Mechanisms and fitness effects of interspecific information use between migrant and resident birds

Jukka T. Forsman, Robert L. Thomson, and Janne-Tuomas Seppänen

Department of Ecology and Evolution, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 d, SE-75236 Uppsala, Sweden and Department of Biology, University of Oulu, PO Box 3000, FI-90014 Oulu, Finland

Interactions with potential competitors are an important component of habitat quality. Due to the costs of coexistence with competitors, a breeding habitat selection strategy that avoids competitors is expected to be favored. However, many migratory birds appear to gain benefits from an attraction to the presence of resident birds, even though residents are assumed to be competitively dominant. Thus far the mechanisms of this habitat selection process, heterospecific attraction, are unknown, and the consequences for resident birds of migrant attraction remain untested. Through heterospecific attraction, migrants may gain benefits if the density or territory location of residents positively reflects habitat quality, and/or they gain benefits through increased frequency of social interactions with residents in foraging or predator detection. In this experiment, we examined the reciprocal effects of spatial proximity on fitness-related traits in migrant pied flycatcher (Ficedula hypoleuca) and resident great tit (Parus major) by experimentally forcing them to breed either alone or in close proximity to each other. Surprisingly, great tits bore all the costs of coexistence while flycatchers were unaffected, even gaining slight benefits. In concert with an earlier study, these results suggest that flycatchers use tits as information about good-quality nest-site locations while benefits from social interactions with tits are possible but less important. We suggest that utilizing interspecific social information may be a common phenomenon between species sharing similar resource needs. Our results imply that the effects of interspecific information use can be asymmetric and may therefore have implications for the patterns and consequences of species coexistence. Key words: cavity nesting birds, habitat selection, interspecific competition, nest-site selection, resident and migrant birds, social information, species interactions. [Behav Ecol 18:888–894 (2007)]

One of the most important factors affecting the fitness of organisms is the choice of environment for reproduction. Choices are complicated by variation in habitat quality with respect to various biotic and abiotic conditions, such as food resource levels, abiotic conditions at the microhabitat level, and the risk of predation that affects the reproductive success of individuals (Robinson et al. 1995; Sinervo and DeNardo 1996; Forsman, Mönkkönen, Helle, and Inkeröinen 1998; Martin 2001; Thomson, Forsman, Mönkkönen, et al. 2006; Thomson, Forsman, Sardá-Palomera, and Mönkkönen 2006). Potential competitors are another important component of habitat quality. Coexistence with competitors usually results in fitness costs that can be due to direct interactions such as resource competition (e.g., Brown and Davidson 1977; Gustafsson 1987; Wedin and Tilman 1993; Martin PR and Martin TE 2001a) or indirect interactions mediated by shared predators or parasites (apparent competition, Holt 1977; e.g., Martin 1995; Holt and Lawton 1994; Martin PR and Martin TE 2001a). Consequently, avoidance of potential competitors is expected to be the best strategy in breeding habitat selection (see Martin PR and Martin TE 2001a, 2001b).

Sometimes, however, animals are paradoxically attracted to the presence of potential competitors. Studies conducted in northern forest bird communities show that later arriving passerine migrant birds use the presence or density of earlier established resident tit species as a cue for habitat quality and are attracted to them (for a review, see Mönkkönen and Forsman 2002). This habitat selection process was coined heterospecific attraction by Mönkkönen et al. (1990). Residents are present year round, initiate breeding before the arrival of most migrants, and have ample time to assess the quality of habitats. Therefore, their presence or relative density in the landscape can be assumed to reflect habitat quality through direct (habitat selection) or indirect (habitat-dependent mortality in winter) processes. Quick habitat selection is important for migrants because their breeding success rapidly declines with delayed onset of breeding (Klomp 1970). Experiments to date show that augmented resident titmouse densities yield increased species number and density of migrant birds (Mönkkönen et al. 1990, 1997; Forsman, Mönkkönen, Helle, and Inkeröinen 1998; Thomson et al. 2003; see also Elmberg et al. 1997). In addition, pied flycatchers (Ficedula hypoleuca), potential competitors with resident tits (Parus spp.) (Haartman von 1957; Slagsvold 1975; see also Gustafsson 1987), prefer tit proximity in breeding site selection and gain fitness benefits in terms of a higher number and condition of nestlings (Forsman et al. 2002).

The ultimate mechanism of heterospecific attraction remains unknown. Migrants are suggested to benefit through hastened and more accurate breeding habitat selection if the density or territory location of tits indicate high-quality habitats or nest sites (Forsman et al. 2002; Mönkkönen and...
The fitness benefits of heterospecific attraction reported before them and to assess whether social interactions contribute to sequences of heterospecific proximity in both the migrant and resident tits (Gustafsson 1987). However, these flycatchers may also have negative impacts on residents (Sasvári et al. 1987). Mutually positive interactions between organisms on the same trophic level exist in certain environmental conditions in plant and sessile animal assemblages (Bertness and Callaway 1994; Bruno et al. 2003), but examples among mobile vertebrates are much sparser (but see Dickman 1992, ungulates).

In this study, we examine the reciprocal fitness-related consequences of heterospecific attraction to tits as a result, been assumed to be either neutral (commensal interaction) or positive (mutualistic interaction). Crucially, however, this assumption has not been explicitly experimentally examined.

Experimental evidence suggests that migratory collared flycatchers (*Ficedula albicollis*) suffer from competition with resident tits (Gustafsson 1987). However, these flycatchers may also have negative impacts on residents (Sasvári et al. 1987).

We experimentally forced pied flycatchers and great tits (*Parus major*) to breed either alone or in close proximity to each other at random locations and tested whether this results in mutualistic (both benefit), commensal (one benefit and other is unaffected), competitive (both suffer), or even parasitic (one benefit and other suffers) interactions. In addition, by comparing the results of this study with those of Forsman et al. (2002), we are able to distinguish between mechanisms behind the positive fitness consequences of heterospecific attraction to migrants. As residents in that study were free to choose their nest sites, the improved performance of attracted migrants can be explained by microhabitat quality, quicker onset of, and social benefits during breeding. Here, our experimental design removed the effects of nest-site location and quality on breeding success, which has rarely been done in the wild. Therefore, if flycatchers breeding in proximity to tits do not exhibit improved reproductive output compared with flycatchers breeding alone, the benefits found in Forsman et al. (2002) did not result from social benefits but mainly through microhabitat quality and quicker onset of breeding. If, however, improved reproductive output occurs here also, social benefits from breeding in association with tits also play a significant role.

METHODS

The experiment consisted of 3 treatments: 1) great tits and pied flycatchers breeding alone (>120 m to the nearest conspecific or heterospecific neighbor) and 3) flycatchers and tits breeding as neighbors (nest boxes 20 m apart). These distances were believed to result in a spatial arrangement of nest boxes that is free from plot-scale effects of conspecific and heterospecific density that affect individual success and yet bring about potential positive or negative effects of the heterospecific proximity at the nest-site scale (see Forsman et al. 2002). All initiated tit nests within the study plots were assigned to treatments in spring. Instead of a fully randomized design, we randomly assigned a treatment to every second nest to avoid accumulation of any treatment in some plots due to chance. When the first nest box became occupied by a great tit (hair in the box), it was randomly assigned a treatment to either breed “alone” or “with neighbor.” The next occupied box within the same area was then assigned to the other treatment; the following occupied box was again randomly assigned and so forth. To control for effects of nesting site quality, tit boxes were gradually (over 5 days) moved ~50 m in a random direction during egg laying. Despite our study sites appearing homogeneous from a human perspective, it is likely to the small-scale spatial variation or microhabitat differences especially in microclimatic factors (Horvath 1964; Walsberg 1985) exist. From the bird’s perspective, altering nest-site location by ~50 m should effectively control for the habitat quality in the vicinity of nests.

Individual site choice of flycatchers was also randomized. We placed 3–4 empty nest boxes, 40 m apart, at a distance of 70 m from great tit nests assigned to the “neighbor” treatment. By that time, most great tit nests were already relocated and free from individual choice as far as it is possible in these species and that all pairs went through similar moving manipulation. Adult birds were not caught but, the experimental procedure should control for any effects of adult phenotypic variation on response variables. Experimental procedures were approved by the ethical committee of the University in question and by the North Ostrobothnia Regional Environment Centre.

We monitored the date of first egg, clutch size, start of incubation, hatching date, and the number and the condition (body mass, length of tarsus, and wing) of nestlings when the oldest chicks were 13 days of age. We used a digital balance (accuracy ± 0.1 g) for body mass measurements, callipers for tarsus (±0.02 mm), and ruler (±1 mm) for wing and tail measurements. In 2003, all the measurements were done by J.T.F. and in other years by R.L.T. Nestling condition measurements were averaged within a brood, and these fitness-related measures were used as the treatment response variables. In the analyses of nestling number, condition, and survival, we used only those broods that had at least one nestling at the age of 15 days. The effect of treatments on response variables

Forsman 2002). Proximity to tits might also yield enhanced predator detection or foraging efficiency via social interactions (Mönkkönen et al. 1996; Forsman, Mönkkönen, Hele, and Kermo 1998; Forsman and Mönkkönen 2002; Saino and Krama 2002). Also unknown are the consequences to resident tits that stem from migrants using heterospecific attraction as a habitat selection strategy. Owing to resident tits’ larger body size and prior occupation of resources, they have traditionally been regarded as dominant competitors over migrants (MacArthur 1972; Herrera 1978). The effect of heterospecific attraction to tits has, as a result, been assumed to be either neutral (commensal interaction) or positive (mutualistic interaction). Crucially, however, this assumption has not been explicitly experimentally examined.

Experimental evidence suggests that migratory collared flycatchers (*Ficedula albicollis*) suffer from competition with resident tits (Gustafsson 1987). However, these flycatchers may also have negative impacts on residents (Sasvári et al. 1987).
RESULTS

Number of nests, timing, and clutch size

A total of 51 great tit nests were included in the analyses across the 3 study years (12 + 11 + 28), out of which 27 were breeding with a neighbor and 24 alone. For flycatchers, the 56 nests in 3 study years (16 + 12 + 28) were equally assigned to each treatment (28 nests each). Great tits tolerated the moving of their nest boxes less well than pied flycatchers. In general, great tits are more sensitive to disturbance prior to the nesting period than flycatchers. About 25% (n = 20) of the initial experimental tit broods failed to produce offspring. Failures were partly due to nest predation (8%) and aggressive takeovers by pied flycatchers (Slagsvold 1975) but also probably due to the experimental procedure. Of the failed tit nests, excluding depredated nests, 45% and 55% were in the neighbor and alone treatments, respectively, suggesting that the treatment did not affect the probability of abandonment. The actual number of aggressive pied flycatcher takeovers of tit nests is difficult to estimate because flycatchers may swiftly occupy abandoned tit nests, which afterwards resembles a takeover. Nevertheless, pied flycatchers are able to takeover tit nests, usually before tits have started incubation (Forsman JT, Thomson RL, Seppänen JT, personal observation). Adverse weather also caused tit brood failures, especially in 2004, when there was a long cold spell in May when many tits were feeding nestlings. Of the initial pied flycatcher nests, about 3% were depredated and ~9% abandoned.

There were no differences between treatments in the average onset of egg laying, clutch size, and hatching date (results not shown in detail) in either great tit or pied flycatcher broods. This suggests that, as planned, manipulations did not affect the initial investment in offspring, and any differences between treatments likely occurred after hatching. On average, great tits began egg laying on 13 May, laid 10 eggs, and hatched on 7 June. The average onset of egg laying in pied flycatchers took place on 26 May; they laid 6.5 eggs that hatched on 15 June.

Number, survival, and body mass of nestlings

In the great tit, treatment effects on the number of nestlings and their average body mass differed in 2004 compared with 2003 and 2005 (see Figure 1 for the qualitatively different treatment effects). We therefore analyzed data from 2004 separately. In 2004, the treatment term remained in the final model for the number of tit nestlings at 13 days. Indeed, great tits breeding with flycatchers produced 3.5 nestlings less (52%) than tits breeding alone (F_{1,10} = 7.29, P = 0.022, R^2 = 42.5%; AIC of the model −23.16 vs. −4.47 for the second best model including date of the first egg) (Figure 1a). However, treatment did not significantly affect nesting body mass in 2004 (Figure 1b). This is largely due to the low number of great tit chicks in nests breeding in association with flycatchers (less sibling competition). Furthermore, in 2004, the survival of tit nestlings from hatching to 13 days old in the neighbor treatment was considerably lower (40.4%) than in the alone treatment (80.5%) (treatment: effect [standard error] = −1.75 [0.58], Wald = 9.03, degrees of freedom [df] = 1, P = 0.003; AIC of the model −5.77 vs. −4.01 for the second best model including the onset of egg laying). In 2003 and 2005, treatment effects on great tit nesting number and mass were parallel. Tits breeding alone in 2003 produced 0.34 nestlings more that were 1.66 g heavier than those of tits breeding with flycatchers, whereas the corresponding numbers in 2005 were 0.21 chicks and 1.54 g, respectively. We therefore pooled the great tit data from years 2003 and 2005. Treatment did not affect great tit nesting number (F_{3,35} = 0.094, P = 0.762) (Figure 1c), but nesting body mass was 1.55 g lower (8.8%) when breeding with flycatchers than when breeding alone (the final model included only treatment; F_{1,34} = 4.66, P = 0.038, R^2 = 12.0%; AIC of the model −81.91 vs. −80.02 for the second best model including clutch size) (Figure 1d). In 2003 and 2005, tit nestling survival from hatching to 13 days differed, but treatment effects were parallel, and the data was again pooled. In 2003, nesting survival in the neighbor and alone treatments was 66.2% and 68.5% and in 2005 87.3% and 93.7%, respectively. Treatment did not have a significant effect on the survival of tit nestlings (treatment: effect [SE] = −0.40 [0.50], Wald = 0.65, df = 1, P = 0.420).

In the pied flycatcher, treatment effects did not differ between years (see Figure 1). However, to compare the effects of treatments with those of the great tit, data on nesting number and their body mass from 2003 to 2005 were pooled and 2004 was analyzed separately. In contrast to the great tit, treatment had no significant effect on nesting number, body mass (Figure 1a–d), or survival (average survival across all years in the neighbor = 95.08% and alone = 95.73% treatments) of flycatcher nestlings.

Nestling wing length

Treatment also had qualitatively different between-year effects on nestling wing length, and these data were analyzed separately. In the great tit, 2003 differed from the other years; tit nestlings raised in the neighbor treatment had 12.4% shorter wings than those in the alone treatment (the final model included only treatment: F_{1,10} = 5.63, P = 0.039, R^2 = 36.0%; Figure 2a) (AIC of the model −24.89 vs. −20.47 for the second best model including clutch size), whereas in 2004 and 2005, there was no treatment effect. In the pied flycatcher, 2005 was different from the other years; after accounting for the effect of onset of egg laying, flycatcher nestlings raised in
the neighbor treatment had 1.8 mm (3.4%) longer wings than those in the alone treatment (model $R^2 = 36.8\%$; treatment: $F_{1,23} = 5.53$, $P = 0.044$; onset of egg laying: $F_{1,23} = 7.44$, $P = 0.012$; Figure 2a) (AIC of the model $-84.65$ vs. $-81.56$ for the second best model including clutch size). In 2003 and 2004, there was no difference in nestling wing lengths between treatments.

Nestling tarsus length

In the great tit, nestling tarsus length was pooled across study years. There was a strong effect of year on tarsus length ($F_{2,42} = 65.26$, $P < 0.0001$), but treatment effects were parallel among years. After accounting for year effect, treatments had no effect on tarsus length of great tit nestlings ($F_{1,42} = 1.85$, $P = 0.181$; Figure 2b). In the pied flycatcher, treatment did not affect the tarsus lengths of nestlings in 2003. However, in 2004 and 2005, treatment effects were qualitatively different. In these years, flycatcher nestlings raised in proximity to tits had 0.33 mm (more than 4 times the standard error of the mean; 0.076 mm) longer tarsus than those breeding alone ($F_{1,33} = 9.36$, $P = 0.004$, $R^2 = 22.1\%$; Figure 2b) (AIC of the model $-141.73$ vs. $-139.18$ for the second best model including clutch size).

DISCUSSION

In recent years, there has been increasing interest in understanding how animals gather information from other individuals...
and use it in decision making (termed social information, for reviews, see Valone and Templeton 2002; Danchin et al. 2004). Most studies exploring social information use are constrained to a within-species context (but see Coolen et al. 2003; Parejo et al. 2005). Our results reported here, in concert with earlier studies (Mönkkönen et al. 1990, 1997; Forsman, Mönkkönen, Helle, and Inkeröinen 1998; Forsman et al. 2002; Thomson et al. 2003), emphasize that the presence of an individual conveys information about the quality of the site to individuals of other species with some ecological overlap. Such interspecific information use has earlier went largely unnoticed but is probably common in nature (for review, see Seppänen et al. 2007) and also seems to be adaptive (Forsman et al. 2002).

Consequences for flycatchers

In an earlier experiment, we showed that pied flycatchers preferred the presence and close proximity of tits in breeding habitat selection and gained fitness benefits (more and heavier nestlings with longer wings) as a result (Forsman et al. 2002). In the present study, flycatchers breeding together with titmice had nestlings somewhat larger (longer tarsus) than flycatchers breeding alone. However, the positive effects of living with tits occurred in only some years and were not as strong as observed in Forsman et al. (2002). For example, in Forsman et al. (2002), the average body mass of flycatcher nestlings breeding with tits was 0.46 g (3.2%) heavier than in flycatchers breeding alone, whereas in the present study, flycatcher chicks in the neighbor treatment were 0.20 g (1.4%) lighter than those reared in the alone treatment (difference not statistically significant). Also, the positive effect on the wing length of nestlings was only observed in one year. In this study, the positive effect of tit proximity on the wing length compared with breeding alone was about the same as in the earlier study (1.8 mm [3.5%] and 1.2 mm [2.3%], respectively). Positive effects on nestling tarsus length were somewhat stronger in this study than in the earlier (0.35 mm [1.9%] and 0.07 mm [0.3%, not statistically significant], respectively).

Importantly, unlike in Forsman et al. (2002), this study manipulated great tit and pied flycatcher nest-site selection to a random location 50 m away, which should control for the habitat quality in the vicinity of the nest for both species (Haartman von 1956; Naef-Daenzer 2000). This suggests that the increased flycatcher reproductive success in Forsman et al. (2002) mainly resulted from the quicker decision making and enhanced likelihood of finding high-quality microhabitats through heterospecific attraction, although social factors may also have some contribution (see below). Resident birds have time to assess the quality of sites and settle at the best sites. It is therefore very likely that a site occupied by a tit is of a higher quality than a randomly chosen site. By settling in close proximity to a tit nest, flycatchers are assured of a good breeding site while simultaneously saving much of the time and energy required to search for a nest site. This suggests that flycatchers may also have some contribution (see below).

Social interactions with tits may also be of importance because in some years flycatchers gained benefits from breeding in proximity to tits. Flycatchers may gain benefits through mechanisms similar to those operating in conspecific (Morse 1970) or in heterospecific (Savari 1992; Dolby and Grubb 1998) aggregations, that is, enhanced foraging success and/or predator protection. Many other migrants aggregate with resident birds during the breeding period, and both foraging benefits (Mönkkönen et al. 1996) and predator protection (Forsman, Mönkkönen, Inkeröinen, and Reunanen 1998; Forsman and Mönkkönen 2001) have been suggested. Occurrence of social interactions may have been hindered by our experimental design that kept population densities of tits and flycatchers relatively low. Benefits of social interactions may become more apparent at moderate population densities when some minimum group size for foraging, for example, can be reached. The ultimate mechanism of heterospecific attraction may thus be both acquisition of good-quality breeding sites and benefits via social interactions with heterospecifcs.

Consequences for tits

The results of this study suggest that, surprisingly, resident great tits seem to be the suffering party in the interaction resulting from the process of heterospecific attraction. Depending on the year, great tits breeding with pied flycatchers produced fewer nestlings of poorer condition than solitary breeding tits. Even though the splitting of data due to among-year variation resulted in moderate sample sizes for some analyses, in general, flycatchers negatively affected the condition traits of tit nestlings, potentially decreasing their survival probability after fledging and future reproductive potential (Lindström 1999). Although all breeding pairs were treated equally (see methods), this result must be interpreted with care. Great tits are sensitive to disturbance prior to hatching, and moving boxes to random locations may have caused stress, which, coupled with presence of flycatcher in the neighbor treatment, may have unduly exacerbated differences between procedural effects of treatments. Savari et al. (1997), however, found correlative evidence of asymmetric interactions between tits and flycatchers; collared flycatchers negatively affected the breeding success of great tits, whereas the impact of tits on flycatchers was less clear. This suggests that our observed treatment effects in great tits are probably real and not confounded by the experimental procedure. In contrast, flycatchers breeding in proximity to tits were not affected negatively in any year and in some years benefited especially in terms of longer tarsus of nestlings, which is positively associated with survival and future breeding habitat quality (Lindén et al. 1992; Lindström 1999).

The nature of interactions between tits and flycatchers

How should we then categorize the interaction between flycatchers and great tits? The consequences of interspecific competition can be asymmetric but usually result in costs for all involved parties (e.g., Martin PR and Martin TE 2001a). Using long-term breeding data, Savari et al. (1987) found that hatching success and the number of fledglings in the great tit were negatively correlated with the density of collared flycatchers, a close relative of the pied flycatcher, whereas effects of tits on flycatchers were less clear and apparent only at highest tit densities. This suggests that our results may suggest a mixed strategy of both tits and flycatchers to take over their nest cavities (Slagsvold 1975; Savari et al. 1987;
Forsman JT, Thomson RL, Seppänens J-T, personal observation. The interactions between flycatchers and tits are therefore complex and do not seem to entail costs for both species in all conditions (see also Mönkkönen et al. 2004). This and other studies (Gustafsson 1987; Sassavari et al. 1987) suggest that the net result of interactions may depend on the population density of species and the scale of measurements. Because flycatchers lag 10–14 days behind tits in breeding, the tits’ peak in food consumption overlaps with late incubation and early hatching period of flycatchers, which is when their need for food increases. The exploitative competition by tits on flycatchers seems to outweigh the benefits only at moderate tit densities upwards (Gustafsson 1987; Sassavari et al. 1987), so that the net effect for flycatchers at low tit density and close proximity remains positive (Forsman et al. 2002; this study). Flycatchers in turn seem to affect tits via interference competition so that the proximity of a single flycatcher neighbor is influential even at low population densities (this study). Thus, the interactions between flycatchers and tits may vary depending on the local conditions. At low tit densities or at the nest-site scale, interactions resemble exploitation where pied flycatchers use tits in breeding site selection and gain benefits while tits seem to suffer. At higher tit densities and at the population level, interaction resembles more interspecific competition in which all parties suffer. Collared flycatchers indeed seem to take the effects of population densities of tits into account in breeding habitat selection because habitats with intermediate tit densities are preferred over high densities (Forsman JT, Hjernquist MB, Taipale J, Gustafsson L, unpublished data). There is also some evidence from other birds that later arriving species use the presence of the earlier established species in their breeding site selection (Slagsvold 1980; Groom 1992; see also Martin PR and Martin TE 2001b), the net result of which may be positive for the later arriving birds but can conceivably be negative for the earlier established bird via direct or apparent competition (see Martin PR and Martin TE 2001a,b).

To conclude, the results of this study highlight the importance of information transfer between individuals of different species regarding shared resources. Such a mechanism can clearly influence the patterns and consequences of species coexistence and should perhaps be incorporated in models attempting to explain it.

FUNDING

Academy of Finland (project no. 202388 to J.T.F.), European Commission (Marie Curie Intra-European Fellowship, project MEIF-CT-2003-500554 to J.T.F.), and Ella and Georg Ehrnrooth Foundation and Oulun Yliopistokunnan tukiäätiö (R.I.T.).

We thank L. Gustafsson, M. Mönkkönen, and 2 anonymous reviewers for comments on the earlier drafts of this paper.

REFERENCES


Forsman JT, Thomson RL, Seppänen J-T, personal observation. The interactions between flycatchers and tits are there-


