

# Contrasting responses of migration strategies in two European thrushes to climate change

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## Abstract

Migration is a widespread strategy that enables animals to escape harsh winter conditions. It has been well documented that migration phenology in birds is changing in response to recent climate warming in the northern hemisphere. Despite the existence of large temporal and geographical scale ringing data on birds in Europe, changes in migration strategies in relation to climate warming have not been well studied, mainly because of a lack of appropriate statistical methods. In this paper, we develop a method that enables us to investigate temporal changes in migration strategies from recoveries of dead ringed birds. We estimated migration probability as the ratio between recovery probabilities of conspecific birds originating from different countries but potentially wintering in the same country. We applied this method to two European thrushes: the entirely migrant redwing *Turdus iliacus*, and the partially migrant blackbird *T. merula*. We tested for an immediate and a 1-year lagged relationship between our migration probability and climatic covariates (i.e. mean winter temperature in France and the North Atlantic Oscillation). Using ringing-recovery data collected in Finland, Germany, Switzerland and France from 1970 to 1999, we detected contrasting responses in these two species, likely related to their different migratory behaviours. Both species showed a decline in the probability for northern and eastern birds to winter in France. The entirely migratory redwing exhibited a year-to-year plastic response to climate, whereas the decline in the partially migrant blackbird was smooth, suggesting underlying genetic processes. The proposed method, thus, allows us to identify useful indicators of climatic impacts on migration strategies, as well as highlighting differences between closely related species.

*Keywords:* climate change, migration behaviour, NAO, plastic response, *Turdus iliacus*, *Turdus merula*

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## Introduction

There is now a large amount of evidence that climate affects a wide variety of biological processes, across a wide variety of organisms (Stenseth *et al.*, 2002; Walther

*et al.*, 2002). Because of their popularity, birds have received a large attention from the public. As a result, many studies that aimed to link climate change and biological processes have been performed on European and North American birds (Evans, 1997; Zalakevicius & Zalakeviciute, 2001; Cotton, 2003). The timing of seasonal activity, also named phenology, has been the source of a prodigious number of studies. In particular, there have been studies to show changes in the average laying dates (Crick *et al.*, 1997; Forchhammer *et al.*, 1998; Brown *et al.*, 1999; Crick & Sparks, 1999; Inouye *et al.*, 2000; Both & Visser, 2001; Van Noordwijk, 2003; Frederiksen *et al.*, 2004). Although harder to substantiate, changes in geographical distribution (Thomas &

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Lennon, 1999) and in demographic traits have also been documented (for review see Crick, 2004). Studies about changes in migration have mainly considered phenological aspects through migration dates (Bradley *et al.*, 1999; Both & Visser, 2001; Cotton, 2003; Jenni & Kéry, 2003). Despite the evolutionary implications of changes in migration patterns for avian populations (Fretwell & Lucas, 1970; Hestbeck *et al.*, 1991), other aspects of migration such as changes in migration routes have been less studied. Many bird species use migration to escape harsh winter conditions in their breeding areas. Migration is an energy-demanding and often dangerous activity. If wintering areas closer to the breeding area become suitable because of an improvement of winter conditions related to global warming, and if there is enough genetic variation and/or phenotypic plasticity, then birds might abandon previous wintering areas.

Until recently, practical difficulties in field studies (Spendelov *et al.*, 1995) and limitations of available approaches to statistical inference about movement of individuals among locations have been two main obstacles in investigating movements in birds. In recent decades, telemetry has appeared as a powerful tool to investigate animal movement, particularly long-distance migration (Berthold *et al.*, 2002; Bairlein, 2003). However, this innovative technique suffers from a lack of background data and can only be applied for relatively large species, and it is, thus, not appropriate for tracking changes in bird movements following global warming. Recent developments in capture–recapture methods (namely multistate capture–recaptures models), based on the pioneer work of Arnason (1972), have considerably improved the ability to study animal movement (Nichols *et al.*, 1992; Spendelov *et al.*, 1995; Bennetts *et al.*, 2001; Cam *et al.*, 2004). When animals are followed at several sites, multistate models provide estimators of movement by modelling the probability to move between sites over time (Kendall & Nichols, 2004). However, these models cannot be used with ring-recovery data, where individuals are at most recovered once at the time of their death (Brownie *et al.*, 1985). A large number of bird species, in particular migratory species that are traditionally hunted, have been the object of long-term ring-recovery studies in Europe (for a detailed account of the history of bird ringing, see Campbell & Lack, 1985). Although these data are unsuitable for multistate modelling, they have been collected over large spatial and temporal scales and potentially represent a valuable tool for providing indicators of changes in bird movements in response to climate.

In this paper, we studied the temporal change in migratory movements in relation to climate using

ring-recovery data. Ring-recovery models were originally developed to estimate survival rate in the presence of a variable recovery rate (Brownie *et al.*, 1985), in populations sometimes segregated based on phenotypic traits (e.g. sex, age, size, ...). So far, geographical segregation has been limited to estimating survival rates in different areas, but the potential for investigating migration with recovery models has been overlooked. In the context of migratory birds and when ringing and recovery area differ, measured recovery rate actually encompasses two parameters: migration rate from ringing area to recovery area and recovery rate in recovery area (i.e. true recovery rate). Conspecific birds originating from the same geographic area are likely to have the same survival rate and the same true recovery rate in a given area at a given occasion, given they are there. Therefore, if the recovery rate varies between conspecific birds originating from different countries after accounting for a potential difference in survival according to their origin, we can conclude that migration rate varies. We investigated temporal change in migratory movements in relation to climate in two European thrushes, the redwing *Turdus iliacus* and the blackbird *T. merula*. Redwings have a northerly breeding distribution, from Iceland through Scandinavia to Russia. This species is almost entirely migratory, and the wintering area encompasses almost all European and Mediterranean countries, Turkey and Northern Africa (Snow & Perrins, 1998). On the other hand, blackbirds breed in most European and Mediterranean countries, and only northern and eastern populations are fully migratory (Snow & Perrins, 1998). Many populations are partially migratory, i.e. a fraction of the population migrates some distance every year while the rest of the population remains on the breeding grounds (Terrill & Able, 1988). These two species were selected because of their contrasting migratory strategies and of the large amount of data available. In redwings, which are completely migratory, we expected a decline in the mean migration distance in response to climate through phenotypic plasticity and/or microevolution. In blackbirds, where both migrants and nonmigrants coexist, we predicted a more complex response to global change. On one hand, we predicted a decline in the mean migration distance of migratory individuals. On the other hand, we predicted a decline in the proportion of migrants given the cost of migratory activities. Because migration traits are likely under genetic control (Berthold & Querner, 1981; Berthold & Helbig, 1992; Berthold & Pulido, 1994; Pulido *et al.*, 1996), we expected the change in the proportion of migrants to be less affected by year-to-year climatic variation than a plastic change in migratory distance. Practically, we used (i) data from redwings ringed in

Finland or in France and subsequently recovered in France and (ii) data from blackbirds ringed in Switzerland and Germany or in France and subsequently recovered in France. We estimated the probability for thrushes to migrate to France. We then modelled this probability as a function of local and large-scale climatic variables to investigate if climate could be responsible for changes in the migration patterns in thrushes.

## Material and methods

### *Brownie et al. ring-recovery models*

Ring-recovery data come from birds that have been ringed, released and are subsequently accidentally found dead and reported or intentionally harvested, retrieved and reported by hunters (Brownie *et al.*, 1985; Williams *et al.*, 2002). Ring-recovery models focus on the estimation of survival rates along with probabilities associated with the sampling process (Williams *et al.*, 2002). The general situation, which motivated the pioneer work of Brownie *et al.* (1985), considers a migratory bird population subject to annual sport hunting. It assumes that ringing of individuals occurs once a year. In the context of European thrushes, ringing occurs during the breeding season, just before the hunting season. Ringed birds released each year are recovered as a result of hunting, where a ringed bird is harvested and retrieved, and the ring number reported to the relevant ringing centre. Two types of parameters are estimated:  $S$ , the annual survival probability, and  $f$ , the recovery rate (i.e. probability that a ringed bird alive at the beginning of the year is harvested, retrieved and the ring number reported).

### *Field methods and data sources*

For blackbirds, we considered birds ringed in Switzerland and southern Germany and in France, and subsequently recovered in France. Blackbirds breed throughout this region, and birds are, therefore, ringed as pullus (i.e. nestling or chick, unable to fly, still able to be caught by hand), or as 'full-grown' (i.e. full-grown bird ringed in calendar year of its birth). The total numbers of birds ringed in southern Germany and Switzerland from 1970 to 1999 were, respectively, provided courtesy of the Max Plank Research Centre for Ornithology and the Swiss Ornithological Institute. For the total number of blackbirds ringed in France, we used data available at the Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO).

For redwings, we considered birds ringed in Finland or in France, and subsequently recovered in France. In Finland, ringing is mainly performed during the breed-

ing season. Birds are therefore ringed as 'pullus' or as 'full-grown'. The total number of thrushes ringed in Finland from 1970 to 1999 was provided courtesy of the Finnish Museum of Natural History. In France, ringing mainly occurs during the postbreeding migration (September–October), and to a lesser extent during the prebreeding migration (March). Therefore, only full-grown redwings were ringed in France.

Information about recoveries from 1970 to 1999 in France regarding to their origin (i.e. Finland, Germany, Switzerland and France) were provided by the European Union for Bird Ringing (EURING). Hunters were the major source of recovery data, but we included all recoveries provided by EURING (i.e. natural and anthropogenic), even when cause of death was unknown.

### *Statistical analysis*

Ring-recovery models make the assumption that each individual marked at time  $t$  has the same probability of surviving to time  $t+1$  (Brownie *et al.*, 1985). Furthermore, these models assume that the individuals are identical in the probability of being recovered dead (Brownie *et al.*, 1985). We verified that the data met these assumptions by assessing the fit of two general time-dependent models: (i) the Seber–Robson–Young full-time dependent model (model 0) and (ii) an extension of this model where the first-year recovery rates are allowed to differ (model 1). This latter model is useful if the ring reporting rate is quite different the first year after ringing (Brownie *et al.*, 1985). Using the goodness-of-fit test (GOF) provided by software ESTIMATE (Brownie *et al.*, 1985), we estimated which of these two models can be used as starting point for model selection.

In blackbirds, GOF tests were only estimable on birds ringed in France as full grown. Both model 0 ( $\chi^2 = 62.89$ ,  $df = 47$ ,  $P = 0.06$ ) and model 1 ( $\chi^2 = 91.76$ ,  $df = 73$ ,  $P = 0.07$ ) fitted the data. In redwings, GOF tests were only estimable on birds ringed in Finland as full grown. The low number of recoveries did not allow us to test model 0. Model 1 fitted the data ( $\chi^2 = 31.52$ ,  $df = 23$ ,  $P = 0.08$ ). We found no evidence for overdispersion for either species, and, thus, no evidence for deviation from the assumption that the fates of the individuals are independent of each other, (i.e. that the data follow a multinomial distribution (Anderson *et al.*, 1994)). Facing the lack of data, we generalized the GOF results to other groups. For both species, we considered  $\{S(a_2 \times t \times area) f(a_2 \times t \times area)\}$  as a general model, where survival rate ( $S$ ) and recovery rate ( $f$ ) were time-dependent ( $t$ ) with two relative age classes ( $a_2$ ) and differed between ringing areas ( $area$ ). The two relative age class effect means

**Table 1** Notations used in the model presentation

Notations	Meaning
(a) Time- and age-dependence designs	
$t$	Time dependence
$g$	Group
$area$	Area effect
$a_1 \times pull$	True two classes age effect
$a_2$	Two classes relative age effect
(b) Covariates	
$T$	Linear temporal trend
$WT$	Mean winter temperature in France 1970–1999
$WT^\#$	Mean winter temperature of the previous year
$NAO$	North Atlantic Oscillation index
$NAO^\#$	North Atlantic Oscillation index of the previous year

that survival and recovery rates the first year after ringing differ from survival and recovery rates in the following years. Survival and recovery rates in the following years were assumed to be identical for birds ringed as pulli and birds ringed as adults.

All models were run in programme MARK (White & Burnham, 1999). We followed basic capture–mark–recapture methodology (Lebreton *et al.*, 1992), and based model selection on the small-sample-size adjusted Akaike's information criterion (AICc; Burnham & Anderson, 2002). The model with the lowest AICc is the most parsimonious model, and provides the best description of the structure in the data as it has the best balance between overfitting (hence loss of precision) and underfitting (hence bias) of the data (Burnham & Anderson, 2002). In the first step, we addressed the influence of time, ringing area and age on survival and recapture rate (Table 1a). In the second step, we used temporal covariates to model survival and recovery rate (Table 1b).

#### *Modelling changes in migration behaviour: the probability of migration*

Although the ring-recovery approach developed by Brownie *et al.* (1985) has been initially developed to estimate survival rate, we used this approach to investigate migration behaviour. For illustrating our approach, let us imagine the fate of a bird ringed in country A during the breeding season and subsequently recovered in country B during or after its postbreeding migration. Given that this bird has survived, the probability for a bird ringed in country A to

be recovered in country B  $f_{A \rightarrow B}$  is

$$f_{A \rightarrow B} = P_{A \rightarrow B} \times P_B \times f_B, \quad (1)$$

where  $P_{A \rightarrow B}$  is the probability for a bird ringed in country A to immigrate to country B,  $P_B$  is the probability to stay in country B and  $f_B$  is the probability of recovery for a bird in country B. Let us imagine now a bird ringed and subsequently recovered in country B. The probability for this bird to be recovered in country B  $f_{B \rightarrow B}$  is

$$f_{B \rightarrow B} = P_B \times f_B. \quad (2)$$

Assuming that the probability of recovery in B and the probability of leaving or staying in B are equal regardless of the origin of birds, the probability for a bird ringed in country A to migrate to B is given by the recovery ratio

$$\frac{f_{A \rightarrow B}}{f_{B \rightarrow B}} = \frac{P_{A \rightarrow B} \times P_B \times f_B}{P_B \times f_B} = P_{A \rightarrow B}. \quad (3)$$

Modelling the probability for a bird ringed in country A to migrate to country B is equivalent to modelling the relationship between  $f_{A \rightarrow B}$  and  $f_{B \rightarrow B}$ . We modelled the recovery ratio as the difference of recovery rates on a log scale using the log link function implemented in software MARK (White & Burnham, 1999). Doing so enabled us to back-transform the difference on the log scale to obtain the ratio on the real scale. In order to investigate the impact of climate on migration probability  $P_{A \rightarrow B}$ , we tested the significance of climatic covariates in explaining the total temporal variation in the difference between recovery rates of birds ringed in areas A and B. In our modelling notation, the area effect was denoted  $t \times area$  or  $t + area$  (i.e. multiplicative and additive effect, respectively). The notation for testing the significance of a covariate  $x$  was denoted  $area \times x$ .

#### *Covariates*

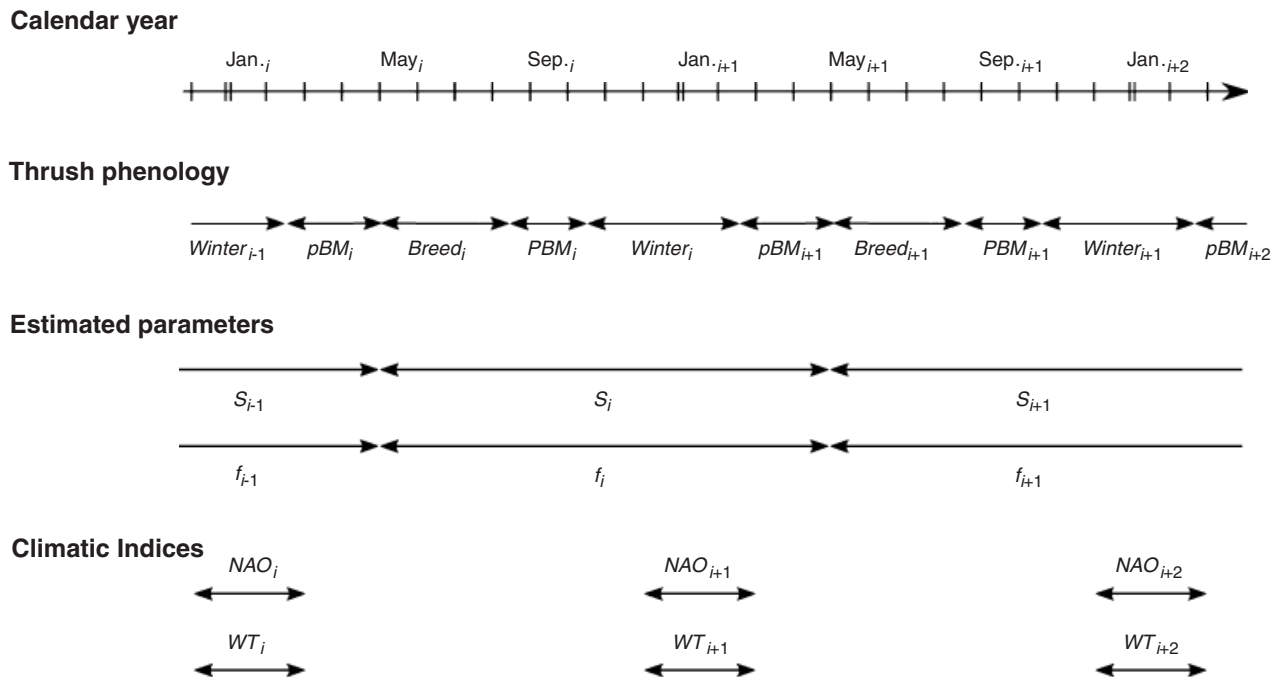
We considered three covariates in our study (Table 1b). The first covariate considered was a temporal trend (denoted ' $T$ '). This covariate is sometimes useful for capturing a long-term tendency in a demographic parameter. We subsequently tested two climatic covariates. We first investigated the contribution of temperature on demographical parameters in thrushes. Daily temperatures for the period 1950–2000 were provided by Météo France for three meteorological stations (i.e. Paris, Lille and Bordeaux). We considered the mean Winter Temperature ( $WT$ ) from December to February. Following Hallett's statement that large-scale climate indices seem to predict ecological processes better than local weather (Hallett *et al.*, 2004), we also tested the influence of the North Atlantic Oscillation ( $NAO$ ). This index quantifies

the atmospheric circulation in north-western Europe and is tightly linked to large-scale patterns in European winter conditions: a positive NAO index indicates warm, wet winters dominated by westerly winds and *vice versa* (Hurrell, 1995; Marshall *et al.*, 2001). The winter NAO index (December–February), has been demonstrated to affect a wide variety of animals (i.e. from invertebrates to large herbivores) in different habitats (i.e. marine and terrestrial Fromentin & Planque, 1996; Post & Stenseth, 1998, 1999; Greene & Pershing, 2000; Sims *et al.*, 2001; Solow, 2002; Stenseth *et al.*, 2003), and notably bird populations (Sillet *et al.*, 2000; Thompson & Ollason, 2001; Barbraud & Weimerskirch, 2003).

In European thrushes, the breeding season lasts from April to mid-August (Snow & Perrins, 1998). Because ringing starts at the beginning of the breeding season, the estimation of demographic parameters overlaps 2 calendar years (Fig. 1). For instance, the annual survival rate in year *i* is defined as the probability that a bird survived winter *i* + 1 (December–March *i* + 1) and survived until April *i* + 1 (Fig. 1). Recovery rate in year *i* is defined as the probability for a bird to be recovered from April *i* to May *i* + 1 (Fig. 1). Testing the relevance of climatic covariates for demographic parameters requires proper synchronization of the covariate with the demographic parameter we want to test. For instance, since winter NAO index for year *i* is computed from December *i*–1 to February *i* (Hurrell, 1995), it overlaps

survival rate in year *i*–1 (Fig. 1). Therefore, survival rate from April year *i* to April *i* + 1 was correlated with *WT* and *NAO* estimated from December of calendar year *i* to February of year *i* + 1 (Fig. 1). Regarding the effect of climate on recovery rate and migration probability (i.e. difference in recovery rate between birds from distinct ringing site), we tested two biological hypotheses: (i) we first test an immediate effect of climate in which the climate experienced by a bird will drive recovery within the same year and (ii) we then tested whether a lagged effect of climate experienced during the previous year will affect recovery during the following year. The first hypothesis was tested by correlating recovery and migration rates from April year *i* to April *i* + 1 with *NAO* and *WT* estimated from December of year *i* to February of year *i* + 1, whereas the alternative hypothesis was tested linking recovery and migration rates from April year *i* to April *i* + 1 with *NAO* and *WT* estimated from December of year *i*–1 to February of year *i* (Fig. 1) respectively denoted *NAO*<sup>#</sup> and *WT*<sup>#</sup> (Table 1b).

Both climatic covariates used here show clear temporal trends. For instance, the winter NAO index has exhibited considerable variability over the past 100 years and three major phases can be described: (i) From the turn of the century until about 1930, the NAO was high contributing to the higher-than-normal temperatures in Europe during this period. (ii) From the early 1940s until the early 1970s, the NAO index exhibited a



**Fig. 1** Phenology of European thrushes, demographic parameters and climatic indices in relation to calendar year. Jan., January; Sep., September; *Winter*, wintering season; *pBM*, prebreeding migration; *Breed*, breeding season; *PBM*, postbreeding migration; *S<sub>i</sub>*, survival rate; *f<sub>i</sub>*, recovery rate; *NAO*, winter North Atlantic Oscillation index; *WT*, mean winter temperature.

downward trend. (iii) Since 1975, the NAO has remained in a strongly positive phase, and displayed an upward trend (see review in Marshall *et al.*, 2001). This positive trend in winter NAO index is generally associated with global warming (Marshall *et al.*, 2001). In order to capture separately the impacts of a global warming trend and of deviations from the trend, we ran models with both a temporal trend and the climatic parameter of interest (thereafter denoted  $T + WT$  and  $T + NAO$ ).

We used ANODEV (Skalski *et al.*, 1993) to estimate the significance of these covariates in explaining the temporal variation in the parameter of interest. We also estimated the proportion of the total temporal variation explained by climatic and nonclimatic covariates as

$$V = \frac{\text{deviance}(\text{constant model}) - \text{deviance}(\text{covariate model})}{\text{deviance}(\text{constant24 model}) - \text{deviance}(\text{time - dependent model})}$$

## Results

### Blackbirds

Without accounting for any temporal covariate, model selection favoured a model with constant survival and time-dependent recovery rate (Table 2, model 11  $\{S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t) + \text{area}\}$ ). In this model, survival rate during the first year of life was lower than during the following years (0.24 vs. 0.44 and 0.34 vs. 0.60 for Swiss-German and French birds, respectively; Fig. 2). Age effect was best modelled when only

**Table 2** Modelling age- and time-variation in survival ( $S$ ) and recovery ( $f$ ) rates of blackbirds ringed in Switzerland and southern Germany or in France and recovered in France from 1970 to 1999

Models	AICc	np	Dev.
1. $S(a_2 \times t \times \text{area}) f(a_2 \times t \times \text{area})$	24880.57	230	555.05
2. $S(a_2 + t \times \text{area}) f(a_2 \times t \times \text{area})$	24771.41	175	556.16
3. $S((a_1 \times \text{pull} + t) \times \text{area}) f(a_2 \times t \times \text{area})$	24748.91	175	533.65
4. $S(t \times \text{area}) f(a_2 \times t \times \text{area})$	24769.41	174	556.16
5. $S(a_1 \times \text{pull} + t + \text{area}) f(a_2 \times t \times \text{area})$	24733.48	148	572.33
6. $S(a_1 \times \text{pull} + t) f(a_2 \times t \times \text{area})$	24736.27	147	577.12
7. $S(a_1 \times \text{pull} + \text{area}) f(a_2 \times t \times \text{area})$	24719.52	120	614.46
8. $S(a_1 \times \text{pull} + \text{area}) f(a_2 + t \times \text{area})$	24705.38	63	714.44
9. $S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t \times \text{area})$	24701.18	63	710.24
10. $S(a_1 \times \text{pull} + \text{area}) f(t \times \text{area})$	24703.41	62	714.47
<b>11. <math>S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t + \text{area})</math></b>	<b>24673.21</b>	<b>35</b>	<b>738.30</b>
12. $S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t)$	24735.94	34	803.03
13. $S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + \text{area})$	24784.82	6	907.92

np: number of estimable parameters; Dev.: deviance.

applied for birds ringed as pulli. Therefore, it appeared to be a true age effect as true age is only known for birds ringed as pulli. The difference in survival between ringing areas could be regarded as additive. Recovery rate also presented a true age effect and was different between ringing areas. The difference in recovery rates between areas was best modelled with an additive effect.

No covariates were significant in explaining temporal variation in survival rate (Table 3). For both areas, recovery rates in blackbirds showed a highly significant declining trend from 1970 to 1999 (Table 3;  $P < 0.01$ ). Regarding climatic covariates, only  $WT$  of the current year explained a significant part of the total variation in recovery rate (Table 3; on its own:  $P = 0.04$ ; in presence of temporal trend:  $P = 0.01$ ). None of the other tested

climatic covariates explained a significant part of the total variation in recovery rate (Table 3). The temporal variation in the difference in recovery rate between ringing areas, which is a measure of the probability for Swiss or German blackbirds to migrate to France, showed a significant linear decrease over time ( $r = -0.23$ ) and explained about 36% of the total variance in recovery differences (Table 3,  $P < 0.01$ , Fig. 3). A model with a linearly declining difference in recovery rate between areas, (i.e.  $\{S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t + \text{area} + T \times \text{area})\}$ ), provided the lowest AICc (AICc = 24664.98;  $np = 36$ ; Fig. 3). Finally, none of the tested climatic covariates explained a significant part of the variation in recovery differences (Table 3).

### Redwings

Without accounting for temporal covariates, model selection in redwings was quite similar to blackbirds. Model selection also favoured a model with constant survival and time-dependent recovery rate (Table 4, model 9  $\{S(a_1 \times \text{pull} + \text{area}) f(a_1 \times \text{pull} + t \times \text{area})\}$ ). Age effect on survival was a true age effect, involving only birds ringed as pulli. Again, survival rate during the first year of life was lower than during the following years (i.e. 0.23 vs. 0.46 for Finnish birds, 0.20 for French full-grown birds) and the difference in survival between ringing areas could be regarded as additive. Recovery rate also presented a true age effect. Contrary to blackbirds, the difference in recovery rate between ringing areas was not additive but multiplicative.

Redwing data showed a slightly significant decline in survival rate from 1970 to 1999 (Table 5,  $P = 0.04$ ). Regarding climatic covariates, winter climatic indices

**Table 3** Effect of covariates on survival, recovery and migration rates of blackbirds ringed in Switzerland and southern Germany or in France and recovered in France from 1970 to 1999

Covariate	Survival		Recovery		Migration	
	Dev.	V	Dev.	V	Dev.	V
Unconstrained time dependence	687.90		738.30		710.24	
Time constancy	738.30		907.92		738.30	
T	730.29	<0.01	809.97	0.58**	728.07	0.36**
WT	737.91	<0.01	883.21	0.14*	737.89	0.01
WT <sup>#</sup>	736.12	0.04	907.13	<0.01	738.28	<0.01
T + WT	737.91	<0.01	794.92	0.21*	728.05	<0.01
T + WT <sup>#</sup>	736.07	0.04	805.44	0.06	728.07	<0.01
NAO	735.36	0.06	905.13	0.01	737.79	0.02
NAO <sup>#</sup>	737.84	0.01	905.66	0.01	737.71	0.02
T + NAO	734.86	0.07	809.68	<0.01	728.07	<0.01
T + NAO <sup>#</sup>	737.72	0.01	807.78	<0.01	728.07	<0.01

Dev.: deviance, V, proportion of the temporal variance in survival explained by the covariate and significance of the covariate in superscript (\*\* $P \leq 0.01$ ; \* $0.01 \leq P < 0.05$ ). For models with both a temporal trend and a climatic covariate, the value of V given indicates the proportion of the remaining variation explained by the covariate once the trend has been accounted for.

of the previous year failed to explain variation in survival rate, either on their own (Table 5,  $P = 0.20$  and  $0.79$  for  $NAO^{\#}$  and  $WT^{\#}$ , respectively) or in the presence of a temporal trend (Table 5,  $P = 0.60$  and  $0.47$  for  $NAO^{\#}$  and  $WT^{\#}$ , respectively). Winter  $NAO$  index of the current year was not significant on its own (Table 5;  $P = 0.24$ ). However, it became significant and explained 15% of the total variance in survival in the presence of a temporal trend (Table 5,  $P = 0.04$ ).  $WT$  of the current year was highly significant, either considered on its own (Table 5,  $P = 0.03$ ) or in presence of a temporal trend (Table 5,  $P < 0.01$ ). When detrended,  $WT$  explained about twice more of the total variation in the annual survival rate than  $NAO$  (Table 5;  $V = 42\%$  vs.  $15\%$ ). The relationship between survival rate and  $WT$  was positive (slope =  $0.14$ ), suggesting that survival increased when  $WT$  was high. Combining temporal trend and  $WT$  in survival rate modelling (explicitly  $\{S(a_1 \times pull + area + T + WT) f(a_1 \times pull + t \times area)\}$ ) provided the lowest AICc (AICc =  $376.61$ ;  $np = 65$ ; Fig. 2).

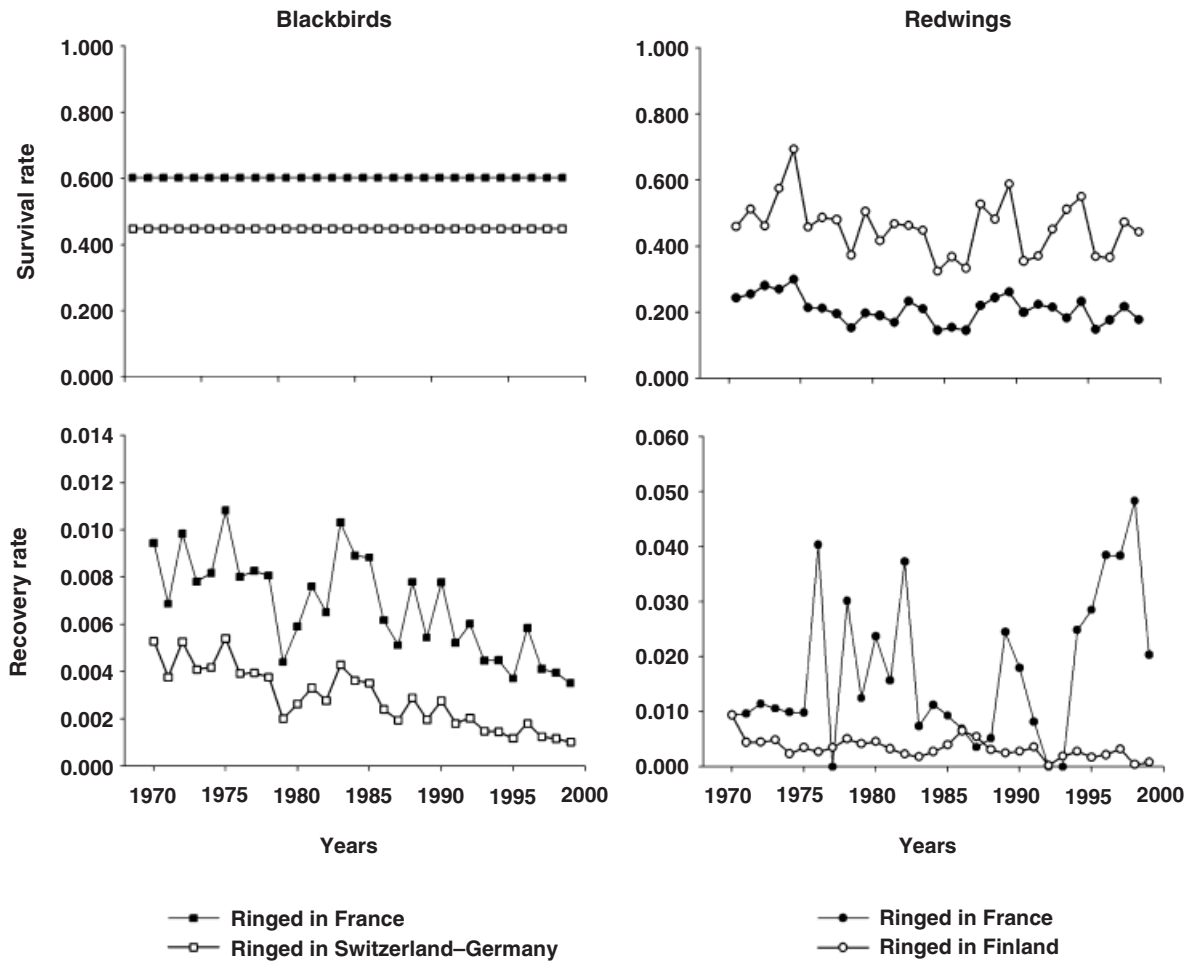
For recovery rate, significant trends were found from 1970 to 1999 (Table 5,  $P < 0.01$ ). Interestingly, the trends were different according to birds' ringing origin: recovery rate for birds ringed in Finland and subsequently recovered in France declined (slope =  $-0.40$ ), whereas recovery rate increased over the same period for birds ringed and recovered in France (slope =  $0.43$ ). Although  $NAO$  was nonsignificant regardless of the year considered, the  $WT$  of the previous winter explained a significant part of the total variation in recovery rate (Table 5,  $P = 0.04$ ). However,  $WT$  of the previous winter was not significant when the temporal trend was present,

suggesting that the relationship between  $WT$  and the recovery rate was likely due to the trend in  $WT$ .

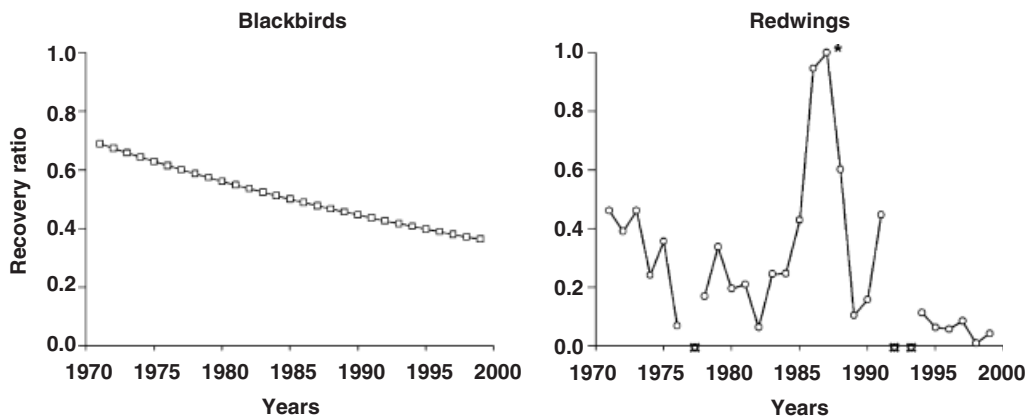
The differences in recovery rates between areas, which is as a measure of the probability of Finnish redwings to migrate to France, presented a decreasing temporal trend ( $r = -0.60$ ) that explained more than 60% of the total variance in the difference between areas (Table 5,  $P < 0.01$ ). Except for  $WT$  of the previous winter, all climatic covariates (i.e.  $WT$  and  $NAO$  of the current year and  $NAO$  of the previous year) were significant on their own but became nonsignificant in the presence of a temporal trend (Table 5). As previously mentioned, this suggested that relationships between these covariates and the differences in recovery rates between areas were due to the temporal trend previously detected. The only significant climatic covariate that remained significant in presence of a temporal trend (i.e.  $WT$  of the previous winter) explained 18% of the total variation in the difference in recovery rates between areas (Table 5). The relationship between  $WT$  of the previous year and the difference in recovery rate between areas was negative when the temporal trend was included ( $r = -0.27$ ), suggesting that the probability for redwings ringed in Finland to migrate to France was lower after birds have experienced a warm year (Fig. 3).

## Discussion

This study investigates the effect of climate on migration pattern in two species of European thrushes: (i) redwings ringed in Finland and France and subsequently recovered in France and (ii) blackbirds ringed



**Fig. 2** Survival and recovery rates of blackbirds (left column) and redwings (right column) recovered in France from 1970 to 1999 according to their ringing origins. Estimates from the models  $\{S(a_1 \times pull + area) f(a_1 \times pull + t \times area + T \times area)\}$  and  $\{S(a_1 \times pull + area + T + WT) f(a_1 \times pull + t \times area)\}$  for blackbirds and redwings, respectively.



**Fig. 3** Migration probability, defined as the ratio between recovery rates, for blackbirds ring in Switzerland and southern Germany and recovered in France (left column) and redwings ringed in Finland and recovered in France (right column) from 1970 to 1999, relative to birds ringed in France;  $\square$  migration probability were not estimable; \* migration probability estimated in 1986 was greater than 1 because recovery rate in Finnish redwings was greater than French redwings (cf. Fig. 2).



in Switzerland/Germany and France and subsequently recovered in France. Assuming that conspecific recovery rate in a given area is the same, the use of ring-recovery modelling (Brownie *et al.*, 1985) enabled us to tease apart the probability of migration (i.e. measured as the ratio of recovery rates in a single area of two sets of conspecific birds originating from different countries).

Preceding our investigations of climate effect on migration, we first had to adequately model temporal variation in survival rate. Temporal trend and climatic covariates were tested against survival rate in order to capture variance associated with these covariates and to

minimize the risk of confounding effects in recovery rate modelling. Although it was not our primary interest, modelling survival provided interesting evidence of relationships with climate. The more southerly distributed species, the blackbird, did not show any pattern in temporal variation in survival rate. No decline or increase was detected, and survival was not found to be affected by climate. However, the more northerly species, the redwing, provided strong evidence of pattern in temporal variation of survival rate. Unsurprisingly, survival rate of redwings ringed in Finland and France and recovered in France was found to be correlated with the *WT* of the current year. Increased mortality during winter is usually only indirectly due to low temperatures, although small birds may freeze to death during cold nights. The redwing being smaller than the blackbirds (ca. 50% Snow & Perrins, 1998), it is more likely to be affected by cold. More commonly, the problem is related to a decrease in the amount and availability of food, particularly when temperatures drop below 0 °C or during heavy snow cover. Freezing and snow cover will often make the access to critical food resources more difficult, especially for redwings which feed on fruits and soil invertebrates (Snow & Perrins, 1998).

Regarding recovery rates, both species showed a link with at least one tested climate covariate (i.e. *WT* for blackbirds and *WT*<sup>#</sup> for redwings). Because recovery rate is a combination of harvesting (i.e. hunting and retrieving) and reporting rates (Williams *et al.*, 2002), recovery rate was not expected to be related to climate. The lack of a relationship between recovery rate and *WT*<sup>#</sup> when a temporal trend is included in redwings

**Table 4** Model selection for time- and age-variation in survival (*S*) and recovery (*f*) rates of redwings ringed in Finland or in France and recovered in France from 1970 to 1999

Models	AICc	np	Dev.
1. $S(a_2 \times t \times area) f(a_2 \times t \times area)$	9766.78	230	288.53
2. $S(a_2 + t \times area) f(a_2 \times t \times area)$	9658.37	175	290.53
3. $S(a_1 \times pull + t \times area) f(a_2 \times t \times area)$	9643.13	175	275.29
4. $S(t \times area) f(a_2 \times t \times area)$	9656.36	174	290.53
5. $S(a_1 \times pull + t + area) f(a_2 \times t \times area)$	9616.40	148	302.72
6. $S(a_1 \times pull + t) f(a_2 \times t \times area)$	9623.48	147	311.81
7. $S(a_1 \times pull + area) f(a_2 \times t \times area)$	9581.70	120	324.16
8. $S(a_1 \times pull + area) f(a_2 + t \times area)$	9536.66	63	393.31
9. $S(a_1 \times pull + area) f(a_1 \times pull + t \times area)$	<b>9531.57</b>	<b>63</b>	<b>388.22</b>
10. $S(a_1 \times pull + area) f(t \times area)$	9535.21	62	393.86
11. $S(a_1 \times pull + area) f(a_1 \times pull + t + area)$	9630.97	34	545.68
12. $S(a_1 \times pull + area) f(a_1 \times pull + t)$	9769.30	33	686.00
13. $S(a_1 \times pull + area) f(a_1 \times pull \times area)$	9625.63	6	596.35

np, number of parameters; Dev., deviance.

**Table 5** Effect of covariates on survival, recovery and migration rates of redwings ringed in Finland or in France and recovered in France from 1970 to 1999

Covariate	Survival		Recovery		Migration	
	Dev.	V	Dev.	V	Dev.	V
Unconstrained time dependence	366.96		388.22		388.22	
Time constancy	388.22		596.35		545.68	
<i>T</i>	385.09	0.14*	517.16	0.38**	449.52	0.61**
<i>WT</i>	382.13	0.29**	574.55	0.10	494.54	0.32**
<i>T</i> + <i>WT</i>	376.61	0.42**	509.28	0.06	447.33	0.19
<i>WT</i> <sup>#</sup>	388.17	0.02	567.55	0.14*	473.41	0.46**
<i>T</i> + <i>WT</i> <sup>#</sup>	384.73	0.02	509.12	0.06	438.25	0.18**
<i>NAO</i>	387.16	0.05	585.39	0.05	505.72	0.25**
<i>T</i> + <i>NAO</i>	382.34	0.15*	511.79	0.04	449.20	0.03
<i>NAO</i> <sup>#</sup>	386.94	0.06	575.38	0.10	505.41	0.25**
<i>T</i> + <i>NAO</i> <sup>#</sup>	384.90	0.01	507.28	0.08	449.19	0.03

Dev., deviance; *V*, proportion of the temporal variance in survival explained by the covariate and significance of the covariate in superscript \*\**P* ≤ 0.01; \*0.01 ≤ *P* < 0.05). For models with both a temporal trend and a climatic covariate, the value of *V* given indicates the proportion of the remaining variation explained by the covariate once the trend has been accounted for.

confirms our expectations, suggesting that the correlation between recovery rate and *WT* was likely due to the trend in the climatic signal, rather than the climatic signal itself. However, it remains unclear why *WT* of the current year in presence of a temporal trend explained a significant part of the total variance of the recovery rate of blackbirds.

Modelling the difference in recovery rates between ringing areas enabled us to investigate temporal variation in migration patterns in relation with climate. Our study showed contrasting responses between blackbirds and redwings. In blackbirds, migration probability declined from 1970 to 1999 but short-term relationships with climate were weak. These results are in part in accordance with our expectations for a partially migratory species facing global warming. Migration is an energy-demanding and often dangerous activity (Berthold, 2001). If breeding areas become suitable for wintering because of climatic amelioration, residency might be favoured compared with migratoriness, explaining the decrease in the probability to migrate into France. As also predicted, given that residency and migratoriness are partially inherited (Berthold, 1991, 2001; Berthold & Pulido, 1994; Pulido *et al.*, 1996), migration probability was not directly affected by year-to-year climatic variation. This decline in migrant fraction is in agreement with predictions made from genetic studies in other partially migratory species facing global warming (Berthold, 1991; Berthold & Pulido, 1994; Pulido *et al.*, 1996). However, although a fraction of the population migrates some distance every year in blackbirds (Snow & Perrins, 1998), a 1-year-lagged response to climate variation (as found in 'Redwings') was not detected (Table 2). Two hypotheses might explain this result. Firstly, the absence of a relationship between migration and climate in blackbirds could suggest that changes in migration distance are under genetic control, as previously found in other partially migratory species (Adriaensen & Dhondt, 1990; Berthold & Helbig, 1992). The increase of temperature might have favoured short-distance migrants, leading to a decrease in the probability for a bird to migrate in France. This assumption is confirmed by the significant decrease in migration distances found in blackbirds from Germany from 1995 to 2002 (Fiedler *et al.*, 2004). Ringing-recovery data in blackbirds confirmed the hypothesis that an increase in the proportion of residents, accompanied by a decrease in migration distance, is a common response in partially migratory species facing global warming (Berthold & Helbig, 1992; Berthold & Pulido, 1994; Pulido *et al.*, 1996). While climate change is likely to be the main factor responsible for the observed changes in migratory behaviour in blackbirds, anthropogenic pressure may have accel-

erated the process. Thrushes are traditional game species for hunters in south-western France and northern Spain (Claessens, 1990; Roux *et al.*, 2000). For blackbirds originating from Germany and Switzerland, hunting activities in South-western France and Spain only target medium-distance migratory birds en route to their wintering areas. This anthropogenic selective pressure is likely to accelerate both the tendency towards residency and the shortening of migration distances if genetically determined. Secondly, phenotypic plasticity might occur in blackbird populations, but remain undetected because it involves other variables affecting survival and recovery rate (e.g. capacity to forage in a wider range of climate or improved metabolic response to a wider set of temperature). Plasticity in these traits might be important factor affecting migration response in blackbirds. However, such plastic responses will likely not be directly related to mean *WT*, but rather to its variance over time.

In redwings, migration probability also declined from 1970 to 1999 but, contrary to blackbirds, we detected short-term relationship with climate. When modelled together, a temporal trend and *WT* of the previous year explained 68% of the total variance in migration probability in redwings. *WT* on its own (i.e. deviation from the increasing trend exhibited by *WT*) explained 18% of the total variance in migration probability. The relationship between *WT* of the previous year and migration probability was negative over the time-period considered, indicating that the warmer the temperature, the fewer Finnish redwings migrated toward France in the next year. This 1-year lagged response suggested a plastic response to climate: the higher the *WT* redwings experienced the previous winter, the more likely are they to cut short their migration. As winter conditions improve with global warming in Europe, one might expect that areas where winter conditions previously prevented wintering will become suitable. As a consequence, the probability for redwings to migrate in France is expected to decrease. The negative temporal trend detected in our proxy of migration probability argues in favour of this hypothesis. This response was consistent with our initial assumptions and highlighted that mechanisms that drive change in migration behaviour in redwings are different from blackbirds'. Response to climate in redwings was actually more complex than a 1-year lagged response. We tested the significance of a covariate defined as the number of years elapsed since the last cold year (cold years were defined as mean *WT*  $\leq -3$  °C). This covariate, which can be considered as a memory effect, explained a very large part of the total variation in the difference in recovery rate between birds ringed in Finland and birds ringed in France (deviance = 427.25;  $V = 0.75$ ,  $P < 0.01$ ).

The relationship between the so-called memory effect and the migration probability was negative, suggesting that the probability of migrating to France is high immediately after a cold year and becomes progressively lower as time goes on.

Our study suggested that ring-recovery data, collected over large temporal and geographical scale and centralized by EURING, are valuable tools to provide reliable indicators, particularly of environmental changes such as global warming. Birds have the capacity to be important bioindicators, because their popularity among the general public and because these indicators are both biologically meaningful and relatively easy to understand for a general public. Fiedler *et al.* (2004) disagreed with this, arguing that only a fraction of 30 short-distance or partial migrants from Germany exhibited a response in accordance with expectations facing global warming (i.e. decrease in mean recovery distance and wintering at higher latitudes). Although our study focused on a lower number of species, we believe that our conclusions are robust because our modelling account for changes in recovery probabilities. Although our failure to detect climate effect in blackbirds might originate from changes in reporting rates of hunted birds as pointed out by Fiedler *et al.* (2004), the significant short- and long-term relationships between climate and migration probability make this unlikely. Our study provided a basis for choosing species likely to be good candidates as bioindicators of climatic change using ring-recovery data. Both redwings and blackbirds exhibited a response to climate change, but the redwing might be a better candidate because plastic responses to climate are not hidden by genetic processes as in blackbirds. Although harder to estimate than migration distance or change in wintering latitude, migration probability is easily interpretable. We predict that other entirely migratory species have a similar potential for indicating the impacts of global warming.

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