Evidence for the impact of global warming on the long-term population dynamics of common birds

Romain Julliard[*], **Frédéric Jiguet** and **Denis Couvet**

Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, 55, Rue Buffon, F-75005 Paris, France
[*] *Author for correspondence (julliard@mnhn.fr).*

Taking the opportunity in 2003 of the exceptionally warm spring in France as a natural simulation of possible future climate, we analysed common bird productivity using the French long-term capture–recapture national monitoring scheme. Two-thirds of the 32 species studied had an above-average productivity in 2003. However, this gain in productivity was not consistent among species, with a relatively low productivity for species exhibiting a long-term decline and relatively high productivity for stable or increasing species. Such links between long-term and short-term dynamics suggest that the impact of increasingly warm springs on productivity is a major component of the recent population dynamics of a variety of common bird species.

Keywords: capture–recapture; Europe; France; country-wide long-term monitoring; productivity

1. INTRODUCTION

Detailed demographic studies have shown how climate-dependent demographic parameters are affected by climate change (e.g. Dunn & Winkler 1999; Saether *et al.* 2000; review in Walther *et al.* 2002; Parmesan & Yohe 2003). However, few empirical studies have provided evidence that this short-term demographic variation hinders the conservation status of the species considered, i.e. have an impact on their long-term and large-scale dynamics. This is partly a result of a strong intrinsic methodological short-coming: the conservation status of a given species is a unique event. In other words, we lack replication, especially because pressures are long-term and global. One possible variable is species identity, i.e. what makes a given species more at risk from global change (e.g. Julliard *et al.* 2003). Another possible approach is to take advantage of the fact that climate change involves not only gradual changes in average parameters, but also the occurrence of exceptional climatic conditions, which may anticipate possible future climate conditions (Schneider & Root 1996).

The present paper combines these two possibilities by looking at the response of a set of common bird species to a particularly warm spring, in terms of their long-term dynamics. The spring of 2003 was much warmer than usual in France (Météo-France 2004). Since 1989, the abundance and demography of common bird species have been monitored in France by means of standardized point counts and capture–recapture (Julliard & Jiguet 2002). Here we compare productivity indices (proportion of young among captures) between spring 2003 and previous years. We evaluated among-species variation in such relative 2003 productivity indices, and linked it with the long-term status of these species (average annual population growth rate since 1989, estimated from the point count survey). We show that, among the 32 species analysed, declining species had a poor reproductive season in 2003, whereas increasing species tended to have an above-average reproductive season. Such a relationship between these short- and long-term dynamics provides further evidence that the long-term dynamics of species is significantly related to global warming.

2. METHODS

The climate in France has been warming over the past century, particularly since the mid-1970s (Moisselin *et al.* 2002). The temperature increase was rather spatially homogenous over France and occurred in all four seasons analysed separately (Moisselin *et al.* 2002). Nevertheless, March–June 2003, with average temperatures of 2.56 °C above the 1950–2000 average, was by far the warmest spring recorded since 1950 (Météo-France 2004). Between 1989 and 2002, spring was already much warmer than usual, with 1.25 °C above the 1950–1988 average. Standard deviations of average spring temperatures were similar for the two periods: *ca.* 0.6 °C. Given such a level of variation, and assuming that average temperatures are distributed normally around a fixed average, a spring as warm as 2003 should occur *ca.* every 300 years.

Productivity estimates are based on the proportion of juveniles among samples of individuals captured during spring, using mist-netting on constant effort sites. Standardization on constant effort sites relies on the fixed position and number of nets used per site (between 10 and 50), and on a fixed number and similar dates of capture sessions per site (usually between three and five, depending on the site, with dates ranging from the beginning of May to the end of July, and covering at least two months for a given site (Julliard & Jiguet 2002)). Each individual captured is individually ringed to avoid double counting, and the species and age (breeding adults or young of the year) are determined unambiguously from plumage by experienced volunteer bird ringers. The scheme started in 1989. Sites monitored similarly in 2003 and in at least one other year were selected ($n = 60$ sites, with an average of 5 years per site for a total of 298 site-years). For each selected site, species captured in 2003 and in at least one more year, and for which at least one adult and one juvenile were captured, were selected. After selection, all species with at least 150 individuals captured were retained ($n = 32$), excluding five reedbed specialists (bluethroat *Luscinia svecica*; sedge warbler *Acrocephalus schoenobaenus*, reed warbler *A. scirpaceus*; bearded tit *Panurus biarmicus*; and reed bunting *Emberiza schoeniclus*), for which local factors (e.g. drought) are likely to override any global effect. The resulting dataset represents 742 species-sites, with 3835 measures of productivity based on 53 800 different individuals captured. Because climate is likely to affect species differently according to their feeding, migrating and reproductive behaviour, species were assigned to one of four categories (migrating status attributions were based on Yeatman-Berthelot (1991)): seed-eating passerines (house sparrow *Passer domesticus*; bullfinch *P. pyrrhula*; chaffinch *Fringilla coelebs*; greenfinch *Carduelis chloris*, goldfinch *C. carduelis*; linnet *C. cannabina*; yellowhammer *E. citrinella*; and cirl bunting *E. cirlus*; $n = 8$), strict sedentary species (greater spotted woodpecker *Dendrocopus major*; long-tailed tit *Aegithalos caudatus*; coal tit *Parus ater*; marsh tit *P. palustris*; willow tit *P. montanus*; blue tit *P. caeruleus*; great tit *P. major*; and short-toed treecreeper *Certhia brachydactyla*; $n = 8$), trans-Saharan migrants (nightingale *L. megarhynchos*; marsh warbler *A. palustris*; melodious warbler *Hippolais polyglotta*; whitethroat *Sylvia communis*; lesser whitethroat *S. curruca*; garden warbler *S. borin*; and willow warbler *Phylloscopus trochilus*; $n = 7$) and the remaining (i.e. non-seed eating) partial and short-distance migrants (wren *T. troglodytes*; dunnock *Prunella modularis*; robin *Erithacus rubecula*; stonechat *Saxicola torquata*; blackbird *Turdus merula*; song
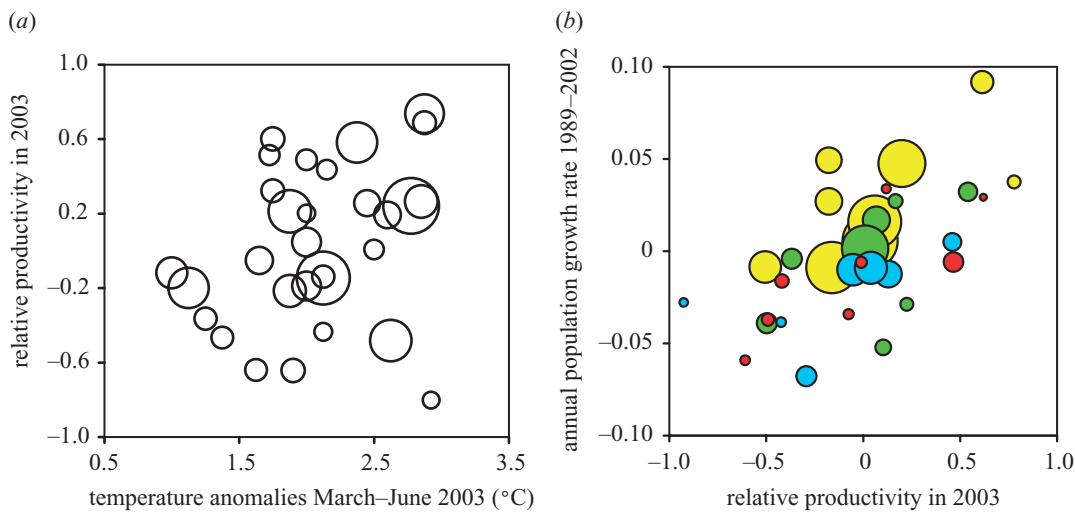
Figure 1. (a) Relative 2003 productivity of French common birds is under the influence of temperature anomalies during spring and (b) explains recent population trends of the species considered. Each circle is one site or group of neighbouring sites (a), or one species (b); the size of the circle is proportional to the precision of the relative productivity estimate (1/(s.e.^{2}), adjusted for over-dispersion. Relative productivity was further standardized within species groups: red, seed-eating; green, sedentary; blue, trans-Saharan migrants; yellow, partial or short-distance migrants.

thrush *T. philomelos*; Cetti's warbler *Cettia cetti*; blackcap *S. atricapilla*; and chiffchaff *Phylloscopus collybita*; *n* = 9).

The long-term trends for the species considered were estimated as the average annual population growth rate from 1989 to 2002 (taken from Julliard *et al.* (2003), updated from year 2002). These trends are chiefly based on the French point count survey, which is statistically independent of the capture–recapture scheme. These trends have been shown to be fairly consistent across western Europe (Julliard *et al.* 2003).

Productivity variation was analysed using standard logistic regression (binomial error) of the proportion of juveniles among individuals caught. To account for among-species and among-sites variations in productivity, all models included species, sites and species–sites interaction effects. We explored whether relative 2003 productivity varied across site and across species using a categorical variable separating 2003 from other years (Y2003). Sites variation and species variation in 2003 relative productivity were tested with the appropriate interactions with Y2003. Site : Y2003 interaction was further modelled with site-specific temperature anomalies during spring (obtained from Météo-France 2004). Species : Y2003 interaction was modelled with the categorical species group defined above and with the long-term trend for the species' French population. Because the data were slightly over-dispersed (residual deviance/residual d.f. = 1.95), we used the *F*-statistic to test specific hypotheses. All s.e. values presented are adjusted for over-dispersion.

3. RESULTS

Among-sites variation in the 2003 relative productivity of common birds was significantly associated with spatial variation in temperature anomalies (site-specific temperature anomalies effect on relative 2003 productivity, nested to site : Y2003 effect adjusted for species : Y2003: $F_{1,58}$ = 9.31, p = 0.003; residual site : Y2003 effect: $F_{58,3002}$ = 1.70, p = 0.0008; figure 1a). The unexplained spatial variation in relative productivity may partly be a result of interactions between temperature and local drought conditions (which were not measured in our study). In addition to among-sites variation, relative 2003 productivity was quite variable among the 32 species studied: productivity was particularly good for seed-eating species (+23 ± 9%, *n* = 8), sedentary species (+13 ± 3%, *n* = 8), and trans-Saharan migrants (+16 ± 5%, *n* = 7), but near average for the remaining partial or short-distance migrants (−4 ± 3%, *n* = 9). Within each of these groups, there was a consistent

trend for species declining over the past 15 years to have had a relatively low productivity in 2003, and for increasing species to have had a relatively high productivity (species-specific trend effect on relative 2003 productivity, nested to species : Y2003 effect, adjusted to site : Y2003 effect: $F_{1,27}$ = 10.39, p = 0.003; residual species : Y2003 effect: $F_{27,3002}$ = 0.64, p = 0.92; figure 1b). In particular, species as diverse as willow warbler, lesser whitethroat, marsh warbler, bullfinch, linnet or willow tit showing consistent large-scale long-term declines across western Europe (Gregory *et al.* 2002; Julliard *et al.* 2003) had a low reproductive success in 2003.

4. DISCUSSION

Although standardized capture–recapture monitoring schemes have been used systematically in the UK since 1983 (known as the 'Constant Effort Site' scheme; Peach *et al.* 1996) and since 1994 in North America (known as 'Monitoring Avian Productivity and Survival'; DeSante *et al.* 1999), few studies have used such datasets to examine temporal variation in productivity. The productivity index integrates many demographic parameters: breeding probability, number of clutches, clutch size, hatching success, fledging success and survival of fledglings during the dependent phase. However, the productivity index may be biased by variation in laying date: if young leave the nest early, they are more likely to be captured than if they had hatched and left the nest late, and so the productivity index (i.e. the proportion of juveniles in the captured sample) would be high. There is an abundant literature on the influence of temperature on laying date, and on whether such a relationship is adaptive, genetically determined, and how it is influenced by climate warming: the laying date should anticipate by about one month the time of maximum food abundance, which should match the nestling period (e.g. Thomas *et al.* 2001). The response of species to climate warming will thus in part depend on their degree of adaptive plasticity, or on their level of genetic diversity, for laying date (Visser *et al.* 1998). That high temperatures affected

our productivity measure through the advancement of laying date is likely, and this may explain the relationship between spatial variation in the 2003 relative productivity and site-specific temperature anomalies (figure 1*a*). Whether it is the main biological mechanism explaining the variable response of species or a mere artefact cannot be inferred from our data.

Variation in relative 2003 productivity between species was modelled together with (and therefore controlling statistically for) variation between sites. Hence, the relationship between relative productivity in 2003, and long-term population change (figure 1*b*), cannot, for example, be a result of declining species being associated with sites with relatively low productivity in 2003. Interestingly, previous studies of populations (in years of unexceptional temperature) have found a negative relationship between long-term trends and current productivity: declining species tend to have an increased productivity and increasing species tend to have a reduced productivity, most probably because of regulation by density dependence (Siriwardena *et al.* 2000). Our results thus appear specific to 2003, that is, a year with an exceptionally warm spring that was outside the range of recent spring temperatures. Coincidentally, the period 1989–2002, during which population trends of the species were quantified, also corresponded to a period with many warm springs (11 out of the 12 warmest springs of 1950–2002), yet less warm than spring 2003. During this period, many common bird species have increased or decreased (e.g. 81 out of the 105 species considered in the UK; Raven *et al.* 2003). During the even warmer 2003 spring, we found that decreasing species had an (even?) poorer productivity, whereas increasing species had an (even?) better productivity than in the previous year.

DeSante, D. F., O'Grady, D. R. & Pyle, P. 1999 Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. *Bird Study* **46** (Suppl.1), S178–S188.

Dunn, P. O. & Winkler, D. W. 1999 Climate change has affected the breeding date of tree swallows throughout North America. *Proc. R. Soc. Lond.* B **266**, 2487–2490. (doi:10.1098/rspb.1999.0950)

Gregory, R. D., Wilkinson, N. I., Noble, D. G., Robinson, J. A., Brown, A. F., Hughes, J., Procter, D., Gibbons, D. W. & Galbraith, C. A. 2002 The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–2007. *British Birds* **95**, 410–448.

Julliard, R. & Jiguet, J. 2002 Un suivis intégré des populations d'oiseaux communs en France. *Alauda* **70**, 137–147.

Julliard, R., Jiguet, F. & Couvet, D. 2003 Common birds facing global changes: what makes a species at risk? *Global Change Biol.* **10**, 148–154.

Météo-France 2004 Le climat pour la France en 2003. See www.meteo.fr/meteonet/actu/archives/dossiers/bilan2003.

Moisselin, J. M., Schneider, M., Canellas, C. & Mestre, O. 2002 Climate change over France during the 20th century: a study of long-term homogenized data of temperature and rainfall. *La Météorologie* **38**, 45–56. [In French with English summary.]

Parmesan, C. & Yohe, G. A. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.

Peach, W. J., Buckland, S. T. & Baillie, S. R. 1996 The use of constant effort mist-netting to measure between-year changes in the abundance and productivity of common passerines. *Bird Study* **43**, 142–156.

Raven, M. J., Noble, D. G. & Baillie, S. R. 2003 The breeding bird survey 2002. BTO research report 364. Thetford, UK: British Trust for Ornithology.

Saether, B. E., Tufto, J., Engen, S., Jerstad, K., Rostad, O. W. & Skatan, J. E. 2000 Population dynamical consequences of climate change for a small temperate songbird. *Science* **287**, 854–856.

Schneider, S. H. & Root, T. L. 1996 Ecological implications of climate change will include surprises. *Biodivers. Conserv.* **5**, 1109–1119.

Siriwardena, G. M., Baillie, S. R., Crick, H. Q. P. & Wilson, J. D. 2000 The importance of variation in the breeding performance of seed-eating birds for their population trends on farmland. *J. Appl. Ecol.* **37**, 1–22.

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. & Speakman, J. R. 2001 Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291**, 2598–2600.

Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond.* B **265**, 1867–1870. (doi:10.1098/rspb.1998.0514)

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395.

Yeatman-Berthelot, D. 1991 *Atlas des oiseaux de France en hiver*. Paris: Société Ornithologique de France.