Do weather conditions affect the dynamics of bearded tit *Panurus biarmicus* populations throughout the year? A case study from western Poland

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Climate change is considered to be one of the factors explaining a recent increase of bearded tit populations. To test this hypothesis, the effect of weather conditions on breeding and wintering populations in western Poland between 1986 and 2005 was studied. Weather did not influence annual changes in the breeding population, whereas non-breeding numbers were positively associated with spring and autumn temperatures. There was a slight trend for earlier egg laying related to higher March–April temperatures. These results suggest that the bearded tit may potentially benefit from climate warming through a prolonged breeding season which in turn could enable more broods to be raised. This conjecture was supported by the fact that the bearded tit showed a strong tendency to start breeding early, well before conditions for maximal clutch size, breeding success and egg volume occurred.

Introduction

Birds are considered an ideal model group for examining the impact of climate changes on animal populations (Walther *et al.* 2002). Weather conditions affect birds' phenology, breeding performance and winter survival which in turn influence population dynamics and distribution (Crick 2004, Dunn 2004, Sæther *et al.* 2004). Increasing air temperatures (Houghton *et al.* 2001) affect birds differently depending on their life histories and geographical distributions. Altricial species of northern temperate climates may profit from milder weather conditions before and at the beginning of the breeding season (Sæther *et al.* 2004). In the case of sedentary species, population growth is caused by higher winter survival (Sæther *et al.* 2000). Despite the number of relevant papers (*see* Sæther *et al.* 2004 for a review), our knowledge of the relationship between bird populations and climate is not yet sufficient. Long-term data, needed for analysis, are available only for a limited set of species and locations. These species are represented mainly by common woodland and farmland species (Sæther *et al.* 2004). However, the response of marshland bird species to climatic conditions may be quite different than in woodlands, mainly due to food resource dynamics (Schaefer *et al.* 2006). Another problem is

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that studies rarely examine the impact of weather conditions at different times of the year.

The bearded tit *Panurus biarmicus* is a small. sedentary passerine (13-18 g), a year-round occupant of littoral vegetation, mainly reed (Phragmites australis) stands (Cramp 1998). Since the middle of the 1980s it has shown a significant increase in many European countries. Simultaneously, the species has expanded its range into northern and eastern parts of the continent (Gosler & Mogyorósi 1997). Gosler and Mogyorósi (1997) explained these changes as a response to climate warming, as the species is suspected of being highly sensitive to harsh winter conditions (Spitzer 1972). Indeed, in several long-term studies on bearded tit populations, marked declines were noted after hard winters (e.g. Björkamn & Tyrberg 1982, Campbell et al. 1996). However, there are virtually no studies in which the linkage between bearded tit population changes and weather conditions were investigated using multiple variable models (but see Peiró & Macià 2002). Despite this, the bearded tit is often considered as a model species for reflecting climate dependent population changes (Burton 1995).

The Polish population of bearded tit reflects the European trends, both in number of breeding pairs and north-eastward range expansion (Tomiałojć & Stawarczyk 2003). There is also evidence that rising temperatures during winter and early spring may affect the phenology (Tryjanowski *at al.* 2002, Ptaszyk *et al.* 2003), breeding performance (Ptaszyk *et al.* 2003, Tryjanowski *et al.* 2004a) and life-history traits (Tryjanowski *et al.* 2004b) of other bird species in Poland.

In the current paper, we attempt to verify the hypothesis that climate warming has caused expansion of the European population of bearded tit. It has been assumed that the bearded tit population increase may be caused by two, not mutually exclusive, mechanisms. In the first case, milder winter conditions may have led to a greater number of surviving birds (tub hypothesis, Lack 1954, Sæther *et al.* 2004). The second theory states that the between-season change in population size is related to the weather during the breeding season because this influences the inflow of new recruits into the population (tap hypothesis, Sæther *et al.* 2004). To test both hypotheses we modeled year-to-year changes in the bearded tit with weather conditions as independent variables. The greatest variation in temperature during the bearded tit breeding season in Poland occurs in early spring. For this reason we also seek relationships between temperature during this time and breeding phenology. Possible advantages of changes in the timing of breeding were assessed from the distribution of breeding performance parameters during the breeding season.

Material and methods

Study area

We surveyed the breeding population of the bearded tit at Łoniewskie Lake (102 ha) near Osieczna, western Poland (51°54'N, 16°41'E). The site holds one of the largest and oldest-known populations of the species in Poland (Tomiałojć & Stawarczyk 2003). The lake is of the eutrophic type, with littoral emergents composed mainly of *Phragmites australis, Typha angustifolia, Juncus* sp. and *Carex* sp. Neither the area of emergent vegetation nor the water depth changed markedly during the studied period (for more details *see* Stępniewski 1995).

Data from the non-breeding period were collected at 14 locations near Poznań (52°27'N, 16°57'E, Fig. 1) in 1985–2002. The area is part of the Wielkopolska Lakeland with domination by intensive farmland. Small marsh patches, ponds and streams are common in the studied area. For further description of the area *see* Surmacki and Stępniewski (2003).

Bird census

With the exception of 1993 we censused the breeding population each year from 1986 to 2005. The number of breeding pairs was estimated by means of observations of the reproductive behaviour of adult birds (nest building, changeover of mates during incubation, nestling provisioning). The observations were performed from the top of a stepladder throughout the

breeding season (as Gilbert et al. 1998). The population was estimated at the beginning of the breeding period (i.e. before the end of April) to avoid recounting the same pairs raising consecutive broods. In this way, an accurate map of nest-site locations was constructed. In order to estimate the start of the breeding season each year, the study area was surveyed at 1-2 day intervals starting from 15 March. Between 3 and 26 nests were found each year and monitored throughout the season which constituted 13%-100% (mean 46.3%) of the total nest number (Stępniewski 1995, Surmacki et al. 2003). The nests were visited as infrequently as possible to avoid abandonment. Where possible, the firstegg date was calculated from direct observation or by back-counting. Three breeding parameters were calculated: breeding success, clutch size and mean egg volume in a clutch (cm³). Broods were classified as "successful" - at least one chick fledged or "unsuccessful" - no chicks fledged. Egg size was examined because it can positively influence chick survival in the first days of life, and thus affect the whole reproductive output of birds (Williams 1994). For more information on bird census and breeding biology studies see Stepniewski (1995), Surmacki et al. (2003). All fieldwork was performed by one person (J. Stępniewski).

Data on non-breeding bearded tits came from casual observations gathered by dedicated birdwatchers between 1985 and 2003. This was a part of a long-term project (1979–2003) on all bird species in the Wielkopolska region coordinated by the Department of Avian Biology and Ecology at Adam Mickiewicz University. Birdwatchers provided their observations on special cards with the following information completed: date, location, number of birds. In total, 93 observations of 748 individuals were gathered at 14 sites in the area described above (Fig. 1). The number of observations made per site varied between 1 and 44. Only observations made between September and February were analyzed.

Statistical analysis

We used stepwise backward regression models to detect the possible influence of weather on breed-



Fig. 1. Location of study sites. Filled circle (\pounds) = Loniewskie Lake (breeding site), Open circles = nonbreeding sites. Figures within circles refer to the number of observations made in a particular site, Rectangles = weather stations in Przybroda (P) and Turew (T), Grey area = the city of Poznań.

ing and non breeding population changes. The following independent variables were used in the analysis of the breeding period: (1) mean temperature in January, (2) total number of days with snow cover ≥ 10 cm depth, (3) mean temperature in April-June, (4) total precipitation in April-June, (5) mean temperature in August-October preceding the breeding season. The variables that were used in the analysis of the population outside the breeding season were: (1) mean temperature in January, (2) total number of days with snow cover ≥ 10 cm depth, (3) mean temperature in April-June preceding the non-breeding period, (4) total precipitation in April–June preceding the non-breeding period, (5) mean temperature in August-October. All the variables selected can be considered as important during the bearded tit life cycle. January is the coldest month in Poland and the deep snow cover is suspected to decrease bearded tits' survival (Parslow 1973, O'Sullivan 1976). The majority of active nests in the studied population occur between April and June (Stepniewski 1995). Low temperatures and high rainfall at that time may reduce breeding success (Stępniewski 1995). Between August and October the peak dispersal of young birds takes place (Cramp 1998). Weather data for the breeding site were obtained from the Field Station of the Polish Academy of Science at Turew ca. 20 km north-east of Łoniewskie Lake. Weather data for the non-breeding season were collected at the Field Station of the August Cieszkowski Agricultural University of Poznań in Przybroda, located approximately in the middle of the study area (Fig. 1).

The dependent variables used in stepwise regression models were the total number of pairs breeding at the lake (breeding season) or the total number of birds recorded between September and February (non-breeding season). In the case of non-breeding data, there was a possibility that the recorded data could be biased due to between-year differences in birdwatchers' activity. For this reason, non-breeding numbers were expressed as the number of bearded tits divided by the total number of all observation cards (including other species) returned by birdwatchers in that particular year.

In the time series analysis, data for a particular year are often determined by the data of the previous year. For this reason, both dependent and independent variables were transformed into indices representing the change between year y and year y - 1. The seasonal variability of breeding parameters was illustrated as 15-day moving averages (Vanicsek & Ludvig 1992, Ludvig et al. 1995). Time trends in the start of breeding were analyzed by linear regression weighted by the number of nests. Two separate models were created; one for the annual median date of egg laying and the other for the first egg laying dates for the population. It was assumed that clutches initiated in March and April are the first attempts of breeding pairs. Only these broods were included in the analysis. Information on these from 1986, 1993, 1995 (for the first egg in the population only) and 2001 are lacking and were therefore not included. To determine the effect of egg laying date, clutch size and year of study on breeding success, successful broods (n = 49) were compared with failed ones (n = 46)using logistic regression in a backward stepwise approach (Hosmer & Lemeshow 1989). Seasonal

trends in mean egg volume and clutch size were analyzed by linear regression. In the analysis of seasonal trends in breeding success, egg volume and clutch size, data from all years were used. In order to standardize timing of breeding, the date of clutch initiation was calculated as the number of days from the first egg date (day zero) for the population in a given year. All analyses were performed with the statistical package STA-TISTICA (StatSoft, Inc. 2003) and SPSS/PC+ (Norusis 1994).

Results

We tested for trends in weather parameters in both breeding (1986–2005) and non-breeding sites (1985–2003). In the breeding site, there was a negative significant trend for the duration of snow cover (linear regression: $F_{1,19} = 11.94$, p = 0.003, b = -0.62, SE = 0.18) and marginally significant negative trend for spring precipitation (linear regression: $F_{1,19} = 4.02$, p = 0.06, b = -0.42, SE = 0.21). In the non-breeding site, there was significant positive trend for spring temperature (linear regression: $F_{1,18} = 12.40$, p = 0.002, b = 0.66, SE = 0.18) and autumn temperature (linear regression: $F_{1,18} = 13.93$, p = 0.002, b = 0.64, SE = 0.18). In all other cases trends were not significant (P > 0.05).

Both breeding and non-breeding populations of bearded tit showed a gradual increase until 2000, then sharply declined (Fig. 2). The number of breeding pairs and the non-breeding population index were significantly correlated (r = 0.78, p < 0.01, n = 16). However, there was no significant correlation when population changes were compared (r = 0.26, p = 0.38, n = 14).

None of the weather variables significantly affected breeding population changes ($F_{5,11} = 1.09, p = 0.31, R^2 = 0.005$; autumn temperature: b = 0.73, SE = 4.28, t = 0.17, p = 0.87, January temperature: b = 0.63, SE = 0.79, t = 0.80, p = 0.44, spring precipitation: b = -0.09, SE = 0.06, t = -1.40, p = 0.18, spring temperature: b = -2.02, SE = 1.94, t = -1.04, p = 0.31, snow cover: b = 0.22, SE = 0.44, t = 0.49, p = 0.63). In contrast, changes in the non-breeding population were linked with climatic conditions ($F_{5,12} = 6.44, p = 0.01, R^2 = 0.39$). The mean spring temperature



Fig. 2. Changes in breeding and non-breeding populations of bearded tit in 1986–2004. Breeding data from 1993 are lacking.



Fig. 4. The number of clutches and the clutch size in 15-day moving averages. 0 = the first egg day for the population.

was positively associated with the change in number of observed birds (b = 3.11, SE = 0.87, t = 3.57, p = 0.003). Mean August–October temperature was included in the model, although it was only marginally significant (b = 2.27, SE = 1.25, t = 1.82, p = 0.09). January temperature (b= -0.23, SE = 0.28, t = -0.83, p = 0.42, spring precipitation (b = 0.01, SE = 0.02, t = 0.14, p =0.89) and snow cover (b = -0.26, SE = 0.22, t =-1.18, p = 0.26) were excluded from the model.

Bearded tits did not show any trend in the median clutch initiation date during the study period (linear regression: $F_{1,15} = 0.71$, p = 0.40, b = -0.14, SE = 0.16). However, a significant trend was observed for the first egg date for the population (linear regression: $F_{1,14} = 28.87$, p < 0.001, b = -0.53, SE = 0.10). Moreover, the first



Fig. 3. Correlation between mean March–April temperatures and the first egg dates for the population. 0 = 1 March.



Fig. 5. The average egg volume (cm^3) in a clutch and breeding success in 15-day moving averages (0 = the first egg day for the population). The vertical line indicates the date when the highest number of broods occurred.

egg date for the population was related to mean March–April temperature (linear regression: $F_{1,14}$ = 84.02, p < 0.001, b = -2.63, SE = 0.29, Fig. 3).

The maximum number of initiated broods was observed at the beginning of the season, then it decreased (Fig. 4). Similar changes were observed for clutch size, but the decline was markedly less steep (linear regression: $F_{2,117} = 16.93$, p < 0.001, b = -0.013, SE = 0.003, Fig. 4). The breeding success showed two peaks; firstly, on about the 35th day and the second smaller peak on about the 65th day from the beginning of the season (Fig. 5). However, results of logistic regression showed that the date of clutch initiation, clutch size or year did not affect breeding success significantly ($\chi^2 = -9.96$,

df = 13, p = 0.53). The mean egg volume showed a slight increase in the course of the breeding season (linear regression: $F_{1.74} = 7.37$, p = 0.01, b = 0.001, SE = 0.0004, Fig. 5).

Discussion

In contrast to previous predictions, our results did not provide any evidence for the impact of severe winters on populations of bearded tit. The first possible explanation is that birds wintered far from their breeding quarters, so they were simply not exposed to the weather conditions used in the analysis. In the east German population of bearded tits about one third of the birds overwinter 100-700 km southwest from their breeding (or natal) sites (Dürr et al. 1999). Similar movements were also observed among the Czech and Slovak populations (Hořák et al. 2003). In the studied population, however, the situation appears to be different. We analyzed recovery data of birds ringed on their breeding grounds (as adults and nestlings) in a radius of 35 km from Łoniewskie Lake between 1991 and 2004 (J. Stepniewski et al. unpubl. data). Of 23 controlled during the following winter, only two moved over 150 km. The rest wintered on the breeding site (n = 10) or within 8 km (n = 11). These results suggest that the bearded tit population in western Poland is chiefly sedentary. Even if the majority of birds overwintered within the studied site and died because of unfavourable conditions, they might be replaced by incomers from adjacent populations. In the studied population 9 birds ringed abroad were caught or seen during the breeding season in Łoniewskie Lake; two from the Czech Republic, four from east Germany and 3 of unknown origin (J. Stepniewski et al. unpubl. data). The data from Germany, the Czech Republic and Slovakia also confirm the mixing of individuals between populations as far as 600 km apart (Dürr et al. 1999, Hořák et al. 2003). In an isolated and sedentary population studied in Spain a negative effect of winter temperatures on population fluctuation was found (Peiró & Macià 2002).

Favourable weather conditions during the breeding season may affect reproductive success and therefore also population dynamics in two ways. First, by providing better conditions for brood raising and nestling survival. The second possibility refers to multi-brooded species, whose seasonal reproductive success depends not only on the fate of a single brood but also on the number of broods that a particular pair can raise. Crick et al. (1993) demonstrated that in these species there is a strong selection to start laying eggs earlier, even before optimal conditions for raising nestlings. This tendency is also present in species with frequent replacement broods (e.g. Kosiński 2001). Thus, earlier nesting initiation can theoretically lead to an increased number of broods, and consequently to population growth. The bearded tit raises up to four regular broods (beside repeated broods after losses, Stepniewski 1995, Cramp 1998) with the latest nesting attempts occurring in August (Stępniewski 2000). Our data showed slight advancement of egg laying dates in bearded tit, which was related to warmer March-April weather. Moreover, seasonal changes in breeding performance parameters and in the number of breeding pairs fit the model created for multibrooded species by Crick et al. (1993). There is a strong tendency in the bearded tit to start breeding in the early phase of the season, markedly before optimal circumstances occur (maximum egg volume, maximum clutch size and the highest breeding success, Figs. 4 and 5). Thus, we may expect that in seasons with warm springs they have enough time to raise more broods. The question remains, why was a positive effect of spring temperatures detected in the wintering population but not in the breeding one? Possibly the positive effect of the warm spring might be blurred by winter mortality and movements, and not maintained through to the following breeding season. Thus, spring temperature may act as a proximate factor regulating the nonbreeding population. Another variable positively influencing non-breeding population dynamics of the bearded tit was August-October temperature. This effect may be explained in two ways. Firstly, between August and September birds make a decision whether to stay within the breeding area or move farther (see Cramp 1998). It is possible that favourable temperature conditions, especially in late autumn, encourage birds to overwinter in the breeding (natal)

area. Secondly, during a warm autumn, birds may have better access to food, which improves their general condition and consequently their winter survival chances. Insects, which form the main summer diet, are still active and accessible during fine autumn weather. Moreover, it has been proved that production of reed seeds, which are the basic winter food, are positively affected by temperatures between August and October (McKee & Richards 1996).

According to our results, climatic conditions may have only a limited impact on bearded tit populations; confined mainly to weather during the breeding season. Nevertheless, we should be aware of the fact that the species has a distinctly patchy distribution and that the studied population could be a part of a larger metapopulation. Moreover, populations of the same species may react to weather conditions depending on their geographical distribution (Both *et al.* 2004). For these reasons further surveys embracing larger populations at different locations are required.

Conclusions

- Our survey did not provide evidence that harsh winter conditions are the main factor limiting bearded tit populations.
- 2. Changes in bearded tit populations are more likely to be caused by weather conditions during the breeding season (tap hypothesis). However, direct evidence came only from analysis of the wintering population. It is possible that the positive effect of warm springs on the breeding population is partially blurred by the winter mortality and autumn migration and thus not detectable in the following season.
- 3. Bearded tit slightly advanced egg laying dates during the studied period and this process was related to milder March–April periods. These results suggest that climate warming can be beneficial for the species through prolonging the breeding season and consequently raising more broods. This assumption is supported by the fact that bearded tits tend to start reproduction as early as possible, even before conditions for optimal breeding performance are reached.

4. Higher autumn temperatures were positively correlated with a rise in the non-breeding population. This effect may be linked to better foraging conditions and, therefore, also winter survival.

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