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Authors: Reif, Jiří, Telenský, Tomáš, Šťastný, Karel, Bejček, Vladimír, and Klvaňa, Petr

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Relationships between winter temperature and breeding bird abundance on community level: importance of interspecific differences in diet

Jiří REIF[1]*, Tomáš TELENSKÝ[1], Karel ŠŤASTNÝ[2], Vladimír BEJČEK[2] and Petr KLVAŇA[3]

[1] *Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Benátská 2, CZ-128 01 Praha 2, Czech Republic; e-mail: jirireif@yahoo.com*
[2] *Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, CZ-165 21 Praha 6, Czech Republic*
[3] *Bird Ringing Centre, National Museum, Hornoměcholupská 34, CZ-102 00 Praha 10, Czech Republic*

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Abstract. Winter weather limits populations of resident bird species. Although many small-scale or species-specific studies illustrated this fact, our knowledge of interspecific differences in population responses to winter temperatures is incomplete due to lack of community-level studies. For this purpose, we have used long-term monitoring data on breeding bird populations of 37 common bird species wintering in the Czech Republic. We predicted that species will differ in their relationship between winter temperature and abundance with respect to their body mass and dietary niche. Smaller species having relatively higher energy expenditure should show closer relationship between breeding abundance and winter temperature than larger species. Concerning dietary niche, abundance of species feeding on animals should be more affected by temperature than abundance of species feeding on plants or omnivorous species. Our results confirmed the second prediction: populations of species preying on animals followed winter temperatures more closely than populations of species feeding on both animals and plants. Food-mediated mortality is probably more important than direct effects of low temperatures. In general, relationships between abundance and temperature were relatively weak in most species and we suggest that possible changes in winter temperatures may not seriously affect populations of common breeding birds in the Czech Republic.

Key words: climate, food type, body size, abundance, bird assemblage, population regulation

Introduction

Harsh winter weather strongly affects populations of resident bird species and there are several ways to such density regulation (Newton 1998). First, low temperatures can directly kill individuals that are not able to adjust their thermal regulation to conditions of higher energetic demands (Bakken et al. 1991). Second, birds' food requirements increase in colder periods to cover higher energy expenditure needed to keep body temperature constant. Under conditions of food shortage, some bird individuals are not able to satisfy their energy demands and they die due to lack of food (Lahti et al. 1998, Robison et al. 2007). Food accessibility might be lower in winter either due to low temperatures when the prey is hidden in refuges to prevent freezing or due to snow or ice cover (Rolstad & Rolstad 2000). Therefore, breeding abundance of many resident bird species is dependent to large extent on weather conditions in the preceding winter (Newton 1998). For this reason, temperature in winter months became an integral part of models predicting species' responses to global climatic changes in terms of distributional shifts (Huntley et al. 2007, Doswald et al. 2009).

Although these models do not discriminate among species-specific ecological characteristics (but see Doswald et al. 2009), we suggest that population

* *Corresponding Author*

response to winter climate does need not to be universal within resident bird species.

Empirical studies of the relationships between population abundance and climatic conditions are not very common on community level (Jones et al. 2003). Most of the current knowledge is based on studies performed on species level in local scale (e.g. Holmes et al. 1986, Virkkala 2004) showing adverse effects of harsh winters on selected resident species due to lower food supply or temperature-mediated mortality (Lahti et al. 1998, Newton et al. 1998, Sæther et al. 2000, Robinson et al. 2007, Siriwardena et al. 2007). Climatic conditions in the Czech Republic, a central European country situated in transition zone between oceanic and continental climate (Tolasz et al. 2007), offer good opportunity to explore the effects of winter temperature variation on bird populations. Due to occurrence of both harsh and mild winters we can expect remarkable variation in bird populations caused by annual fluctuations of climatic conditions. Moreover, long tradition of annual monitoring of bird populations in this country (Janda & Šťastný 1984) provided high quality data on breeding abundance for number of species enabling a community level analysis (Reif et al. 2006).

For such an analysis, we have selected species with high proportion of individuals staying on breeding grounds during winter (Cepák et al. 2008). We have related breeding abundance of each species to average temperature of the preceding winter to express its dependence on winter weather. We have predicted that the species would differ in responses of their populations to winter weather due to the influence of ecological differences among species. First, efficiency of thermal regulation increases with body mass (Aschoff 1981, Meehan et al. 2004). Therefore, we expected that abundance of larger species would follow changes in temperature less closely than abundance of smaller species. Second, the effects of temperature might act through food supply (Lahti et al. 1998, Robinson et al. 2007). We can expect that species with different dietary niches would differ in dependence of their abundance on winter temperature. Accessibility of seeds and other plant tissues should be less dependent on temperature compared to the food of animal predators because their prey can actively hide in places enabling survival during the period of low temperatures (Avery & Krebs 1984, Carrascal et al. 2001, Zmihorski & Rejt 2007). Therefore, we can predict that abundance of species feeding on animals (carnivores and insectivores) should be more affected by temperature than abundance of species feeding on plants (e.g. seed-eaters) or omnivorous species. The aim of this paper was to test these two predictions using Czech bird monitoring data.

Material and Methods

Data

We used data from the Breeding Bird Monitoring Programme (BBMP) for the assessment of breeding bird population changes between 1982 and 2007 in the Czech Republic. BBMP is a large-scale generic bird monitoring scheme based on fieldwork of skilled volunteers (Janda & Šťastný 1984, Reif et al. 2006). All 335 census sites are scattered throughout the whole territory of the country and they form a representative sample of the Czech landscape (Reif et al. 2008a). Standardized point counts are used as a field method with 20 points visited two times per breeding season (to detect both early and late breeding species) at each census site. During one visit, all birds seen or heard were recorded for five minutes on each census point. In each year, abundance of a species at a given census site was calculated as the mean number of individuals from both visits (see Reif et al. 2007, 2008a for more details on field methods).

Wintering of bird species in the Czech Republic was assessed using information from the Atlas of bird migration in the Czech Republic and Slovakia (Cepák et al. 2008) based on all known ringing recoveries until 2002. For purposes of this study, we have selected 37 species with more than 75% of Czech breeding population wintering on the territory of the country (Cepák et al. 2008) and having good record in BBMP data at the same time (see Reif et al. 2008b). For these species (Table 1), we have obtained information about their body mass from local ornithological monographs (Hudec 1983, 1994, Hudec & Šťastný 2005) and about their winter diet from Bejček et al. (1995). We have recognized following categories of species' dietary niche: species feeding on animals (n = 9, three carnivorous species and six insectivorous), species feeding on both animals and plants (n = 15, including four omnivorous corvids), species feeding on plants only (n = 13, all but one were seed-eaters).

Winter temperatures were supplied by the Czech Hydrometeorological Institute as monthly means for December, January and February in each year from 1982 to 2007 (Table 1). Temperatures were positively correlated across years among all months but the correlation coefficients were relatively low and only one relationship was significant ($r_{\text{December–January}} = 0.46$, $P = 0.018$, $r_{\text{December–February}} = 0.22$, $P = 0.286$, $r_{\text{January–February}} = 0.28$, $P = 0.166$, $N = 26$ in all cases). Therefore, particular months were treated separately in following analyses.

Table 1. *Mean temperatures in particular winter months (December, January, February) in the Czech Republic measured from 1982 to 2007. Note that December temperatures were measured in the preceding calendar year (i.e. in December 1981 for the winter 1982 etc).*

Winter	December	January	February
1982	-3.1	-5.3	-2.1
1983	0.8	2.4	-3.2
1984	-1.2	-1.0	-1.7
1985	-0.8	-7.8	-5.6
1986	1.8	-1.6	-7.4
1987	-0.6	-7.9	-1.8
1988	0.5	1.3	0.9
1989	1.0	-0.2	2.5
1990	0.2	-0.3	3.6
1991	-1.0	-0.2	-4.5
1992	-2.0	-0.1	1.4
1993	-1.4	-0.1	-2.9
1994	1.6	1.7	-1.2
1995	1.0	-1.8	3.4
1996	-2.6	-4.6	-4.6
1997	-4.9	-4.5	1.5
1998	0.8	0.2	2.8
1999	-1.7	-0.4	-1.5
2000	-0.2	-2.2	2.3
2001	0.6	-1.5	0.4
2002	-3.4	-1.2	3.4
2003	-2.9	-2.3	-4.1
2004	-0.5	-3.7	0.7
2005	-0.6	-0.2	-3.4
2006	-1.1	-5.9	-2.8
2007	2.3	3.0	2.7

Statistical analyses

We have transformed abundance of each bird species into annual indices using log-linear models in TRIM 3.51 with the effects of individual census sites and years included into the model formula (Pannekoek & van Strien 2001). Log-linear models are standard tools for analysis of bird monitoring data based on counts and having Poisson distribution of errors. Serial correlation and over-dispersion from Poisson distributions were taken into account. The value of the index was set at 100% in 1982 as the first year.

As breeding bird abundance often shows density dependence it is impossible to relate abundance to environmental variables directly over time (Piha et al. 2007). We have adopted approach introduced by Sæther et al. (2003) expressing annual growth rate (r) of population of each species:

$$r = N_{t+1}/N_t \quad (1)$$

where N_t is the index of population abundance (computed using log-linear models, see above) in the year t. In the next step, we have related the logarithm of annual growth rate of the breeding population of a given species to winter temperature controlling for the effect of N_t:

$$\log(r) = a + bZ + cN_t \quad (2)$$

where Z is a vector of environmental variables (mean temperature in a given winter month in our case) and a, b and c are model parameters. Parameter b indicates the effect of winter temperature, parameter c indicates the effect of density dependence. As Z and N_t were not correlated, multicollinearity was not a problem in this regression model. To assess the strength of the effect of winter temperature on population of each species we used partial correlation coefficient calculated in the model. The more positive correlation, the higher dependence of species' breeding abundance on temperature in the preceding winter. We ran separate models for each of the winter months (i.e. December, January and February, respectively). As a result, each bird species obtained three different partial correlation coefficients, corresponding to respective months, quantifying the effects of winter weather of its population.

In the next step, we have modelled partial correlation coefficients as functions of body mass and dietary niche and their interaction across species. Partial correlation coefficients corresponding to different months were included together into a common model with the effect of "month" as an additional explanatory variable. This approach enabled us to test whether the partial correlation coefficients were more positive in one month compared to the others and thus to judge which part of winter has the strongest limiting effect on bird populations. Moreover, it was possible to focus on the interactions between different variables, testing, for instance, whether the effect of body mass is different in December compared to January. This approach also did not elevate the probability of Type I error.

Finally, we have performed linear mixed-effects models with random effects of species, genera, families and orders to control for the effects of phylogenetic relatedness of the focal species (expressed by taxonomy). Mixed-effects models were fitted using lme function in R package nlme (R development core team 2005) using maximum likelihood method recommended for comparison of models with different fixed effects structures (Crawley 2007). We have also used mixed-effects models to examine the within- and between-taxon-variability of partial correlation coefficients from the relationships between abundance and winter temperature. For this purpose, we used restricted maximum likelihood method which is independent on fixed effects (Crawley 2007). Classification of species to orders and families was based on information from Sibley & Monroe (1990) and to genera on information from Dudley et al. (2006). Body mass was log-transformed for statistical analyses to achieve normality. Partial correlation coefficients showed normal distribution among species (Kolmogorov-Smirnov tests: $d_{December} = 0.09$, $d_{January} = 0.11$, $d_{Febraury} = 0.09$, all $P > 0.20$).

Results

Temperature in winter months explained small part of annual variation in breeding abundance of particular bird species (Table 2). Generally, partial correlation coefficients indicating the strength of dependence of annual growth rates of species' populations on winter

Table 2. *Characteristics of 37 resident bird species with breeding populations monitored between 1982 and 2007 in the Czech Republic. Species are sorted with respect to their winter diet to: plant-eating species (P), animal-eating species (A), and species feeding on both animals and plants (A+P). Partial correlation coefficients (partial r) with corresponding significance levels (p) revealed by linear models show the effects of temperature (Temperature) in particular winter months (separate set of models were run for December, January and February) and species' abundance in previous breeding season (Abundance), respectively, on annual population growth rates of particular species. Species showing signifficant effect of temperature (at least in one month) are in bold.*

Species	Diet	Body mass (g)	December				January				February			
			Temperature		Abundance		Temperature		Abundance		Temperature		Abundance	
			partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*	partial r	*p*
Cygnus olor	P	10250	-0.26	0.212	-0.54	0.007	-0.11	0.624	-0.58	0.003	-0.10	0.626	-0.59	0.002
Anas platyrhynchos	A+P	1063	-0.01	0.974	-0.28	0.193	0.01	0.980	-0.27	0.200	0.41	0.047	-0.31	0.141
Buteo buteo	A	848	-0.12	0.563	-0.59	0.002	0.21	0.330	-0.60	0.002	0.51	0.011	-0.61	0.001
Falco tinnunculus	A	220	-0.02	0.938	-0.66	0.000	0.19	0.385	-0.68	0.000	0.29	0.176	-0.64	0.001
Perdix perdix	P	365	0.37	0.075	-0.43	0.034	0.18	0.406	-0.38	0.069	0.12	0.565	-0.33	0.110
Phasianus colchicus	P	1163	0.20	0.355	-0.56	0.004	0.09	0.661	-0.54	0.006	0.00	0.993	-0.53	0.007
Streptopelia decaocto	P	198	0.33	0.112	-0.20	0.355	0.60	0.002	-0.25	0.245	0.28	0.183	-0.29	0.168
Alcedo atthis	A	41	0.20	0.347	-0.44	0.030	0.48	0.019	-0.50	0.012	0.45	0.026	-0.58	0.003
Picus viridis	A	191	-0.08	0.717	-0.42	0.040	0.26	0.222	-0.39	0.057	-0.08	0.721	-0.41	0.045
Dryocopus martius	A	310	0.09	0.659	-0.35	0.092	0.07	0.008	-0.37	0.531	-0.07	0.731	-0.37	0.076
Dendrocopos major	A+P	81	0.27	0.206	-0.61	0.001	0.29	0.170	-0.52	0.009	0.00	0.996	-0.64	0.001
Dendrocopos minor	A+P	21	-0.21	0.322	-0.81	0.000	-0.26	0.228	-0.80	0.000	0.17	0.440	-0.80	0.000
Troglodytes troglodytes	A	10	0.54	0.007	-0.44	0.032	0.80	0.000	-0.74	0.000	0.49	0.015	-0.65	0.001
Turdus merula	A+P	93	0.56	0.005	-0.20	0.349	0.74	0.000	-0.40	0.056	0.35	0.095	-0.41	0.046
Aegithalos caudatus	A	8	0.00	0.987	-0.39	0.062	-0.22	0.292	-0.34	0.101	0.05	0.815	-0.38	0.068
Poecile palustris	A+P	11	-0.02	0.941	-0.39	0.061	-0.31	0.139	-0.40	0.052	-0.29	0.173	-0.46	0.025
Poecile montanus	A+P	11	0.16	0.442	-0.65	0.001	-0.10	0.648	-0.61	0.002	0.19	0.382	-0.67	0.000
Lophophanes cristatus	A+P	11	0.03	0.546	-0.44	0.130	-0.19	0.363	-0.41	0.047	-0.31	0.142	-0.41	0.046
Periparus ater	A+P	10	-0.29	0.172	-0.51	0.011	-0.26	0.224	-0.48	0.018	0.12	0.587	-0.51	0.012
Cyanistes caeruleus	A+P	10	0.17	0.437	-0.62	0.001	-0.03	0.873	-0.65	0.001	-0.10	0.632	-0.66	0.000
Parus major	A+P	12	-0.01	0.973	-0.56	0.005	-0.32	0.127	-0.54	0.006	-0.21	0.329	-0.59	0.003
Sitta europaea	A+P	19	0.02	0.935	-0.50	0.014	0.06	0.781	-0.52	0.010	0.36	0.086	-0.56	0.004
Certhia familiaris	A+P	23	0.34	0.101	-0.62	0.001	0.02	0.933	-0.63	0.001	0.28	0.189	-0.62	0.001
Certhia brachydactyla	A	9	0.15	0.498	-0.58	0.003	0.10	0.637	-0.60	0.002	0.02	0.923	-0.58	0.003
Garrulus glandarius	A+P	161	-0.10	0.652	-0.46	0.023	0.30	0.159	-0.37	0.073	0.12	0.577	-0.46	0.025
Pica pica	A+P	200	-0.22	0.300	-0.54	0.006	0.05	0.806	-0.55	0.005	-0.42	0.042	-0.54	0.006
Corvus monedula	A+P	230	0.22	0.311	-0.43	0.037	-0.01	0.973	-0.42	0.040	-0.06	0.796	-0.42	0.038
Corvus corone	A+P	506	0.00	0.983	-0.40	0.053	-0.08	0.714	-0.44	0.032	-0.08	0.696	-0.44	0.031
Passer domesticus	P	32	0.13	0.531	-0.28	0.182	0.28	0.190	-0.21	0.322	-0.12	0.582	-0.28	0.181
Passer montanus	P	23	0.29	0.173	-0.53	0.008	0.28	0.179	-0.52	0.009	0.14	0.506	-0.50	0.013
Fringilla coelebs	P	23	0.04	0.838	-0.22	0.301	0.05	0.827	-0.21	0.316	-0.03	0.893	-0.21	0.320
Carduelis chloris	P	28	-0.03	0.893	-0.32	0.134	-0.15	0.497	-0.34	0.104	0.39	0.061	-0.09	0.693
Carduelis carduelis	P	17	0.08	0.712	-0.54	0.007	0.09	0.674	-0.55	0.005	0.36	0.083	-0.53	0.008
Carduelis flammea	P	11	-0.35	0.097	-0.33	0.114	-0.18	0.400	-0.40	0.052	-0.15	0.497	-0.39	0.059
Loxia curvirostra	P	41	0.10	0.646	-0.64	0.001	0.23	0.277	-0.64	0.001	0.05	0.832	-0.64	0.001
Pyrrhula pyrrhula	P	28	0.35	0.095	-0.64	0.001	-0.08	0.704	-0.58	0.003	-0.02	0.916	-0.57	0.003
Emberiza citrinella	P	29	-0.01	0.959	-0.22	0.294	-0.23	0.272	-0.25	0.238	-0.44	0.030	-0.32	0.127

temperature were positive (mean$_{December}$ = 0.08 ± 0.04 (standard error), mean$_{January}$ = 0.08 ± 0.05, mean$_{February}$ = 0.07 ± 0.04) indicating that winter weather affects breeding population of Czech birds to some extent. The values of partial correlation coefficients did not differ among months ($F_{2, 108}$ = 0.01, P = 0.992) suggesting no indication of higher importance of some months compared to others for limiting of bird populations.

Only one species, winter wren (*Troglodytes troglodytes*), was significantly affected by temperatures in all three focal months. Five species were significantly affected by temperatures in one or two months: blackbird *Turdus merula* (December and January), kingfisher *Alcedo atthis* (January and February), buzzard *Buteo buteo* (February), mallard *Anas platyrhynchos* (February), collared dove *Streptopelia decaocto* (January). Majority of the focal species (63–78%, depending on the month used for the analysis) showed significant negative dependence of population growth rate on abundance in the previous breeding season, none showed positive dependence (Table 2).

Species' dietary niche was a significant predictor of the interspecific variation in the strength of the relationship between breeding abundance and temperature in particular winter months (month: $F_{2, 106}$ = 0.01, P = 0.991; dietary niche: $F_{2, 106}$ = 4.08, P = 0.020). Abundance of species feeding on animals followed winter temperatures more closely than abundance of species feeding on both animals and plants (post-hoc contrasts: difference between feeding on animals and feeding on both animals and plants P = 0.013, difference between feeding on animals and feeding on plants P = 0.151, difference between feeding and plants and feeding on both animals and plants P = 0.540, Fig. 1). The effect of dietary niche did not differ among particular winter months as indicated by non-significant interaction between month and dietary niche (month: $F_{2, 102}$ = 0.01, P = 0.991; dietary niche: $F_{2, 102}$ = 3.99, P = 0.022; month x dietary niche: $F_{4, 102}$ = 0.37, P = 0.829). In contrast to the significant effect of dietary niche on the relationship between breeding abundance and temperature, this relationship was not affected by body mass (month: $F_{2, 107}$ = 0.01, P = 0.992; body mass: $F_{1, 107}$ = 0.26, P = 0.609). The effect of body mass did not differ among months (month: $F_{2, 105}$ = 0.01, P = 0.992; body mass: $F_{1, 105}$ = 0.26, P = 0.609; month x body mass: $F_{2, 105}$ = 0.92, P = 0.400).

The significant effect of dietary niche and no effect of body mass remained consistent over various designs of linear models: after simultaneous testing the effects of dietary niche and body mass (month: $F_{2, 105}$ = 0.01, P = 0.991; dietary niche: $F_{2, 106}$ = 4.06, P = 0.020; body mass: $F_{1, 106}$ = 0.28, P = 0.595), after including the interaction between dietary niche and body mass (month: $F_{2, 103}$ = 0.01, P = 0.991; dietary niche: $F_{2, 103}$ = 4.12, P = 0.019; body mass: $F_{1, 103}$ = 0.29, P = 0.592; dietary niche x body mass: $F_{2, 103}$ = 1.81, P = 0.169), after including interaction between month and dietary niche and interaction between month and body mass, respectively (month: $F_{2, 97}$ = 0.01, P = 0.991; dietary niche: $F_{2, 97}$ = 4.02, P = 0.021; body mass: $F_{1, 97}$ = 0.28, P = 0.597; dietary niche x body mass: $F_{2, 97}$ = 1.77, P = 0.176; month x dietary niche: $F_{4, 97}$ = 0.37, P = 0.827; month x body mass: $F_{2, 97}$ = 0.99, P = 0.373). Reversed order of explanatory variables in the linear models showed the same significant terms (results not shown).

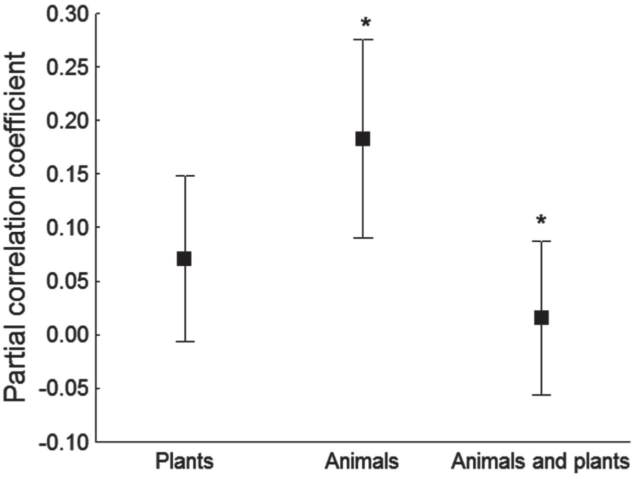

Fig. 1. *Mean (±95% confidence interval) strengths of relationships between species' breeding abundance and winter temperature (quantified by partial correlation coefficients) in the Czech Republic in three groups of resident bird species defined by species' winter diet (i.e. species feeding on animals, plants, or both animals and plants). Groups significantly different from each other according to results of post-hoc contrasts are marked with asterisks. See Methods section for more details on computation of relationship between breeding abundance and winter temperature.*

Linear mixed-effects models examined the fixed effects of month, diet and body mass given the random effects of species relatedness expressed by their species, genus, family and order status. These analyses did not reveal any significant results implying strong effect of phylogeny on ability of the explanatory variables to explain interspecific variability in the relationships between breeding bird abundance and winter temperature: model with dietary niche (month: $F_{2, 72} = 0.02$, $P = 0.984$; dietary niche: $F_{2, 13} = 0.43$, $P = 0.658$), model with body mass (month: $F_{2, 72} = 0.02$, $P = 0.984$; body mass: $F_{1, 6} = 0.00$, $P = 0.999$), model with interaction between dietary niche and month (month: $F_{2, 68} = 0.02$, $P = 0.984$; dietary niche: $F_{2, 13} = 0.42$, $P = 0.668$; dietary niche x month: $F_{4, 68} = 0.70$, $P = 0.596$), model with interaction between body mass and month (month: $F_{2, 70} = 0.02$, $P = 0.983$; body mass: $F_{1, 6} = 0.00$, $P = 0.999$; body mass x month: $F_{2, 70} = 1.89$, $P = 0.159$), model with interaction between dietary niche and body mass (month: $F_{2, 72} = 0.02$, $P = 0.984$; dietary niche: $F_{2, 13} = 0.43$, $P = 0.657$; body mass: $F_{1, 4} = 0.00$, $P = 0.968$; dietary niche x body mass: $F_{2, 4} = 0.79$, $P = 0.513$), the most complex model (month: $F_{2, 66} = 0.02$, $P = 0.984$; dietary niche: $F_{2, 13} = 0.41$, $P = 0.673$; body mass: $F_{1, 4} = 0.00$, $P = 0.969$; dietary niche x body mass: $F_{2, 4} = 0.75$, $P = 0.530$; month x dietary niche: $F_{4, 66} = 0.70$, $P = 0.593$; month x body mass: $F_{2, 66} = 1.87$, $P = 0.162$). All results were robust to different orderings of explanatory variables in the models (results not shown).

Finally, we have examined the random effects of species' taxonomonic categorization alone on the variability in partial correlation coefficients between breeding abundance and temperatures in particular winter months. Variability at the species level was highest for December (75%) and February (79%), respectively, and second highest for January (40%). Variability at the family level was the second highest for two months (December 25%, February 13%). For January, the variability explained at the family level was even the highest among all taxonomic levels (49%). The order level contributed to substantial part of variation for February (8%), and the genus level for January (12%). For the remaining months, order and genus levels had negligible contributions to variability in partial correlation coefficients (less than 1% in all cases).

Discussion

Our examination of relationships between breeding abundance and winter temperature in 37 common bird species wintering in the Czech Republic revealed four main patterns: (i) relationships were generally weak in most species, only six species showed significant partial correlation between population growth rate and temperature in at least one of the three winter months (December, January or February); (ii) the strength of these relationships was affected by diet: species preying on animals had stronger relationship between abundance and winter temperature than species feeding on both animals and plants; this pattern was consistent across all winter months; (iii) body mass did not affect the strength of the relationship between abundance and temperature; (iv) populations of more than two thirds of species showed density dependence (negative in all cases).

The first and fourth patterns imply that winter severity is not a very important component of population regulation of resident bird species in the Czech Republic. Intrinsic population processes seem much more important as most of the species showed significant negative density dependence. It means that annual change in breeding abundance of a species depends more on its abundance in the previous year than on temperature in winter. This finding is in contrast with the strong effect of climate on spring arrival dates. In central Europe, several studies described dependence of mean arrival dates of migrants on temperatures in spring or on the Northern Atlantic Oscillation index (Hubálek 2003, Tryjanowski et al. 2005, Hubálek & Čapek 2008). Climatically-induced shift in arrival date might translate into change in breeding abundance resulting in population decline of species not able to adjust their arrival on breeding grounds to warmer climate (Tryjanowski et al. 2005, Møller et al. 2008). Putting these findings together with the results of our study, we suggest that abundance of central European birds in the breeding season is strongly affected by spring temperature (Tryjanowski et al. 2005, Reif et al. 2008b) but the effect of winter temperature is weak (this study). However, we should bear in mind that winter weather was expressed as monthly temperate means. Although mean temperature is frequently used to test the effects of winter conditions on animal populations (e.g. Jones et al. 2003, Huntley et al. 2007, Link & Sauer 2007), use of such mean can mask the effects of temperature anomalies such as short periods of deep frost that may limit bird abundance more directly. Future studies can focus on performance of various measures of winter severity in bird population models.

The second and third patterns indicate that winter climate in the Czech Republic impacts upon bird populations indirectly through food supply rather than directly in which case the effect of body mass would be expected. Dietary niche thus seems to determine the effect of winter temperature on breeding bird populations: species feeding on both animals and plants (including omnivorous species) showed weaker relationships to temperature than species feeding on animals. This effect of dietary niche was consistent over particular winter months implying that none of the months have stronger limiting effect on bird food supply compared to the others. Results of our study expand on initial findings of Robinson et al. (2007) reporting high importance of dietary differences for relationships between abundance and winter temperature in 10 passerine species.

Low temperatures may reduce the activity of potential prey (especially invertebrates) and/or the prey might be less accessible (Avery & Krebs 1984, Rolstad & Rolstad 2000). The first factor might explain relatively close relationship between abundance and temperature in winter wren. Abundance of this species showed the tightest relationships to temperature, significant in all winter months. Indeed, Cannell et al. (1999) included the index of winter wren breeding abundance among indicators of climatic change in Great Britain as its abundance signalised impacts of winter severity on animals very clearly. Our data confirm indicative potential of this species. Reduced prey accessibility was probably important for limitation of populations of carnivorous species in our data because all species with this dietary specialisation were among those with the strongest abundance-temperature relationships. Ice cover on rivers and water bodies probably restricted accessibility of food for kingfisher (Keller et al. 1989, Kelly & Van Horne 1997), snow cover hid movements of small rodents (Solonen 2006), the main component of diet of kestrel (*Falco tinnunculus*) and buzzard (Zmihorski & Rejt 2007, Riegert et al. 2009). In contrast, species with wider dietary niche may switch to the food type temporary available to prevent starving during unfavourable weather conditions (Brandle et al. 2002). This explanation, however, is conditional on broad dietary niche on the level of particular individuals (Colles et al. 2009) and this assumption remains to be tested in species in our data.

Most of the species showed negative density dependence in population growth rate. This result corresponds to findings of Greenwood & Baillie (1991) and Newton et al. (1998), who reported poor breeding performance of common birds following the years of high abundance. Presence of density dependence confounds the effects of environmental factors on abundance and the studies searching for determinants of population changes need to separate the effects of extrinsic and intrinsic factors (Link & Sauer 2007, Piha et al. 2007). However, even recent studies apply direct correlations between species' abundance and the factor of interest (Wesołowski et al. 2009), although such analyses might produce substantially flawed results. As the recent mathematical tools enable to include a simple population model into statistical tests (Sæther et al. 2003) we urge to use this approach.

Our mixed-effects models showed that the effects of dietary niche on the strength of the relationship between abundance and winter temperature were insignificant if the taxonomic relatedness of the focal species was taken into account. Although the strength of abundance-temperature relationships varied considerably among species, about one fourth (or even more, depending on which of the winter months was used in the models) of the variability was found at the family level. Moreover, bird diet is specific for higher taxa (Bennett & Owens 2002) and closely related species within families or genera often feed on similar food (Price 2008). As a result, the effect of dietary niche was weaker if the phylogenetic component of variability (expressed in taxonomic categories) was highlighted. Nevertheless, significant phylogenetic effects do not preclude use of the results for conservation praxis (Thomas 2008). For instance, from the effect of winter temperatures on populations of species feeding on animals we can infer that these species may be particularly sensitive to human disturbance on wintering sites. Such disturbance could reduce the amount of time needed by the birds to search for their animal food. Therefore, such disturbance should be limited at least in the species of conservation concern like kingfisher.

Our results might be useful for considerations about results of modelling of species' potential responses to climatic change (Diniz-Filho et al. 2009). Such predictions often use models with only a few climatic variables including winter temperature (e.g. Huntley et al. 2007). We have found that the effect of winter temperature on breeding bird abundance is relatively weak at least in the conditions of the Czech Republic and its strength is modified by species' dietary niche. Therefore, predictive models with sole climatic variables might be too simplistic and the patterns of species' diversity and abundance predicted by these models not realistic. Inclusion of some ecological characteristics of the focal species such as dietary niche might result in improvement of predictive power of such models.

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