

# Climate change can alter competitive relationships between resident and migratory birds

MARKUS P. AHOLA, TONI LAAKSONEN, TAPIO EEVA and  
ESA LEHIKOINEN

Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland

## Summary

1. Climate change could affect resource competition between resident and migratory bird species by changing the interval between their onsets of breeding or by altering their population densities.
2. We studied interspecific nest-hole competition between resident great tits and migrant pied flycatchers in South-Western Finland over the past five decades (1953–2005).
3. We found that appearance of fatal take-over trials, the cases where a pied flycatcher tried to take over a great tit nest but was killed by the tit, increased with a reduced interspecific laying date interval and with increasing densities of both tits and flycatchers. The probability of pied flycatchers taking over great tit nests increased with the density of pied flycatchers.
4. Laying dates of the great tit and pied flycatcher are affected by the temperatures of different time periods, and divergent changes in these temperatures could consequently modify their competitive interactions. Densities are a result of reproductive success and survival, which can be affected by separate climatic factors in the resident great tit and trans-Saharan migrant pied flycatcher.
5. On these bases we conclude that climate change has a great potential to alter the competitive balance between these two species.

**Key-words:** density effect, *Ficedula hypoleuca*, long-term trend, *Parus major*, timing of breeding.

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## Introduction

Interspecific competition is one of the major factors determining the distribution and abundance of species and thus also species composition at the community level (MacArthur & Levins 1967). In a stable environment, competition between two species over common resources should lead to niche differentiation or local extinction of the weaker competitor (Hardin 1960). Fluctuations of environmental conditions such as climate and food abundance can, however, favour different species in different situations, allowing even relatively similar species to coexist (Chesson & Huntly 1997; Sætre, Post & Král 1999; Qvarnström *et al.* 2005). Thus, climate change could affect the competitive relationships among species. For example, it has been

suggested that migratory bird species could face difficulties compared to residents because changes in their wintering areas and along migration routes do not necessarily reflect those taking place in their breeding areas (Berthold *et al.* 1998). Both resident and migratory species may be able to adapt to changes through selection, but individuals of resident species are expected to be in a better position to adjust behaviourally to warming spring temperatures and an advanced phenology of their food items.

Climate change may affect the competitive relationships between resident and migratory birds in at least two different ways. First, climate change may affect the timing of breeding, as well as the time interval between the onsets of breeding, of competing species. When the onsets of breeding of two species are close to each other, severe competition over certain limited resources (e.g. breeding holes) is most likely (Slagsvold 1975). The timing of breeding in many bird species has advanced during recent decades and is affected by prebreeding temperatures at their breeding grounds

(e.g. Crick & Sparks 1999). For migratory species the timing of breeding also depends on when they arrive in the target area (Both & Visser 2001; Ahola *et al.* 2004). It is predicted that climate warming will be stronger overall at higher latitudes (IPCC 2007), but these general temperature trends are likely to be complicated by geographical and within-season temporal variations (Easterling *et al.* 1997; Ahola *et al.* 2004; Hüppop & Winkel 2006). Such spatial or temporal differences may affect differentially the timing of breeding in competing species that are influenced by the temperatures of different areas and/or time periods during their prelaying time. Divergent changes in the breeding times of resident and migratory species might therefore also affect their competitive situation.

Secondly, climate change may affect the severity of competition by altering the population densities of competing species. Species densities might change either in the same or in opposite directions, depending on how climate affects survival and reproductive patterns. The timing of breeding and, consequently, the availability of food for nestlings affect breeding success (Lack 1968; Perrins 1970). Some studies have shown a mismatch between timing of breeding and optimal food availability for offspring as a result of climate change (Visser *et al.* 1998; Both & Visser 2001). This mismatch has caused declines in breeding success (Moss, Oswald & Baines 2001) and population size (Both *et al.* 2006). Weather and food conditions affect birds' survival year-round. For example, winter survival depends on local circumstances at their wintering grounds (Møller & Szép 2005; Szép *et al.* 2006). For resident and migratory species, the conditions experienced during the non-breeding period are likely to differ as they spend much of this time at different latitudes. Under these circumstances densities of different species might develop in different ways causing changes in the severity of interspecific competition. For example, if winters become milder in breeding areas migratory birds may face higher densities of residents on arrival, and thereby stronger competition for food and nest sites, which would be unfavourable for migratory species (e.g. Berthold *et al.* 1998; Lemoine & Böhning-Gaese 2003).

Interspecific competition is often difficult to study because resource needs and interactions are usually both complex and hard to measure. Breeding-site competition in hole-breeding species is an exception, as the number of nest-holes is easy to control and a critical limiting factor for them (Gustafsson 1988; Newton 1994). It has been shown that the availability of nest-holes affects strongly the intensity of nest-site competition between hole-breeders (Tompa 1967), which makes it beneficial for birds to occupy a breeding hole and territory as early as possible. In fact, among hole-nesters the resident strategy is more widespread than among open-nesters (von Haartman 1968).

We studied breeding-site competition between two hole-breeding passerines which differ in their wintering

habits. The great tit (*Parus major* L.) and the pied flycatcher (*Ficedula hypoleuca* Pallas) share a common distribution over Europe and western Russia (Cramp & Perrins 1993). They coexist in the same habitats, use the same food resources (Eeva, Lehikoinen & Pohjalainen 1997; Eeva, Ryömä & Riihimäki 2005) and breed mainly in similar tree holes and artificial nest-boxes (e.g. Cramp & Perrins 1993). In most parts of its range the great tit is a sedentary species, although periodic short-range irruptions are a regular phenomenon (Cramp & Perrins 1993). The pied flycatcher is a long-distance migrant and winters in tropical Africa, south of the Sahara desert (Lundberg & Alatalo 1992). The two species are known to compete for nest-holes (Slagsvold 1975; Lundberg & Alatalo 1992; Källander 1994; Newton 1998), although the great tit starts breeding earlier and thus has a head-start in nest-hole competition (Slagsvold 1976).

Conflicts can be harmful for both species. As great tits start breeding earlier, they choose their territories and nest-holes without pied flycatchers' influence. Pied flycatchers are physically weaker than great tits and therefore cannot take over tit nests by force. Flycatchers may try to take over occupied nest-holes by interrupting the owners, causing them to abandon their nests, or simply by rapid nest-building upon the tit's nest. In the latter case, the attempt should be made before the start of the incubation period, when the tits are not continually in the vicinity of their nests (reviewed by Slagsvold 1975). The take-over attempts, however, may lead to the death of the pied flycatcher (e.g. von Haartman 1957; reviewed by Slagsvold 1975; Merilä & Wiggins 1995). None the less, pied flycatchers benefit if they can take over a nest-hole when there are either no alternative sites available, or when the obtained hole is in a better territory than unoccupied ones.

It is known that climate change has affected the timing of breeding, survival and population densities of birds, but we are not aware of any direct evidence about the effects of climate change on interspecific resource competition. We studied the roles of the timing of breeding and population densities in determining the intensity of nest-site competition between the great tit and the pied flycatcher. In this way, our aim was to find out whether the climate change could change or has changed the competitive relationship between the two species.

## Materials and methods

### DATA

Breeding data were used from two nest-box studies in SW Finland. The first data set was collected by Lars von Haartman during his long-term study in Askainen (60°30' N, 21°45' E). This data set included data on both great tits and pied flycatchers from 1953 until 1994 (with missing data for 1958, 1990 and 1992). The number of nest-boxes studied each year varied from 79 (1993) to 155 (1983) (median = 134,  $n = 39$  years). The

second data set was collected by T. E. and E. L. in Harjavalta ( $61^{\circ}20'N$ ,  $22^{\circ}10'E$ ) during 1991–2005. From the Harjavalta data we excluded all nesting attempts that were within 3 km of a polluting industrial complex known to affect the breeding parameters of tits and pied flycatchers (e.g. Eeva, Lehikoinen & Pohjalainen 1997). Further from the industrial complex, there were from 131 (2001) to 599 (1995) nest-boxes studied per year (median = 478,  $n = 15$  years). The two study areas are c. 95 km apart. In both areas nest-boxes were checked at least once a week, and usually more often during the egg-laying period. Laying dates were determined from the number of eggs observed during the laying period, and only nesting attempts considered to be the first ones per female during each year were used (for details see Laaksonen *et al.* 2006). Eventually, there were data on 2442 pied flycatcher, 883 great tit, 176 blue tit (*Cyanistes caeruleus* L.), 74 coal tit (*Periparus ater* L.) and nine crested tit (*Lophophanes cristatus* L.) nests from Askainen. Respectively, data on 2607 pied flycatcher, 1245 great tit, 229 blue tit, 76 coal tit, 44 crested tit and 11 willow tit (*Poecile montanus* Conrad) nests were used from Harjavalta.

We tested the similarity of laying dates in the two study areas using data from three common years (1991, 1993 and 1994). A two-way analysis of variance (ANOVA) showed that there was much more variation among years than between locations in the laying dates of both great tits (year:  $F_{2,337} = 43.96$ ,  $P < 0.0001$ ; location:  $F_{1,337} = 4.04$ ,  $P = 0.05$ ,  $n = 66$  for Askainen and  $n = 275$  for Harjavalta) and pied flycatchers (year:  $F_{2,795} = 530.86$ ,  $P < 0.0001$ ; location:  $F_{1,795} = 2.81$ ,  $P = 0.09$ ,  $n = 141$  for Askainen and  $n = 658$  for Harjavalta). We also examined the densities of pied flycatchers and all tit species (measured as proportions of nest-box occupancy) in the two study areas during the 3 years. For the density of tits, we used all tit species because, as well as great tits, the other species occurring in the area affect the availability of the nest-boxes for the arriving pied flycatcher. These other species are, however, involved only rarely in conflicts for nest-boxes as they start breeding earlier and occur in smaller numbers than great tits in both areas. Densities were regularly lower in Harjavalta: on average by 9.5% units for tits (Askainen: 32.0, 29.1, 32.0; Harjavalta: 21.4, 22.7, 20.5) and 1.5 for pied flycatcher (Askainen: 42.4, 44.3, 41.4; Harjavalta: 41.9, 43.9, 37.7). To take the between-location density difference into account when considering the trend in density over years, we corrected the densities of Harjavalta by adding to them the average between-location difference from the 3 years. In order to see whether the corrected values represented the true density trend more clearly than the uncorrected values, we correlated both with regional data from southern Finland during 1983–2005 (Väistönen 2006); our data with corrected values had a much higher correlation with the population trend index of tits than had the data with uncorrected values (corrected:  $r = 0.80$ ,  $P < 0.0001$ ,  $n = 22$ ; uncorrected:  $r = 0.59$ ,  $P = 0.0039$ ).

Thus, using the correction was justified when studying the density trend in the combined data. In the main analyses of the determinants of the competition intensity, we used the uncorrected data and separate data-points from the two different locations, because the realized relative densities are the ones experienced by birds in both study areas.

#### NEST-HOLE COMPETITION

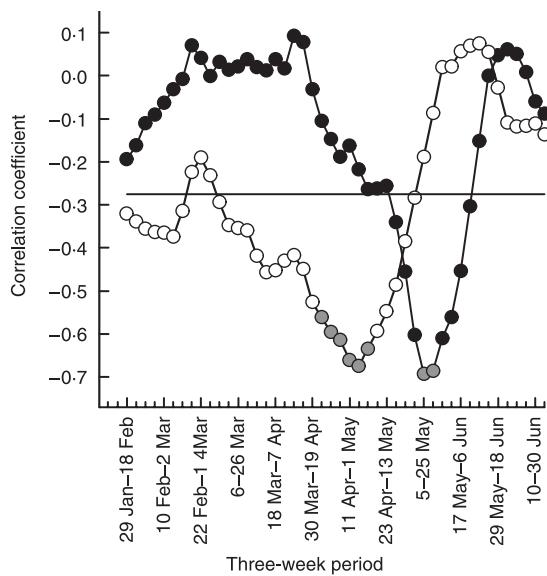
Two types of situation were interpreted to represent competitive conflicts between great tits and pied flycatchers: (1) fatal take-over attempts by pied flycatchers (hereafter fatal attempts), where a flycatcher male or female was found dead or lethally injured at a great tit's nest; and (2) possible take-overs, where a flycatcher nest appeared on top of a tit's nest within 1 week from the last sign of progress on the tit nest. Cases where flycatchers built nests on top of great tit nests that were abandoned for other reasons were not included. Such reasons were, for example, capturing of the female great tit during egg-laying or incubation period at last visit preceding the abandonment of the nest; the death of the great tit nestlings due to a cold and/or rainy weather period; or the tit nest destruction by some predator, deduced from, for example, disappearance of eggs or nestlings or from other remains of a predation event. One should be aware that while the fatal attempts are clear evidence of straight conflicts we cannot, even after careful consideration of each case, be completely sure that all the great tit nests that were taken over were abandoned due to pied flycatcher behaviour. To be certain, we would need continuous monitoring data from the nest-boxes. In any event, the occurrence of the possible take-over cases can be considered to indicate the competitive pressure against nest-holes as the nests were, in any case, inhabited quickly after abandonment. Obviously, both measures are simply indicators of the intensity of nest-hole competition between tits and flycatchers, as conflicts also take place frequently without leaving any traces. Apart from the risk of injury, the cost of such competitive conflicts is realized in terms of both time-loss and a loss of territory quality, when individuals are forced to move to suboptimal territories (Winge & Järvi 1987).

We modelled the occurrence of annual fatal attempts and possible take-overs (separate models for both measures) in all great tit nests using a multiple logistic regression (procedure GENMOD in SAS), where the response variable was of type 'events/trials' (e.g. number of fatal attempts/number of great tit nests). We used the following explanatory variables: (i) interval between yearly median first egg-laying dates of the great tit and the pied flycatcher (in days; hereafter laying date interval); (ii) density of tits; and (iii) density of pied flycatchers (measured as percentages of occupied nest-boxes). The final density of pied flycatchers is obviously determined after conflicts have taken place. None the less, we believe that the final density is a useful indicator of the

number of pied flycatchers attempting to breed in the area each year, as a proportion of the nest-boxes always remained unoccupied. We ran the two analyses first with all the explanatory variables and all their interactions and then, stepwise, dropped out the non-significant factors, starting from the highest-order interactions. We then performed regression analyses to determine whether there have been changes in the central determinants of laying date interval and the degree of nest-box competition during the past five decades. All the analyses were conducted with SAS 9.1.

#### DETERMINATION OF RELEVANT TIME PERIODS FOR TEMPERATURES EXPLAINING THE TIMING OF BREEDING

In order to understand what determines the laying date interval, we needed to know how temperatures of different periods of spring are correlated with the timing of breeding in both species. We used daily mean temperatures for Turku ( $60^{\circ}30' N, 22^{\circ}16' E$ ), obtained from the Finnish Meteorological Institute, as base data for weather factors potentially explaining the timing of breeding. For both species, we determined the species-specific prebreeding periods whose temperatures best explained variation in the timing of breeding. This was conducted by first correlating the median breeding times against mean temperatures of several overlapping 3-week periods (starting at 3-day intervals from 29 January onwards). Correlations between great tit laying dates and average 3-week temperatures strengthened continuously from the period starting on 24 March until the strongest negative correlation was obtained with temperatures from 14 April–4 May (Fig. 1). After that correlations weakened quickly, but remained significant until the period 2–22 May (Fig. 1). For the pied flycatcher, the correlations were non-significant before an abrupt strengthening during the 3-week periods starting between 23 April and 5 May (Fig. 1). They also weakened fast after the most negative correlation was reached with the period 5–25 May (Fig. 1). In a second step of this analysis, we widened the original 3-week periods with the highest correlations in 3-day steps from either their beginning or end, or from both, in order to find a period for each of the species which would be the most important in explaining their timing of breeding. The importance was measured with the adjusted  $R^2$  from the regression analyses between the temperatures of the compared periods and the yearly median laying dates. The period that best explained the timing of breeding was 2 April–7 May (length 36 days) for great tits and 5–28 May (length 24 days) for pied flycatchers (Fig. 1; comparison results not shown). Temperatures of these species-specific periods were used as explanatory weather variables for the timing of breeding. We are confident that this approach is superior to using monthly averages of temperatures, especially as we are interested in the species-specific determinants for the timing of breeding.



**Fig. 1.** Identification of the most important prebreeding periods for the laying dates of the great tit (○) and the pied flycatcher (●) during 1953–2005. The figure presents Pearson's correlation coefficients between yearly median egg-laying dates and mean temperatures of the overlapping 3-week periods (starting at 3-day intervals; note that only every fourth period is shown in the x-axis tick label). The grey dots indicate the extended periods whose temperatures best explained the timing of breeding in each species (2 April–7 May for great tits and 5–28 May for pied flycatchers; see Material and methods). Correlation coefficients below the horizontal line are statistically significant at  $P < 0.05$  ( $n = 54$ ).

## Results

### CONFLICT CASES AND THEIR CONSEQUENCES

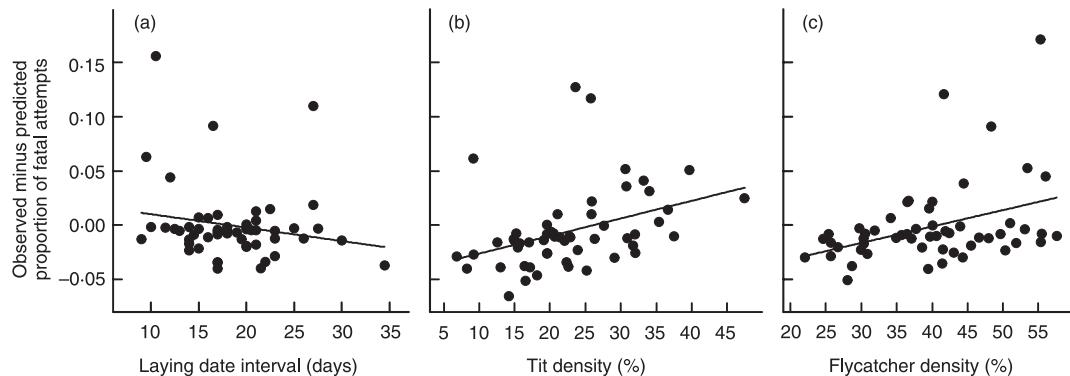
During 1953–2005 there were 53 dead flycatchers found as evidence for fatal attempts, and 20 cases were considered as possible take-overs. Most victims of the fatal attempts were males, and most often both the fatal attempts and possible take-overs happened during the egg-laying period in the great tit nest. The remaining cases occurred mainly during the nest-building or incubation periods, but a couple of fatal attempts happened even during the nestling stage (Table 1). Interestingly, 15 of the 53 cases, where a flycatcher was killed in a great tit nest, ended up with great tit abandonment and 11 of them with a breeding of another flycatcher. The abandonment in these cases was connected clearly to the appearance of the carcass in the nest.

### FACTORS AFFECTING CONFLICT PROBABILITY

The probability of fatal attempts increased with a shorter laying date interval and with a higher density of tits or pied flycatchers (Fig. 2a–c; Table 2a). The probability of possible take-overs increased with increasing pied flycatcher density (Table 2b), whereas laying date interval or tit density had no obvious effect on it

**Table 1.** Frequencies of different types of conflicts during each breeding phase of the great tit

	Nest-building	Egg-laying	Incubation	Nestling	Unknown	$\Sigma$
Fatal attempts	10	19	15	2	7	53
of which by females	2	3	2	0	2	9
males	8	16	13	2	5	44
Possible take-overs	4	12	4	0	0	20
All conflicts	14	31	19	2	7	73



**Fig. 2.** Individual effects of (a) laying date interval, (b) density of tits, and (c) density of pied flycatchers on the probability of the fatal attempts after the effect of the other two explanatory factors has been removed. On the y-axis there is the deviation of the observed proportion of fatal attempts from that predicted by the model which contains only the other two explanatory factors (excluding the one on the x-axis).

**Table 2.** Effects of individual explanatory factors in the models for occurrence of (a) fatal take-over attempts and (b) possible take-overs by pied flycatchers. The factors in the table are in reverse order in which they were dropped out from the model, i.e. the first dropped factor is at the last row in the table. The results for the factors left in the final models are shown in bold type. Dispersion (deviance/d.f.) for full model explaining the probability of fatal attempts was 1.01 and that for the final model was 1.04. Respective values for models explaining possible take-overs were 0.71 and 0.72

Explanatory variable	d.f.	$\chi^2$	<i>P</i>
(a) Fatal take-over attempts			
Laying date interval (LDI)	50	<b>5.54</b>	<b>0.019</b>
Flycatcher density (FD)	50	<b>19.22</b>	<b>&lt; 0.0001</b>
Tit density (TD)	50	<b>20.21</b>	<b>&lt; 0.0001</b>
LDI × TD	49	0.84	0.36
LDI × FD	48	1.53	0.22
FD × TD	47	0.98	0.32
LDI × FD × TD	46	2.35	0.13
(b) Possible take-overs			
Flycatcher density (FD)	52	<b>7.24</b>	<b>0.0071</b>
Laying date interval (LDI)	51	2.63	0.11
LDI × FD	50	1.8	0.17
Tit density (TD)	49	0.4	0.53
LDI × TD	48	0.08	0.77
FD × TD	47	0.04	0.83
LDI × FD × TD	46	0.11	0.74

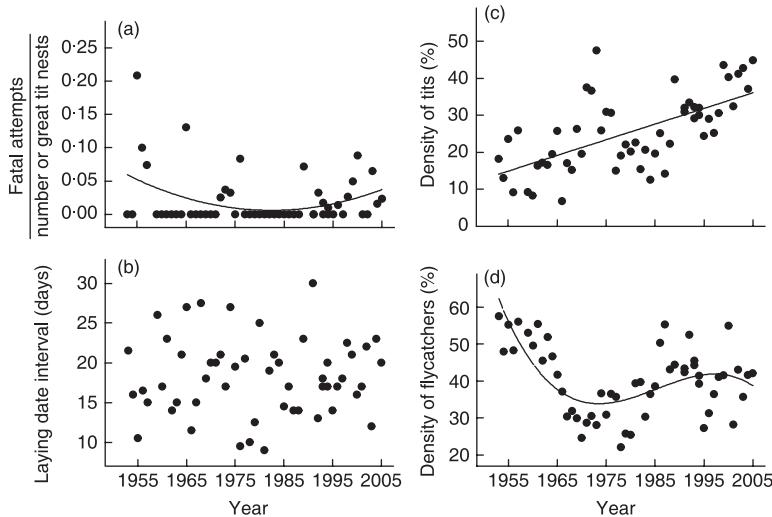
(Table 2b). There were no significant interactions between the explanatory variables in the analyses (Table 2a,b).

The probability of fatal take-over attempts in great tit nests varied greatly, having a number of years with

no cases observed. The highest values appeared during the first two decades of the study period (year:  $P = 0.01$ ; year $^2$ :  $P = 0.02$ ; Fig. 3a). The probability of possible take-over cases showed no significant trend, but the number of cases was relatively low. The probability of fatal attempts and probability of take-overs were correlated positively ( $r = 0.46$ ,  $P = 0.0005$ ).

Laying dates did not change significantly either in great tits or in pied flycatchers during the period 1953–2005 (great tit:  $b = 0.01 \pm 0.04$ ,  $t = 0.22$ ,  $P = 0.83$ ,  $n = 54$ ; pied flycatcher:  $b = 0.03 \pm 0.03$ ,  $t = 0.86$ ,  $P = 0.39$ ,  $n = 54$ ). Accordingly, there was no trend in their laying date interval ( $b = 0.02 \pm 0.05$ ,  $t = 0.41$ ,  $P = 0.68$ ), but this varied substantially among years [average laying date interval:  $18.5 \pm 5.3$  (SD); Fig. 3b]. There was a linear increasing trend in the density of tits ( $b = 0.42 \pm 0.07$ ,  $t = 5.93$ ,  $P < 0.0001$ ; Fig. 3c). The density of pied flycatchers first decreased clearly from the 1950s to the 1970s, then increased until the middle of the 1990s, and after that tended to decrease again. A third-order trend fitted the data (year, year $^2$ :  $P < 0.0001$ , year $^3$ :  $P = 0.0014$ ; Fig. 3d).

Temperatures of the species-specific prebreeding periods explained about half the variation in timing of breeding in both species: laying was earlier when it was warm (great tit:  $b = -2.13 \pm 0.29$ ,  $t = -7.26$ ,  $P < 0.0001$ , adj  $R^2 = 0.48$ ; pied flycatcher:  $b = -1.37 \pm 0.19$ ,  $t = -7.07$ ,  $P < 0.0001$ , adj  $R^2 = 0.47$ ). Importantly, with regard to competition, almost half the variation in the laying date interval was explained by the difference in the temperatures of these time-periods. The laying date interval decreased with higher temperature difference



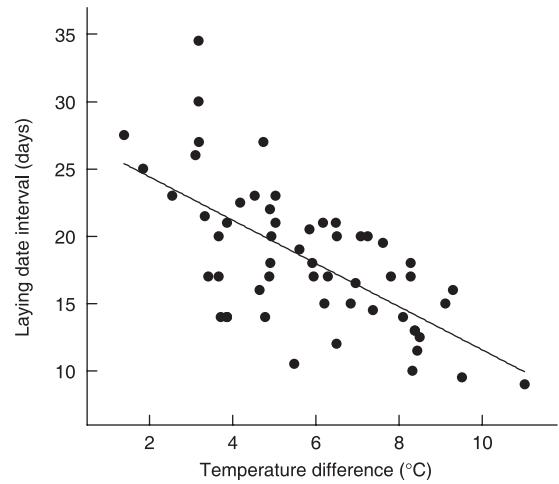
**Fig. 3.** Trends over time in (a) probability of fatal take-over attempts by pied flycatchers, (b) laying date interval between great tits and pied flycatchers, (c) density (nest-box occupancy) of tits and (d) density of pied flycatchers.

( $b = -1.61 \pm 0.25$ ,  $t = -6.40$ ,  $P < 0.0001$ , adj  $R^2 = 0.42$ ; Fig. 4). This indicates that the temperatures of the two periods are independent enough to influence the timing of each species differently, and thereby alter the competitive relationship between them. However, the temperatures have not changed significantly differently (trend for the difference:  $b = -0.029 \pm 0.02$ ,  $t = -1.51$ ,  $P = 0.14$ ; year  $\times$  species interaction on temperature trends:  $F = 1.95$ ,  $P = 0.17$ ), although when examined separately there was a warming trend in the prebreeding temperature for great tits ( $b = 0.046 \pm 0.012$ ,  $t = 3.72$ ,  $P = 0.0005$ ), whereas the trend for pied flycatchers was not significant ( $b = 0.017 \pm 0.016$ ,  $t = 1.03$ ,  $P = 0.31$ ).

## Discussion

Our results show that competition for nest-holes between the resident great tit and migratory pied flycatcher increases when the onsets of their breeding are closer to each other and when the densities of tits and/or pied flycatchers are high. All these factors can be affected by climate change, indicating that climate change has a great potential to affect the strength of interspecific competition.

The onsets of breeding in the two species are affected by the temperatures of separate, species-specific time-periods. Accordingly, almost half the variation in the laying date interval is explained by the difference in these temperatures. Diverging temperature trends in these prebreeding periods would thus change the competitive balance between the two species. This could very well happen, as it has been shown that climatic trends can vary among different time-periods, even when these periods are short and temporally close to each other. For example, the significant warming of spring temperatures in SW Finland during the past three decades has concerned only c. 10 days at the end of April (Ahola *et al.* 2004). The spring phenology of pied flycatchers is also affected by conditions at southern



**Fig. 4.** Relationship between difference of mean temperatures of the species-specific periods ( $T_{\text{pied flycatcher}} - T_{\text{great tit}}$ ; period 5–28 May for pied flycatcher and 2 April–7 May for great tit), and laying date interval between the two species.

latitudes. Temperatures along the migration route affect the timing of their arrival, which in turn affects the timing of breeding (Ahola *et al.* 2004; Hüppop & Winkel 2006). On the basis of previous literature, it could be predicted that if the laying date interval between these two species decreases pied flycatchers should have better chances for successful nest takeovers, as fewer great tits will have had time to reach the incubation phase when flycatchers arrive to occupy their territories (Slagsvold 1975). Our results did not show any clear effect of laying date interval on the possible take-overs, but the interval nevertheless affected the number of fatal take-over attempts.

Climate change can alter the densities of competitors by affecting their reproductive output or their survival. While breeding success affects the size of the population at the end of the breeding season, conditions during the non-breeding season determine how many individuals survive to breed the following year (Møller & Szép 2005; Szép *et al.* 2006). In some populations, both great tits and pied flycatchers have found to breed increasingly late in relation to peak food availability for nestlings (Visser *et al.* 1998; Both & Visser 2001; Sanz *et al.* 2003). This mistiming during the recent decades, as a consequence of climate change, has also led to decreases in population sizes (Both *et al.* 2006). In our study populations there has been a decreasing trend in the clutch size of pied flycatchers (Laaksonen *et al.* 2006), which is a possible factor contributing to the observed decreasing population density.

We are currently not aware of any studies on how climate change has affected or will affect survival in these species. We did not find any clear trend in their conflict probabilities in SW Finland during the recent decades of climate warming, although both fatal attempt and possible take-over probabilities were highest during the 1950s and 1960s. However, the population densities of trans-Saharan migrant pied flycatchers have

decreased during the past five decades, whereas those of resident great tits and other tit species have increased. This indicates that, at least partly, different factors affect the survival and/or breeding success of these species.

Among many other factors, interspecific competition may affect birds' breeding success and survival, and thus have some influence on their population dynamics. Pied flycatchers may benefit if they succeed to take over nest-holes in high quality territories. On the other hand, they face a risk of being killed while trying to intrude into nest-holes already occupied by great tits and dying would, of course, reduce their fitness fatally. In the case of choosing a territory with a free nest-hole a pied flycatcher avoids the risk of death, but if the quality of that alternative territory is lower the choice reduces its expected fitness. For a great tit, losing a nest obviously decreases its fitness. However, even a fatal take-over trial by a pied flycatcher may affect a great tit's breeding success negatively, as in many cases the carcass in the nest caused nest abandonment. The cases observed may even underestimate how often this could happen in nature, as the carcasses were often removed when found. On the other hand, the fatal trials can also benefit other flycatcher individuals as most of these cases ended up with a flycatcher nest on top of the great tit nest. At the population level, the occurrences of the negative and positive effects on individuals' fitness determine the effects of competition on each species population dynamics. We could not show any immediate effects of competition to population density or laying date of the pied flycatcher. However, there were clear changes in densities of both pied flycatchers and tits, but in this paper we did not study the effects of, for example, wintering survival and breeding success, which we consider to be more important factors than the competition in determining the population densities.

The availability of nest-holes is limited by the number of birds occupying them, but depends ultimately on the existence of suitable holes in forests. Nest-hole densities are typically higher in nest-box areas than in natural environments (Lundberg & Alatalo 1992), and a low density of nest-holes increases the frequency of fatal take-over attempts (Merilä & Wiggins 1995). It is therefore likely that competition pressure between hole-breeders is even higher in environments devoid of nest-boxes. However, the availability of nest-holes is not the only critical factor for hole-breeders. In our study areas, a number of nest-boxes were left empty every year. This fits with the earlier results, that territory quality has a great importance for pied flycatchers (Alatalo, Lundberg & Glynn 1986), as some individuals choose to make a risky take-over attempt rather than selecting a freely available, empty nest-box.

In conclusion, the severity of competition between great tits and pied flycatchers is affected by both the timing difference in their breeding and by their breeding densities. Over recent decades, the timing of breeding has changed variably in different populations of great tits and pied flycatchers. The changes have, at least

partly, followed the warming or cooling of ambient spring temperatures (Winkel & Hudde 1997; McCleery & Perrins 1998; Cresswell & McCleery 2003; Visser *et al.* 2003; Both *et al.* 2004). Breeding success and the population sizes of some populations have decreased, due probably to difficulties in coping with climate change (Moss, Oswald & Baines 2001; Both *et al.* 2006). Our data showed that climate change has great potential to alter the competitive balance between these two species. Whether such changes exist in other populations, and how those changes are distributed geographically, are intriguing topics for future research.

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