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Rapid change in host use of the common cuckoo *Cuculus canorus* linked to climate change

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Parasites require synchrony with their hosts so if host timing changes with climate change, some parasites may decline and eventually go extinct. Residents and short-distance migrant hosts of the brood parasitic common cuckoo, *Cuculus canorus*, have advanced their phenology in response to climate change more than long-distance migrants, including the cuckoo itself. Because different parts of Europe show different degrees of climate change, we predicted that use of residents or short-distance migrants as hosts should have declined in areas with greater increase in spring temperature. Comparing relative frequency of parasitism of the two host categories in 23 European countries before and after 1990, when spring temperatures in many areas had started to increase, we found that relative parasitism of residents and short-distance migrants decreased. This change in host use was positively related to increase in spring temperature, consistent with the prediction that relative change in phenology for different migrant classes drives host-use patterns. These findings are consistent with the hypothesis that climate change affects the relative abundance of different host races of the common cuckoo.

Keywords: coevolution; host race; migration; migration distance; phenology; response to climate change

1. INTRODUCTION

Parasites exploit their hosts by timing emergence and reproduction to the annual cycle of the host [1]. Numerous examples show that the timing of changes in hormone level, body temperature or other aspects of reproductive physiology of the host suffice to synchronize the reproductive cycle of the parasite with that of the host [1], and synchrony of the reproductive cycle of brood parasites with that of the hosts also occur in the cuckoo [2].

Recent climate change has prompted the hypothesis that many biological interactions between species, or between species and the environment, are mistimed

because phenology of one partner has changed more than that of another and is thus sub-optimal with respect to reproduction or survival. As a case in point, caterpillars that are the prey of birds like the great tit *Parus major* now emerge earlier, so their avian predator, by consequence, breeds later than optimal with respect to this major larval food source (e.g. [3]). Likewise, avian predators such as the sparrowhawk *Accipiter nisus* have not advanced their reproductive phenology despite the fact that their avian prey now breed considerably earlier [4,5]. Many questions remain unresolved with respect to such mistiming because all organisms must adjust their phenology not just to a single interacting species, but to many different species, be they parasites, predators, competitors or commensals.

Brood parasitic birds, fishes and insects exploit parental care by their respective hosts for successful reproduction

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[6,7]. Thus, the reproductive cycles of the host and the parasite are synchronized because the parasite will be unable to reproduce in the absence of a host nest and a host providing parental care. Brood parasitic cuckoos such as the common cuckoo *Cuculus canorus* rely on a variable number of hosts, with some being specialists and others generalists ([6]; Davies 2000). The common cuckoo is characterized by a large number of host races that each specializes on a particular host species to which its eggs are adapted in terms of coloration, spottiness (e.g. [8,9]) and egg size [9–11]. The timing of breeding may vary among host races simply because different host species reproduce at different times [2,12]. However, not all cuckoo host races breed during the peak of breeding of their hosts. Though this is the case for some, such as the host race exploiting the long-distance migratory reed warbler *Acrocephalus scirpaceus* [2], the host race that parasitizes the resident or short-distance migratory robin *Erithacus rubecula* exploit relatively late-breeding members of their host population [2]. Indeed different host races of the cuckoo breed at staggered times throughout the season and those that co-occur in sympatry with other host races appear to shift their reproductive season such that there is less overlap, in a pattern of reproductive character displacement for timing of breeding (A. P. Møller *et al.* 2010, unpublished data).

Climate change has affected timing of migration and timing of breeding of different bird species (reviews in [13,14]). Long-distance migratory birds seem to have altered the timing of their spring migration less than short-distance migrants, and reproductive phenology has changed accordingly with residents resembling short-distance migrants [13,15,16]. The common cuckoo, a long-distance migrant, has advanced its migration phenology very little during the second half of the twentieth century (mean rate of advancement of arrival date by common cuckoo is only 0.13 d yr^{-1}), similar to its long-distance migratory hosts ([17]; mean rate of advancement 0.15 d yr^{-1}). By contrast, short-distance migrants have advanced their spring phenology considerably (mean rate of advancement 0.37 d yr^{-1}), potentially causing mismatch in the timing of reproduction of cuckoo host races using resident and short-distance migrant hosts [17]. Such differences in timing of reproduction of hosts and parasites could have profound effects on the relative abundance of different host races, and therefore also on the reproductive success of the hosts and their population dynamics.

The objectives of the present study were twofold. First, we tested to which extent the relative frequency of residents and short-distance migratory hosts has changed after 1990 by comparing host use during two periods before and after 1990, when climate change has been particularly strong [18]. Second, if climate change is driving the change in relative frequency of different cuckoo host races, we should expect spatial heterogeneity in temporal change of host use reflecting spatial heterogeneity in climate change. While spring temperatures have increased by more than 2°C in parts of Scandinavia since 1990, other areas such as parts of Eastern Europe have experienced little or no change in temperature [18]. In other words, we should expect the change in use of residents and short-distance migratory hosts to be negatively

correlated with the change in spring temperature. We used an extensive database of more than 32 000 cases of common cuckoo parasitism from Europe to test these predictions.

2. MATERIAL AND METHODS

(a) Database

We established a database of all known cases of cuckoo parasitism in Europe (West of the Ural Mountains) based on an extensive survey of museum collections, nest record schemes, bird ringing databases, publications and web sites. Despite any noise in the data, there is a biologically meaningful signal that can be interpreted in the light of temperature change and geographical variation. We attempted to assemble an exhaustive list of all cases of cuckoo parasitism with information on date, locality and host species. Any observation that did not include information on host species was excluded. We made an exhaustive list of natural history museums in Europe with the help of local ornithologists in different countries, but also included all large natural history museums in North America that might have data. We contacted more than 500 museum collections, requesting information. If we did not obtain a response, we sent two additional emails requesting information. In the case of large collections, or collections representing areas for which we had little information, we made additional efforts to obtain data, for example, by asking colleagues to obtain the information. We also requested information on other collections of cuckoo eggs or databases with information on cuckoo parasitism. Furthermore, we collected all published information on cuckoo parasitism with the requirement that the data included the information listed above. Any publication was thoroughly searched for other references that might also contain information. The sources of information and all contributors are listed in electronic supplementary material, appendix S1.

In total, the database consists of 32 843 records of cuckoo parasitism with information on host species, year, locality and additional information. We took great care to avoid any cases of multiple records of the same observation by checking records against the data already recorded. If in doubt, we excluded a possible duplicate record. We used information from more than 12 722 cuckoo eggs recorded by Moksnes & Røskaft [19], and included in the database listed above, for estimating approximate mean and standard deviation of laying date of cuckoos in different countries. This information was used for estimating change in temperature during biologically relevant periods for the cuckoo.

We made two kinds of explicit tests to test for heterogeneity in sampling effort in our database. First, we split the entire dataset into two temporal halves (1850–1940 and 1941–2009), and we subsequently tested whether the proportion of cuckoo eggs in nests of different host species was significantly repeatable among periods. Such repeatability (R) would be expected if natural habitats in different countries remained relatively stable, and if these habitats determined the distribution and the abundance of different hosts. Indeed, this analysis showed highly significant repeatability ($F = 9.31$, $r^2 = 0.90$, $p < 0.0001$, R (s.e.) = 0.81 (0.05)). Second, we had quantitative information on parasitism rates of different host species for 15 countries. We tested whether parasitism rate (i.e. the proportion of nests of any given host species that was parasitized by the cuckoo in a

given country) was positively associated with relative frequency of parasitism (the proportion of all cuckoo eggs in a given country that were found in the nests of different hosts) for these 15 countries. If relative frequency of cuckoo eggs in nests of different host species reflected parasitism rates, we would expect a strong positive correlation. Indeed, the amount of variance explained exceeded 65 per cent in these 15 tests. This information does not suggest that the data are biased.

(b) Frequency of cuckoo hosts with respect to migration

We classified all cuckoo hosts as long-distance migrants wintering in Sub-Saharan Africa or in the Indian Sub-continent ($n = 49$ species), or otherwise as short-distance migrants or residents ($n = 73$ species), using Cramp & Perrins [20] as a source.

We used 1990 as a cut-off point in the analyses because temperature has increased the most since 1990 [18]. In fact, temperature trends estimated at the cuckoo laying period (see below) for individual countries were significantly smaller before 1990 than from 1990 onwards ($t_{22} = 9.74$, $p < 0.0001$; mean (s.e.) 1958–1989: -0.001 (0.005) °C yr⁻¹; 1990–2009: 0.078 (0.007)). In addition, the actual choice of year was not crucial because the proportion of short-distance migrants that were hosts was highly repeatable in different countries for the periods 1985–2009, 1990–2009 and 1995–2009 ($F_{22,46} = 29.09$, $r^2 = 0.93$, $p < 0.0001$, R (s.e.) = 0.90 (0.04)).

(c) Changes in spring temperature

We estimated temperature trends at the country level from 1958 to 2009 using daily 2 m temperatures obtained from the ECMWF ERA-Interim data (http://data-portal.ecmwf.int/data/d/interim_daily/) for 1989–2009 and ERA-40 data (http://data-portal.ecmwf.int/data/d/era40_daily/) for years before 1989. The use of different data sources is justified as the ERA-Interim data did not include years before 1989 and ERA-40 data did not include years after 2002. As biologically relevant measure of climate, we used mean daily temperatures recorded in the interval centred symmetrically around the mean cuckoo parasitism dates in individual countries spanning two standard deviations around these dates. This analysis is based on the assumption that cuckoos have laid on specific dates, but were able to lay earlier or later depending on the duration of the breeding season of the host. Data from adjacent countries may be statistically non-independent because these tend to share the same climatic conditions. To identify countries where recent climate change has occurred at similar rates, we estimated temporal trends in temperature for 1958–1989 and 1990–2009 (see above), and then computed the difference in the slopes of temperature trend lines between these two study periods. Neighbouring countries were lumped according to the results of a hierarchical cluster analysis (method UPGMA) on these differences in temperature trends. Countries that were classified in the same cluster, but did not border on each other or on the same third country were forced into different clusters. Cluster analyses based on six other hierarchical clustering methods gave very similar classifications (details not shown). The relative frequency of parasitism was then recomputed by pooling all cases recorded in any given cluster of countries in either period. Temperature trends for each cluster were computed by averaging temperature trends for

individual countries and using country area as a weighting factor. A total of 12 clusters including between one and five countries were thus identified (electronic supplementary material, appendix S2). Slight modification of clustering (e.g. separation of Denmark from the Scandinavian cluster) did not alter the results qualitatively. These different clusters of adjacent countries with similar change in climatic conditions over the last decades should be considered statistically independent observations with respect to climatic effects.

Summary data for all variables are reported in electronic supplementary material, appendix S2.

(d) Population trends

Because short- and long-distance migrants may differ in population trends, such differences could potentially account for changes in the relative frequency of hosts with short migration distance. We extracted information on population trends for common breeding birds in Europe, using Voříšek [21] as a source.

(e) Statistical analyses

We analysed change in relative frequency of host use (i.e. the number of cuckoo eggs in nests of residents or short-distance migrants relative to the total number of cuckoo eggs reported) in the period 1990–2009 in relation to change in spring temperatures in different countries or clusters using generalized linear model analyses with PROC GENMOD in SAS 9.1.3, with the events/trials syntax. In these analyses, host use during 1958–1989 was entered as a covariate. Parameter estimates were corrected for over-dispersion using the deviance/d.f. ratio as a scaling factor.

3. RESULTS

(a) Change in relative frequency of host use in relation to migration distance

We first analysed the change in frequency of use of resident and short-distance migrant hosts in the two periods (before 1990 versus from 1990 onwards) and among countries, analysing host use as a binary response variable in a model with country and time period as factors. We found significant heterogeneity ($\chi^2_1 = 175.68$, $p < 0.0001$) among countries in relative frequency of cuckoo eggs laid in nests of short-distance migratory hosts ranging from 0.110 to 0.728 before 1990 and from 0 to 0.916 from 1990 onwards. The mean frequency of hosts that were residents or short-distance migrants was 0.429 (s.e. = 0.035; median = 0.404) before 1990, but only 0.299 (s.e. = 0.054; median = 0.228) from 1990 onwards, and this decline in the use of resident and short-distance migrant hosts was significant ($\chi^2_1 = 21.96$, $p < 0.0001$).

We carried out the same analysis using clusters of adjacent countries that had experienced similar changes in temperature owing to recent climate change. Residents and short-distance migrants became rarer in the pool of parasitized hosts in the more recent period, and this proportion varied with geographical area (model corrected for over-dispersion; effect of period: ($\chi^2_1 = 6.85$, $p = 0.0089$; effect of country aggregation: $\chi^2_1 = 44.43$, $p < 0.0001$). Thus, clustering did not affect the conclusions.

Populations of residents and short-distance migrants versus long-distance migrants differed somewhat in their long-term population trends. Long-distance migrants

decreased in abundance while residents and short-distance migrants did not change ($t_{88} = 2.27$, $p = 0.026$; residents and short-distance migrants: mean (s.e.) = 0.0004 (0.0038), $n = 50$; long-distance migrants: mean (s.e.) = -0.0117 (0.0036), $n = 40$). This difference in population trends of hosts should have resulted, other things being equal, in an increase in the relative frequency of parasitism of residents and short-distance migrants, long-distance migrants having become overall less abundant. Nonetheless, we found a decrease in the parasitism of residents and short-distance migrants.

(b) Change in use of resident and short-distance migratory hosts in relation to changing spring temperatures

In areas where temperature has increased more we found a greater decrease in the proportion of cuckoo eggs found in nests of hosts that were residents and short-distance migrants over the last two decades (figure 1; model corrected for over-dispersion; effect of temperature trend: $\chi_1^2 = 9.27$, $p = 0.0023$, coefficient = -31.00 (10.30); effect of relative parasitism in the first period: $\chi_1^2 = 2.04$, $p = 0.153$). The same analysis run on clusters gave similar results ($\chi_1^2 = 11.42$, $p = 0.0007$, coefficient = -27.88 (8.24); effect of relative parasitism rate in the first period: $\chi_1^2 = 1.00$, $p = 0.317$). Inclusion of change in temperature trends between the two periods did not alter the results qualitatively (change in temperature trend on country-level data: $\chi_1^2 = 5.28$, $p = 0.022$; clustered data: $\chi_1^2 = 5.59$, $p = 0.018$).

Because our data stem from different sources from different times we wanted to assess whether uncontrolled temporal trends could be influencing our results. To test for this we calculated the mean collection year for the two time periods from each country and took their difference, which represents the average time span between our past and current parasitism observations. Models based on country data where we included the difference (in years) between the mean date of parasitism events between the two periods within countries confirmed the negative covariation between relative parasitism rate of residents and short-distance migrants and temperature trend in the second period (binomial model as above; temperature trend: $\chi_1^2 = 8.23$, $p = 0.0041$; effects of parasitism rate in the first period: $\chi_1^2 = 1.70$, $p = 0.192$; time difference: $\chi_1^2 = 0.07$, $p = 0.798$). A model including change in temperature trends rather than temperature trends in the second period led to qualitatively similar results (temperature trend: $\chi_1^2 = 4.70$, $p = 0.029$; effects of relative parasitism rate in the first period: $\chi_1^2 = 0.53$, $p = 0.466$; time difference: $\chi_1^2 = 0.27$, $p = 0.603$). Thus including this variable in the models that examine relative parasitism of residents or short-distance migrants between time periods or as a function of increasing spring temperature did not change the conclusions.

4. DISCUSSION

In summary, different host races of the common cuckoo have changed their abundance as reflected by an increasing frequency of parasitism of long-distance migratory hosts. This change in relative frequency of host use with respect to migratory strategy was related to change in spring temperature. These relationships may have consequences for

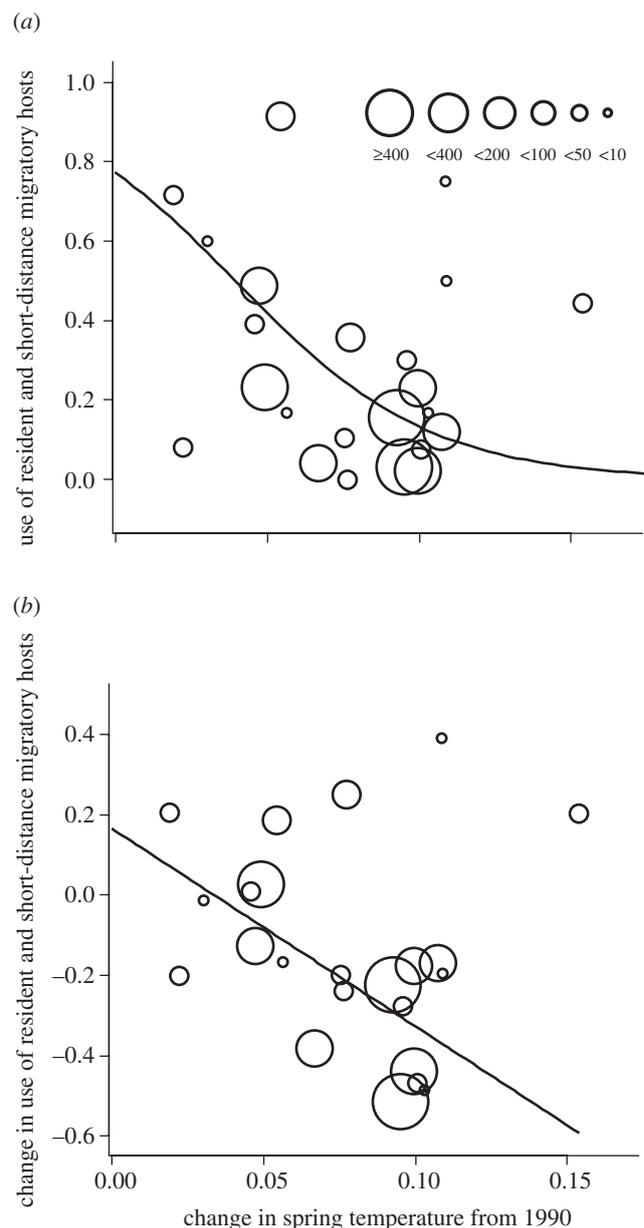


Figure 1. (a) Relative parasitism rates of resident and short-distance migratory birds during 1990–2009 in relation to annual change in spring temperature ($^{\circ}\text{C yr}^{-1}$) during 1990–2009. The line is drawn according to the best-fit binomial model controlling for relative parasitism rates before 1990 (see §3). (b) Change in relative parasitism rate of resident and short-distance migratory hosts in different European countries (frequency in 1990–2009 minus frequency before 1990) in relation to annual change in spring temperature during 1990–2009 ($^{\circ}\text{C yr}^{-1}$). The line is drawn based on the parameters of a linear regression weighted by the number of cases of parasitism after 1990 in each country and is shown to illustrate the negative relationship. See text for the appropriate binomial general linear model analysis. In both panels, the size of the symbols corresponds to the number of cases of parasitism reported during 1990–2009. Each circle represents a different European country in the two panels, and the size of circles reflects sample size as indicated at the top of the figure.

the relative population size of different host races of cuckoos and potentially for their risk of extinction.

We documented a change in relative frequency of brood parasitism in different host species of the

common cuckoo. Cuckoos have declined in abundance by 6 per cent since 1980, but not at all since 1990 [21], so a reduction in parasitism rate would be expected during the early part of our study, but not after 1990. Residents and short-distance migrants are now relatively less commonly used as hosts than long-distance migrants. Thus factors other than a general decline in breeding populations of cuckoos have to be invoked. This change in host use by the common cuckoo was what we predicted based on differences in migratory phenology of the cuckoo and its resident, short-distance and long-distance migratory hosts [17]. This implies that common resident and short-distance migratory hosts of the cuckoo such as robin, dunnock *Prunella modularis* and meadow pipit *Anthus pratensis* are less represented as hosts, while long-distance migrants-like reed warbler *A. scirpaceus* become more so (for a rare exception, see [22]). We consider this difference in response to be linked directly to inter-specific changes in breeding date among hosts of the cuckoo. Such changes in breeding date are common and highly heterogeneous among host species [14]. We hypothesize that mismatch in phenology will be common and not specific to the common cuckoo and its host races. Indeed, Møller [23] has shown that a louse-fly commonly parasitizing a bird host now emerges relatively earlier during the reproductive cycle of the host than just a few years ago. Such changes in relative phenology of parasites are more likely for parasites with a free-living part of their life cycle when they may experience different climatic conditions [24]. In fact, it is such parasites rather than parasites living continuously on their hosts that have changed in abundance or phenology in response to climate change [23].

The second major finding of this study was that the change in the relative frequency of residents and short-distance migrants as hosts could be predicted by changing temperatures. Countries with increasing spring temperatures had a greater decrease in relative frequency of resident and short-distance migratory hosts than countries with little or no change in temperature. This finding mirrors the result by Both *et al.* [25] showing that change in timing of reproduction by the pied flycatcher *Ficedula hypoleuca* could be predicted by changes in local temperature.

Changes in relative frequency of parasitism of different hosts with respect to migration may have consequences for risk of extinction of cuckoo host races. We suggest that changes in migration and breeding phenology of hosts may affect the relative reproductive success and hence the population size of different host races that are adapted to their specific hosts. Davies & Brooke [26] have already shown that the abundance of different host races changes over time. Furthermore, Krüger *et al.* [27] have shown that parasitic cuckoos experience greater rates of species and sub-species formation and extinction than do non-parasitic cuckoos. While such elevated risks of extinction may be attributed to parasitism and coevolution, the present study suggests that differential effects of climate on hosts could also play a role. Indeed different host races of the common cuckoo breed at different times because some host species differ in mean timing of breeding by more than one month ([2]; A. P. Møller *et al.* unpublished data), and early-breeding and late-breeding host races should be differentially sensitive to

effects of climate change. Though current climate change is dramatic, such phenomena also occurred previously, for example, following repeated past glaciations. Therefore, cuckoos in their evolutionary history probably experienced repeated climate-induced phenological shifts of some host species that may have influenced the abundance of some host races to the point of bringing these to extinction.

In conclusion, we have shown that resident and short-distance migratory hosts of the common cuckoo became less-frequently parasitized during 1990–2009 compared with earlier periods for different European countries. This decrease in relative representation of resident and short-distance migratory hosts increased with greater change in spring temperatures during breeding since 1990, consistent with the hypothesis that the change in host use by the common cuckoo is at least partially driven by climate change.

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