

Presence of other species may counter seasonal decline in breeding success: a field experiment with pied flycatchers *Ficedula hypoleuca*

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Seasonal decline in breeding success limits fitness in many bird species nesting in the temperate, boreal and arctic zones. Factors affecting this decline, especially if the decline is reduced, can thus have significant ecological and evolutionary importance. In an experiment designed to investigate fitness consequences of heterospecific attraction, no seasonal decline in breeding success was observed for pied flycatchers *Ficedula hypoleuca* breeding in the presence of resident titmice *Parus* spp., whereas a pattern of steep decline was observed for birds breeding in areas where residents were removed. Randomisation of removal treatment and pied flycatcher territories with respect to arrival date leaves enhanced foraging that results from the presence of resident titmice during breeding as the best, albeit currently hypothetical, explanation for the observed absence of a seasonal decline. Among terrestrial vertebrates, reports of this kind of direct positive interactions are rare.

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Seasonal decline in breeding success is a widespread phenomenon in bird reproduction (Klomp 1970, Perrins 1970, Crick et al. 1993, Smith and Moore 2005), affecting fitness similarly for most temperate, boreal and arctic species, and is therefore of considerable ecological and evolutionary importance. Mechanisms suggested to explain this include the 'date' and 'quality' hypotheses (Korpimäki and Wiehn 1998, Hansson et al. 2000, Christians et al. 2001, Wardrop and Ydenberg 2003). The 'date' hypothesis postulates that the observed seasonal decline in breeding success results from environmental constraints that increase as the breeding season progresses (Verboven and Verhulst 1996, Brinkhof and Cave 1997, Siikamäki 1998, Sanz 1999). In contrast, the 'quality' hypothesis proposes that the seasonal decline emerges from the lower intrinsic quality of late breeders (e.g. Hipfner et al. 1999). In one well-studied species, the pied flycatcher *Ficedula hypoleuca*, the steep decline pattern is shown to result from

increasing energy constraints throughout the season, consistent with the 'date' hypothesis (Lundberg and Alatalo 1992, Siikamäki 1998, Hemborg 1999).

Thus far the seasonal decline in breeding success has been treated as a within-species phenomenon, detached from the context of other coexisting species. The presence of other species, however, may affect the manifestation of a decline if the result of the interspecific interaction affects the proximate mechanism(s) behind the phenomenon. Interactions with heterospecifics may bring advantages compared to interactions with conspecifics, such as resource facilitation or more diverse food and foraging habitat selection and predator detection while the resource overlap might be smaller (Dickman 1992). While positive interspecific interactions in sessile plant and coral communities are better understood (Stachowicz 2001), positive interactions in terrestrial vertebrate communities still lack the level of attention called for by Dickman (1992) 10 years ago.

One example documented to occur and leading to fitness benefits is heterospecific attraction. Migrant passerines at northern latitudes have been shown to be attracted to (Mönkkönen et al. 1990, 1997, Timonen et al. 1994, Forsman et al. 1998) and derive fitness benefits from breeding associations with resident titmice *Parus* spp. (Forsman et al. 2002). This is likely due to a sooner onset of breeding caused by using resident presence as a cue for finding good breeding patches (Mönkkönen et al. 1999), and possibly also due to direct benefits of interspecific aggregation (Forsman et al. 2002).

Birds have the cognitive capability to observe conspecifics in order to facilitate breeding decisions (Lundberg and Alatalo 1992, Danchin et al. 1998, Doligez et al. 1999, 2002, Frederiksen and Bregnballe 2001), and foraging (Templeton and Giraldeau 1996, Heinrich and Pepper 1998, Smith et al. 1999, Marchetti and Drent 2000, Emery and Clayton 2001, Sonerud et al. 2001). Conceivably these capabilities could be transferred to extract information from heterospecifics too, and interspecific aggregations might well lead to enhanced foraging through reduced vigilance costs or copying foraging choices of knowledgeable neighbours (Slagsvold 1980, Barnard and Thompson 1985, Clergeau 1990, Møller 1992, Mönkkönen et al. 1996, Forsman and Mönkkönen 2001). In northern breeding areas resident titmice and the pied flycatcher have similar ecological requirements, with slightly differing foraging techniques (Lack 1966, Lundberg and Alatalo 1992). Compared to migrant conspecifics, residents are likely to be more knowledgeable of food and shelter distribution, and better adapted to local predator behaviour.

If interspecific competition is relatively weak despite similar feeding ecology (due to, for example, ephemerally superabundant resources, or populations being limited by predators or weather; Forsman and Mönkkönen 2003), the above suggests that breeding success of birds nesting in close association with heterospecifics should decline less as the breeding season progresses than of birds breeding with conspecifics or alone, if the decline results from an energy constraint and interspecific aggregation leads to enhanced foraging. To explore this possibility, we compared the seasonal decline in breeding success between pied flycatchers breeding either in the presence or absence of resident titmice, in an experimental setting where territory or parent quality were unlikely to explain differences. Other results from this experiment regarding the fitness consequences of heterospecific attraction are published elsewhere (Forsman et al. 2002).

Methods

The study was conducted in 2000 on nine separate forest patches in coastal lowland agricultural landscape south

of the town Oulu, Finland (N 64°50', E 24°30'). Patches ranged from 7 to 21 ha in size with relatively homogeneous vegetation of middle-aged birch *Betula* spp. and sparse distribution of large aspen *Populus tremula*, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* trees. Resident titmice were attracted to all patches by providing food (fat and sunflower seeds) and a surplus of nest boxes for overnight shelter throughout the winter. Thus, pre-removal conditions were the same at all patches.

We assigned the patches into three blocks based on size and forest age, and one patch was drawn randomly from each block for removal treatment. From March onwards, all resident titmice (*Parus major*, *P. caeruleus* and *P. montanus*) were removed from these patches by daily mist-netting and by sealing the nest boxes. Removal was total and was completed before the arrival of pied flycatchers. At the rest of the patches, hereafter "titmice presence" patches, titmice were allowed to establish breeding normally (average density 0.49 pairs/ha), after which we sealed the remaining vacant boxes before the arrival of the first migrants. Resulting titmice density in titmice presence patches was elevated or roughly equal compared to the previous year (cf. 'addition treatment' in Forsman et al. 2002).

Nest box locations for pied flycatchers were assigned randomly to intersections of a 50 × 50 m grid on the patch, and were at least 25 m from the patch edge or titmice nest. Initially all these boxes were sealed. As the settling phase of the experiment began on May 8th, two random boxes were opened at all patches. From then on we visited the patches daily, opening one or two random boxes if vacant boxes had become occupied, always leaving two vacant boxes (min. 100 m apart) available. We terminated the settling and sealed the remaining vacant boxes at all patches fourteen days later, when the first flycatcher egg was observed. The purpose of the above procedure was to randomise territory locations within the patch and between the males, in order to reduce the correlations between male quality, arrival date and territory quality. It also resulted in pied flycatcher densities that did not differ significantly between treatments at the end of settling phase (Removal: average 0.39 pairs/ha, Presence: average 0.44 pairs/ha), thus avoiding differential effects of conspecific density. As pied flycatcher females choose mates (Alatalo et al. 1986) and adjust their clutches (Siikamäki 1995) based on territory quality instead of male quality, male quality was unlikely to affect clutch size. Settling was terminated on the appearance of the first egg to avoid including secondary nests in the experiment as most flycatcher males attempt to pair with a secondary female after laying (Lundberg and Alatalo 1992).

A total of 45 females and 41 males were aged as either young (second calendar year) or older by estimating the

coloration and wear of the outermost greater wing coverts (Lundberg and Alatalo 1992, Jenni and Winkler 1994). Early in the breeding season experienced observers can achieve 90% accuracy with this method (Lundberg and Alatalo 1992). However, as our estimation was done at the end of the nestling period and without extensive previous experience in ageing, accuracy may be lower here. We determined laying and hatching dates by daily visits to each box. Offspring were measured 13 days after hatching, measuring body mass ($\pm 0.5\text{g}$), wing length ($\pm 1\text{mm}$) and tarsus length ($\pm 0.05\text{mm}$).

Broods surviving to 13 days of age with both parents present were included in the analysis. Thus, out of 36 pairs that laid clutches in the six presence patches, 23 (64%) were included, and out of 14 pairs in the three removal patches, 9 (64%) were included. In the statistical analysis we used ANOVA with tit density treatment as a fixed factor and patches (within treatments) as a nested random factor. We used nested design in order to account statistically for the effect of a common external factor, i.e. the patch, on pairs breeding within the same patch (Scheiner 2001). To test for the difference in seasonal effect on clutch and brood sizes between treatments we included laying date (for clutches) or hatching date (for broods) as a covariant in the ANOVA. If the interaction term between treatment and date is statistically significant, then the null hypothesis of similar decline pattern in both treatments is rejected. A similar analysis was performed for decline in offspring quality, measured as offspring size. Measures were averaged over brood and reduced to one composite measure, describing offspring size with principal component analysis. Conceivably brood size can affect the size of individual offspring. We therefore added brood size to the ANOVA model as a covariant to remove its effect on offspring size, and then examined the interaction between treatment and hatching date as above. Again, a significant interaction term would suggest different effects of time between treatments. Equalities of error variances were checked with Levene's test (Levene 1960). We also initially entered parent ages as covariates into the models, but because their effects were not statistically significant these variables were removed from the final models.

Results

The observed overall proportion of young birds was 67%. The frequency of young birds was slightly higher in the removal treatment than in the presence treatment, especially for females (Fig. 1). However, the frequency differences between treatments are not statistically significant (Fisher's Exact Test, males: $P = 0.494$, females: $P = 0.094$).

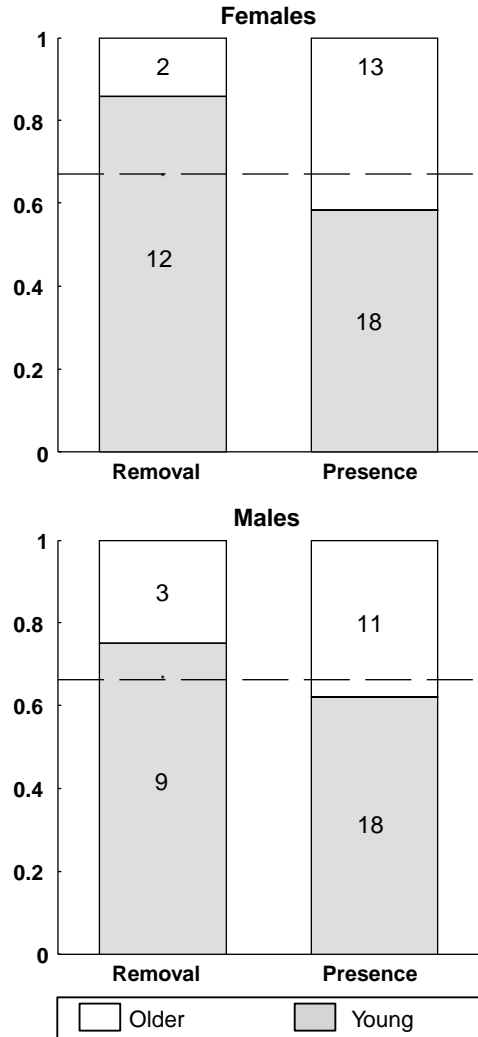


Fig. 1. Proportions of young (second calendar year) and older pied flycatchers in the two treatments. Dashed lines represent the observed total proportions of young birds (0.67 of females, 0.66 of males). Actual numbers of individuals are shown on the bars.

Proportion of breeding attempts not included (single parents and failures) in the analysis did not differ between treatments (36% in both cases), nor did the laying dates (Mann-Whitney $U_{5,13} = 31.5$, $P = 0.920$).

Variation in clutch size was not explained by interaction between treatment and laying date ($df = 1$, $MS = 0.265$, $F = 0.6$, $P = 0.447$), nor by laying date alone ($df = 1$, $MS = 0.003$, $F = 0.007$, $P = 0.993$), thus indicating no effect of laying date on clutch size. Brood size declined steeply as a function of hatching date in the removal treatment (Fig. 2). In contrast, no decline was observed in the presence treatment, resulting in a significant interaction between treatment and hatching date ($df = 1$, $MS = 2.635$, $F = 7.458$, $P = 0.013$).

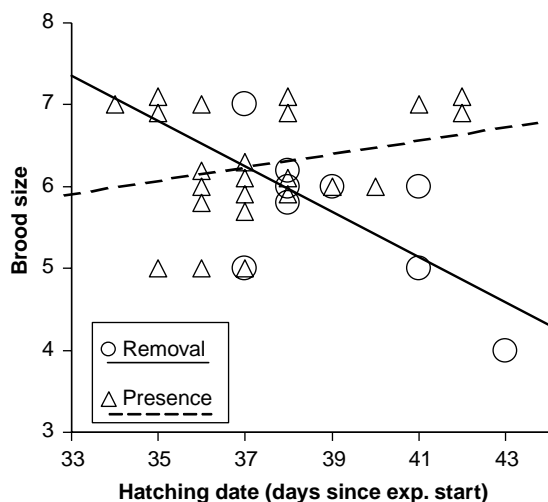


Fig. 2. The effect of hatching date on brood size in different treatments. A strong seasonal decline is evident in the removal treatment, whereas the relationship is slightly positive in the presence treatment. Multiple values at the same point have been slightly displaced vertically for presentation.

The principal component analysis extracted one factor (eigenvalue = 1.786, explaining 59.5% of the total variance), correlating strongly with all three offspring size measures (wing length: 0.609, tarsus length: 0.924, body mass: 0.748). We thus interpreted the factor as representing offspring size. Although the seasonal decline in the removal treatment appears steeper compared to that in the presence treatment (Fig. 3), the interaction term was not statistically significant ($df = 1$, $MS = 1.778$, $F = 2.357$, $P = 0.140$). The effect of overall hatching date was a statistical borderline case ($df = 1$, $MS = 3.08$, $F = 4.083$, $P = 0.057$).

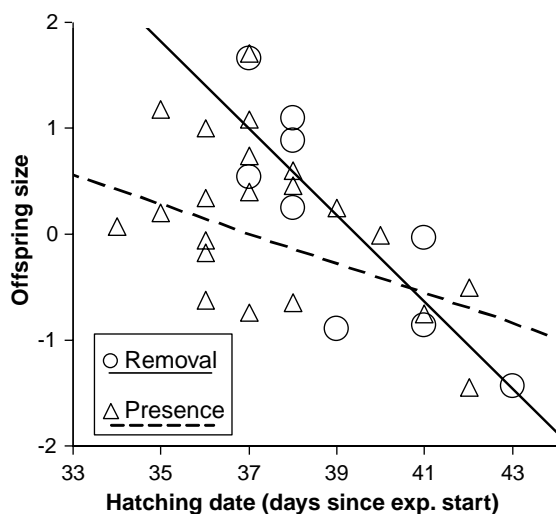


Fig. 3. The effect of hatching date on offspring size. Seasonal decline is evident in both treatments.

Flycatchers in the presence treatment had typically earlier hatching dates, due to the combined effect of later arrival and longer time-lag between arrival and laying in the removal treatment. This phenomenon and the main treatment effects are discussed in Forsman et al. (2002).

Discussion

Flycatchers breeding with or without titmice did not show any decrease in clutch size with time. In contrast, the brood size of flycatchers in titmice presence patches did not decrease with time, whereas a steep pattern of decrease was observed in removal patches. The forest structure in experimental patches was homogeneous and treatments were randomised, as were the nest sites both within patches and in respect to arrival dates. Possible remaining random effects of patches themselves were accounted for in the nested analysis design, thus the quality of nest sites cannot explain these results. Furthermore, as no patterns were observed for clutch size, the difference in brood size decline patterns was due to factors acting during the incubation and nestling phases. Lundberg and Alatalo (1992) also describe greater seasonal decline in fledgling number than in clutch size. Overall, offspring size tended to decline with date (Fig. 3.), although this is not statistically significant. The trend is similar in both treatments, and thus the presence of titmice apparently did not affect the decline in offspring quality.

Seasonal decline in clutch and brood size has been repeatedly observed for this and other bird species, with no explicit removal of other species. Here clutch size in both treatments, and brood size in the presence treatment, did not decline with date at all. This apparent inconsistency is likely explained by the limited duration we allowed for settlement (14 days, for reasons explained in Methods). Allowing the very latest pairs and secondary females to breed would probably have resulted in some decline in the above cases. In addition, the admittedly low sample size might prevent detecting a subtle decline, but then again, the statistically significant difference in brood size decline is then even more striking.

The original experiment, designed to investigate fitness effects of heterospecific attraction (Forsman et al. 2002), cannot distinguish between the 'date' and 'quality' hypotheses for seasonal decline in breeding success, and therefore not between possible processes leading to its absence by the presence of residents. However, Siikamäki (1998) studied seasonal decline in pied flycatcher breeding success by delayed breeding and supplementary feeding experiments, only ca. 250 km south from our experiment. It was clearly shown that increasing energy constraints, not parent quality, were responsible for the seasonal decline in breeding success.

Lundberg and Alatalo (1992) also provide support for this hypothesis. Assuming declining resource availability, or increasing energy demand (for example due to moult) for late breeders, was the cause for seasonal decline of breeding success in our experiment as well, we can present hypotheses on mechanisms leading to mitigation of this effect by resident bird presence.

In the presence of titmice, flycatcher foraging was perhaps enhanced, alleviating the normal seasonal energy constraint. Such enhancement could result from improved predator monitoring and avoidance (Forsman and Mönkkönen 2001), or copying of foraging locations or techniques. Supplementary feeding has been observed to counter seasonal decline (Siikamäki 1998). Many studies suggest that facilitative effects indeed occur not only within species (Sonerud et al. 2001), but also between individuals of different species utilising same resources (Mönkkönen et al. 1996, Whiting and Greef 1999, Forsman and Mönkkönen 2001, Coolen et al. 2003). In removal patches the increasing energy constraints for late pied flycatcher parents would not be dampened, leading to smaller broods. The fact that decline patterns for clutch size were not observed, lends some support to this.

Another possible hypothesis is that flycatcher parents optimise their clutch sizes, or correct brood sizes by ignoring either an egg or a hatchling, to fit perceived and conjectured resource levels. If presence of residents in the habitat selection phase predicts high habitat quality throughout the breeding phase, flycatchers in the experiment may have fitted their brood size to this conjectured resource level. However, as the quality of the nest site was in reality random, this would have led to larger-than-optimal brood size, unless some foraging benefits were actually derived from resident presence. As optimisation decisions are likely to occur during pied flycatcher breeding, at least for laying decisions (Lundberg and Alatalo 1992, Hemborg 1999), this proposed explanation perhaps deserves attention too.

On the other hand, if the 'quality' hypothesis explains the decline in breeding success, then enhanced foraging is not necessarily implied. Doligez et al. (2002) showed that collared flycatchers *Ficedula albicollis* are attracted to patches where conspecific breeding success is high. Conversely, young and unsuccessful males disperse from patches where reproductive success is high, presumably to avoid competition (Doligez et al. 1999). Consistent with this, the proportion of young birds, both male and especially female, was slightly lower in the titmice presence treatment compared to the removal treatment. This would thus explain our result if seasonal decline concerns young and poor quality individuals more than older birds. However, we did not find significant effect of parental age.

Although processes leading to eradication of a seasonal decline in breeding success by resident bird presence

are currently hypothetical, it is nevertheless clear that in addition to competition, co-existing heterospecific individuals can have positive effects on individual fitness and thus evolution.

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