen korrelaatio muutto- ja paikkalintujen tiheyksien välillä johtuisi lajienvälisestä kilpailusta.

Lajien reviirien päällekkäisyyksiä tutkittiin soittamalla peipon ja pajulinnun laulua vuosina 1989 ja 1990 kolmenlaisilla tutkimuspisteillä: a) tiaisenpesäpisteillä, joissa pesi hömö- tai talitiainen kokeen suoritusvuonna b) kontrollipisteillä, joissa tiaispari oli pesinyt edellisenä vuonna muttei tutkimusvuonna, ja c) satunnaispisteillä, jotka oli valittu satunnaisesti tutkimusalueelta. Jos lajienvälinen kilpailu näkyisi lajien tilasuhteissa, tiaisenpesäpisteillä pitäisi olla vähemmän muuttolintujen positiivisia atrappivasteita kuin muilla pisteillä.

Atrappivasteiden jakautumista selvitettiin log-lineaarisilla malleilla, jotka soveltuvat riippuvuuksien testaamiseen luokitelluissa aineistoissa. Vuonna 1990 tutkimuspisteillä oli paljon vähemmän positiivisia atrappivasteita kuin vuonna 1989. Tämä johtui mahdollisesti muuttolintujen vuosienvälisistä tiheysvaihteluista. Kilpailuhypoteesin mukaista reviirien päällekkäisyyksien välttelyä ei ilmennyt vaan muuttajien positiiviset vasteet kerääntyivät tiaisenpesäpisteille enemmän kuin voisi satunnaisesti odottaa. Kerääntymistä tapahtui etenkin vuonna 1989. Kontrolli- ja satunnaispisteiden informaation perusteella tämä lajienvälinen kerääntyminen ei johtunut habitaattivaikutuksista. Tulos antaa tukea Mönkkösen ym. (1990) ehdottamalle hypoteesille, jonka mukaan muuttajat voisivat käyttää paikkalintujen läsnäoloa merkkinä sopivista pesimähabitaateista.

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