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Temperature during egg formation and the effect of climate warming on egg size in a small songbird

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ABSTRACT

The predicted effects of recent climate warming on egg size in birds are controversial, as only two long-term studies have been reported, with contrasting results. Long-term data on egg size variation are analyzed in relation to ambient temperatures in a southern European population of pied flycatchers where breeding phenology has not matched the spring advancement in the last decades. Cross-sectional, population analyses indicated that egg breadth, but not egg length, has decreased significantly along the 16-year period, leading to marginally non-significant decreases in egg volume. Longitudinal, individual analyses revealed that despite females consistently laying larger eggs when they experienced warmer temperatures during the prelaying and laying periods, there was an overall negative response – i.e. decreasing egg volume and breadth with increasing spring (May) average temperatures – across individuals. This trend is hypothesised to be caused by the mismatched breeding phenology, in relation to climate warming, of this population. Except in the unlikely cases of populations capable of perfectly synchronising their phenology to changes in their environment, maladjustments are likely for traits such as egg size, which depend strongly on female condition. Slight changes or absence thereof in breeding dates may be followed by mismatched dates, in terms of food abundance, for optimal egg formation, which would be reflected in smaller average egg size, contrary to early predictions on the effects of climate warming on bird egg size.

1. Introduction

Evidence has accumulated in the last few years that recent climate warming has affected the breeding date of some bird populations in North America and Europe, to variable degrees depending on species and geographical location (Parmesan and Yohe, 2003; Visser et al., 2003; Both et al., 2004). For logistic reasons, there are fewer studies examining effects of climate warming on traits other than breeding date or clutch size (Sanz, 2002), with the notable exceptions of the studies by Järvinen (1987) and Tryjanowski et al. (2004). Both these authors examined long-term patterns of population variation in egg size aiming to reveal correlations with increasingly warmer ambient temperatures in their study areas. Järvinen (1987) found an increase of average egg size with warmer temperatures in northern Finnish populations of pied flycatchers (*Ficedula hypoleuca*), while Tryjanowski et al. (2004) found exactly the opposite trend in a red-backed shrike (*Lanius collurio*) population in Poland.

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Järvinen (1987) predicted, on the basis of the positive relationship between ambient temperatures and average egg sizes he observed in a 19-year study, that climate warming could play a positive effect on some traits such as egg size, 'beneficial' in the sense that a large egg size usually enhances hatching success (Potti and Merino, 1996; Saino et al., 2004). At least in some species larger eggs also result in larger hatchlings, increased growth and development and, ultimately, increased fledging success (Williams, 1994). The pioneer study of Järvinen (1987), based on a cross-sectional population analysis, may nowadays be criticized for a lack of control for other factors in a design that, furthermore, has very low statistical power (Przybylo et al., 2000). Further, as noted by Tryjanowski et al. (2004), predictions about the consequences of climate warming on egg size are not straightforward. This is because egg size is only one of the traits that may be affected by climate warming (Both and Visser, 2005), among many others that may be phenotypically and genetically correlated with it (e.g. individual size or condition; see Potti, 1993; Smith et al., 1993; Williams, 1994; Christians, 2002; Yom-Tov, 2001; Lifjeld et al., 2005). Furthermore, adjustment of egg size to changes in environmental phenology, if any, will depend to a certain degree on a previous adjustment of bird phenology to the phenology of the changing environment. There is evidence that some bird populations, including that studied here, have not substantially advanced their breeding dates in spite of their habitats having experienced increasingly earlier onsets of the springs in the last few decades. In some populations, this has led to mismatches between the timing of peak food supply and nestling demands (Sanz et al., 2003; Both et al., 2004, 2006). Changes in egg size could be further proof of such a mismatch, given its usually strong relationship with female mass or indices of body condition (Christians, 2002).

Here I examine long-term trends of egg size in a population of pied flycatchers studied during 16 years to document patterns of its temporal variation and relationships to ambient temperatures. First, I use detailed data on ambient temperatures experienced by individual females during their laying and immediate prelaying periods, to test whether the variation in egg size in this population has any component attributable to an environmental factor that, for an insectivorous bird, is a strong indicator of resource conditions at the start of breeding. Previous work has centred on genetic and maternal effects on egg size (Potti, 1993, 1999a), on maternal effects due to egg size (Potti and Merino, 1994), and on the consequences of egg size on hatching success (Potti and Merino, 1996). Some purely environmental influences on egg size in this population have also previously been suggested (Potti, 2007), for instance larger eggs were laid in nestboxes of high quality (as measured by rates of nestbox occupancy; Potti, 1993). Increased temperatures experienced by females during laying have been reported to affect positively the egg size of pied flycatchers and other insectivorous passerines (Ojanen et al., 1981; Nager and Zandt, 1994; Perrins, 1996; Stevenson and Bryant, 2000; Hargitai et al., 2005). However, there has been little previous long-term work – as opposed to short-term or experimental studies, which abound (Williams, 1994; Christians, 2002) – on the influence of ambient temperature on the egg size of any altricial bird species that has simultaneously controlled for a set of important factors that may independently affect egg size, such as study year (Hargitai et al., 2005), female mass (Järvinen, 1991; Potti, 1993) or the already mentioned identity effects. Using general linear models (GLM), I test simultaneously for the importance of effects related to ambient temperatures on the egg volume produced by female pied flycatchers, once these relevant influences are taken into account. The longitudinal analysis also examines whether the increased spring warming across the study period, as expressed by decadal variation in average May temperatures (Sanz et al., 2003) has affected egg size. Finally, I explore the fitness consequences of egg size variation and place it in the wider context of long-term breeding patterns by examining its relationship with hatching success and recruitment to the breeding population.

2. Methods

I studied the egg size of pied flycatchers breeding in nest boxes in a deciduous (*Quercus pyrenaica*) forest in La Hiruela, central Spain, during 16 years (1987–2006, with no egg data for the years 1996, 2002 and 2003). All eggs in clutches (range 3–8) were measured during around the sixth day of incubation with callipers to the nearest 0.1 mm for maximum length (L) and breadth (B) and a mean egg volume (V, in cm^3) was calculated for each clutch using Hoyt's (1979) formula ($V = 0.51LB^2$). The greatest component of variation in egg volume occurs between females, while within-clutch and yearly variation are small (Potti, 1993, 1999a). Egg volume is highly consistent both within clutches and across years and does not vary across the range of female ages (Potti, 1993). Therefore, unique values of egg volumes were obtained by averaging egg volume within a clutch and then across all clutches of individual females.

Females were captured either on the sixth to tenth day of incubation or while feeding nestlings 8–13 days old by means of a trap put within their nest. They were measured for tarsus length (to the nearest 0.05 mm; Potti and Merino, 1994) and weighed with a spring balance (to the nearest 0.1 g). In almost all years, masses recorded in the field significantly increased linearly with the time of capture during the day (Potti and Merino, 1995). To adjust for these differences, I transformed field masses to those predicted at noon by using the slopes of yearly linear regressions of mass on time of capture (Potti and Merino, 1995). Female masses recorded during the incubation and the nestling periods differ significantly, precluding lumping of both. As data were limited in many years to only one of those masses, correlations for both are presented in the cross-sectional analysis. For the longitudinal analyses, I used the mass recorded at incubation, for which sample sizes were larger.

For the analyses concerning egg size and temperature during the period of egg formation I computed a 'temperature-during-prelaying-and-laying' index for each female tailored as a function of her breeding date and clutch size, using the mean daily temperatures experienced by individual females during part of those periods (e.g. Hargitai et al., 2005). To capture most of the temperature range experienced by each female during the period of egg formation in the oviduct (King, 1973), I used the mean of average daily temperatures