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Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis

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Abstract We experimentally tested the conditions where heterospecific attraction is more likely to occur. The heterospecific attraction hypothesis predicts that colonizing or migrant individuals use the presence of resident species as a cue for profitable breeding sites. In other words, increasing resident densities will result in increased migrant densities until the costs of interspecific competition override the benefits of heterospecific attraction. The experiment consisted of a reference and a manipulation year. In the reference year, resident titmice were permitted to breed at intermediate densities whilst in the manipulation year, resident densities were manipulated in nine study plots. Three treatments were performed as low, intermediate and high resident densities and migrant density responses were measured in both years. Relative between-year migrant and resident densities were analyzed by regression analysis. Migrant foliage gleaning guild densities responded linearly and positively, as did densities of habitat generalists, in particular Chaffinch (*Fringilla coelebs)*,. The ground-foraging guild did not show a response. This study provides support for predictions of the heterospecific attraction hypothesis and suggests that information on habitat quality with reference to both food availability and safe breeding sites are important in using heterospecifics as cues. Based on Chaffinch response data, artificially increased resident densities were not high enough for competitive effects between residents and migrants to decrease heterospecific attraction. It seems unlikely that in northern environments natural resident densities will reach high levels where competitive effects would occur, therefore heterospecific attraction will always be beneficial. This study again shows the importance of heterospecific attraction in migrant habitat selection and as a process promoting species diversity in northern breeding bird assemblages.

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Introduction

Negative interactions such as predation and, in particular, interspecific competition (see reviews Cody 1974; Connell 1983; Schoener 1983) have dominated discussions of community ecology. Recently it has been shown that ecological interactions between two species may take the form of a variety of direct and indirect interactions that will ultimately affect species coexistence (Martin and Martin 2001).

Indeed, both positive and negative community processes exist. These processes do not operate alone, but interact in space and time (Elmberg et al. 1997; Menge 2000), with their relative importance being determined by various biotic and abiotic factors present in that specific environment (Thompson 1988; Travis 1996; Menge 2000). Theoretical study has shown that competition need not be the only or dominating interaction. Particularly in seasonal environments (Dodds 1988; Stone and Roberts 1991), or in environments experiencing harsh physical conditions (Bertness and Callaway 1994), positive interactions, where one species benefits and none are negatively affected, are more likely to prevail.

Northern boreal bird communities are a perfect example of a community occurring in such harsh environments. High year-to-year variability in abiotic factors (Järvinen 1979) causes considerable stochastic variation in population numbers of bird species (Järvinen 1979; Helle and Mönkkönen 1986; Haila and Järvinen 1990; Morozov 1993; Haila et al. 1996). Consequently, the densities of northern bird populations are regarded as being below the carrying capacity of the environment (Enemar and Sjöstrand 1972; Enemar et al. 1984; but see Mönkkönen 1990). Harsh environmental conditions also have substantial effects on the separable groups of the breeding community: resident and migrant birds. In the north, resident densities and relative proportions of breeding bird numbers are lower than in more southern areas (Forsman and Mönkkönen 2002). Based on the geographical variation in the proportions of migrant and resident breeding birds, Herrera (1978a, 1978b) proposed that there is diffuse competition between the two groups, and that migrants fit into the community only if there is free "space" after the preoccupation by residents (see also O'Connor 1990; Newton and Dale 1996). However, given the geographical variation in the contribution of residents to breeding bird communities (Forsman and Mönkkönen 2002), the intensity and quality of interactions between those groups may vary. Indeed, Mönkkönen et al. (1990) found that on islands with an increased abundance of resident titmice, there was an increased abundance of migrant passerines and an overlap of breeding territories more than expected by chance (Timonen et al. 1994; Haila and Hanski 1987). This result was in apparent contradiction to that predicted by interspecific competition and they termed the phenomenon 'heterospecific attraction'. In this context, heterospecific attraction (HA) predicts that migrants use residents as cues for good quality habitat to make quick reliable decisions about where to breed, particularly when time for such assessment is limited and delays may be costly (Alatalo and Lundberg 1984; Mönkkönen and Helle 1987). Subsequently, Mönkkönen et al. (1997) and Forsman et al. (1998a) have experimentally tested HA in a North American boreal forest and north European boreal forest, respectively. They have shown that both species number and their abundance increase with increasing resident density.

Recently, Mönkkönen et al. (1999) provided a theoretical background into possible evolutionary benefits of employing this habitat selection strategy. They explored the use of two possible strategies, direct sampling and cue using. They found, due to the high relative cost and time consuming nature of actively sampling habitats (also Danielson 1992), that cue using was beneficial both in a situation with high interspecific competition and when benefits of being with heterospecifics out weigh competition. Assuming residents do provide a reliable sign of the habitat quality, they concluded that in most cases selection would favor those individuals capable of using other species as cues, especially among habitat generalists. The model also predicted that the highest attraction to heterospecifics (residents) would be at medium resident densities, when benefits of aggregating with residents exceed effects of possible competition (see also Forsman et al. 2002).

In the present study, we experimentally investigated HA and the predictions of the theoretical model. We studied the habitat selection of migrants in relation to different resident densities. Our study differs from previous experiments (Mönkkönen et al. 1997; Forsman et al. 1998a) in two main ways. First, we examine the response of a different migrant bird community. It was located farther south than that of Forsman et al. (1998a) and included different species, most noticeably Chaffinch (*Fringilla coelebs)*, an abundant habitat generalist (Raivio and Haila 1990; Väisänen et al. 1998). In addition, higher southern migrant densities allow more species to be included as common species and therefore also in respective guilds. Second, other studies dealing with this problem have relied on two treatments, an addition and removal, in a cross over design, creating either zero or high resident densities, with no truly intermediate densities relative to a reference year (Elmberg et al. 1997; Mönkkönen et al. 1997; Forsman et al. 1998a). We experimentally created a continuum of resident species density that allowed the first testing of the HA model, which predicts that migrants will show strongest attraction at intermediate resident densities, i.e. that the density response is not linear.

Previous studies have indicated that HA is important in foliage-gleaning and ground-foraging guilds (Mönkkönen et al. 1997; Forsman et al. 1998a). A positive response in either these guilds would allow a better understanding of the mechanisms involved in HA. For foliage gleaners, a positive response indicates the importance of food abundance while, for ground foragers, the emphasis would be on safe breeding sites. Hence, we expected both guilds to respond positively also in this study. Because habitat generalists are, by definition, not very tightly associated with any particular structural or floristic component of their environment, we expect them to show positive responses to changing resident densities.

Materials and methods

Experimental design

This experiment took place in the Oulu region, in northern Finland (64°50'N, 25°30'E). Nine forest plots (range 7–22 ha) were selected as study sites, which were clearly defined and in many cases surrounded by open agricultural land. The sites were situated not farther than 10 km from each other and the nearest neighbor distance was approximately 1 km. The vegetation in the plots was dominated by birch (*Betula* spp.), although some had varying densities of Scots pine (*Pinus sylvestris*), spruce (*Picea abies*) and aspen (*Populus tremulus*).

The experiment, using the nine forest plots as treatment areas, lasted 2 years (summers 1999 and 2000). Year 1999 was used as a reference year and no manipulations of resident species densities were done. The year 2000 was the treatment year and manipulations of resident densities were performed. At the beginning of the winter of 1998–1999, open nest boxes were placed on all study plots in densities so as to be in surplus of the possible demand. In addition, food was provided throughout the winter in the form of suet and sunflower seed. During this first year (1999) when no resident density manipulations took place, resident bird species Great Tit (*Parus major*), Blue Tit (*P. caeruleus*) and Willow Tit (*P. montanus*) were allowed to breed at intermediate densities. Early in the winter of 1999–2000 the same density of boxes remained open on all study plots to be used by roosting tits. This ensured an equal impact on the winter insect abundance within the plots which may have been altered had boxes not remained. However, in March 2000 (late winter) we began to manipulate the numbers of the three resident bird species. Three treatments were performed: low, intermediate and high densities of resident species on study plots. In low density plots nest boxes were closed, and due to the forests being young, only a few natural cavities existed in which to roost or breed. In this way residents were forced to leave the plots. If problem individuals did remain they were mist-netted, removed and released far from the plots. In intermediate density plots, the same number of resident pairs were permitted to nest as in the previous season, to simulate the densities of the previous year. High resident density plots contained feeders late into spring in order to encourage pairs to settle in these plots and artificially increase the quality of these habitats. All manipulations ceased before the arrival of the first migrants and resident densities at this time were used in the analysis. The three titmice species were regarded as equal and a pair of any of the three species was counted as a single resident titmice pair. A half pair was counted when a resident pair bred outside, but in the immediate vicinity of the plot <25 m and thus had the potential to influence the experiment. For the assigning of treatments to the different plots, they were divided into three groups each comprising three plots (Table 1). This was done systematically by taking into account both slight differences in vegetation structure (densities of tree species such as pine, spruce) and size of the plots as well as their spatial separation. Within each group the treatments of low, intermediate or high densities were randomly assigned.

During both years the densities of the migrants were measured using the territory mapping method (Koskimies and Väisänen 1988). Each plot was censused 5 times during both experimental years, between 24 May and 24 June. Observations were interpreted as a pair if an individual was singing, giving alarm call or foraging within 100m in at least two census maps in a year. In both years the same person (J.T.F.), to ensure a fixed standard, interpreted the census maps.

Statistical methods

Only the most abundant species, those occurring in at least five plots in a single year, were included in the analyses (species shown in Table 1). This was done because the lower the density of a species in the study plots, the greater would be the influence of chance in determining its presence or absence (see Helle and Mönkkönen 1986) and this would make the existing patterns and responses less clear and difficult to extract. Alone, rare species show no trend (2-tailed regression: df=7, B=0.32, T=−1.298, P=0.235).

All raw abundance data (Table 1) were firstly converted into densities (number of pairs per 10 ha) for each species, to remove the effects of differing plot size. In all of the following statistical tests, we used the manipulation year reference year density difference, which ranges from negative values (low density plots) to positive values (high density plots) of both residents and migrants between treatment years. In this way we were able to control for differences in habitat quality, although possible between-year differences in a single plot will remain. We used regression analysis in testing the effect of resident density change to the change in migrant density.

We analyzed the response of migrants to altered titmice density at three levels. Firstly, we tested the combined response of all species (species listed in Table 1). The second level was the feeding guild and generalist/specialist group. We tested the response in foliage gleaners, which included Willow Warbler (*Phylloscopus trochilus)*, Chaffinch, Garden Warbler (*Sylvia borin*) and also in ground foragers, which were the Redwing (*Turdus iliacus*), European Robin (*Erithacus rubecula*) and Tree Pipit *(Anthus trivialis*). The two feeding guilds should benefit from HA for slightly different reasons. Foliage gleaners should benefit from using the residents as indicators of habitat quality, with respect to food availability and safe, predator-free sites (as resident titmice also belong to this foraging guild), while ground foragers should only benefit from using residents as protection from predators or indication of safe breeding sites. We separated species on their generalist or specialist nature, based on groupings from Raivio and Haila (1990). Habitat generalists included Willow Warbler, Chaffinch, Tree Pipit and Robin, while habitat specialists consisted of Redwing, Spotted Flycatcher (*Muscicapa striata*) and Garden Warbler. Finally we tested the response of the most common species individually. Based on the results of earlier experiments, our statistical hypotheses were 1-tailed and we employed 1-tailed tests. All analyses were performed using SPSS 8.0 for Windows.

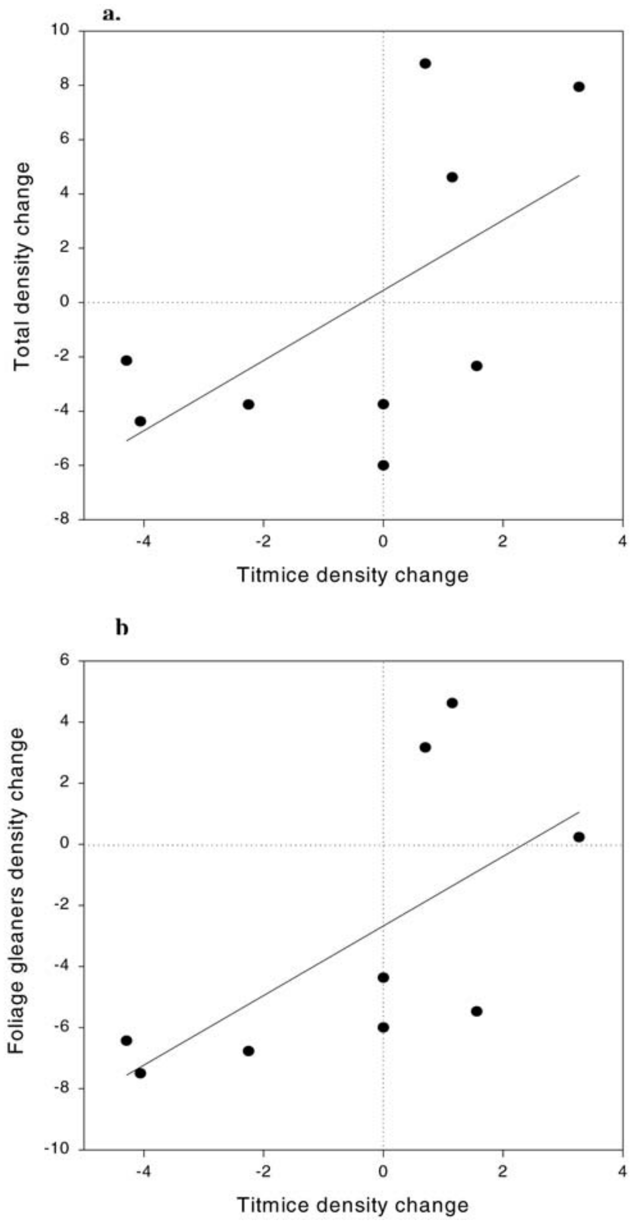

Fig. 1 The change in **a** total density (seven species listed in Table 1) and **b** in density of foliage gleaners (*Phylloscopus trochilus*, *Fringilla coelebs* and *Sylvia borin*) in response to experimentally altered titmice density

Results

Community structure and species richness

We successfully manipulated the densities of the resident species in the second study year (2000), compared to the initial reference year (1999) (Table 1). What resulted was a continuum of resident pair density relative to the control

Table 1 Number of breeding pairs of titmice and migrant species in the study plots during the years 1999 (99) and 2000 (00); treatment indicates the manipulation performed in the respective plots. Abbreviations: titmice, *Parus major, P.caeruleus, P.montanus*; *Phylloscopus trochilus* (*Phy tro*), *Fringilla coelebs* (*Fri coe*), *Anthus trivialis* (*Ant tri*), *Erithacus rubecula* (*Eri rub*), *Sylvia borin* (*Syl bor*), *Muscicapa striata* (*Mus str*), *Turdus iliacus* (*Turili*)

Treatment	Low density						Intermediate density						High density					
Study plots	Alakanava		Ängeslevä		Kärpänaro		Vesikari		Paratiisi		Mikkola		Koivikko		Parras		Nenänperä	
Area	16.0 ha		7.0 ha		13.3 ha		16.0 ha		10.0 ha		14.2 ha		13.0 ha		12.8 ha		21.4 ha	
Year	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00	99	00
Titmice pairs	6.5	0	3	0	3.5	0.5	5	5	5	5	6	7	5	6.5	5	7	5	12
Net pairs	–6.5		–3		–3		0		0		1		1.5		2		7	
Migrant pairs																		
Phy tro	24	16	19	16	16	12	32	22	21	19	24	24.5	14	17	33	22.5	39	36
Fri coe	17	13	8	4	8	4	10	13	9	6	8	13	6	9	7	9	12	16
Ant tri	2	5	3	5	5	7	2	4	4	6	3	6	1	4	5	7	6	8.5
Eri rub	3	3	1	1	0	3	7	6	3	2	0	4	4	2	0	2	4.5	9
Syl bor	0	0	0	2.5	1	0	4	4	2	1	4	3	0	0	2	3.5	2	1.5
Mus str	1	3	1	1	1	0	1	1	2	3	0	1	3	4	1	1	2	9
Tur ili	0	0	0	1	0	0	1	1	2	0	1	1	2	0	0	0	0	2.5
Other species	1	5	2	2	0	0	3	1	5	1	1	3	3	1	4	2	8	7

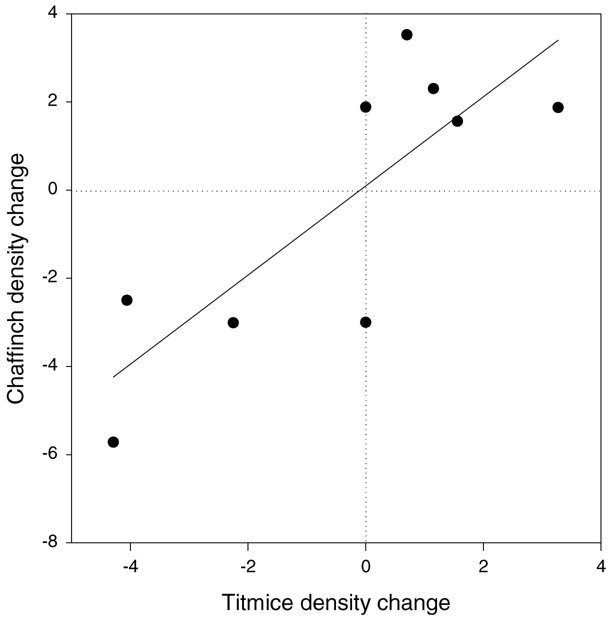

Fig. 2 Chaffinch (*Fringilla coelebs*) density response to experimentally altered titmice density

year (range of change –4.29–3.27), which therefore controlled for plot specific effects.

Density responses

A significant response for the total density (Fig. 1a), density of foliage gleaning species (Fig. 1b) and habitat generalists was observed (Table 2). Foliage gleaners' density was on average lower in 2000 than in 1999, but total densities were more or less equal in both years (Fig. 1; regression line goes through the origin). Slopes close to unity suggest that for every single increment of titmice density there was a corresponding increase in the density of migrant birds. However, these results differ when Chaffinch response data are excluded from these analyses. The abundant species group (regression: T=0.463, P=0.329), foliage gleaning guild (regression: T=0.291, P=0.39) and habitat generalists (regression: T=0.732, P=0.244) responses then become insignificant. The ground-foraging guild and habitat specialists showed no response to the increase in resident densities (Table 2).

Of the seven most abundant species, none showed a strong negative response (Table 3). Only Chaffinch (Table 3; Fig. 2) showed a significantly positive result to increased resident densities. With increasing change in titmice density there was equally large increase in Chaffinch density, a large increase for a single species to undergo. Spotted Flycatcher also showed a near significant positive response (Table 3).

We also examined if species responses were unimodal, where highest migrant densities would be found at intermediate resident densities as predicted by Mönkkö-

Table 2 Regression analysis of migrant guild densities, using most abundant species in Table 1 and subsequent species in each guild, plotted against relative titmice densities; *B* slope of regression; *T* the value of the *t*-test; for each guild the degrees of freedom equals 7 (*n*–2)

Species group	Regression		
	B	T	One-tailed significance
Common species	1.293	1.935	0.047
Foliage gleaners	1.139	2.193	0.032
Ground foragers	0.106	0.338	0.373
Habitat generalists	1.391	2.271	0.029
Habitat specialists	–0.098	–0.279	1.0

Table 3 Regression analysis of relative migrant species densities plotted against relative titmice density; *B* the slope of the regression; *T* the values of the *t*-test; for each species the degrees of freedom equals 7 (*n*–2); species abbreviations are as in Table 1

Species	Regression		
	B	T	One-tailed significance
Phy tro	0.357	0.773	0.233
Fri coe	1.011	3.638	0.004
Ant tri	–0.105	–1.532	1.0
Eri rub	0.129	0.567	0.294
Syl bor	–0.229	–1.224	1.0
Mus str	0.215	1.452	0.095
Tur ili	–0.008	–0.534	1.0

nen et al. (1999). In none of the species groups or individual species did the inclusion of the quadratic term into the regression model significantly improve the model fit, and we can conclude that all responses were linear.

Discussion

Heterospecific attraction predicts that population densities of attracted species will increase as long as the benefits of attraction are higher than the costs of interspecific competition. The current manipulation experiment provided general support for this hypothesis even though this was mainly due to the large response of a single abundant species. The positive change in resident density was associated with a positive change in the total density of migrants, in the density of foliage gleaners, habitat generalists and the Chaffinch. The present results were similar to previous studies concerning heterospecific attraction. In Europe, enhanced resident densities affected positively both the numbers of migrant species and their densities (Forsman et al. 1998a). However, no species or species group showed a clearly unimodal response to altered titmice densities, and therefore our results did not provide support for the unimodal density response of migrants in relation to resident density (Mönkkönen et al. 1999).

Forsman et al. (1998a) found little evidence that the amount of food correlates with species abundances, indicating that species in local scale communities do not seem to be limited or compete for food. Mönkkönen (1990) demonstrated that these local communities seem to be limited, rather by territorial space between conspecifics. The presence of increased migrant densities with increased resident densities clearly demonstrates that migrants may use residents as cues for relatively good breeding patches, therefore extensively colonizing these habitats and leaving other patches uninhabited. This pattern was also shown by Elmberg et al. (1997) in dabbling ducks. In this guild, Mallard (*Anas platyrhynchos*) and Green-winged Teal (*A. crecca*) co-occurred on lakes more than expected by chance alone. Therefore, competition for territories between conspecifics may result from initial positive interactions between heterospecifics, which result in increasing migrant densities in favorable (high resident density) habitats.

The mechanism behind HA is still unclear. However, the benefits of the corresponding process among conspecifics, conspecific attraction, are better known (see Stamps 1988 for review). Conspecific attraction has long been known to affect the habitat selection of animals, such as fish, lizards, insect larvae and birds causing territorial clumping. Stamps (1988, and references therein) reviewed the benefits that may arise from conspecific attraction. She suggested four possible benefits. Firstly, individuals would have increased mating success due to attraction of more females to these territory clusters or increased social stimulation. A second benefit may be predator avoidance and detection. Thirdly, territorial aggregation could improve defense against intruders of the same species. Lastly, conspecifics may provide information about habitat quality, resulting in an easy procedure to assess the habitat quality of prospective breeding sites. Of the above, only predator protection and information on habitat quality can be possible benefits of HA. Interestingly, the benefit from information on habitat quality has only fairly recently been suggested (Stamps 1988) and undergone experimental testing (Reed and Dobson 1993; Muller et al. 1997; Pöysä et al. 1998).

The different response of guilds and species may give a clue to the mechanism of heterospecific attraction. Foliage gleaners showed a significant increase in density with increasing resident densities. Resident titmice also belong to this foraging guild and the positive response indicates the importance of gaining information on the quality of habitat and in particular food availability before settling to breed, as predicted by Mönkkönen et al. (1990). Migrant species may also gain benefits during the breeding season by joining mixed-species foraging flocks (see Mönkkönen et al. 1996), which are known to relay foraging benefits to the participants (Morse 1970; Sasvári 1992; Hino 1998). In addition, species such as Spotted Flycatcher, which showed a positive trend in the present study, may benefit from the beating effect (Swynerton 1915). Mönkkönen et al. (1996) showed it to be a frequent flock member and this may further enhance HA in guilds such as aerial feeders where feeding benefits may be obtained. Possible benefits gained from predator avoidance and detection may also be important. It has been shown that individuals forage closer to heterospecifics during periods of higher perceived predator densities (Forsman et al. 1998b) and that certain species in these flocks may warn others of predators (Sullivan 1984).

The ground foraging guild did not show a response to manipulations in our study, suggesting that HA is unimportant in species belonging to other foraging guilds, where information on habitat quality relating to food availability is not applicable. The present results are similar to those obtained in a North American bird community (Mönkkönen et al. 1997). The possible benefits gained by ground foragers would be predominantly that of predator avoidance (see Slagsvold 1980) and detection. During the breeding season, however, ground-foraging species appear not to be regular members of mixed-species foraging flocks (Mönkkönen et al. 1996), in which benefits such as predator detection would be gained.

It is also predicted that habitat generalists should show HA (Mönkkönen et al. 1997; Forsman et al. 1998a; Mönkkönen et al. 1999). Dall and Cuthill (1997) suggest that because generalists need to gather a large amount of information about the environment compared with specialists, the sampling strategy may be more costly. Therefore, by trying to reduce these costs it would be beneficial for generalists to use residents as cues. The present study provided support for this prediction. Generalists as a group and the Chaffinch in particular showed a highly significant response to augmented resident densities, although Willow Warbler, also a generalist species, did not. Chaffinch is ecologically very similar to one resident species, Great Tit, and they forage in a very similar manner. Indeed, they have been shown to compete in certain conditions (Reed 1982). The territories of these two species were shown to overlap with territories of resident tits more than would be expected by chance (Timonen et al. l994). They have also previously been shown to respond positively to artificially increased resident densities (Mönkkönen et al. 1990). The highly positive response of the Chaffinch we observed is even more significant because adult birds in this species exhibit strong breeding site tenacity (Mikkonen 1983). Chaffinch densities in study plots with increased density of titmice increased by some 30–60% in relation to densities in 1999 (Table 1). Assuming that young individuals are the most prone to use HA and that the adult survival rate in small passerine birds like Chaffinch is about 60% (see, e.g., Dobson 1990), then the proportion of young birds in breeding populations is somewhere between 30 and 50%. Therefore, the response we observed is about at a maximum for species with site fidelity.

Year-to-year variation in survival rates and hence in the proportion of young individuals in a population may explain variation between species and years (studies) in species-specific responses to changes in resident densities. "Populations have a certain age and size structure which can effect outcomes of interactions" (Thompson 1988), clearly this structure will change yearly and could explain the lack of response in some species in the present study. For example, we found no response of Redwing, whereas in Forsman et al. (1998a) this species showed the most significant positive response of all species present. Likewise, Willow Warbler has previously been shown to respond positively to increased resident densities (Mönkkönen et al. 1990), but we found no response. There was a pronounced decrease in the density of Willow Warblers between 1999 and 2000 (average densities were 18 vs. 15 pairs/10 ha, respectively), and there simply may not have been enough young individuals in the population for a significant response to emerge (see also Timonen et al. 1994). We therefore still suggest that HA may be a community wide process, but that responses may vary dramatically between years depending on the population structure.

The present study was conducted to test the predictions of the theoretical model (Mönkkönen et al. 1999). Study plots in the present study were manipulated to have increased resident densities, however, the increased densities never reached those high enough to result in less pronounced HA and not near those densities where competition would be expected. Mönkkönen (unpublished data) studied the relationship between Chaffinch and titmice densities across the whole of Europe and found that only at titmice densities above 20 pairs/10 ha negative density relationships between these species can be found. In northern Europe, where resident densities are invariably low (Forsman and Mönkkönen 2002), positive and linear relationship prevailed. In our study the highest titmice densities were about 5.5 pairs/10 ha. We suggest that in harsh northern environments, where resident densities are severely limited, resident densities will rarely, if ever, reach the levels required for competitive interactions. Thus residents should settle in high quality sites and HA will always be a positively important strategy for migrants when selecting a breeding patch in the north.

This suggestion agrees with results of experimental studies on the fitness effects of competition vs. heterospecific attraction. Gustafsson (1987) demonstrated competition between resident titmice and the migrant Collared Flycatcher (*Ficedula albicollis*) in Gotland. In his plots increased titmice densities were 27 pairs/10 ha (see also Sasvári et al. 1987). However, in an experiment conducted in northern Finland, where augmented titmice densities were only up to 6 pairs/10 ha, the presence of resident tits resulted in positive fitness consequences in the Pied Flycatcher (*Ficedula hypoleuca*) compared to the zero density treatment of titmice (Forsman et al. 2002). The apparent discrepancy between these two studies is probably explained by the different environmental conditions and low density of titmice, which is insufficient for competitive interactions to emerge.

Indeed, information gained on habitat quality makes more empirical sense between heterospecifics, where territories can overlap, than conspecifics where territories are mutually exclusive. Conspecifics would be expected to compete more than similar, but slightly different heterospecifics, as found in the relationship between

Great Tit and Chaffinch (Reed 1982). Knowing that HA does exist, it is now important to examine which of the possible benefits individuals using this strategy may gain. As for conspecific attraction (Smith and Peacock 1990; Ray et al. 1991; Reed and Dobson 1993; Reed 1999), HA results in non-random dispersal and habitat selection, where the presence of a second bird species will influence where individuals of the species settle to breed. HA will also therefore have profound influences on conservation biology and metapopulation theory and should also be incorporated into theory of this nature.

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