Extreme temperature drop alters hatching delay, reproductive success, and physiological condition in great tits

Michał Gładalski1 • Miroslawa Baňbura2 • Adam Kaliński1 • Marcin Markowski1 • Joanna Skwarska1 • Jarosław Wawrzyniak1 • Piotr Zielinski3 • Jerzy Baňbura1

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Abstract
It has been suggested that extreme weather events may be treated as natural experiments that may unravel the mechanisms by which birds adjust their phenology and breeding parameters to environmental variability. In 2017, a sudden and heavy drop of temperatures for several days affected many European bird populations. This event occurred during the laying–early incubation period in the great tit (Parus major) population in central Poland, causing a large delay in hatching and had sustained reproductive consequences. This cold snap occurring once breeding activity had already started in 2017 was followed by the warm and invariable breeding season of 2018. This natural experiment had an essential influence on great tit reproductive parameters. We found a significant difference in hatching date, number of fledglings, hatching success, and fledging success between 2017 and 2018. In 2017, there were about two fledglings per nest fewer than in 2018. Fledging success was positively associated with hatching delay in 2017, while the relation was negative in 2018. Hatching success differed significantly between both years, being higher in 2018. Mean level of hemoglobin (used as index of body, physiological condition) in the blood of nestling great tits was higher in 2017 than in 2018. We argue that the moment of hatching may be (at least in some years) more tightly related to the moment of maximum food demand of tit nestlings than the traditionally used laying date. Also in extreme years, phenotypic plasticity of hatching delays may be insufficient to adjust the timing of breeding to the upcoming extreme weather events. Further examining its limits may be an important goal for future research.

Keywords Climate change • Birds • Laying date • Thermal conditions • Delayed breeding time • Breeding success • Body condition

Introduction
There is still little information about how climate change and extreme weather events may influence breeding traits and reproduction parameters in animals (Charmentier et al. 2008; Pipoly et al. 2013; Charmentier and Gienapp 2014; Gładalski et al. 2016, 2018a; Mainwaring et al. 2017; van de Pol et al. 2017; Wingfield et al. 2017). Therefore, it was suggested that those extreme weather events may be treated as natural experiments that could shed light on the mechanisms by which birds adjust their breeding characteristics to environmental variability (Jentsch et al. 2007; Bailey and van de Pol 2016; Marrot et al. 2017). Radchuk et al. (2019) in their meta-analysis focusing on birds suggest that the evolutionary load imposed by incomplete adaptive responses to ongoing climate change may be threatening the persistence of species. In addition, examining the limits of phenotypic plasticity of those breeding characteristics may be an important goal for future research (Gładalski et al. 2014; Wesołowski et al. 2016; Chevin and Hoffmann 2017; Bonamour et al. 2019).

Variation in ambient temperature affects all life stages of organisms (Stearns 1992). Extreme weather episodes may disturb life history strategies of various species and may have complex effects on fitness (Haftorn 1988; Chamberlain and Pearce-Higgins 2013; Whitehouse et al. 2013; Mainwaring...
and Hartley 2016). In birds, extremely cold spells may induce egg rejection behavior (this behavior could serve as a mechanism for maternal clutch size adjustment in passerines in response to extreme cold periods, Shitikov et al. 2019), negatively influence hatching success (in white storks, Ciconia ciconia, frost during incubation may negatively influence the hatching success, Tobolka et al. 2015), or lead to higher nest mortality (extreme weather events may cause high late mortality even for stork nestlings older than 30 days, Tobolka et al. 2015; extreme drought may alter breeding success in willow flycatchers, Empidonax traillii, Theimer et al. 2018). Extremely cold spell may also cause much lower biomass of nestlings (low temperatures and long-lasting heavy and frequent rain may cause lower amount of food and may cause difficulty with feeding nestlings, Whiteshote et al. 2013), cause large hatching delay (Whitehouse et al. 2013; Gładalski et al. 2018a), or even cause egg freezing and egg cracking, resulting in the loss of whole clutches (Hale 1933, Musselman 1939, Indykiewicz 2015). Little is known about the flexibility of the hatching delay (a difference between the expected date and the observed hatching date was considered as a hatching delay) and its consequences on breeding parameters (Kluen et al. 2011; Lee and Lima 2017).

In insectivorous passersines, like tits, temperature has a crucial influence on the optimal laying date and reproduction, because it affects trophic conditions for egg formation, conditions for incubation, and the timing of peaks in spring caterpillar abundance – the main food source for the nestlings (Perrins 1991). 2017 was not, in general, an abnormal-...
We calculated the expected hatching dates as follows: first egg date + clutch size +12 (incubation in great tits normally lasts 13 days, and the female often starts to incubate 1 day before completing the clutch (García-Navas and Sanz 2011, Gladalski et al. 2018a)). The difference between expected date and observed hatching date was considered as a hatching delay (positive values mean a delay, while negative values mean that hatching occurred before the expected date). In calculations, the mean laying dates were expressed as days from 1 March. In Fig. 1, we used laying–early incubating warmth sums, which were calculated as the sums of the mean daily temperatures for a period of 7 days starting from the 4th day since the first egg date to characterize thermal conditions during egg laying (Gładalski et al. 2018a).

The individual nestling values of hemoglobin concentration were treated as unit records and analyzed using mixed linear models, brood ID being included as a random factor to control for clustering; degrees of freedom were approximated by the Satterthwaite method (Heck et al. 2010). Effects of year and study area on the hemoglobin concentrations (with controlling for wing length, number of fledglings, hatching delay, and interaction between years and hatching delay) were modeled in an ANCOVA style (Crawley 2002). Effects of year, study area, and hatching delay on fledging success (fledging success refers to the proportion of eggs resulting in fledglings) and hatching success (refers to the proportion of eggs resulting in hatchlings) were calculated using a generalized linear model with binomial error distribution, the approximation of degrees of freedom by the residual method, applying logit link function (Crawley 2002; Heck et al. 2012). Generalized linear and linear mixed modeling was performed using IBM SPSS Statistics 22 software (Heck et al. 2010, 2012; IBM SPSS 2013).

**Results**

The patterns of variation in temperatures in April, during the first half of the breeding season, were very different between 2017 and 2018 in Łódź (Figs. 1, 2). Mean warmth sums during laying–early incubating were very low in 2017 in comparison with 2018 (Fig. 1).
In 2017, the sudden, long-lasting drop of temperature took place at the time of egg laying by tits and caused large hatching delays in great tits (mean 4.64 ± 2.61 SD days) in comparison with relatively invariable, warm spring in 2018 (mean − 0.52 ± 1.07 SD days) (Fig. 3; \( F_{1,169} = 254.3, P < 0.001 \)) . Those extremely different thermal conditions caused large differences in physiological condition of nestlings and fledging success in both years, but there was also a significant difference in hatching success. Clutch size was not significantly different between 2017 and 2018 (2017 mean 9.01 ± 1.41 SD, 2018 mean 8.96 ± 2.02 SD; \( F_{1,169} = 0.32, P = 0.57 \)), but the number of fledglings was significantly different (2017 mean 4.38 ± 2.90 SD, 2018 mean 6.33 ± 3.25 SD; \( F_{1,169} = 14.59, P < 0.001 \), Fig. 3). Fledging success was significantly different between the years, being higher in 2018, with other significant effects being hatching delay and interaction between year and hatching delay (Table 1). Fledging success was positively associated with hatching delay in 2017 (\( b = 0.41 ± 0.10 \) SE; Wald \( \chi^2 = 17.13, P < 0.001 \)), while the relation was negative in 2018 (\( b = -0.33 ± 0.10 \) SE; Wald \( \chi^2 = 11.98, P = 0.001 \)). Hatching success was significantly different between the years, being higher in 2018, and was significantly different between both study areas, being higher in the forest site (Table 1). Hatching success was not significantly related to hatching delay. This suggests that the length of delay did not proportionally affect hatching success, but the very occurrence of the hatching delay was influential (year: 2017 hatching delays vs. 2018 no hatching delays).

Controlling for wing length, number of fledglings, and hatching delay, the level of hemoglobin was higher in 2017 than in 2018 with significant interaction between year and number of fledglings (Table 2, Fig. 3). The level of hemoglobin was more negatively associated with the number of fledglings in 2017 (\( \text{est} = -4.61, t = -5.51, \text{df} = 358.86, P < 0.001 \)), while the relation was negative in 2018 (\( \text{est} = -1.30, t = -2.52, \text{df} = 284.22, P = 0.012 \)).

**Discussion**

We found that a sudden drop of temperatures causing a cold snap in the breeding season of 2017 caused a larger hatching delay and lower fledging and hatching success than in 2018. An average great tit brood produced about two fledglings per nest fewer in 2017 than in 2018, whereas clutch size was not significantly different between 2017 and 2018. Fledging success was also positively associated with hatching delay in 2017, while the relation was negative in 2018. Hatching success differed significantly between 2017 and 2018 and between both study areas, being higher in the forest site. Mean level of hemoglobin in the blood of nestling great tits was, contrary to our predictions, higher in 2017 than in 2018.

Fig. 3 (A) Mean hatching delay in the great tit in extreme years of 2017 and 2018. Mean laying dates are represented as averages ±95% confidence intervals. (B) Mean number of fledglings in the extreme years of 2017 and 2018. Mean level of fledglings is presented as averages ± standard error. (C) Mean hemoglobin concentration (g/l) in the blood of the great tit nestlings in the extreme years of 2017 and 2018 from a linear mixed model analysis. Mean level of hemoglobin is presented as averages ± standard error

Visser et al. (2006) suggested that quantifying food resources is essential to establishing an understanding of
phenology. When the temperatures are high enough, tit females start producing eggs, and then if there is a sudden temperature drop (and phenology of trees slows down, so the caterpillars for tit nestlings will be available later during the season), they may delay the moment of producing the next egg in a clutch or delay the moment of starting incubation (García-Navas and Sanz 2011; Kluen et al. 2011). During the large temperature drop in 2017, great tits delayed hatching to match nutritional needs of nestlings with caterpillar phenology, but it was not enough. Many of nestlings in that year died because the tree phenology was strongly delayed. When first hatchlings appeared, many of the trees were still leafless, with only young buds present (own observations). Different studies show that the mean number of fledglings per female is lower in years when population/caterpillar mismatch is high (Reed et al. 2013). In our study areas, with subsequent days, the amount of caterpillars grew up, but for the most broods, food conditions were harsh and nestling reduction within the broods was large in 2017 (and the clutch sizes were not significantly different between 2017 and 2018). Certainly, if females did not delay hatching in 2017, the number of dead nestlings would be much larger (and the number of fledglings would be expected to be even lower than it was). In the extreme 2017, larger hatching delay was related to later hatching and larger amounts of food for nestlings, but, in general, in tits, breeding characteristics (clutch size, physiological condition of nestlings, hatching success, fledging success) tend to decline during the course of the breeding season (Verhulst et al. 1995; Verboven and Visser 1998; Kaliński et al. 2019). This negative relation between fledging success and hatching delay was present in the temperature-stable 2018. Tomáš (2015) suggested that most studies conducted on optimal timing of breeding in birds have traditionally considered the date of the first egg as the event that should be related to the time of maximum food availability. In the context of the large hatching delays in 2017 found in our study, we argue that the moment of hatching may be (at least in some years) more tightly related to the moment of maximum food demand of tits’ nestlings than laying date. Another (or supplemental) explanation may be that lower fledging success in the cold year could occur also because of the slower embryonic development as during the cold spell, the temperature for embryos could easily be suboptimal (Haftorn 1988), and maybe the females could not buffer it totally with required amount of incubation (e.g., because they also needed increased food intake to maintain body temperature and condition – e.g., comparing the time females spent with incubation in 2017 and in 2018 could be a test for it). This may lead to increased time to develop to hatching causing the large hatching delay, and it may also cause lower fledging success via greater embryonic/post hatching mortality.

Hatching success also differed between 2017 and 2018, being higher in cold spell free 2018. It may confirm that a cold spell may have negative effects on egg viability (Lee and Lima 2017). On the other hand, the duration of hatching delay had no influence on hatching success, suggesting that the length of hatching delay may be not as significant as the very occurrence of the delay during harsh weather conditions (cold spell in 2017 vs. stable weather in 2018). Hatching success also differed between both study areas, being higher in the forest study site. Our studies on tits suggest that no consistent long-term difference in hatching success occurs between the study areas, with hatching success being higher in the forest in some years and in the urban park in other years, while the long-term means are similar (Gładalski et al. 2017, unpublished data). Therefore, the difference that was found in the present study could be a statistical artifact or a result of some additional unknown factors.

Our previous studies have shown that blood hemoglobin concentration in nestling passerines is a reliable index of individual condition and nutritional state (Kaliński et al. 2015, 2017, 2019). Kaliński et al. (2015) suggested that extreme weather, with large amounts of rain and low temperatures,
may cause depressed hemoglobin levels in the great tit nestlings, because heavy rainfall may prevent parents from efficient foraging on oak leaf-eating caterpillars. In 2017 a mismatch between nutritional needs of nestlings and caterpillar phenology was large enough to cause high levels of nestling reduction within broods. Contrary to the predicted hemoglobin difference, the larger hemoglobin level in 2017 may emerge because of the decreased brood size (they emerged because of higher mortality in the cold year) may allow the survived nestlings to reach higher body condition. Experimental studies show that changes in brood size may affect body condition of nestlings and breeding success of tits (Fargallo and Merino 1999; Neuenschwander et al. 2003; Bańbura et al. 2013).

We agree with Radchuk et al. (2019) that adaptive responses of animals to some effects of climate change may be insufficient. We also agree that extreme weather events may and should be treated as natural experiments and that they could explain and sometimes give the opportunity to explore things that would be very difficult or even impossible to study in a different way. In the light of gathered evidence on climate changes, the future weather will probably become more unstable and extreme. As a consequence, we will probably have plenty of opportunities to study natural experiments of this type in the coming century.

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