Heterospecific attraction among forest birds: a review

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Abstract   In this paper we review the evidence for a habitat selection process where colonizing individuals use other species presence as cues to profitable breeding sites. Our experimental studies in Fennoscandia and North America have shown that density and species richness of migrant birds breeding in the forests respond positively to experimentally augmented titmice densities. We used analytical modeling to analyze ecological conditions, which may favor a habitat selection process where later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites. We compared the fitness of two colonist strategies: colonists could either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Model results suggested that cue-using strategy is more beneficial in most ecological conditions and that this may result in heterospecific attraction. Further field experiments showed that migrant individuals selected nest sites at close vicinity of nesting titmice, and bred earlier and reproduced better. We conclude that heterospecific attraction may be a common and widespread process among forest birds particularly in seasonal environments.

Key words   Experimental studies, Habitat selection, Migrant vs. resident birds, Reproductive output, Species richness

Heterospecific attraction was coined by Mönkkönen et al. (1990) to describe habitat selection process where individuals prefer selecting habitat patches already occupied by individuals of another species. It was hypothesized that particularly migrant birds may use residents as cues to profitable breeding sites in conditions where direct and accurate assessing of the quality of available patches is difficult. Short available breeding time and large year-to-year variation in conditions, both characteristics of northern environments, would presumably render heterospecific attraction a profitable habitat selection strategy.

Temperate and boreal passerine bird communities are comprised of resident and migrant species. Residents have to cope with local conditions on a year round basis but migrants are able to avoid the low phases in food availability by migrating elsewhere for the temperate winter. Individuals of many species show high fidelity to their previous year's breeding territory (Hildén 1965). However, because of high adult mortality approximately half of the individuals in passerine breeding populations are first time breeders who need to make a selection among potential breeding sites. Therefore breeding habitat selection may only be made once in the life of a bird (Cody 1985) stressing the importance of this operation.

Birds obviously use a multiple of cues when selecting breeding sites (Hildén 1965). These include habitat cues, habitat structure, floristics, food resources etc., as well as information on population density (Wiens 1989). Also interactions with other species may influence the occupancy of an area (Cody 1985). The effect of other species on local community diversity may either be positive, such as through heterospecific (see also Slagsvold 1980, Elmberg et al. 1997) or conspecific (Alatalo et al. 1982; Doligez et al. 1999) attraction, or negative through intra- (e.g., Krebs 1971; Fretwell 1972; Mönkkönen 1990) or interspecific (e.g., Reed 1982; Garcia 1983; Gustafsson 1987; Martin & Martin 2001a, b) competition. The presence and density of predators may also decrease the desirability of habitat patches (Mar-

tin & Roper 1988; Järvinen 1990; Suhonen et al. 1994; Hogstad 1995), if settling individuals are able to actively avoid areas with high risk, as appears to be the case (Norrdahl & Korpimäki 1998).

The idea that individuals prefer to settle close to conspecific individuals at least in some species can be traced back many decades (Lack 1948; Svärdson 1949; Kalela 1952). Stamps (1988) reviewed hypotheses to account for such attraction to conspecific individuals. Aggregated distribution may 1) provide protection against predators by means of communal defence or information delivered by neighbours, 2) benefit an individual if settled neighbours reflect habitat quality, 3) provide social stimulus and hence accelerate or improve breeding performance (e.g. pairing), or 4) improve ability to defend against intruders or competitors. In principle, the three first hypotheses may apply to heterospecific attraction as well. First, it has often been shown that individuals of many species may aggregate to breed in colonies or clumps for protection against nest and other predators (Slagsvold 1980). Second, birds are able to recognize vocalizations of heterospecific individuals, e.g. song (Mönkkönen et al. 1996) and warning calls (Forsman & Mönkkönen 2001; Gunn et al. 2000), and therefore birds can make use of information delivered by other individuals. Aggregations of heterospecific individuals may also provide social stimulus if, for example, females are attracted to such 'hot-spots' of singing males, improving or accelerating pairing.

For heterospecific attraction to operate certain ecological conditions must prevail. First, residents must honestly signal the quality of habitat. This seems a rather robust assumption. Resident birds are very likely less time constraint than migrants, and hence, can invest more time and energy in direct assessing of the relative quality of available habitat patches. Migrant birds are more time constrained in their breeding because in their northern breeding areas habitat selection, pairing, nest building, reproduction, and in some species also moulting has to be fulfilled within just few weeks. Even short delays in the onset of reproduction may accrue severe fitness costs (von Haartman 1967; Alatalo & Lundberg 1984; Harvey et al. 1985; Barba et al. 1995). The presence of resident individuals is likely an honest signal of predation risk in a patch, because residents have had time to evaluate the risk of predation or because residents in risky patches have already fallen victims of predation. Habitat selection and predation result in spatial variation in the density of resident individuals in a land-scape. Only if such variation existed, would there be potential for migrants to gain information from resident abundance.

Second, migrant bird responding to this variation should be capable of making a choice between different habitat patches. In other words, heterospecific attraction is more likely applied by a species that have to process much information from the landscape before habitat selection, such as habitat generalists apparently have to do (see Dall & Cuthill 1997). Strict habitat specialists more likely respond directly to structural or floristic composition of habitats. Third, for fitness benefits from heterospecific attraction, residents must not cause serious resource depletion for migrants. If severe competition occurs between residents and migrants, migrants should avoid settling in a patch together with residents (Cody 1985). Therefore, heterospecific attraction is more likely among species that do not compete over food and in conditions where food depletion is not a risk (food limitation less severe).

In this paper we first provide some background information on abundances of birds along biogeographic gradients to exemplify the range of conditions where temperate breeding bird communities develop. In particular, we focus on the relative abundance of migrant and resident species in their breeding assemblages, which form the starting point for our later studies on species interactions in forest bird communities. Secondly, we review the evidence, both theoretical and empirical, for heterospecific attraction among forest birds. We consider the effects of this attraction on both breeding numbers and community structure as well as on fitness components of breeding individuals. Finally, we provide a discussion about the generality, importance and conservation implications of heterospecific attraction.

BIOGEOGRAPHICAL PATTERNS IN THE ABUNDANCE OF RESIDENT AND MIGRANT BIRDS AND IMPLICATIONS FOR HETEROSPECIFIC ATTRACTION

A well-known geographic pattern in northern breeding bird communities is the increase in the proportion of migrant birds of the total species and pair numbers with increasing seasonality (MacArthur 1959; Wilson 1976; Herrera 1978; Morse 1989). Usually migrants comprise a larger share of species and individuals in the north than in the south. This geographical pattern is clear, for example, in western Eu-

rope where the proportion of tropical (trans-Saharan) migrants increases from an average less than 10% in the Mediterranean region to about 50% in Fennoscandia (Herrera 1978; for North American pattern, see e.g. Wilson 1976; Morse 1989).

According to Herrera (1978) such a pattern is because carrying capacity of the environment during the severe season (winter) regulates the size of resident species populations below the levels of summer time carrying capacity, which in turn affects the number of migrants that may enter the habitats. In other words, migrants fit in the breeding assemblages in high numbers only where resident populations are regulated to a low level (see also Morse 1989). Resident birds are usually considered superior competitors over migrants and this interspecific competition would keep migrant numbers low in areas and habitats where resident densities are high (Herrera 1978; O'Connor 1981). The pattern of increasing proportion of migrants toward north may also be because of geographical variation in migrant abundance without any linkage to resident abundance. Helle and Fuller (1988), however, showed that total migrant densities do not vary very much from south to north in Europe indicating that the increasing proportion of migrants toward north is mainly due to decreasing resident abundance.

More detailed new analysis by Forsman and Mönkkönen (see Forsman 2000) showed that while resident densities generally declined with latitude migrant densities tended to peak at mid-latitudes (in central Europe) and were lower both further south and north (Fig. 1). The decrease in resident densities was not linear either, and densities north from 60°N were invariably low whereas further south highly variable. The unimodal density pattern of migrants was common to many genera (*Phylloscopus*, *Fringilla*, and *Turdus*) and suggests that migrant densities at geographical scale vary independently of resident numbers. The current evidence, therefore, does not support the conclusion that competition with residents would cause the geographical pattern in migrant proportions, and calls for alternative explanations.

Forsman and Mönkkönen (see Forsman 2000) also analysed the covariation between titmice (resident) and migrant (several genera) densities in Europe after removing the geographical trends in abundances to find out geographic areas where negative (competition) and positive (e.g. heterospecific attraction) associations between residents and migrants are more
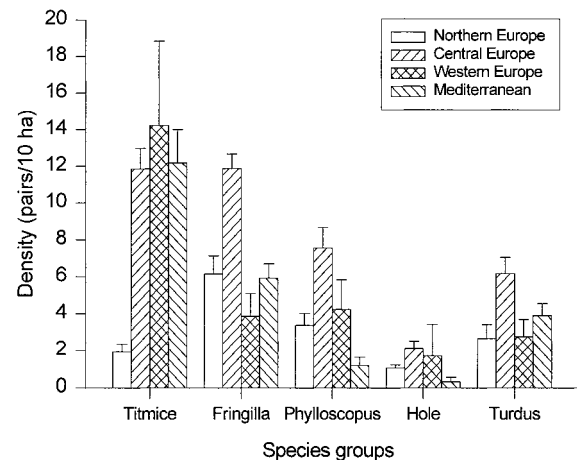
Fig. 1. Density of different forest bird taxa and species groups in different parts of Europe based on published census results (see Forsman 2000). Northern Europe refers to areas north from latitude 60° and southern Europe to areas south from 45°. The area between these latitudes was divided into central Europe (east from 2°E) and western Europe (west from 2°E). Titmice include all European Parus spp. and the Long-tailed Tit (*Aegithalos caudatus*). Generic groups refer to all species in the genus, and Hole denotes hole nesting passerine birds other than Parus spp. (Ficedula hypoleuca, *F. albicollis*, and *Phoenicurus phoenicurus*).

likely than elsewhere. There were many significant positive associations but no significant negative associations. For example, the density of *Fringilla* spp. was positively and significantly associated with titmice densities in northern and central Europe, and that of *Phylloscopus*-warblers in central Europe. This result indicates that positive rather than competitive interactions may prevail between residents and migrants almost irrespectively of the geographic location.

EVIDENCE FOR HETEROSPECIFIC ATTRACTION: NUMERICAL RESPONSES

1) Observational evidence

That birds may be attracted to nest close to other species is a well-known pattern (Durango 1947; Koskimies 1957; Hildén 1964, 1965). Slagsvold (1980), for example, found that Bramblings (*Fringilla montifringilla*) and Redwings (*Turdus iliacus*) preferred to nest in Fieldfare (*Turdus pilaris*) colonies. These species obviously benefited from breeding within Fieldfare colonies because of communal defense against nest predators.

First implications of heterospecific attraction among putative competitor species were found by Reed (1982). He demonstrated that Chaffinch (*Fringilla coelebs*) territories on the mainland of Scotland tended to co-occur with Great Tit (*Parus major*) territories more often than expected by chance alone. In island conditions, however, these two species seemed to compete with each other and occupied non-overlapping territories (Reed 1982). Reed (1982) concluded that the environment on the mainland is richer (more food) than on islands. These results suggest that interspecific interactions may vary considerably according to environmental conditions from competition in situations were resources are limiting (on islands in Reeds case) to positive interactions in others (mainland).

Positive association between territories of two species may also stem from overlapping habitat requirements or from concomitant settling in rich resource. In a playback experiment, where habitat requirements of the species were controlled for, Timonen et al. (1994) demonstrated that two migrants species, the Chaffinch and the Willow Warbler (*Phylloscopus trochilus*), did not avoid settlement near or in resident (*Parus* spp.) territories. Also in this work, there was a tendency that migrants aggregated more than expected at the vicinity of residents. In this experiment, however, food availability was not controlled for and a possibility remained that actually both residents and migrants preferred settling in high quality food patches resulting in positive associations among species.

2) Experimental evidence

To test for numerical response of migrants to resident abundance in their breeding bird assemblages of forest birds we have conducted three rather similar experiments (Mönkkönen et al. 1990, 1997; Forsman et al. 1998). In these studies, we manipulated the occurrence of resident titmice (*Parus* spp.). These manipulations involved winter-feeding and putting up nest boxes to attract titmice on part of the study plots, and removal of titmice from some others. As a result, at the onset of breeding season migrants could make a choice between plots devoid of titmice and plots where titmice densities were augmented. Migrant responses to manipulations were measured by censusing their abundance on experimental plots at the height of the breeding season when breeding pairs possess territories. The experimental design where all plots received both treatments in alternate years ef-

fectively removed any year, food or site related effects on the results (for detailed methodology, see original publications). Heterospecific attraction hypothesis predicts that migrant densities would be higher in plots with titmice than in empty plots.

Our results, encompassing two different continents (Europe and North America) and a variety of conditions from north (Lapland) to south boreal forest zones (Minnesota), were consistent and provided support for the heterospecific attraction hypothesis. The general pattern turned out to be a positive response by migrants to augmented titmice abundance. In all three locations migrant species richness tended to be higher when titmice were present than in absence of titmice (Fig. 2) but this trend was statistically significant only in Lapland. In Lapland and central Finland total migrant abundance responded significantly and positively to augmented titmice abundances, and in central Finland and in Minnesota, foliage gleaners showed a significant positive response. In each area there were one or two individual species showing positive, and none showing negative, response to titmice presence.

The only other study, in addition to our experiments, where the effects of heterospecific attraction on species abundance and community assembly has been addressed is the work by Elmberg et al. (1998) on dabbling ducks. In line with our results, Elmberg et al. (1998) concluded that heterospecific attraction rather than competition affects species co-occurrence in dabbling ducks.

3) Theoretical considerations and a test

Our experiments clearly showed that forest bird species might use each other's presence as cues in breeding habitat selection in a wide variety of environmental conditions. Results from local experimental work, however, do not lend themselves to make far-reaching conclusions about the importance and generality of the heterospecific attraction as a process. Therefore, we used analytical modeling to analyze ecological conditions, which may favor a habitat selection process where later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites (heterospecific attraction) (Mönkkönen et al. 1999). In this model, colonists assessing potential breeding patches could select between high-quality source and low-quality sink patches. Residents occupied a proportion of the source patches. One patch can only foster one pair of colonists. Colonists could
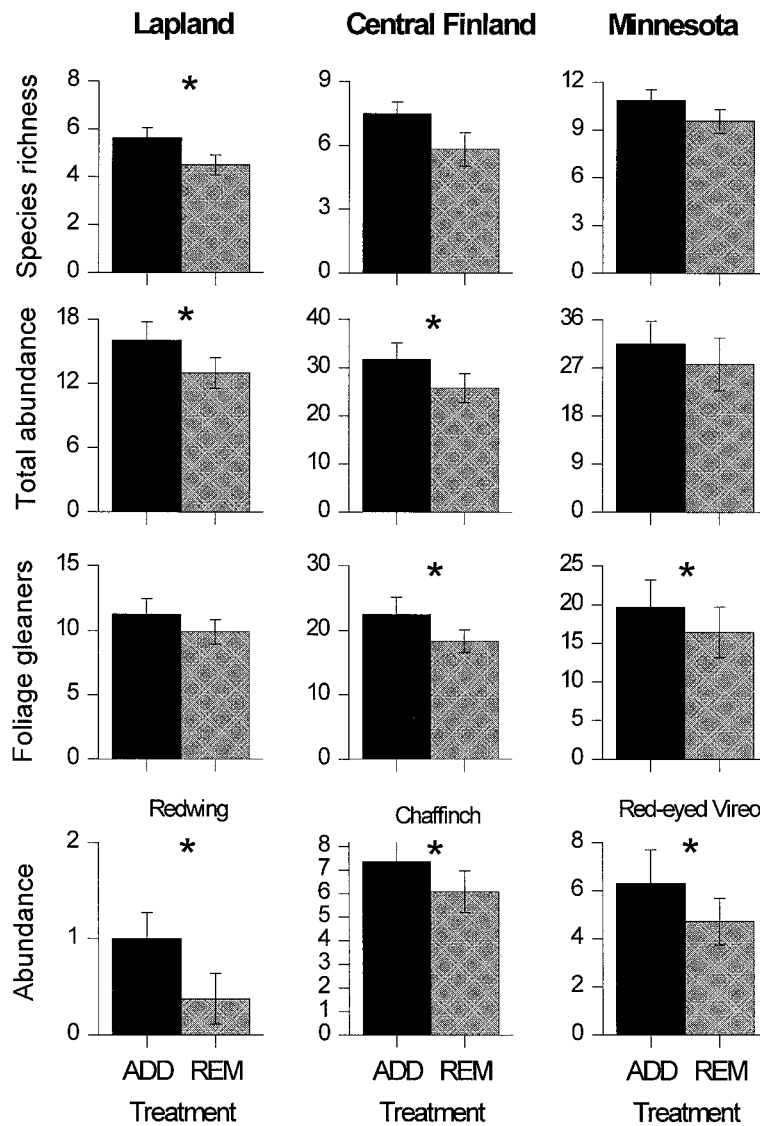
Fig. 2. Mean species richness, mean number of pairs of migrant passerine birds and of foliage gleaning birds in three experimental studies (Lapland, Forsman et al. 1998; Central Finland, Mönkkönen et al. 1990; Minnesota, Mönkkönen et al. 1997). Mean number of pairs for the most strongly responding species is also given (Redwing *Turdus iliacus*, Chaffinch *Fringilla coelebs*, Red-eyed Vireo *Vireo olivaceus*). Error bars denote ±1 SD. ADD refers to augmented titmice density and REM to removal of titmice from the study plots. Asterisk refers to statistically significant (P<0.05) difference between the treatments.

either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Cue-users gained benefit from lowered costs when assessing occupied source patches. We compared the fitness between cue-users and sampler in different ecological conditions and varied, for example, the proportions of sink, empty source and occupied source patches, as well as intensity of competition vs. benefits gained from social aggregations.

We assumed that colonizing individuals use sequential-comparison tactic (SCT) when choosing among patches. It follows from SCT that colonists sample only a limited number of patches (maximum 5 patches). Our model does not result in an ideal distribution because colonists do not necessarily end up selecting the best available patch but the best of the evaluated ones. We used a variant of natural decision theory where sequences can be depicted with decision tree diagrams (for details, see Mönkkönen et al.

1999).

The results of the model indicated that the cue-using strategy is an efficient way to choose the best possible patch both when benefits from social aggregation exceeded the effects of competition (interspecific competition is not strong) but also when interspecific competition is stronger than the benefits (results in avoidance of occupied patches). Samplers can achieve higher fitness than cue-users only if the difference in quality between occupied and unoccupied source patches is low (interspecific interactions weak). This was because the relatively more complicated patch selection procedure of cue-users creates costs, which override the benefits of avoiding the direct assessment of the patch quality, when gains are low. Consequently, cue-using strategy can be used both to avoid competition and to aggregate with heterospecific individuals. Heterospecific attraction would occur whenever colonists gained some benefit from aggregating with residents, which exceeded the effects of competition.

The model also predicted that the strongest attraction to heterospecifics occurs when residents occupy approximately half of high-quality source patches. This is because in such conditions colonists can truly make a choice between empty and occupied source patches. If only few patches are occupied (or empty) chances of finding one are low and choices between empty and occupied source patches are infrequent. In other words, the response of colonists to resident abundance would not necessarily be linear along a whole gradient of resident abundance.

To test this idea we conducted a further experiment in central Finland where resident densities in nine study plot were manipulated create a spectrum of resident densities, relative to previous year's unmanipulated densities (Thomson et al. unpublished). In the first study year titmice were allowed to breed on plots at natural densities, but before the second breeding season their densities were manipulated by feeding, providing nest boxes and removals. Relative changes in migrant densities were analyzed against the difference in titmice densities between years. The hypothesis was that intermediate change in titmice densities would be associated with the highest migrant densities.

The results were only partly consistent with the prediction. There was only very little evidence for a non-linear response. In general the result was a linear response of migrants as shown in Fig. 3 for foliage gleaning guild. This pattern matches well with our
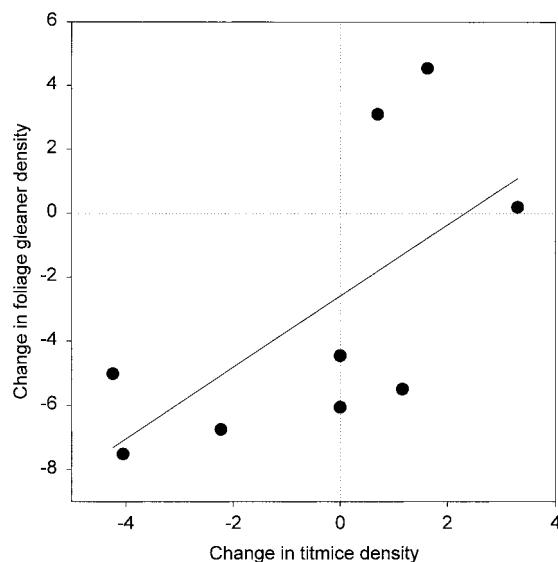
Fig. 3. The change in density of foliage gleaning birds between two consecutive breeding seasons as a response to manipulated titmice density (pairs/10 ha). Titmice densities were decreased (negative change), kept constant, or augmented (positive change) between the years. Foliage gleaners' density significantly increases with increasing titmice density (regression slope $=1.16$, df$=7$, P$=0.032$).

earlier experiments and provide further support for heterospecific attraction. The prediction from our analytical model was not, however, confirmed. This is very likely because we did not manage to create high enough titmice densities in our experiment for non-linear responses to emerge. For example, fitting a quadratic curve to density response of the chaffinch in relation to titmice density suggests that the peak in chaffinch density would be achieved when titmice density is about 10 pairs/10 ha. Only after that point would chaffinch densities start to drop with an increase in titmice densities. Maximum densities in our area were about 6 pairs/10 ha, which is rather high density compared to natural densities in the area, but, however, far below the threshold point for non-linear response.

COLONISATION RATES AND FITNESS CONSEQUENCES OF HETEROSPECIFIC ATTRACTION ON DIFFERENT SPATIAL SCALES

1) Habitat selection across scales

Habitat selection of birds is regarded as a hierarchical procedure during which factors affecting decisions of colonizing birds vary considerably (Hutto

1985). On larger scales the influence of individual choice on selection is probably negligible (Hutto 1985) because the choice of geographical area or macrohabitat (e.g., forest type) is quite likely strongly genetically determined (Partridge 1978). However, the smaller the scale is the larger is the number of the characters and cues of the environment that can be taken into account by an assessing individual.

The multitude of different biotic cues affecting habitat selection suggests that perceptual ranges of birds can be very wide and following decisions show considerable behavioural plasticity. Considering the importance of a certain factor in habitat selection, however, it is crucial to take into account the scale where the process takes place and whether or not the selection decisions are adaptive. Cues that are used during the selection process may be either nested across different scales or their effect may take place on one level only. Our earlier work on heterospecific attraction emphasize its effect on habitat patch selection but Timonen's et al. (1994) study suggested that it may operate on smaller scales as well, such as on territory level. To examine the importance of heterospecific attraction in more detail we conducted a set of experiments, which involved two intersecting spatial scales: habitat patches in the landscape and territories within a patch (Seppänen et al. unpublished). In the landscape level we manipulated the densities of resident birds (*Parus* spp.) inhabiting isolated forest patches embedded on an agricultural landscape. In the territory level experiment we studied the settlement of migrant birds in relation to nest of *Parus* spp. In both experiment we used the Pied Flycatcher as a model species.

2) Colonisation rates

If heterospecific attraction is used by Pied Flycatchers (*Ficedula hypoleuca*) when selecting breeding habitat patches, they should first select patches of high titmice density. There was a tendency that Pied Flycatchers preferred high tit density patches to zero density patches. Both the first male flycatcher of each study plot and the average arrival day of males tended to be slightly earlier on high tit density plots than on zero plots, though not statistcally significantly (Seppänen et al. unpublished). Female flycatchers had no response whatsoever to the treatments.

On the level of territories Pied Flycatchers were let choose between two nest boxes: the other was close (25 m) and the other one was farther away (100 m) from an active tit nest. If heterospecific attraction is used at this scale, nest boxes adjacent to a tit nest would be preferred to more distantly located nest boxes. On the territory level, males clearly preferred nest boxes closer to the tit nest to the nest boxes farther away. In 25 set-ups, out of the total 36 cases, males selected first the box closer to the tit nest first. The observed distribution differed significantly from random pattern (1-tailed P=0.014 based on resampling). Likewise, females preferred settling to close by nest-boxes to those farther away (23 vs. 12 boxes selected first, respectively; 1-tailed P=0.043). It is known that female flycatchers select the nesting site according to the quality of the site and not according to the quality of the male (Alatalo et al. 1986). Therefore, we can consider female preference as independent of male selection even though males arrive first from migration. In this experiment we cannot completely rule out the possibility that both titmice and flycatcher, independently, chose higher quality sites.

3) Fitness consequences

At least equally as important as the scale issue is whether the habitat selection is adaptive or not. Even though heterospecific attraction results in positive association between titmice and migrant densities, it does not necessarily indicate that using heterospecific cues is beneficial in terms of reproductive success (see Pulliam 1988; Martin 1998). We tested if heterospecific attraction results in an increased fitness in the Pied Flycatcher by comparing reproductive success in patches where tits nested with patches devoid of tits using the abovementioned experimental arrangement.

In general, the presence of titmice had a positive effect on the reproductive success of the Pied Flycatcher (Seppänen et al. unpublished). Flycatchers were able to start egg-laying earlier, and the time delay from the female arrival to the first egg was on average 1.7 days shorter in patches where tits were present than in patches devoid of tits. Moreover, nestlings hatched 1.7 days earlier, and there were on average 0.6 more nestlings in broods in patches with tits than in patches without tits. Fledglings growing up in the neighborhood of titmice were larger than in the nests farther away.

The results of these two experiments clearly indicate two things. First, heterospecific attraction seems to be an adaptive habitat selection strategy in terms of reproductive success in the Pied Flycatcher. Second, the effect of heterospecific attraction on habitat selection and fitness is potentially working on two over-

lapping scales; the presence of tits is first used in roughly comparing the quality of habitat patches at the landscape level followed by a more fine-tuned small scale nest site selection with preference to neighborhood of tit nest sites (see also Timonen et al. 1994). The results of the experiments also provide an example of nested habitat selection across scales with possibly cascading effects from titmice presence in the landscape in terms of higher occupation rates and reproductive success.

DISCUSSION

To summarize, boreal forest environment provide an example of a system where using resident species as cues is a profitable strategy in the breeding habitat selection of migrant birds. The experiments conducted on two continents indicate that heterospecific attraction of migrants to titmice increase the diversity and total abundance in local breeding communities. Migrant birds apparently use titmice abundance in comparing the relative quality (food and/or predators) of habitat patches. Our work at the biogeographic scale suggests that heterospecific attraction might not be restricted to boreal conditions but may be a wide spread process in forests bird communities. Analytical modeling approach suggested that this sort of cueing from residents in most cases creates fitness benefits and is therefore selected for. This was further shown in experiments on titmice and Pied Flycatchers. We observed that flycatchers preferred areas of high tit density in their settlement and, moreover, their reproductive success was higher in patches with tits than without them.

Recent theoretical study has suggested that positive interspecific interactions are plausible, common and intensive in a wide variety of environmental conditions. For example, Dodds (1988) showed that in highly seasonal ("boom and bust") environments, positive interactions, such as facilitation and mutualism, are selected for. Similarly, Bertness and Callaway (1994) suggested that positive interactions should be particularly common in communities under a severe physical stress (e.g., in highly variable or seasonal environments) and/or experiencing high consumer (predation) pressure. Bird communities in temperate and particularly in boreal settings occur in conditions that very likely meet these conditions: seasonality is pronounced producing a large difference in resource levels between summer and winter (Blake et al. 1994) and predation pressure on adults, nests and

young birds is heavy (Hanski et al. 1996; Solonen 1997).

We were able to show fitness benefits for Pied Flycatchers from settling in patches with titmice, but many earlier studies, conducted further south in temperate forests, have also shown competitive interactions between flycatchers (Pied Flycatcher or Collared Flycatcher, *F. albicollis*) and tits (Slagsvold 1975; Sasvari et al. 1987; Gustafsson 1987, 1988; Merilä & Wiggins 1995). For example, Gustafsson (1987) showed that tits affected negatively the fitness of collared flycatchers. Potential reason for these seemingly contradictory results is in the difference in densities of residents among studies. In these southern studies titmice densities have usually been 2–5 times higher than the highest densities in our study areas (4–5 pairs/10 ha). Contrasting results in our and Gustafssonson's (1987) study suggests that interspecific interactions may change along with different densities of potential competitors. This matches well with the results of our analytical model, which predicted stronger attraction to residents at intermediate abundance (see above).

The results of the experimental studies indicate that birds' readiness to follow heterospecific cues varies among places and species. Not all species responded positively to increasing resident densities in our experiments, and there obviously is much variation in within-species responses to resident densities according to local conditions. In what conditions are species more apt to using heterospecific cues? Young birds selecting their first nesting sites are very likely more susceptible to use heterospecific cues than older individuals, which usually return to their previous year's breeding site. Young birds might also be better off by using heterospecific residents than conspecific as cues because the presence of conspecifics may not reflect relative quality of the breeding sites in the current year but rather conditions in the past when site selection was made. Given the extensive between-year variation in conditions taking one's cue from residents is quite likely more beneficial. It follows that the intensity of heterospecific attraction should vary according to the proportion of young individuals in the breeding population. We earlier referred to habitat generalists as being a species group apt to hetereospecific attraction because they are not very tightly dependent on any particular habitat feature. In two Finnish experiments (Mönkkönen et al. 1990; Thomson et al. unpublished), we found that the Chaffinch, an acknowledged habitat generalist,

showed the strongest response to increased titmice density. In the northernmost experiment (in this area the Chaffinch is relatively few in number) the Brambling had also a positive response to augmented tit densities (Forsman et al. 1998). Brambling is also a habitat generalist and, in addition, does not show site-fidelity to previous year's breeding sites (Enemar et al. 1984; Mikkonen 1983). Brambling is therefore free to use external cues in order to find as good breeding habitat as possible.

The results of the experiments on Pied Flycacher provide also some evidence about the processes behind the heterospecific attraction. We have earlier suggested that the presence and density of tits is used to make quick assessment of relative quality among habitat patches in the landscape. Our results showed, that indeed, high tit density patches and nest boxes closer to the nest of tit were colonized earlier indicating that tits were used as a measure of the patch and site quality resulting in increased fitness. Female flycatchers in patches where tits were present showed shorter time lags between arrival and the onset of egg-laying. Pied Flycatchers, as many other birds, are time constrained in their breeding and an early start of the breeding has a positive effect on the reproductive output (e.g., von Haartman 1967; Lundberg & Alatalo 1992). Our results also suggest that flycatchers may also benefit from the tits through enhanced feeding efficiency or predator vigilance.

At the landscape level, heterospecific attraction results in a clumped distribution of individuals and species, a common pattern in nature (Hanski et al. 1993). This would explain the common observation that some seemingly suitable habitat patches remain empty. If colonization of patches is more generally dependent on the presence of individuals of other species, this would further complicate population dynamics in patchy landscapes. For example, metapopulation models, for the sake of realism, should incorporate interspecific interactions such as heterospecific attraction. Given the increasing fragmentation of landscapes taking interspecific interactions into account when assessing individual dispersal and population viability is becoming increasingly important. For example, many old-forest associated resident species in Fennoscandia show declining population trends because of habitat loss and fragmentation (e.g. Haila & Järvinen 1990). This may have negative effects on migrant species as well, if colonization rates in remaining patches depend critically on heterospecific cues.

Our experiments focused only on migrant birds' habitat selection and fitness, and provided no evidence of whether heterospecific attraction results in a mutualistic relationship where also residents benefit from migrants' presence or benefits are asymmetric accruing only to migrants. This remains as a challenge for future studies. The experiments in temperate forests have so far encompassed only the high end of the resident density gradient; resident densities in nest-box studies may be unnaturally high compared to natural densities (e.g. Wesolowski et al. 1987). It would be interesting to see results from an experiment similar to our flycatcher work conducted in temperate settings where numerical response and fitness effects were studied over the whole gradient of resident densities. These results would further test for the importance and intensity of interspecific interactions (both negative and positive) and even reveal threshold conditions where originally positive interactions turn into negative ones.

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