Biological Conservation 172 (2014) 109–116

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Birds protected by national legislation show improved population trends in Eastern Europe

Jaroslav Koleček [a,b,c,*], Matthias Schleuning [c], Ian J. Burfield [d], András Báldi [e], Katrin Böhning-Gaese [c,f], Vincent Devictor [g], José María Fernández-García [h], David Hořák [i], Chris A.M. Van Turnhout [j,k], Oksana Hnatyna [l], Jiří Reif [a,m]

[a] Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University in Olomouc, 17. listopadu 50, CZ-77146 Olomouc, Czech Republic
[b] Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, CZ-60365 Brno, Czech Republic
[c] Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, D-60325 Frankfurt (Main), Germany
[d] BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, United Kingdom
[e] MTA Centre for Ecological Research, Lendület Ecosystem Services Research Group, Alkotmány u. 2-4, Vácrátót 2163, Hungary
[f] Department of Biological Sciences, Goethe University, Max-von-Laue-Straße 9, D-60438 Frankfurt (Main), Germany
[g] Institut des Sciences de l'Evolution, UMR 5554-CNRS, Université Montpellier II, Montpellier Cedex 05, France
[h] Hazi Foundation, Granja Modelo, s/n, 01192 Arkaute, Álava, Spain
[i] Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-12844 Praha 2, Czech Republic
[j] Sovon Dutch Centre for Field Ornithology, P.O. Box 6521, 6503 GA Nijmegen, The Netherlands
[k] Department of Animal Ecology, Institute for Wetland and Water Research, Radboud University Nijmegen, Toernooiveld 1, 6500 GL Nijmegen, The Netherlands
[l] Department of Zoology, Faculty of Biology, Ivan Franko National University of Lviv, Hrushevskyi St. 4, UA-79005 Lviv, Ukraine
[m] Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Benátská 2, CZ-12801 Praha 2, Czech Republic

A R T I C L E I N F O

Article history:
Received 27 May 2013
Received in revised form 15 February 2014
Accepted 23 February 2014

Keywords:
Conservation effectiveness
Ecological trait
Environmental legislation
Global change
Life history strategy
Population growth rate

A B S T R A C T

Protecting species is one of the major focuses of conservation efforts. However, large-scale assessments of the effects of species protection on animal populations are rare. Protection has been shown to benefit birds in Western Europe and in the United States, but not yet in Eastern Europe, where modern environmental legislation was only established in the early 1990s after political changes. We compared the population trends of bird species between 1970–1990 and 1990–2000 in ten Eastern European countries for species protected since 1990s and unprotected species, controlling for effects of species' phylogeny and traits. After 1990, trends in protected species improved more than in unprotected species. This suggests that national legislation has helped prevent declines of the protected species, although there was a high variability in population trends among countries. In particular, there was great improvement in the population trends of protected species in countries providing 'narrow and deep' protection to few species. In contrast, trends of protected species remained nearly unchanged in countries providing 'broad and shallow' protection to most species, while few unprotected species had adverse population trends in these countries. Although our correlative analysis cannot show causal relationships, the positive relationship between protection and long-term population trends suggests that species protection is a highly relevant tool for conservation. A combination of 'broad and shallow' and 'narrow and deep' protection might be most efficient for securing healthy bird populations for the future.

1. Introduction

Many bird species have declined strongly in the last century from exploitation, land-use changes, climate change and biological invasions (Bonebrake et al., 2010; Williams et al., 2012). In response, policy makers have introduced legislation to protect species by limiting their exploitation and the destruction of their habitats (e.g. Male and Bean, 2005; Williams et al., 2012). Since applying such legislation has financial and other consequences, it

* Corresponding author at: Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, CZ-60365 Brno, Czech Republic. Tel.: +420 605 552 978.

E-mail addresses: j.kolecek@gmail.com (J. Koleček), matthias.schleuning@senckenberg.de (M. Schleuning), ian.burfield@birdlife.org (I.J. Burfield), andrasbaldi@gmail.com (A. Báldi), katrin.boehning-gaese@senckenberg.de (K. Böhning-Gaese), vincent.devictor@univ-montp2.fr (V. Devictor), jofernandez@hazi.es (J.M. Fernández-García), david@natur.cuni.cz (D. Hořák), chris.vanturnhout@sovon.nl (C.A.M. Van Turnhout), sjanka@ukr.net (O. Hnatyna), jirireif@natur.cuni.cz (J. Reif).

http://dx.doi.org/10.1016/j.biocon.2014.02.029
0006-3207/

is important to know whether the protection efforts are really beneficial to the protected species (Hoffmann et al., 2010). Although the benefits of various management applications have been assessed for many species (e.g. Bonebrake et al., 2010; Williams et al., 2012), general assessments of bird protection at the national or international level are far less common (Donald et al., 2007; Voříšek et al., 2008).

The success of bird protection efforts can be assessed by comparing long-term population trends of protected and unprotected species. Legislation might prevent population declines of protected species, and cause more positive population trends in protected species than in unprotected ones. For instance, between 1988 and 2002, the population status of 52% of the 1300 plant and animal species protected under the US Endangered Species Act improved (Male and Bean, 2005). The proportion of species that were stable or improving increased by 64% within 13 years of their official listing, and improving trends were associated with the greatest mean institutional funding per year (Male and Bean, 2005). Using 8838 species/country combinations, Donald et al. (2007) showed that in Western Europe, species subject to special protection under Annex I of the EU Birds Directive were significantly more likely to have positive population trends during 1970–2000 than non-Annex I species. This pattern was not apparent in the same groups of species outside the EU. Moreover, for every additional 1% of a country's land area under EU protection (SPAs), the odds of a species being in more positive population trend classes increased by around 4% across all species (including non-Annex I species), and by around 7% for Annex I species (Donald et al., 2007). A similar approach was used to test the potential effect of hunting in long-term and large-scale trends in waterbird populations (Jiguet et al., 2012). These examples indicate that conservation policies applied over large regions for sufficiently long periods could have positive effects.

Whether protective legislation might also be beneficial in Eastern Europe has never been investigated. This region is important for biodiversity conservation, having a lower intensity of land use resulting in richer biodiversity than in Western Europe (Galewski et al., 2011). It is thus important to know whether species protection also affects population trends in this region (Pullin et al., 2009; Stoate et al., 2009). Since Eastern Europe was under totalitarian governments for much of the 20th century, a new era of nature conservation legislation started after the political changes of the early 1990s. Eastern European countries thus offer a very interesting opportunity to test the effectiveness of species protection.

Current conservation strategies contain a variety of approaches differing in targets and management tools (Brooks et al., 2006). From a perspective of management intensity and breadth of focus, one can discriminate 'narrow and deep' policies investing a high amount of resources into a limited sample of objects, and 'broad and shallow' policies, with a widely applied but modest effort (Vickery et al., 2004). Following this distinction, the national legislations of Eastern European countries on the protection of bird species might be divided as follows: (i) those protecting only the rare, most endangered and/or charismatic species ('narrow and deep'), and (ii) those protecting most species, including non-threatened or common species, leaving only a few (mostly game) species unprotected ('broad and shallow'). Whether these two strategies can have different impacts on population trends remains to be explored. Studies analyzing the impacts of conservation actions on protected species' population status across the globe found that the greatest success was achieved via targeted intensive actions (Butchart et al., 2006; Brooke et al., 2008; Sodhi et al., 2011). One can thus assume that the impact of the 'narrow and deep' strategy will result in more positive population changes in the focal species.

Besides protection, many environmental and life history factors correlate with bird population trends (e.g. Gregory et al., 2007), perhaps affecting species' susceptibility to adverse conditions and therefore the effectiveness of species protection (Böhning-Gaese and Oberrath, 2003; Jiguet et al., 2007; Van Turnhout et al., 2010; Webb et al. 2010). Specifically, it has been observed that habitat specialists, farmland species, seed-eaters, ground nesters, long-distance migrants and species breeding in cooler regions have suffered more from recent environmental changes than habitat generalists, forest species, residents and species breeding in warmer regions (Reif, 2013). Accordingly, correlation of species' ecological and life history traits with avian population trends must be considered when exploring relationships between species' protection status and population changes.

Here, we assess the relationships between species protection and population trends of birds in Eastern Europe, taking into consideration associations with species' traits. If species protection is efficient, we predict that (i) population trends of protected species would be more positive than those of unprotected species. We also predict that (ii) the differences between protected and unprotected species would be greater in countries with 'narrow and deep' protection than in countries with 'broad and shallow' protection.

2. Materials and methods

2.1. Protected species lists

To obtain lists of bird species protected by statute in each Eastern European country, we requested information from experts working for governmental and non-governmental organizations. We received feedback from 14 of the 15 countries contacted, and species lists suitable for our study were supplied for the following ten countries: Belarus, Croatia, the Czech Republic, Estonia, Hungary, Latvia, Moldova, Poland, Slovakia and Ukraine (Table A1). We analyzed legislation that came into effect between 1987 and 1995, i.e. around the time of political changes and approximating to the time period for which population change data are available (see below). As five countries protected 21–52% and the other five 81–92% of bird species, we considered the former group as having 'narrow and deep' protection and the latter as having 'broad and shallow' protection (see Table A1).

2.2. Population trends

We obtained population trends for the time period from 1970 to 1990 from Heath et al. (2000). This time period was considered to be representative for population trends before species protection was established after the political changes in Eastern Europe around 1990. Population trends for 1990–2000 from Burfield and Van Bommel (2004) were representative for the period with protection. Although the length of the periods differed, these are the best long-term data available for comparisons of bird population trends among European countries in different time periods and have been widely used (e.g. Donald et al., 2001, 2007; Sanderson et al., 2006; Jones and Cresswell, 2010). They are the only sources covering all breeding species in the focal countries. To unify the scale for both data sources, we merged the original population trends to three common categories: −1 = species' populations showed >20% decrease or species went extinct; 0 = species' populations were stable with a change of <20% in any direction; 1 = species' populations showed >20% increase. Further, we excluded species with trends specified as "unknown" or "fluctuating". This approach ensured that our database contained only species with reliable measures of population trends and the estimates of trend changes between the time periods can be considered conservative. We also excluded new breeders that colonized a given country during the period 1990–2000 and species that went extinct in a given country in 1970–1990, because the trends of such species could not have been affected by their protection status. As a result, we used data on 306 bird species with population trends in both the 1970–1990 and 1990–2000 time periods (Table A2).

2.3. Traits

To account for the potential influences of other factors on species population trends, we identified 16 species' traits that correlated with population trends in previous studies (e.g. Gregory et al., 2007; Jiguet et al., 2007; Van Turnhout et al., 2010) and included them as explanatory variables in our statistical analyses. These traits characterized species' breeding habitat and dietary niche, nest type and location, migration strategy, life history (for all these traits we used data from Cramp, 1977–1994; Böhning-Gaese et al., 2000; Böhning-Gaese and Oberrath, 2003; Koleček and Reif, 2011) and climatic niche (calculated using data from Hagemeijer and Blair, 1997 and Haylock et al., 2008).

For habitat, dietary and climatic niche, we distinguished between niche position (i.e. mean value) and niche breadth (i.e. range). Habitat niche was based on a classification of species' habitat requirements along a gradient of decreasing vegetation structural complexity and density, from (1) closed forest to (7) open country without trees or shrubs. Species were allocated up to three different values and habitat niche position was calculated as the mean of these values. Habitat niche breadth was determined as the difference between the extreme values. In addition, we used another expression of habitat requirements along a gradient of increasing habitat humidity, from (1) non-humid and (2) wet (e.g. wet meadows and marshlands) to (3) aquatic habitats (e.g. rivers and water reservoirs). Dietary niche position was based on a classification of species into four different trophic levels, as either (1) herbivorous, (2) herbivorous and insectivorous, or omnivorous, (3) insectivorous or (4) carnivorous. Dietary niche breadth was based on a classification of species into (1) obligatory herbivorous (i.e. plant sources only, e.g. *Loxia curvirostra*) or obligatory insectivorous/carnivorous (i.e. animal sources only, e.g. *Buteo buteo* or *Apus apus*), (2) herbivorous and insectivorous/carnivorous (i.e. plant and animal sources, e.g. *Parus major*), or (3) omnivorous (i.e. plant, animal and other sources, e.g. *Corvus corax*). Nest type was scored along a gradient of three levels of increasing nest concealment. Nest location described the height of the nest above the ground, from (1) on or close to the ground, (2) intermediate – i.e. shrubs and lower trees, to (3) high trees. Migration distance was defined as the distance to wintering grounds, distinguishing between (1) residents, (2) short-distance migrants (most of the population wintering north of the Sahara Desert), and (3) long-distance migrants (the major part of the population wintering south of the Sahara Desert). Moreover, we defined migration flexibility as the variation in migration behavior within a species. Thus, we recognized (0) obligatory migrants and obligatory residents (inflexible migration behavior), and (1) facultative migrants (flexible migration behavior). Climatic niche was calculated from maps of mean temperatures in the main three-month species-specific breeding season (mostly April, May and June) for the period 1961–1990 based on temperature data obtained from Haylock et al. (2008) following Jiguet et al. (2007). Climatic niche position was the mean breeding season temperature over the breeding range of each species within Europe (taken from Hagemeijer and Blair, 1997). Climatic niche range was classified as the difference between maximum and minimum temperatures across the European breeding range.

We chose five life history traits, i.e., body mass, egg mass, incubation period, clutch size and number of broods per season, using mean values from published data (Cramp, 1977–1994). As these life history traits are highly correlated, we reduced their number by principal component analysis (PCA) into two independent axes (see also Reif et al., 2010). Each species was positioned along the two most important ordination axes, and these scores were used for further analyses (Fig. A1). We thus suggest that the first ordination axis (PC 1, explaining 55.6% of the variability among species, eigenvalue = 2.78) expressed a gradient from 'slower strategy' (K-selected) species (i.e. those having larger eggs, larger body mass and longer incubation period) to 'faster strategy' (r-selected) species (hereafter the 'first life history axis'). The second axis (PC 2, explaining 19.5% of the variability, eigenvalue = 0.98) expressed a different and (by definition) independent gradient – from species allocating most of their energy to just one breeding attempt per season (i.e. having a single brood and larger clutch sizes) to species spreading their investments across multiple breeding attempts per season – i.e. having multiple broods and smaller clutch sizes (hereafter the 'second life history axis').

2.4. Data analysis

We tested the statistical effect of species protection in the 1990s by comparing population trends between protected and unprotected species relative to the reference population trends in 1970–1990. We used linear mixed effect models (using the libraries nlme and lme4; Bates, 2010; Pinheiro et al., 2010) in R (R Development Core Team, 2005) assuming a normal distribution of errors (Crawley, 2012). The response variable was species' population trend expressed using three categories on an ordinal scale (-1, 0, +1). Thus wholly positive trends would yield an average value of 1, wholly negative a value of -1 and stable or even mixture, would oscillate around a value of 0. The residuals of the statistical models followed a normal distribution, and formal tests of residual normality did not indicate a violation of the model assumptions.

The explanatory variables with fixed effects were: time period (i.e. 1970–1990 and 1990–2000), protection status, species' traits (11 traits and 2 life-history PCA axes) and country. The interaction of a given explanatory variable with the time period quantified the effect of this variable on the change in population trends between the two time periods across species and countries. In the case of protection status, we included a three-way interaction term between time period, protection status and country to test the country-specific effects of species protection on species trends. However, we did not estimate country-specific effects for trait variables, since the models would be too complex and since we did not expect interactions between species traits, time period and country.

Population trends of species are often considered to be evolutionarily conserved and it is recommended to take the phylogenetic relatedness among species into account in comparative analyses across species (see e.g. Thomas, 2008; Diniz-Filho et al., 2013). Therefore, we controlled for the potential impact of common evolutionary history on the observed relationships. We accounted for phylogenetic relatedness among species, expressed as species nested in genus nested in family, as random effects in all models (see Lockwood et al., 2002; Jiguet et al., 2010). We also fitted linear models without the random effects of bird taxonomy and compared the model fit between the two models with a likelihood ratio test.

To select the best subset of the trait variables, we applied an information-theoretic approach (Burnham and Anderson, 2002) using the "dredge" function in the R library MuMIn (Bartoń, 2010). To reduce the possible confounding effects of overfitting, we performed the analyses in two steps. We first selected the variables with the highest explanatory power within the following six groups of related traits: (i) habitat niche, (ii) dietary niche, (iii) climatic niche, (iv) migration strategy, (v) nest type and location and (vi) life history axes (Table 1). Within each group, models containing all possible combinations of trait variables and their twofold interactions were assessed using the Akaike Information Criterion for small sample sizes (AIC_c). We averaged across all models within each group, obtaining model-averaged coefficients with confidence intervals (Johnson and Omland, 2004). The terms whose confidence limits did not include zero were selected for the next step. In the second step, we combined the selected terms into one model, which was further reduced by the same assessment procedure, dropping the variables whose confidence limits included zero. The final model thus contained the selected traits and the variables time period, protection status and country. The significance of fixed effects in the final model was assessed with a type-II analysis of deviance using Wald chi^2-tests that is independent of the sequence of factors in the final model. The three-way interaction of time period, protection status and country indicated whether the population trends of the protected species improved (or deteriorated) more than the trends of unprotected species between the time periods in particular countries. For visualizing the effects predicted by the final model, we calculated predicted values of avian population trends estimated by the final model to reveal the country- and period-specific effects of species' protection status. This enabled us to examine the statistical effects of protection status (i) across all countries, (ii) for the two groups of countries defined by their protection strategy ('broad and shallow' vs. 'narrow and deep' protection), and (iii) for every individual country.

3. Results

The final model obtained by selection among trait variables (Table A3; Appendix A) showed large differences in the population trends of 306 bird species between the time periods 1970–1990 and 1990–2000, both between countries and between species with different protection status and traits (Tables 1 and 2).

3.1. Species protection

There was a significant interaction between protection status and time period (Table 1), with the protected species improving their trends between the time periods significantly more than the unprotected species (estimate = 0.38, SE = 0.14, t = 2.64, model R^2 = 0.17, p = 0.008). Across the region, protected species had more negative population trends than unprotected species in 1970–1990, but trends of both groups became similar in 1990–2000 (Fig. 1). That is, population trends of protected species improved in the second time period, while unprotected species had similar trends in both periods (Fig. 1). The rate of decline of protected species was approximately halved after the onset of protection (Fig. 1). Nevertheless, mean population trends remained negative irrespective of species' protection status in 1990–2000 (Fig. 1).

The positive association of protection with population trend was observed both in countries with 'narrow and deep' protection, as well as in countries with 'broad and shallow' protection (Table 2). However, these two different protection strategies were associated with marked differences in the patterns of changes in protected and unprotected species' trends. In the 'narrow and deep' countries, trends of protected species improved markedly after protection in the 1990s (Fig. 2). The population trends of unprotected species were more positive than those of protected species between 1970 and 1990, but improved only slightly during

Table 1
Analysis of the deviance of the final linear mixed effects model including the effects of species' traits and legislation on changes in population trends of 306 bird species in 1990–2000 relative to 1970–1990. Mixed effects models accounted for avian phylogenetic relatedness by including family, genus and species as nested random effects. The significance of effects was assessed with a Type II analysis that is independent of the sequence of factors in the model using a Wald chi^2-test. Species' population trend was expressed using three categories on an ordinal scale (−1, 0, +1). PC 1 expresses a gradient from 'faster strategy' (r-selected) to 'slower strategy' (K-selected) species. PC 2 depicts a gradient from species allocating most of their energy to just one breeding attempt per season to species spreading their investments to multiple breeding attempts per season.

Explanatory variable	Df	Chi^2	P
Protection status	1	5.15	0.023
Country	9	142.37	<0.001
Time period	1	7.67	0.006
PC 1	1	5.92	0.015
PC 2	1	2.83	0.092
Nest location	1	9.74	0.002
Migration flexibility	1	3.11	0.078
Protection status × country	9	31.94	<0.001
Protection status × time period	1	31.77	<0.001
Country × time period	9	74.13	<0.001
PC 2 × time period	1	10.67	0.001
Nest location × time period	1	6.86	0.009
Migration flexibility × time period	1	11.93	0.001
Protection status × country × time period	9	17.61	0.040

Table 2
Estimates of the statistical effects of protection between 1970–1990 and 1990–2000 in 10 Eastern European countries, obtained from the three-way interaction "protection status × country × time period" for each country as calculated in the final model (see Table 1). The statistical effect of protection on population trends is relative to the time period before the legislation came into effect (1970–1990) and relative to unprotected species.

Country	Estimate	SE	t	P
'Narrow and deep' protection				
Ukraine	0.63	0.13	4.80	<0.001
Latvia	0.08	0.14	0.59	0.555
Belarus	0.38	0.14	2.64	0.009
Moldova	0.07	0.13	0.52	0.602
Czech Republic	0.12	0.12	1.10	0.271
'Broad and shallow' protection				
Estonia	0.35	0.15	2.41	0.016
Slovakia	0.15	0.15	0.99	0.322
Hungary	0.14	0.21	0.65	0.516
Croatia	0.59	0.20	2.92	0.004
Poland	0.26	0.21	1.20	0.232

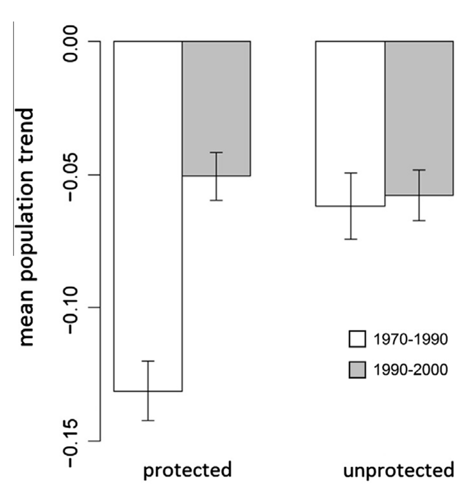

Fig. 1. Population trends (±SE) of 306 species protected and unprotected since 1990s in 10 Eastern European countries in 1970–1990 and 1990–2000 (see Table 1). The values of population trends shown in the figure are predicted values estimated by the final model. This model related observed trends to species protection status and ecological traits across particular countries. Species' population trend was expressed using three categories on an ordinal scale (−1, 0, +1). Wholly positive trends would yield an average value of 1, wholly negative a value of −1 and stable or even mixture, a value of 0.

Fig. 2. Population trends (±SE) of 306 species protected and unprotected since 1990s in Eastern European countries under 'narrow and deep' and 'broad and shallow' protection in 1970–1990 and 1990–2000 (see Table 1). The values of population trends shown in the figure are predicted values estimated by the final model. This model related observed trends to species protection status and ecological traits across particular countries. Species' population trend was expressed using three categories on an ordinal scale (−1, 0, +1). Wholly positive trends would yield an average value of 1, wholly negative a value of −1 and stable or even mixture, a value of 0.

1990–2000 (Fig. 2). In the countries with 'broad and shallow' protection, population trends of protected species did not change significantly between the periods (Fig. 2). At the same time, population trends of unprotected species deteriorated in these countries: positive population trends in 1970–1990 became negative trends in 1990–2000 (Fig. 2).

The relation of protection to bird population trends varied considerably among countries (Fig. A2). The countries with the most significant protection effects over time were Belarus, Croatia, Estonia and Ukraine (Table 2).

3.2. Traits

Population trends were significantly related with four trait variables, and three of these correlations changed between the two periods (Table 3). In 1970–1990, facultative migrants had more positive population trends than obligatory migrants or residents, but this relationship disappeared in 1990–2000. In 1970–1990, ground nesting species had more negative population trends than the above-ground nesting species, but this difference in population trends was significantly weaker in 1990–2000 (Table 3). In both time periods, r-selected species had more negative trends than K-selected species (PC 1). At the same time, species allocating energy to a few breeding attempts had more negative trends than species spreading their investments into multiple breeding attempts (PC 2). This relationship was observed in 1970–1990, but was not detectable in 1990–2000.

Table 3
Effects of species' traits on population trends of 306 bird species in two time periods (1970–1990 and 1990–2000) in 10 Eastern European countries as revealed by the final linear mixed effects model (see Table 1 for the analysis of deviance table of this model and for a brief description of PC 1 and PC 2). The main effect (i.e. the terms without interactions) refers to the relationship between a given trait and the population trend in the first time period; the interaction term (i.e. a term × time period) refers to the change in trends between the first and second time period. The main effect of PC1 refers to the relationship with the population trends in both periods because the interaction term was not included in the final model.

Trait variable	Estimate	SE	df	*t*	*P*
Migration flexibility	0.15	0.05	139	2.96	0.004
Migration flexibility × time period	−0.14	0.04	3360	−3.42	0.001
Nest location	0.11	0.03	139	3.84	<0.001
Nest location × time period	−0.05	0.02	3360	−2.62	0.009
PC 1	−0.04	0.02	139	−2.42	0.017
PC 2	0.07	0.03	139	2.70	0.008
PC 2 × time period	−0.06	0.02	3360	−3.25	0.001

3.3. Phylogenetic relatedness

The model containing taxonomic information as random effects explained a significantly larger proportion of the variability in bird population trends than the linear model without this random effect (Likelihood ratio = 438.4, $P < 0.001$). This suggests that phylogenetic dependency played a significant role and justifies our effort to control for its effects. However, variance partitioning among random effects showed that the residual variance was by far the most important component of the overall variance in the random effect part (accounting for 76.9% of the variability). Family explained 4.7% and genus explained less than 0.1% of the variability. Species had the most notable effect, explaining 18.4% of the variability in population trends.

4. Discussion

Our results show that legislation for species protection was significantly related to bird population trends in Eastern Europe. After controlling for the effects of species' ecology, life history and phylogenetic relatedness, population trends of bird species protected since the 1990s, after the fall of totalitarian governments, improved more than those of unprotected species. However, trends of both protected and unprotected species remained negative in 1990–2000. Thus, we might have expected an even stronger decline in protected species if they had lacked protection. This pattern suggests that the modern conservation legislation in these countries helped to protect birds, albeit not sufficiently to reverse their declining trends. This is in line with the positive influence of species protection already found in Western Europe (Donald et al., 2007) and North America (Male and Bean, 2005). It is important to note that these two studies examined protected species lists that were uniform over large regions (i.e., European Union and the United States), while our study focused on species lists specific for each country. National-level protection thus most likely also delivers benefits to individual species.

Our simultaneous focus on several countries required a correlative approach, which, unlike manipulative experiments, cannot effectively test for causal mechanisms (Quinn and Keough, 2002). Other unobserved factors could also contribute to the observed changes in avian populations trends, including those originating in environmental and demographic stochasticity (Sæther and Engen, 2002), as well as deterministic factors. Indeed, in the 1990s, when conservation legislation came into effect, Eastern European countries underwent deep socioeconomic and land-use changes that were also reflected in the population trends of some common bird species (Goławski, 2006; Koleček et al., 2010; Reif et al., 2011). For instance, several studies provide evidence that land use changes after the collapse of communism improved population trends of many farmland bird species (Donald et al., 2001; Stoate et al., 2009; Kamp et al., 2011). A similar population increase was found in forest birds due to lower impacts of acid emissions on forest stands (Flousek, 1989). However, a more detailed examination of some protected species suggests a link between legislation and the observed changes in species' abundance in some Eastern European countries. Specifically, a prohibition on poisoning was the direct driver of increasing populations of raptors in Hungary (Harasztha and Bagyura, 1993), while the harvesting levels of some game bird species approached zero after their protection was established in the Czech Republic (Supplementary Table A4) according to Anon. (2013). Relationships between the protection and exploitation of bird populations have been found all over the world (Donázar and Fernández, 1990; Villafuerte et al., 1998; Alonso et al., 2003; Whitfield et al., 2004; Fasola et al., 2010; Williams et al., 2012) and the greatest conservation success was achieved via targeted intensive actions (Butchart et al., 2006; Brooke et al., 2008; Sodhi et al., 2011). Nevertheless, we cannot generalize these examples to all protected species because they differ in their responses to protection, due to differences in their ecological characteristics and evolutionary history. Therefore, positive effects of protection at the species level should be confirmed by more detailed species-by-species approaches that would reveal the impact of legal protection relative to the impacts of other pressures.

Our prediction that bird population in countries with 'narrow and deep' protection should show a greater statistical effect than those with 'broad and shallow' countries was not confirmed. Both countries with 'narrow and deep' and 'broad and shallow' strategies showed positive associations between protection status and change in population trends. However, the patterns of changes in protected and unprotected species' trends differed between the protection strategies. In the 'narrow and deep' countries, protected species showed a great improvement in trends, whereas the trends of unprotected species improved less strongly. By contrast, across all countries with 'broad and shallow' protection (including common species such as *Sylvia atricapilla* or *Parus major* – see Table A2), we found a consistently marked deterioration in the trends of unprotected species after 1990, while protected species had similar trends in both time periods. Thus, it appears that both approaches to species protection might deliver positive, albeit different outcomes for bird conservation. A combination of the two models might achieve the best results overall: a basic level ('broad and shallow') of protection for many species, contributing to support population stability; and more stringent protection ('narrow and deep') for a subset of rare or threatened species, including active support where feasible (Garnett et al., 2003), to facilitate population recovery.

Several species' traits also influenced bird population trends in Eastern Europe. Our findings accord with the pan-European analysis of Sanderson et al. (2006), who observed a significant decline of trans-Saharan migrants in 1970–1990, but not in 1990–2000. Similarly, the declines of ground-nesting species conform to the decline of farmland birds frequently reported in European countries (Donald et al., 2001, 2006). The reduction in the rate of their decline observed in our study may be related to the reduction of agricultural intensity in Eastern Europe after political changes (Donald et al., 2001; Stoate et al., 2009), which resulted in temporary farmland bird recovery in some countries (Reif et al., 2008; but see Báldi and Batáry, 2011). In addition, we found that K-selected species, as well as species spreading their investment into multiple breeding attempts, had more positive population trends than r-selected species and species allocating their energy to just one breeding attempt. Similar relationships have been observed in France (Jiguet et al., 2007) and in the Czech Republic (Reif et al., 2010). Sol et al. (2012) suggested that successful invaders are species that are able to wait longer until environmental conditions are suitable for reproduction (i.e. K-selected species) and, more importantly, those having multiple breeding attempts. The life histories identified above could be generally advantageous for survival under adverse environmental conditions, at least for birds.

Apart from the correlative approach, which was necessary given the large spatial focus and the comparative nature of our study, there are a few additional limitations to take into account when interpreting the results. First, our sample of ten countries, albeit being the best dataset available to address our question, is still relatively small. However, they do cover most of Eastern Europe, aside from Russia, so we are confident that the countries considered form a representative sample of bird populations in the region. Second, although protection is positively related to bird population changes in Eastern Europe in general, we found heterogeneity in the effect of legal protection on population trends across countries, within the broad categories of 'narrow and deep' as well as 'broad and shallow' protection strategies. This variability may allow further insights into the costs and benefits of bird protection in particular countries. Unfortunately, we do not have detailed country-level data to address this variability in a formal analysis. However, the variability in protection effects among countries should be the subject of further work. Third, the number of bird species differed among countries, resulting in imbalanced sample sizes among countries. However, the differences in species numbers were not substantial (from a minimum of 156 bird species in Belarus to a maximum of 221 in Ukraine). In addition, the hundreds of species per country resulted in an extensive dataset with 1854 species-country combinations, making the statistical inference robust to this variation.

In conclusion, our findings suggest positive effects from statutory species protection in Eastern Europe. Protection seems to play an important role in reducing the rate of regional bird population decline. We suggest that updates to national protected species lists should include different protection strategies, according to species' threat levels in a given country. This might combine the prevention of declines of non-threatened species by the 'broad and shallow' approach, and the facilitation of population recovery of the most threatened species by the complementary 'narrow and deep' approach. Since birds are frequently used as environmental indicators at the European level (e.g. Gregory et al., 2005), future studies should explore if national legislation of bird protection might also contribute to the maintenance of other aspects of biodiversity. Furthermore, future studies could investigate the variation in protection effects among countries with more detailed analyses of the enforcement of bird conservation legislation, taking into account other local factors, such as the history and tradition of nature conservation and socio-economic factors. This might aid the further development of national and international animal protection strategies.

Acknowledgements

We wish to thank all the national experts who provided us the information on the respective national legislation or helped us to obtain these data, namely A. Abramczuk, A. Andreev, I. Budinski, S. Bugariu, I. Elts, J. Figelj, I. Hristov, O. Keišs, R. Kucharski, R. Slobodník, S. Trautmann and D. Uzunova. Further, we thank two anonymous reviewers, D. Dawson, M. Schwager, B. O'Hara, M. Krist and K. Weidinger for their valuable comments on data analysis and the earlier drafts of manuscript. D.W. Hardenkopf improved the English. The study was supported by the Ministry of Education of the Czech Republic, Palacký University (grant scheme to graduate students IGA PrF_2011_012, IGA PrF_2012_021 and IGA PrF_2013_007 and a mobility grant to J.K.), Institute of Vertebrate Biology (institutional support RVO: 68081766 to J.K.) and the Deutsche Bundesstiftung Umwelt (AZ 30011/296 to J.K.). M.S. and K.B.G. were supported by the research funding program Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz (LOEWE) of Hesse's Ministry of Higher Education, Research, and the Arts. A.B. was supported by the Hungarian Scientific Research Fund (OTKA K81971). I.J.B. was supported partly by an NGO operating grant from the European Commission (DG Environment, under the LIFE+ programme) to Stichting BirdLife Europe.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.02.029.

References

Alonso, J.C., Palacín, C., Martín, C.A., 2003. Status and recent trends of the great bustard (*Otis tarda*) population in the Iberian peninsula. Biol. Conserv. 110, 185–195.

Anon., 2013. Hunting statistics for the Czech Republic. <http://www.uhul.cz/ke-stazeni/ostatni/myslivecke-statistiky-od-roku-1960> (accessed 01.02.14).

Báldi, A., Batáry, P., 2011. Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. Ibis 153, 875–876.

Bartoń, K., 2010. MuMIn: Multi-Model Inference. <http://CRAN.R-project.org/package=MuMIn> (accessed 21.01.13).

Bates, D.M., 2010. lme4: Mixed-Effects Modeling with R. R Foundation for Statistical Computing, Vienna.

Böhning-Gaese, K., Halbe, B., Lemoine, N., Oberrath, R., 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evol. Ecol. Res. 2, 823–839.

Böhning-Gaese, K., Oberrath, R., 2003. Macroecology of habitat choice in long-distance migratory birds. Oecologia 137, 296–303.

Bonebrake, T.C., Christensen, J., Boggs, C.L., Ehrlich, P.R., 2010. Population decline assessment, historical baselines, and conservation. Conserv. Lett. 3, 371–378.

Brooke, M.D.L., Butchart, S.H.M., Garnett, S.T., Crowley, G.M., Antilla-Beniers, N.B., Stattersfield, A.J., 2008. Rates of movement of threatened bird species between IUCN Red List categories and toward extinction. Conserv. Biol. 22, 417–427.

Brooks, J.S., Franzen, M.A., Holmes, C.M., Grote, M.N., Mulder, M.B., 2006. Testing hypotheses for the success of different conservation strategies. Conserv. Biol. 20, 1528–1538.

Burfield, I.J., Van Bommel, F.P.J. (Eds.), 2004. Birds in Europe. Population estimates, trends and conservation status. BirdLife Conservation Series No. 12. BirdLife International, Cambridge.

Burnham, K.P., Anderson, D., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Butchart, S.H., Stattersfield, A.J., Collar, N.J., 2006. How many bird extinctions have we prevented? Oryx 40, 266–278.

Cramp, S.E. (Ed.), 1977–1994. The Birds of the Western Palearctic, vols. I–IX. Oxford Univ. Press.

Crawley, M.J., 2012. The R Book. John Wiley & Sons.

Diniz-Filho, J.A.F., Loyola, R.D., Raia, P., Mooers, A.O., Bini, L.M., 2013. Darwinian shortfalls in biodiversity conservation. Trends Ecol. Evol. 28, 689–695.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's bird populations. Proc. R. Soc. London B 268, 25–29.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D., Waliczky, Z., 2007. International conservation policy delivers benefits for birds in Europe. Science 317, 810–813.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Van Bommel, F.P.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agric. Ecosyst. Environ. 116, 189–196.

Donázar, J., Fernández, C., 1990. Population trends of the griffon vulture *Gyps fulvus* in Northern Spain between 1969 and 1989 in relation to conservation measures. Biol. Conserv. 53, 83–91.

Fasola, M., Rubolini, D., Merli, E., Boncompagni, E., Bressan, U., 2010. Long-term trends of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. Popul. Ecol. 52, 59–72.

Flousek, J., 1989. Impact of industrial emissions on bird populations breeding in mountain spruce forests in central Europe. Ann. Zool. Fenn. 26, 255–263.

Galewski, T., Collen, B., McRae, L., Loh, J., Grillas, P., Gauthier-Clerc, M., Devictor, V., 2011. Long-term trends in the abundance of Mediterranean wetland vertebrates: from global recovery to localized declines. Biol. Conserv. 144, 1392–1399.

Garnett, S., Crowley, G., Balmford, A., 2003. The costs and effectiveness of funding the conservation of Australian threatened birds. Bioscience 53, 658–665.

Goławski, A., 2006. Changes in numbers of some bird species in the agricultural landscape of eastern Poland. Ring 28, 127–133.

Gregory, R.D., Van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P., Gibbons, D.W., 2005. Developing indicators for European birds. Philos. Trans. R. Soc. B 360, 269–288.

Gregory, R.D., Vorisek, P., Van Strien, A., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., Burfield, I.J., 2007. Population trends of widespread woodland birds in Europe. Ibis 149 (S2), 78–97.

Hagemeijer, W.J.M., Blair, M.J. (Eds.), 1997. The EBCC Atlas of European Breeding Birds. Their Distribution and Abundance. T & AD Poyser, London.

Haraszthy, L., Bagyura, J., 1993. Protection of birds of prey in Hungary in the last 100 years. Aquila 100, 105–121.

Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation. J. Geophys. Res.: Atmos. 113, D20119.

Heath, M., Borggreve, C., Peet, N., Hagemeijer, W.J.M. (Eds.), 2000. European bird populations: Estimates and trends. BirdLife Conservation Series No. 10. BirdLife International/European Bird Census Council, Cambridge.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., et al., 2010. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509.

Jiguet, F., Devictor, V., Ottvall, R., Van Turnhout, C., Van der Jeugd, H., Lindström, Å., 2010. Bird population trends are linearly affected by climate change along species thermal ranges. Proc. R. Soc. London B 277, 3601–3608.

Jiguet, F., Gadot, A.-S., Julliard, R., Newson, S.E., Couvet, D., 2007. Climate envelope, life history traits and the resilience of birds facing global change. Glob. Change Biol. 13, 1672–1684.

Jiguet, F., Godet, L., Devictor, V., 2012. Hunting and the fate of French breeding waterbirds. Bird Study 59, 474–482.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19, 101–108.

Jones, T., Cresswell, W., 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? J. Anim. Ecol. 79, 98–108.

Kamp, J., Urazaliev, R., Donald, P.F., Hölzel, N., 2011. Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations. Biol. Conserv. 144, 2607–2614.

Koleček, J., Reif, J., 2011. Differences between the predictors of abundance, trend and distribution as three measures of avian population change. Acta Ornit. 46, 143–153.

Koleček, J., Reif, J., Šťastný, K., Bejček, V., 2010. Changes in bird distribution in a Central European country between 1985–1989 and 2001–2003. J. Ornit. 151, 923–932.

Lockwood, J.L., Russel, G.J., Gittleman, J.L., Daehler, C.C., McKinney, M.L., Purvis, A., 2002. A metric for analysing taxonomic patterns of extinction risk. Conserv. Biol. 16, 1137–1142.

Male, T.D., Bean, M.J., 2005. Measuring progress in US endangered species conservation. Ecol. Lett. 8, 986–992.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2010.nlme: Linear and Nonlinear Mixed Effects Models. R Foundation for Statistical Computing, Vienna.

Pullin, A.S., Báldi, A., Can, O.E., Dieterich, M., Vassiliki, K., Livoreil, B., Lövei, G., Mihók, B., Nevin, O., Selva, N., Sousa-Pinto, I., 2009. Conservation focus on Europe: major conservation policy issues that need to be informed by conservation science. Conserv. Biol. 23, 818–824.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.

R Development Core Team, 2005. R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna.

Reif, J., 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. Acta Ornithol. 48, 1–16.

Reif, J., Böhning-Gaese, K., Flade, M., Schwarz, J., Schwager, M., 2011. Population trends of birds across the iron curtain: brain matters. Biol. Conserv. 144, 2524–2533.

Reif, J., Vermouzek, Z., Voříšek, P., Šťastný, K., Bejček, V., Flousek, J., 2010. Population changes in Czech passerines are predicted by their life-history and ecological traits. Ibis 152, 610–621.

Reif, J., Voříšek, P., Šťastný, K., Bejček, V., Petr, J., 2008. Agricultural intensification and farmland birds: new insights from a central European country. Ibis 150, 569–605.

Sæther, B.-E., Engen, S., 2002. Pattern of variation in avian population growth rates. Philos. Trans. R. Soc. London B 357, 1185–1195.

Sanderson, F., Donald, P.F., Pain, D.J., Burfield, I.J., Van Bommel, F.P.J., 2006. Long-term population declines in Afro-Palearctic migrant birds. Biol. Conserv. 131, 93–105.

Sodhi, N.S., Butler, R., Laurance, W.F., Gibson, L., 2011. Conservation successes at micro-, mezo- and macroscales. Trends Ecol. Evol. 26, 585–594.

Sol, D., Maspons, J., Vall-llosera, M., Bartomeus, I., García-Peña, G.E., Piñol, J., Freckleton, R.P., 2012. Unraveling the life history of successful invaders. Science 337, 580–583.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., Van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe – a review. J. Environ. Manage. 91, 22–46.

Thomas, G.H., 2008. Phylogenetic distributions of British birds of conservation concern. Proc. R. Soc. London B 275, 2077–2083.

Van Turnhout, C.A.M., Foppen, R., Leuven, R.S.E.W., Van Strien, A., Siepel, H., 2010. Life-history and ecological correlates of population change in Dutch breeding birds. Biol. Conserv. 143, 173–181.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol. Conserv. 119, 19–39.

Villafuerte, R., Viñuela, J., Blanco, J.C., 1998. Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain. Biol. Conserv. 84, 181–188.

Voříšek, P., Reif, J., Šťastný, K., Bejček, V., 2008. How effective can be the national law in protecting birds? A case study from the Czech Republic. Folia Zool. 57, 221–230.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., LeRoy Poff, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol. Lett. 13, 267–283.
Whitfield, D.P., Fielding, A.H., McLeod, D.R.A., Haworth, P.F., 2004. Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. Biol. Conserv. 119, 319–333.
Williams, D.R., Pople, R.G., Showler, D.A., Dicks, L.V., Child, M.F., Zu Ermgassen, E.K.H.J., Sutherland, W.J., 2012. Bird Conservation: Global Evidence for the Effects of Interventions. Pelagic Publishing, Exeter.