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Local weather conditions have complex effects on the growth of blue tit nestlings



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ABSTRACT

Adverse weather conditions are expected to result in impaired nestling development in birds, but empirical studies have provided equivocal support for such a relationship. This may be because the negative effects of adverse weather conditions are masked by parental effects. Globally, ambient temperatures, rainfall levels and wind speeds are all expected to increase in a changing climate and so there is a need for a better understanding of the relationship between weather conditions and nestling growth. Here, we describe a correlative study that examined the relationships between local temperatures, rainfall levels and wind speeds and the growth of individual blue tit (*Cyanistes caeruleus*) nestlings in relation to their hatching order and sex. We found that changes in a range of morphological characters were negatively related to both temperature and wind speed, but positively related to rainfall. These patterns were further influenced by the hatching order of the nestlings but not by nestling sex. This suggests that the predicted changes in local weather conditions may have complex effects on nestling growth, but that parents may be able to mitigate the adverse effects via adaptive parental effects. We therefore conclude that local weather conditions have complex effects on avian growth and the implications for patterns of avian growth in a changing climate are discussed.

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1. Introduction

Environmental conditions have a broad range of effects on reproducing animals and in birds, they may affect the timing of egg laying, clutch sizes, nestling survival rates, patterns of nestling growth and parental provisioning patterns (Wingfield, 1984; Stenseth et al., 2002; Møller, 2012). Birds are usually able to respond to predictable changes in environmental conditions, such as the temporal increases in spring temperatures that have resulted from anthropogenic climate change through shifts in their breeding ranges or the timing of reproduction (Charmantier et al., 2008; Chen et al., 2011). However, they are less able to respond to unpredictable short-term temporal fluctuations in environmental conditions, such as those associated with changes in local weather conditions, through changes in parental provisioning or brooding behaviours (McCarty, 2001; Greno et al., 2008). One of the most important effects that short-term changes in local weather conditions can have on birds is affecting patterns of offspring growth (Krijgsveld et al., 2003; Dawson et al., 2005). This is because the conditions experienced during ontogeny can impair the development of morphological characters and internal organs which

subsequently affects a number of traits with relevance to an individuals' fitness during adulthood, such as the acquisition of social dominance, the acquisition of breeding territories and reproductive partners, breeding success and lifespan (e.g. Magrath, 1991; Both et al., 1999; reviewed by Lindström, 1999; Metcalfe and Monaghan, 2001).

Adverse weather conditions such as low temperatures, high rainfall or high wind speeds or their interactive effects (e.g. Coe et al., 2015) impair growth either directly by chilling them (Dunn, 1975; Bryant, 1978; Quinney et al., 1986; Keller and van Noordwijk, 1994; McCarty and Winkler, 1999; Ritz et al., 1995; Dawson et al., 2005; Pérez et al., 2008; Ardia et al., 2009, 2010; Winkler et al., 2013) and/or indirectly by reducing the ability of parents to catch or transfer prey to the nest (Konarzewski and Taylor, 1989; Becker and Specht, 1991; Boersma and Parrish, 1998; Ritz et al., 1995; Finney et al., 1999; Geiser et al., 2008). In altricial nestlings, these patterns likely represent a trade-off between growth and thermoregulation (Visser, 1998; Rauter and Rever, 2000) because naked young are susceptible to adverse weather conditions. In altricial species however, the female parent often spends the first few days of the nestlings' lives brooding them whilst the male parent searches for food but as the food requirements of the brood increase, then females spend increasing amounts of time foraging until both parents continually search for food. Nevertheless, the trade-off between growth and thermoregulation means that in

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adverse weather conditions, nestlings may have to allocate their limited resources towards sustaining their own body temperatures rather than towards developmental functions such as growth (Skagen and Yackel Adams, 2012; Pérez et al., 2016).

Despite studies showing that adverse local weather conditions result in impaired offspring growth, other studies have provided no, or weak, support for such a relationship (Dunn, 1975; Murphy, 1985; Johnston, 1993; McCarty and Winkler, 1999; Bradbury et al., 2003). For example, local weather conditions were poor determinants of growth in farmland passerine birds (Bradbury et al., 2003) and the amount of sunshine had no effect on the growth of roseate tern (*Sterna dougallii*) chicks, although wind speeds were negatively related to growth (Dunn, 1975). It is unclear why adverse weather conditions do not always impair growth but it may be that the effects are masked by parental effects (Dawson et al., 2005) or by resource allocation patterns whereby nestlings shift resources between various morphological characters (Mainwaring and Hartley, 2012). Further studies are thus required to increase our understanding of how weather conditions influence growth. Further, it may provide useful insights into the effects of climate change on patterns of avian growth. Globally, ambient temperatures (IPCC, 2001), rainfall levels (Marvel and Bonfils, 2013) and wind speeds (Vautard et al., 2010; Young et al., 2011) are expected to increase from anthropogenic climate change (Garcia et al., 2014). There is a need to document the effects of global climate change on ecological systems as whilst there has been a great deal of research into the effects on changes in laying dates in passerine birds in temperate environments (Charmantier et al., 2008; Møller, 2012), the effects of local weather conditions on other aspects of the life histories of birds are less well understood (Dawson et al., 2005).

Here, we study how variation in local temperature, rainfall and wind speeds affected the growth of individual blue tit (*Cyanistes caeruleus*) nestlings in relation to their hatching status and sex. Blue tits are a useful study species because their growth is likely to be affected by adverse weather conditions as it constrains the parents' ability to forage for caterpillars. Blue tit broods hatch with varying degrees of asynchrony with some broods hatching within one day and others hatching out over two or three days, and in these cases the majority of the brood hatches on the first day (Cramp and Perrins, 1993; Stenning, 2008). Early hatched nestlings are larger than their late hatched siblings throughout the growth period (Mainwaring et al., 2010) whilst male nestlings are larger than females throughout (Mainwaring et al., 2011; Mainwaring et al., 2012). Meanwhile, whilst egg constituents, such as lipid content and fatty acids decline (Bourgault et al., 2007), egg mass and volume do not vary through the laying sequence in some populations (Bourgault et al., 2007) but increase through the laying sequence in other populations (Stenning, 2008) thereby enabling late hatched nestlings to mitigate the adverse effects of hatching asynchrony. In this study, we test the following two predictions. First, we predict that the growth of nestlings will be positively affected by high temperatures but negatively affected by high levels of rainfall and wind speeds because high temperatures promote effective foraging and reduce the need to brood the nestlings whilst the converse applies when rainfall and wind speeds are high. Second, we predict that the growth of later hatched and female nestlings will be affected to a greater extent than earlier hatched and male nestlings because they are smaller and hence more likely to lose out when competing for parentally provided food.

2. Material and methods

2.1. Study site and quantifying reproductive parameters

Data were collected from blue tits breeding in deciduous woodland interspersed with small patches of coniferous trees in Lancashire, UK (54°0'N, 02°47'W) during 2004–2006 (Lambrechts et al., 2010). A total of 66 nestboxes were available for hole breeding passerines to occupy and although not all nestboxes were occupied, we only recorded blue tits breeding in the nestboxes. Regular nestbox checks from the beginning of April established the date on which the first egg was laid, assuming that one egg was laid per day (Cramp and Perrins, 1993). Nests were then checked on a daily basis after the sixth egg was laid to establish when incubation began. Nests were left undisturbed during incubation. Then, a couple of days before the predicted hatching date, nests were checked for hatching on a daily basis. We individually marked nestlings on the day that they hatched with an indelible marker pen, meaning that we were able to quantify the exact date of hatching for all of the nestlings. As female blue tits usually begin to incubate their clutch one or two days prior to clutch completion, then broods hatch asynchronously over a period of 2–3 days. Following previous studies (Mock and Forbes, 1995; Mainwaring et al., 2010), we defined those nestlings that hatched on the first day of hatching as early hatched nestlings and those nestlings that hatched on later days as late hatched nestlings.

2.2. Quantifying nestling growth changes

A total of 614 nestlings from 66 broods were measured every two days until the eldest nestlings were 14 days old. We individually tracked individual nestlings by marking them with an indelible marker pen daily until they were six days old when they were fitted with individually numbered metal rings. At each visit, one of us (MCM) quantified the body mass (± 0.1 g; electronic balance), head-bill length (± 0.05 mm; dial callipers), tarsus length (from the depression in the angle of the intertarsal joint to the end of the folded foot) (± 0.05 mm; dial callipers) and right fourth primary length (± 0.5 mm; fixed rule) of all nestlings. Note that whilst body mass and head-bill length were measured every two days from day 2 onwards, tarsus length and fourth primary length were measured every two days from day 6 onwards. Nestling growth changes may vary systematically with nestling age, independent of changes due to local weather conditions and so we included a 'growth period' factor in the analyses with 1 being the growth change between days 2 and 4, 2 being the change between days 4 and 6, 3 being the change between days 6 and 8, 4 being the change between days 8 and 10, 5 being the change between days 10 and 12 and 6 being the change between days 12 and 14. We have previously calculated the repeatability of values for each morphological character and found them all to be repeatable (Mainwaring et al., 2010). For each morphological character, we quantified growth rate changes by calculating the change in the value obtained at a particular visit from the value obtained at the previous visit. After the nestlings were measured at day 14, the nests were left undisturbed for 6 days because nest visits may have caused the nestlings to fledge prematurely. Nests were then checked again at day 20 (± 1) in order to establish fledging success. We only included nestlings that fledged, and as 47 nestlings never fledged, then 567 nestlings from 66 broods were included in the study.

2.3. Molecular techniques

We determined the sex of individual nestlings using standard molecular techniques, as we have previously described elsewhere (Mainwaring et al., 2011, 2012).

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