Positive fitness consequences of interspecific interaction with a potential competitor

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The coexistence of species sharing mutual resources is usually thought to be limited by negative processes such as interspecific competition. This is because an overlap in resource use leads to negative fitness consequences, and traits favouring avoidance of potential competitors, for example in habitat selection, are therefore selected for. However, species interactions are acknowledged to vary from negative (competition) to mutualism, although empirical evidence for positive interspecific interactions from natural communities of other than plants and sessile animals is scarce. Here, we experimentally examined the habitat selection and its fitness consequences of a migrant bird, the pied flycatcher (*Ficedula hypoleuca*), in relation to the presence of competitively superior birds, resident titmice (*Parus* spp.). Experiments were conducted on two spatial scales: landscape and nest-site scale. We demonstrate that pied flycatchers were attracted to and accrued fitness benefits from the presence of titmice. Flycatchers breeding in tight association with titmice initiated breeding earlier, had larger broods and heavier young than solitarily breeding flycatchers. This paradoxical result indicates that species interactions may switch from negative to positive and that the coexistence of species is not always restricted by negative costs caused by other species.

Keywords: habitat selection; heterospecific attraction; species coexistence; positive interspecific interactions

1. INTRODUCTION

Negative interactions are considered to prevail between coexisting species with overlapping resource use. For example, coexistence of potential competitors has been shown to bring about fitness costs in terms of increased competition for food (Minot 1981; Gustafsson 1987; Sasvári *et al.* 1987), nutrients (Tilman 1982; Wedin & Tilman 1993) or increased nest predation (Martin 1993; Schmidt & Whelan 1998). Therefore, traits that minimize temporal or spatial overlap with competing species should be selected for. It has indeed been shown that shared nest predators, for example, may induce spatial segregation or interspecific aggression among coexisting species (Martin 1993; Martin & Martin 2001a). Hence, the concept of coexistence of species is usually based on the idea of minimum tolerance towards co-occurring species.

Interspecific interactions, however, need not always be negative and they may show considerable plasticity depending on the local biotic and abiotic conditions (Travis 1996; Agrawal 2001). Especially harsh and physiologically stressful environments have been suggested to enhance the occurrence of positive interspecific interactions (Bertness & Callaway 1994) and empirical evidence from plant and animal communities seems to support this hypothesis (e.g. Greenbee & Callaway 1996; Bertness & Leonard 1997; Bertness 1999). However, the evidence for positive interspecific interactions mainly comes from plant communities or communities of sessile animals (see Jones *et al.* 1997) and direct fitness benefits resulting from positive interactions in mobile animal communities are scarce (Dickman 1992).

One potential case for positive interspecific interactions among animals is heterospecific attraction of migrants to resident birds. Experiments in Europe and North America have shown that elevated resident titmice densities yield increases in the number of species and abundance of migrant birds, via heterospecific attraction (see Mönkkönen *et al.* 1990), and even species that are potential competitors with titmice are attracted to them (Mönkkönen *et al.* 1990, 1997; Timonen *et al.* 1994; Forsman *et al.* 1998). The idea behind heterospecific attraction is that using residents as a cue in habitat selection is likely to be beneficial because residents indicate good quality habitats in terms of food or safety, or migrants receive feeding or foraging benefits from aggregating with residents (Mönkkönen *et al.* 1996). Residents have all year to assess the quality of habitats and may provide a faster and more reliable cue for migrants than spending time sampling the quality of potential breeding sites, thus yielding a fitness benefit to migrants because the reproductive success of birds declines rapidly with delayed onset of breeding (Klomp 1970; Harvey *et al.* 1985).

Thus far, however, we have not known whether heterospecific attraction is selectively advantageous or neutral. Here, we examined whether heterospecific attraction of a migrant bird to resident titmice (*Parus* spp.) results in fitness benefits for migrants by conducting two separate experiments on two spatial scales: at landscape and nest-site scale. The pied flycatcher (*Ficedula hypoleuca*) was our model species. Both titmice and pied flycatchers are cavity nesters and they feed mainly on arboreal arthropods captured using foliage gleaning and hovering behaviours (Lack 1966; Lundberg & Alatalo 1992; Mönkkönen *et al.* 1996). Therefore, titmice and flycatchers have overlapping resource needs. There is evidence further south suggesting that they compete (von Haartman 1957; Slagsvold 1975) and an ecologically similar species, the collared

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flycatcher (*F. albicollis*), has been shown to suffer severely from competition with titmice (Gustafsson 1987; Sasvári *et al.* 1987; Merilä & Wiggins 1995).

In the landscape scale, before the arrival of migrants, we manipulated the density of breeding titmice in forest patches by increasing their numbers or reducing their density to zero so that arriving flycatchers clearly faced two distinct conditions. In the nest-site scale, flycatchers were allowed to choose their nest-box either close (25 m) or farther away (100 m) from an active titmouse nest. We examined (i) the preference of breeding site selection of flycatchers in relation to the presence of titmice, and (ii) the fitness consequences of selection. On the basis of results of earlier experiments (Mönkkönen *et al.* 1990, 1997; Timonen *et al.* 1994; Forsman *et al.* 1998; see also Elmberg *et al.* 1997) and the predictions of a theoretical model (Mönkkönen *et al.* 1999), we predicted that the presence and proximity of titmice has positive effect on the breeding site selection and fitness of pied flycatchers.

2. METHODS

(a) Landscape scale experiment

The experiment was carried out in nine separate forest patches, 7–21 ha in size, in northern Finland (64°50' N, 24°30' E) during the spring and summer of 2000. The patches were homogeneous, dominated by young to middle-aged birch (*Betula* spp.) and surrounded by agricultural areas. Each patch was randomly assigned to two treatments: removal of titmice (*Parus major*, *P. caeruleus* and *P. montanus*) from three patches and the addition of titmice on six patches with an average density of 4.85 pairs per 10 ha (range 3.1–5.6 pairs per 10 ha). Density manipulation was carried out in March and April, before the arrival of pied flycatchers, and achieved densities prevailed through the whole breeding season.

Female flycatchers choose breeding territory on the basis of site characteristics rather than male characteristics (Alatalo *et al.* 1986). We controlled such effects by randomizing the location of nest-boxes within a patch and by keeping only two nest-boxes open in a day for arriving flycatcher males on each patch. New box(es) were opened only if either of the previous boxes had become occupied. All empty nest-boxes were removed simultaneously from all patches when the first flycatcher egg was observed to avoid secondary nests; polygyny is usual in pied flycatchers and males provide little or no parental care for secondary nests (Lundberg & Alatalo 1992). At the end of the settling process pied flycatcher densities did not vary between treatments ($t_7 = 0.563$, $p = 0.591$), indicating that there were no differential effects of intraspecific competition. Because of this equality of pied flycatcher densities in patches, no measurements of the effects of interactions on tits can be made. However, sometimes especially early arriving pied flycatchers may take over the nest boxes occupied by tits (J. T. Forsman, personal observation) suggesting that titmice may suffer (though rarely) competition with flycatchers.

(b) Nest-site scale experiment

The experiment was carried out in 1999 and 2000 in the same kind of homogeneous birch forests as the landscape scale experiment. There were two nest-boxes available for arriving pied flycatchers in relation to an occupied titmouse nest-box: box A was placed at a distance of 25 m from the titmouse nest and box B at a distance of 100 m. A sealed nest-box was placed 25 m from

box B to control the number of boxes in the neighbourhood of experimental boxes. Thus, there were two unoccupied boxes available in a similar environment, only differing in their proximity to a nesting titmouse.

(c) Measurements and analyses

Arrival dates of pied flycatchers were recorded daily at all patches in the landscape scale experiment, and twice a day in the nest-site scale experiment. Males were identified based on their coloration and on the size and shape of forehead patches (Lundberg & Alatalo 1992). Female arrival was determined either directly or when nest material was observed in the box. For each box we recorded the onset of egg laying, incubation and hatching. Measurements of wing (± 1 mm) and tarsus (± 0.05 mm) length as well as body mass (± 0.5 g with Pesola 30 g string weighing machine) of nestlings were taken 13 days after hatching. In analyses we used average values calculated for each brood. Arrival dates were compared using Mann–Whitney *U*-tests. We used a multivariate analysis of variance (MANOVA) as an *a priori* test (Scheiner 1993) to analyse differences in fitness components between the treatments. For the MANOVA the fitness components were divided into two groups, those describing the whole brood (clutch size, brood size at the age of 13 days, hatching date and survival proportion to the age of 13 days) and those describing the quality of nestlings (wing and tarsus length and body mass), and the test was performed in both groups separately. As the power of MANOVA decreases when the number of response variables increases (Scheiner 1993), we considered a 0.1 *p*-value for Pillai's trace statistic sufficient to proceed to separate *post hoc* tests (*t*-test) for each dependent variable. Based on the results of earlier experiments (Mönkkönen *et al.* 1990, 1997; Timonen *et al.* 1994; Forsman *et al.* 1998) and the predictions of a theoretical model (Mönkkönen *et al.* 1999), our predictions were clearly one-tailed and one-tailed *t*-tests were used for *post hoc* testing. In all analyses equality of variances was checked using Levene's test.

For the nest-site scale experiment a resampling procedure (Resampling Stats 1998) was performed to analyse nest-box preference. Choices were distributed randomly within nest-box arrangements 10 000 times, and the ratio of choices was recorded in each distribution. Dividing the number of ratios where preference was the same or more extreme than observed by 10 000, gives the probability that the observed distribution was achieved by a random process. The preference of females was assumed to be independent of the choices of males as females choose the nest site on the basis of territory quality and not male quality (Alatalo *et al.* 1986), and we observed several times that females forced males to change their primary choice. Differences in fitness components were analysed among those nest-box pairs where both A and B boxes were occupied by a pair of flycatchers ($n = 14$). We used MANOVA and one-tailed *post hoc t*-tests to analyse differences in fitness components between A and B boxes as in the landscape scale experiment. We used SPSS 10.1 software in all statistical analyses.

3. RESULTS

In the landscape-scale experiment, a total of 50 flycatcher pairs settled on the plots. During the settling period, flycatcher males tended to arrive earlier to patches where titmice numbers were increased than on patches where they were removed (1.7 days difference in mean arrival date: $U_{14,35} = 175.0$, one-tailed $p = 0.076$). For

Figure 1. Fitness parameters of the pied flycatcher broods in the addition (ADD) and removal (REM) treatment of resident titmice in the landscape scale experiment. *p*-values refer to the result of the *post hoc t*-test. The average ($\pm$ s.e.m.) (a) clutch size ($p = 0.134$); (b) hatching date measured from the start of the experiment ($p = 0.026$); (c) survival proportion to the age of 13 days ($p = 0.113$); and (d) number of nestlings at the age of 13 days in both treatments ($p = 0.025$).

females no significant difference was observed (difference 0.8 days: $U_{14,35} = 193.5$, one-tailed $p = 0.123$). However, the necessary randomization of nest sites severely limited settling opportunities, and these results thus are conservative. Out of the 50 settled pairs, seven deserted their nest before or during the egg laying and three broods were destroyed after hatching. In addition, during the nestling period we observed that several broods had only one of the parents present. To control that effect, we included in the analyses concerning fitness differences between treatments only those nests that had both parents taking care of the nestlings; in titmice addition areas there were 23 and in removal areas nine such nests. There were differences among variables describing the quality of broods between treatments (MANOVA, Pillai's trace = 0.266, $F_{4,27} = 2.44$, $p = 0.071$). Flycatcher broods hatched 1.7 days earlier (figure 1b) and had 0.6 more nestlings (figure 1d) in patches with titmice than without them. Differences in the clutch size (figure 1a) and survival proportion (figure 1c) were also parallel with our predictions but not statistically significant. Delayed hatching in titmice removal patches was due to delayed egg laying. The time-lag between female arrival and the onset of egg laying was constantly longer during the laying period in patches without breeding titmice (mean difference 1.69 days, $t_{30} = 2.68$, two-tailed $p = 0.012$). The quality of nestlings did not differ between treatments (Pillai's trace = 0.036, $F_{3,28} = 0.35$, $p = 0.790$).

In the nest-site scale experiment, pied flycatcher males and females both preferred the nest-box placed near the titmouse nest. Most males (25 of 36, $p = 0.004$) and females (23 of 35, $p = 0.046$) chose the nest-box close to

Figure 2. Fitness parameters of the pied flycatcher nestlings breeding either close (near) or farther away (far) from an active titmouse nest in the nest-site scale experiment. *p*-values refer to the result of the *post hoc t*-test. The average ($\pm$ s.e.m.) (a) body mass ($p = 0.046$); (b) wing length ($p = 0.034$); and (c) tarsus length of nestlings in both treatments ($p = 0.337$).

the titmouse nest. At this nest-site scale, the quality of flycatcher nestlings differed between treatments (MANOVA, Pillai's trace = 0.286, $F_{3,24} = 3.21$, $p = 0.041$). In the nest-boxes near titmice nests, nestlings were significantly heavier (average difference: 0.46 g) (figure 2a) and had significantly longer wings (average difference: 1.22 mm) (figure 2b) than nestlings in the more distant nest-boxes. The quality of broods did not differ between treatments (MANOVA, Pillai's trace = 0.061, $F_{4,23} = 3.71$, $p = 0.827$).

4. DISCUSSION

The results were in accordance with our predictions and demonstrated that the presence of resident titmice, putative competitors of the pied flycatcher, resulted in fitness benefits for pied flycatchers. First, pied flycatchers were attracted to the vicinity of titmice. Second, at the landscape scale, the mean brood size increased by 0.6 nestlings, an increment of 10.6% compared with the mean brood size on removal patches, while at the nest-site scale, flycatchers breeding in closer proximity of titmice had larger nestlings. In the absence of positive effect of interspecific interactions the opposite is expected: that the removal of titmice frees resources for flycatchers and hence results in higher reproductive success in the removal patches (see Gustafsson 1987). It is thus evident that heterospecific attraction has a strong selective basis.

Our results show that the presence of a putative competitor led to increased fitness of pied flycatchers on both spatial scales. This result was not due to habitat quality because of similar forest structure among forest patches and nest-sites: the main difference was the presence, absence or the proximity of titmice. In the nest-site scale

experiment the nest-box close to the titmouse nest might have been located on a better quality site than the nest box farther away as titmice were able to choose their nesting site. This, however, is unlikely due to the homogeneity of the habitat and the short distance between the nest boxes. The mechanism behind this process is unknown at this point, but our results indicate two possibilities. First, the presence of residents will provide faster resource assessing and acquisition for migrants. This was suggested by the result that flycatchers arrived slightly earlier to titmice addition plots and started egg laying earlier, which resulted in larger broods than for flycatchers in removal plots. Second, titmice may provide direct social benefits through aggregated dispersion, such as enhanced foraging success and reduced vigilance costs (Pulliam & Millikan 1982). This possibility was supported by the result that flycatchers nesting close to titmice nests had larger nestlings than birds breeding farther away, when there was no difference in the timing of breeding. Foraging benefits may also hasten females' endeavours to achieve laying condition, which would explain the result that flycatchers breeding with titmice were able to initiate egg laying earlier than flycatchers on removal areas.

These two possible explanations, enhanced resource acquisition leading to faster breeding patch selection and social benefits, are not mutually exclusive. Actually, differentially manifested fitness benefits on both spatial scales indicate that they act together. At the landscape scale, there were fitness differences between the treatments only in the variables describing the quality of broods, which were due to earlier onset of the breeding in addition plots. Differences in the fitness components in the quality of nestlings probably did not emerge because flycatcher nests in addition plots were randomly distributed and most of the nests were relatively far away from titmice nests, reducing the positive effect of social benefits. At the nest-site scale, the benefits from the presence of titmice for resource acquisition and breeding patch selection for arriving flycatchers were the same irrespective of which nest-box was chosen (near or farther away from titmice). Consequently, the onset of breeding did not differ between the box types and neither did the quality of broods. However, flycatchers breeding close to titmice had a possibility to constantly gain feeding and vigilance benefits throughout the whole breeding season, which could explain heavier nestlings compared with birds breeding farther away from the titmice. Thus, heterospecific attraction to residents may have cumulating, differentially expressed benefits to migrants on different spatial scales.

Gustafsson (1987) has carried out a similar experiment with the collared flycatcher further south, in Sweden, and his results conflicted with ours: higher resident bird densities resulted in lowered reproductive success for the collared flycatcher. However, these studies differed in two important aspects. Resident densities were 2–5 times higher in Sweden (up to 27 pairs per 10 ha) than in our study area (up to ca. 5 pairs per 10 ha), and his titmice removal was not complete, unlike in our study. Taken together, Gustafsson's and our results indicate that the direction and the result of interspecific interactions may change as a function of the density of putative competitor(s). At low density (when negative effects of coexistence presumably do not exceed the benefits) posi-

Figure 3. The change in the direction and result of interspecific interaction of species 2 with increasing density of potential competitor (species 1). At region A, where the density of species 1 is low, positive effects of the presence of species 1 prevail over negative and result in heterospecific attraction and increasing fitness of species 2. At high competitor densities (region C), negative effects of competition prevail, and species 2 suffers from the presence of species 1. Species 2 will reach its maximum fitness and/or density at the intermediate densities of species 1 (region B).

tive interactions prevail as shown in our study. With increasing density, the benefits of aggregated dispersion level off, and later interaction turns into competition, as shown by Gustafsson (1987). This scenario, presented in figure 3, resembles the Allee-effect (Allee *et al.* 1949) for a single population, where population growth or individual fitness reaches its peak at intermediate population density. At low density, mating success or communal protection against predators, for example, is drastically reduced while at high density intraspecific competition intensifies, both resulting in lowered fitness (Courchamp *et al.* 1999; Stephens & Sutherland 1999). We hypothesize that a similar pattern may arise in interspecific interactions: that individual fitness or the direction of interspecific interactions, everything else being equal, is a nonlinear, unimodal function of the density of putative competitor(s) (figure 3). With increasing competitor density the benefits from social aggregations become gradually outweighed by the negative effects of interspecific competition. This outline matches well with the theoretical examination of interspecific interactions (Mönkkönen *et al.* 1999), where attraction to heterospecifics is predicted to switch to avoidance if competition becomes too strong. It is, however, important to recognize the most important mechanism of interspecific interactions. If, for example, nest predation is the driving force in species coexistence (see Martin 1993), avoidance of or aggressions against individuals of different species sharing same nest-site preferences may always be beneficial (Martin & Martin 2001a,b).

Differences in geographical location and abiotic conditions may further explain and emphasize the qualitative difference between our and Gustafsson's results. Positive interspecific interactions have been suggested to prevail in stressful conditions (Bertness & Callaway 1994) and it has traditionally been supposed that due to environmental instability, northern breeding bird communities are not saturated (Järvinen 1979), and competition for resources

is therefore relaxed. This may produce a qualitative latitudinal gradient in the result of species interactions. In intertidal communities, it has indeed been shown that differences in abiotic conditions may cause changes in species interactions on a geographical scale (Leonard 2000). Variation in the nature and outcome of species interactions in relation to the density of heterospecifics and variation in abiotic conditions clearly call for more attention for better understanding the coexistence of species.

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