The effect of climate change on partial migration – the blue tit paradox

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Abstract

Climate change has proven to affect various aspects of the migration of birds. In response to milder winters making the habitat more profitable and increasing the survival of residents, the migratory fraction of partially migratory populations has been predicted to decline. We studied the blue tit *Parus caeruleus*, a common partial migrant in southern Sweden. The numbers migrating at Falsterbo, a migratory passage site in SW Sweden, has increased during the last decades, in parallel with increasing winter and annual temperatures. Migration data from Falsterbo were compared with yearly indices of the size of the breeding population as estimated by the Swedish National Bird Monitoring Programme. Over the study period 1975–2004, also the breeding population has increased in size. The proportion of blue tits migrating each year did not change over the study period, or possibly even increased slightly, which is in contrast to how climate change has been predicted to influence populations containing both migratory and resident individuals. The most important factors determining the intensity of blue tit migration in a given year was the size of an important winter food source, the beech mast crop (more migrants at lower crops) and the size of the breeding population (more migrants at higher densities).

Keywords: beech mast, breeding population size, habitat quality, *Parus caeruleus*, temperature, winter food

Received 16 February 2006; revised version received 17 May 2006 and accepted 23 May 2006

Introduction

The ongoing global warming rapidly alters the conditions for many living organisms (Easterling *et al.*, 1997; Walther *et al.*, 2002; Moberg & Jones, 2005). Migratory birds are annually globetrotting the Earth and are therefore thought to be particularly sensitive to global warming (Berthold, 2001). It is of vital importance for the existence of many migratory bird populations that individuals can sense and respond to changes in the environment (Berthold, 2001). Indeed, in recent decades migratory birds have started to arrive earlier in spring, breed earlier and depart later in autumn in northern Europe (van Noordwijk *et al.*, 1995; Visser *et al.*, 1998; Lindström & Agrell, 1999; Hüppop & Hüppop, 2003; Jenni & Kery, 2003; Gordo *et al.*, 2005; Stervander *et al.*, 2005).

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Global warming is predicted to have profound effects also on partial migrants (Berthold, 1999). Among partial migrants, a fraction of the population consists of migratory individuals, whereas the other fraction stays on or close to the breeding grounds (Terrill & Able, 1988). Experiments have shown that given strong directional selection, complete residency, as well as complete migration can evolve from a partially migratory population within a few generations (Berthold *et al.*, 1990). Survival of individuals from the sedentary proportion of a partially migratory population is thought to be density dependent (Lundberg, 1988). Everything else being equal, milder winters will most likely result in increasing numbers of individuals that can be sustained on a given resource (notably food) on the breeding grounds in winter. Birds becoming residents will therefore increase their survival probabilities in a warmer climate, which will favour residency over the migratory alternative (Berthold, 2001). In partially migratory populations, the proportion of migratory individuals

has, therefore, been predicted to decrease in times of global warming (Berthold, 1999, 2003).

The blue tit *Parus caeruleus* is a small passerine bird breeding in deciduous forests over large parts of Europe (Perrins, 1979). It is a partial migrant over much of its breeding range and the numbers of migrants are known to vary drastically between years (Ulfstrand, 1962; Frelin, 1979; Winkel & Frantzen, 1991; Heldbjerg & Karlsson, 1997). Large numbers of migrants are normally found in years with poor crops of beech (Fagus) seeds (an important winter food source) and/or high population densities (Ulfstrand, 1962; Winkel & Frantzen, 1991; Heldbjerg & Karlsson, 1997).

There is still a debate whether partial migration is mainly genetically or phenotypically controlled (Berthold, 2001). Among blue tits there is a predominance of juveniles and females on migration (Smith & Nilsson, 1987; Heldbjerg & Karlsson, 1997). This was interpreted by Smith & Nilsson (1987) as evidence of a phenotypical explanation for partial migration, (i.e. the individuals lowest in rank migrate). However, since also adults are found on migration (Heldbjerg & Karlsson, 1997), and migratory behaviour could be gender-specifically genetically programmed, Berthold (2001) suggested that the patterns of partial migration in blue tits nevertheless can be genetically based.

In continental Europe the proportion of blue tits on migration has been reported to decline over three decades (1960–1989) (Winkel & Frantzen, 1991), in line with the predictions for partial migrants in a climate warming situation (Berthold, 2003). However, somewhat paradoxically, there has been a dramatic increase during the last decades in the number of blue tit migrants at Falsterbo, Sweden (Heldbjerg & Karlsson, 1997). This is not just a local phenomenon, because the blue tits originate from the whole of southern Sweden (Heldbjerg & Karlsson, 1997). The increase in migrant numbers is seemingly in contrast to the climate-warming-related prediction for partial migrants posed by Berthold (2003). However, over the same period there has also been a general increase with about 50% in the size of the Swedish breeding population (Lindström & Svensson, 2005). Given that high densities may result in higher numbers of migrants in a partially migratory population (see references above), the increase in population size may be the main cause of the increasing numbers of migrant. Hence, it remains to be investigated if the *proportion* of migrants in the Swedish blue tit population has declined along with climate warming.

We analyse the relationship between the size of the Swedish blue tit breeding population and the number of migrants recorded at Falsterbo. Based on Berthold (2003), we predict that the proportion of migrants is decreasing as a response to global warming. We also analyse the underlying causes behind the between-year variation in migrant numbers and discuss which factors may be important in the population dynamics of the Swedish blue tit population.

Materials and methods

Falsterbo at the south-western tip of Sweden is an important migratory passage site for birds breeding in Fennoscandia (Rudebeck, 1950; Alerstam, 1978; Roos, 1984; Karlsson *et al.*, 2005). It is situated on a narrow peninsula stretching out into the strait of Öresund and migratory birds following coastlines concentrate there. Our data on blue tit migration originate from two different programmes: visual observations and standardized ringing.

Visual observation counts of migrants were conducted daily from 1 August to 20 November by one or two observers at the south-western tip of the Falsterbo Peninsula. Observations began at dawn and lasted until 14:00 (CET). From 1973 to 2000, the counts were carried out by Gunnar Roos and from 2001 and onwards by Nils Kjellén (Roos, 2001; Kjellén, 2004). The counts are a part of the National Monitoring Programme run by the Swedish Environmental Protection Agency. We used observations from 1975 to 2004, the time period for which there is also data on the breeding population size (see below).

Falsterbo Bird Observatory (55°23′N, 12°49′E) carries out standardized ringing of birds in the Falsterbo lighthouse garden (Karlsson *et al.*, 2005). The garden is situated about 800 m from the site where the visual counts are carried out. The standardization of ringing started in 1980. In autumn, birds are mistnetted daily from 21 July to 10 November using a maximum of 21 nets. The number of nets is adjusted depending on weather and wind conditions (Karlsson *et al.*, 2002). The nets are opened at dawn and taken down 6 h later or until less than 10 birds are captured in the last hour. Mistnets are emptied every half hour, more often in damp weather conditions (Karlsson *et al.*, 2005). Since 1983, nearly all blue tits trapped have been aged and sexed. We, therefore, used autumn data from 1983 to 2004 for our analyses. The number of blue tits captured in spring is almost negligible and was, therefore, not included in our analysis.

Estimates of the size of the Swedish blue tit breeding population come from The Swedish Bird Survey, which is run by the Department of Animal Ecology, Lund University, as a part of the National Monitoring Programme of the Swedish Environmental Protection Agency. The data included here comes from the Summer Point Counts, a programme that started in 1975

(Lindström & Svensson, 2005). The fieldwork is almost exclusively conducted by volunteers. The observers chose their own route and identify 20 points (stops) in such a way that the same birds are not heard or seen at two points. In woodland, this distance is at least 200 m and in open terrain 300–400 m. At each point, all birds seen and heard during five minutes are noted. Each route is monitored once a year, normally in May or June at approximately the same date and time of day (Lindström & Svensson, 2005). About 90% of the routes are situated in the southern half of Sweden, which also is where the major part of the blue tit population is breeding. Yearly indices of population size were calculated using TRIM 3.2 (TRends and Indices for Monitoring data) (Pannekoek & van Strien, 2001). TRIM allows for missing counts using estimation, and yields yearly indices using Poisson regression (for further details, see Pannekoek & van Strien, 2001).

Mean monthly and annual temperatures from the weather station at Falsterbo lighthouse were obtained from the Swedish Metrological and Hydrological Institute (SMHI).

As a measure of autumn and winter food abundance a given year we used a beech mast index ranging from 0 to 5, as estimated annually in several plots in Stenbrohult, central southern Sweden (Nilsson, 1985). Beech seeds are an important winter food source (Ulfstrand, 1962). Production of beech seeds (i.e. mast crops) is known to be synchronized over large areas. For example, our index of beech mast production is strongly correlated with the Danish beech mast index monitored by the Danish Forest and Nature Agency (Heldbjerg & Karlsson, 1997) ($r_s = 0.88$, $P < 0.001$). We, therefore, feel confident that our beech mast index is representative for large parts of the breeding range of Swedish blue tits.

Time series of migration counts, breeding population estimates and temperatures were analysed using Pearson linear regression. Migration counts were adjusted to control for the effect of two different observers (Kjellén, 2002). The migration counts were ln-transformed to reach normality. We also tested for a correlation between the time series of migration counts and breeding population size. To avoid a spurious correlation due to temporal trends in the data, we used the standardized residuals of the regression of the time series on year. To test whether the proportion of migrants in the blue tit population has declined or increased over time, the change over time in two ratios was analysed using linear regression. The first ratio is the number of adults trapped, divided by the breeding population index (for the years 1983–2004). In this way only adults occur in our data. If partial migration is mainly under genetic control (Berthold, 2001), this may be the most appropriate measure of population dynamics. The second ratio is the total number of migrants from visual observations divided by the breeding population index (for the years 1975–2004). In this ratio also juvenile migrants are included, and may, therefore, better mirror phenotypically controlled migration. Both ratios were square root transformed (Sokal & Rohlf, 2001).

In order to explain the annual variation in observed migration, we set up a range of likely models, which we evaluated with Akaike information criteria corrected for small sample size, AIC_c (Burnham & Anderson, 1998). We standardized the included variables to evaluate the relative effect of each variable on the model. Variables included in the models were breeding population size index, beech mast index and mean temperature in May. Lacking comparable long-term data on fledgling success in blue tits, we used mean May temperature as a proxy for fledgling success, assuming higher breeding success at higher temperatures (Järvinen & Vaisanen, 1984; van Noordwijk *et al.*, 1995; Eeva *et al.*, 2000; Cresswell & McCleery, 2003; Julliard *et al.*, 2004). Statistical analyses were carried out in SPSS 11.5 and Excel 2003.

Results

Over the last 30 years, the annual mean temperature at Falsterbo increased with about 0.05 °C yr^{-1} ($R^2 = 0.219$, $P < 0.01$). The mean temperature in February, the coldest month, also increased significantly (+ 0.11 °C yr^{-1}, $R^2 = 0.13$, $P = 0.047$). January temperatures remained unchanged (+ 0.04 °C yr^{-1}, $R^2 = 0.02$, $P = 0.5$). The beech mast index varied markedly between years (average beech mast crop = 2.17 ± SD 2.05), but did not change over the time period 1975–2004 ($r_s = 0.08$, $P = 0.7$).

There was a strong tendency for an increase in the number of blue tits counted during visible migratory passage in the years 1975–2004 (ln-transformed number of migratory blue tits = 0.092 × year−175.5, $R^2 = 0.115$, $P = 0.067$, Fig. 1a). With one more year added (2005), a year otherwise not included in the analysis, the relationship is statistically significant ($R^2 = 0.129$, $P = 0.048$). The size of the breeding population in Sweden during the same time period increased significantly (index of breeding population size = 0.01 × year−20.11, $R^2 = 0.403$, $P < 0.001$, Fig. 1b). As expected from two increasing trends, they were significantly positively correlated ($r = 0.602$, $P < 0.001$). More importantly, the yearly residuals were strongly positively correlated ($r = 0.532$, $P < 0.01$, Fig. 2), suggesting that when the breeding population size is large, more birds will migrate.

Blue tit migration recorded in the standardized ringing was strongly correlated to the numbers from
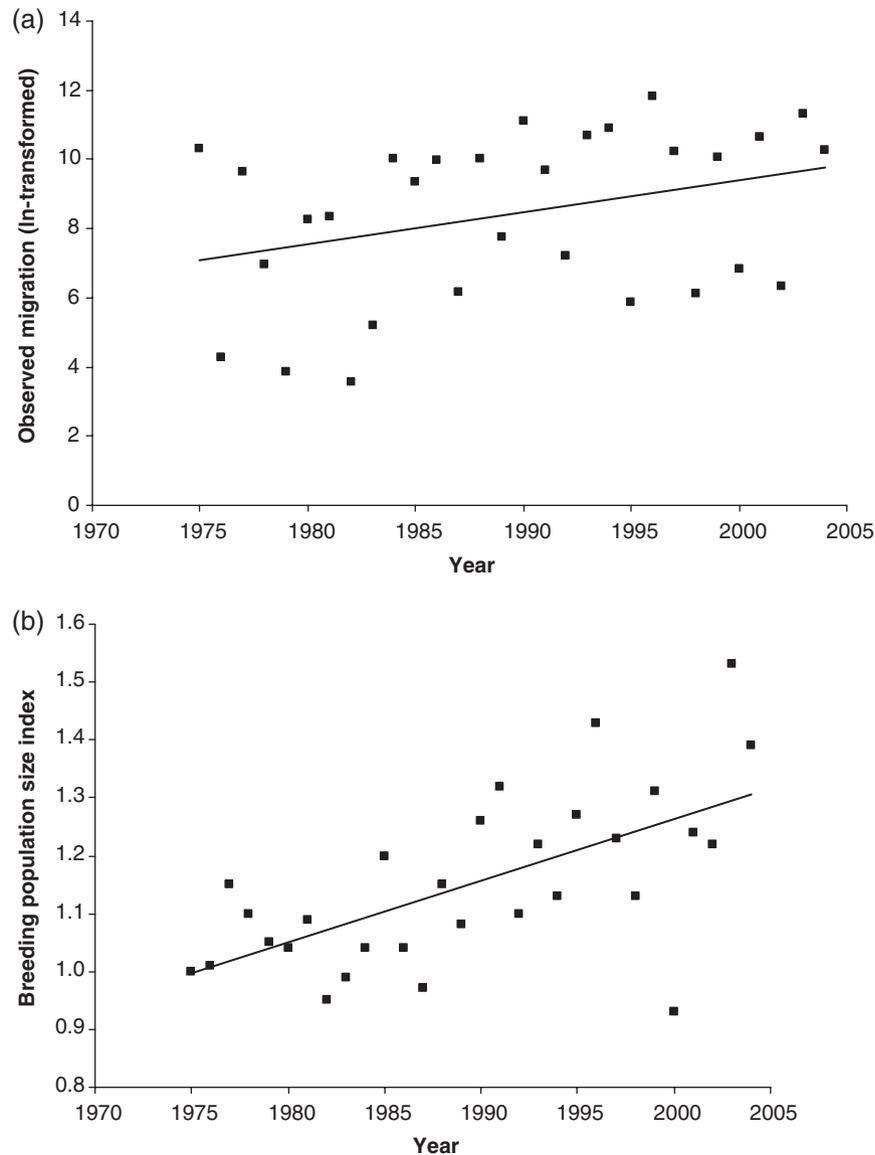
Fig. 1 (a) Trends in observed migration (ln-transformed counts to reach normality) and (b) breeding population size of the blue tit during 1975–2004.

the visible observation counts ($r = 0.97$, $P < 0.001$). Both our estimates of proportion of migrants (observed migrants/breeding population index and adult migrants trapped/breeding population index, respectively) tended to increase over the respective study periods, which is contrary to the prediction of a significant decrease in the proportion of migrants (Fig. 3a, ratio all observed migrants/breeders, $R^2 = 0.10$, $P = 0.082$; Fig. 3b, ratio adult trapped migrants/breeders, $R^2 = 0.14$, $P = 0.086$, but note that the second relationship depends heavily on the low numbers of adult migrants in 1983). Thus, we found no indication that the proportion of migrants in the population has declined over our study period, rather the opposite.

When evaluating six different models of predicting the observed migratory intensity of blue tits (Table 1), we found the model consisting of beech mast index, breeding population size index, and May temperature to be the most parsimonious model (with the lowest AIC_c). The model can be written as migration = 8.37–$1.21 \times$ beech mast index + $1.04 \times$ breeding population size index + 0.70 May temperature. The beech mast index had the largest impact on the observed blue tit migration (effect size = −1.21). In contrast to the other factors affecting the intensity of blue tit migration, the effect of beech mast was negative, implying that low beech mast crops were associated with high migratory intensity. The relative effect of breeding population size
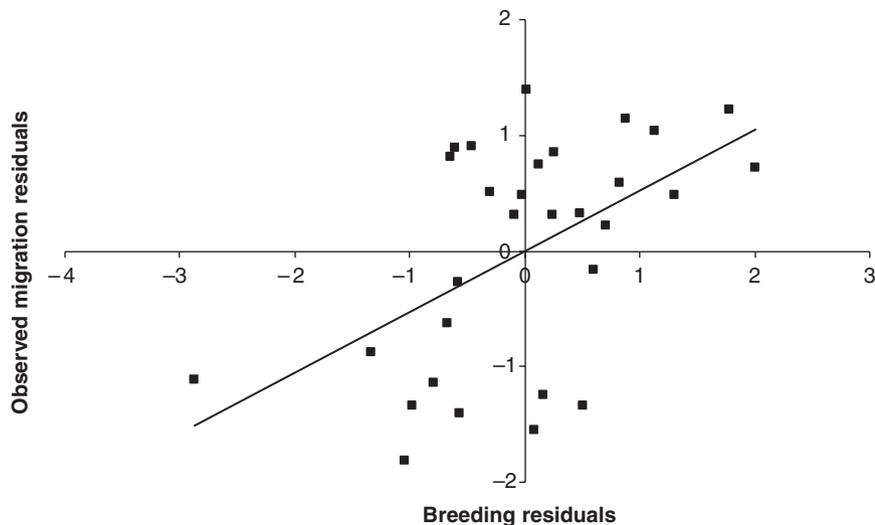
Fig. 2 Yearly residuals (from the long-term trend) of observed migration in relation to the yearly residuals (from the long-term trend) of breeding population size during 1975–2004. Relatively many migrants were found in years when the breeding population was relatively large.

on migratory intensity was higher (1.04) than the effect of the temperature in May (0.70). Small breeding populations and low temperatures in May are thus reducing the migratory intensity of blue tits in autumn. The second best model, including only the beech mast and breeding population size indices, differed with only 2.15 units from the best model. Given the small difference and that the ecological meaning of May temperature (the variable differing between models) is somewhat uncertain, both models can be considered equally good at explaining the variation in observed migratory intensity (Table 1).

Discussion

There has not only been a general warming trend at a global level (Easterling *et al.*, 1997), but also at more regional levels. Moberg & Jones (2005) showed that the winters in central and western Europe during the last half of the past century has overall become milder. At Falsterbo, the mean annual and, more importantly, February temperatures increased over the period 1975–2004. February is often the coldest month of the year and it is likely that temperatures then are critical for the survival of residents (Hildén, 1982; Newton, 1998). There is a high correlation among temperatures measured across large parts of Sweden (Alexandersson, 2002), suggesting that the Falsterbo temperatures are representative for the recruitment area of blue tits passing Falsterbo on migration. We, therefore, find it appropriate to discuss the migration habits of the partially migratory Swedish blue tit population in a global warming perspective.

By studying a single species, we do not aim to test the generality of Berthold's hypothesis. However, the blue tit is a common and well-studied partial migrant at Falsterbo (Heldbjerg & Karlsson, 1997), its population changes are well known (Lindström & Svensson, 2005), and the ecology is well studied, including its food preferences (Ulfstrand, 1962). Thus, the possibilities to detect and describe the influence of warmer climate on a partially migratory bird species should be unusually good.

The proportion of migrants within the Swedish blue tit population did not decrease over the last decades. Thus, we found no support for the prediction by Berthold (2003), that under a climate warming scenario the migratory habit among partial migrants should decline or even cease. If anything, both our estimates of the proportion of migrants, the ratio of adult migrants to the size of the breeding population and the ratio of total migrant number to the size of the breeding population, may have increased with time. Should partial migration mainly be under genetic control (Berthold, 2001), the first estimate may be the most appropriate. Migratory adults are likely to have migrated already during the preceding years as juveniles (cf. Heldbjerg & Karlsson, 1997), giving us a measure of population density that do not just represent a "surplus" in the form of this year's production of young. Should the number of migrants be explained mainly by exogenous factors, where subdominant individuals are forced to migrate (Smith & Nilsson, 1987; Lundberg, 1988), the second estimate, including all migrants when calculating the proportion of migrants, may be more appropriate. We conclude that the proportion of migrants in the Swedish blue tit
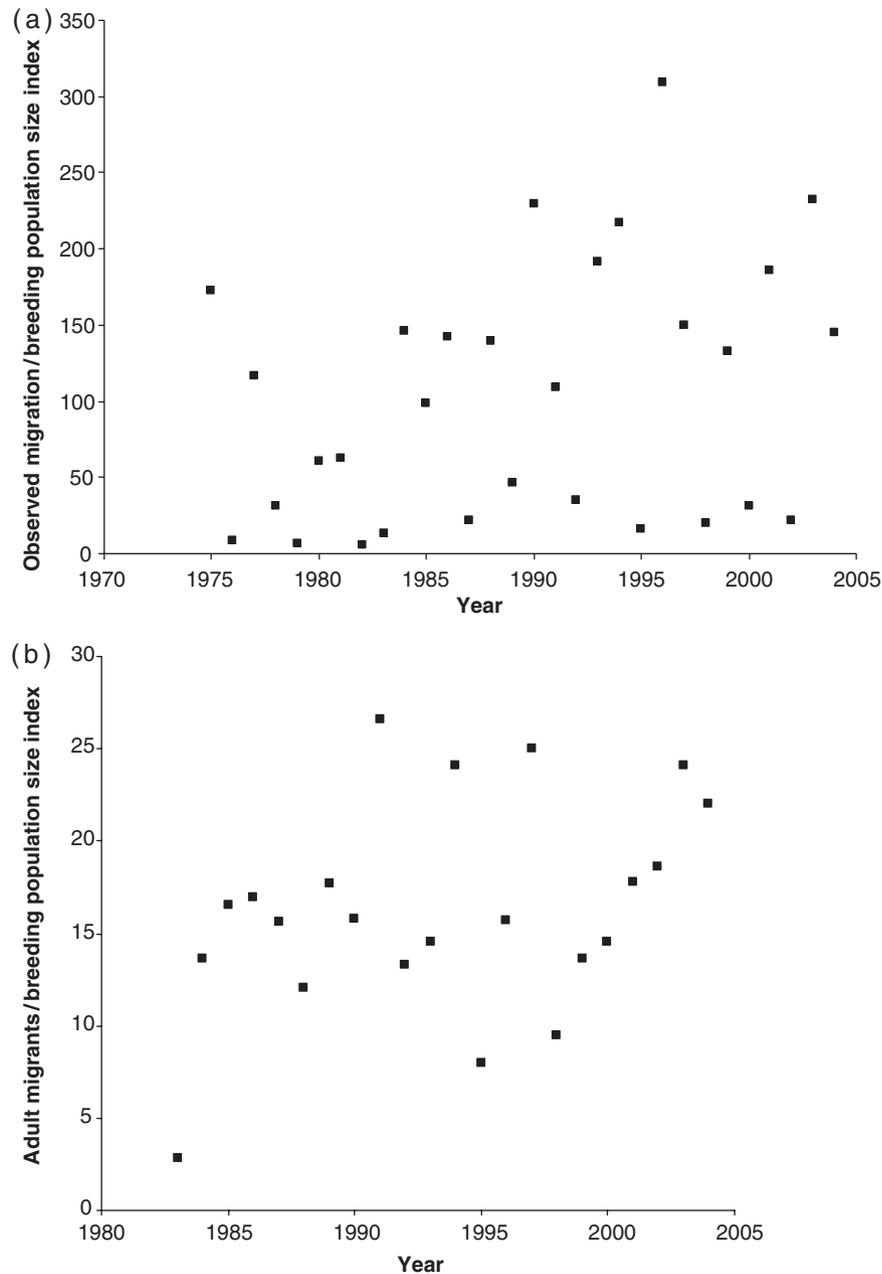
Fig. 3 (a) The ratio of all migrants from observed migration counts (1975–2004) over breeding population size. (b) The ratio of adult migrants recorded in the standardized ringing (1983–2004) over breeding population size. Ratios are square-root transformed according to Sokal & Rohlf (2001).

population has not declined along with a warmer climate regime. If any change has occurred, the blue tits have become more migratory. Although we with this type of analysis cannot completely exclude that a warmer climate has influenced the proportion of migrants in the predicted direction, it is clear that if it has, other factors have been far more important in shaping blue tit migration dynamics, and then in a direction opposite to the predicted.

When evaluating various factors with the potential to influence the number of migratory blue tits, the beech mast index and the breeding population size index had the strongest influence. There were more migrants in years with fewer beech seeds, higher breeding density and higher temperature in May. The effect of temperature in May was the weakest and its ecological significance somewhat uncertain. We will, therefore, focus the discussion on the first two variables. The most simple

Table 1 Alternative models for explaining the annual variation in observed blue tit migration, with number of estimated parameters (K), Akaike information criteria corrected for small sample size (AIC_c), AIC_c differences (Δ_i) and explanatory power of models (R^2)

Model	K	AIC_c	Δ_i	R^2
Beech + breeding pop + May temp	4	114.63	0	0.63
Beech + breeding pop	3	116.78	2.15	0.56
Breeding pop	2	120.55	5.92	0.45
Beech + May temp	3	120.92	6.29	0.49
Beech	2	125.36	10.73	0.35
May temp	2	136.21	21.58	0.05

explanation to the increase in migrants at Falsterbo is that the breeding population has increased in size. Everything else being equal, if there are more birds around, more birds will migrate. Whether the constant (or possibly increasing) proportion of migrants in the population is due to a constant proportion of genetically disposed migrants (Berthold, 2001), or due to more behaviourally-mediated migrants in years of high population density (Smith & Nilsson, 1987), is not possible to determine with the present data.

Are there alternative explanations to the higher number, and possibly higher proportion, of migrants than simply a larger population size? One alternative would be that some important autumn or winter resource have deteriorated. However, this is unlikely. First, the size of beech mast crops in our study area has not declined with time. Further, the crop size of beech trees increases strongly with tree size (Nilsson & Wästljung, 1987) and the number of large trees has increased in Sweden (Swedish National Forest Inventory), partly because the stands of beech has been protected since 1974. Thus, the amount of beech seeds may even have increased over the study period, providing increasing resources of food. Second, the winter population, as measured by standardized point counts (corresponding to the summer point counts used for our analysis), has also increased in size (Lindström & Svensson, 2005). Both these factors speak against deteriorating winter conditions causing more birds to migrate. However, although more birds in total can be sustained in south Sweden during winter, we cannot exclude that there are fewer resources *per bird*, resulting in more birds choosing, or being forced, to migrate.

Another reason for more birds to migrate would of course be that genetically controlled migrants have succeeded at least as well as the residents, due to increasingly more favourable conditions along the migration route or in winter quarters they reach, which would favour migration as a strategy. The area of suitable winter habitat, deciduous forests, has increased markedly in Denmark and further south (Anon, 2003). However, in the Danish Bird Survey, the blue tit has increased in numbers only during breeding, and remained stable in winter (Heldbjerg, 2005), indicating that conditions on the wintering grounds for the increased inflow of migrants has not suddenly become more favourable. Theoretical work on coexistence of migrant and resident strategies in partially migratory populations has indicated unequal balancing of the fitness benefits (Lundberg, 1988; Kokko & Lundberg, 2001) (i.e. migrants are doing the best of a bad job). Unfortunately, there is no information available on the fitness of blue tits with different migratory strategies. However, in the partially migratory European robin *Erithacus rubecula*, residents were clearly selected for by having both higher survival and higher reproductive success than migrants (Adriaensen & Dhondt, 1990).

The present analysis has emphasized the importance of population density and food abundance for blue tit migration. Although these factors may well in turn be influenced by climate change, we conclude that the partially migratory Swedish blue tit population over three decades of a climate warming scenario has not become less migratory. This shows that the effect of climate change on bird migration systems are by no means as easy to predict, or as general, as we may think.

Acknowledgements

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