



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

Michał Gładalski¹ · Mirosława Bańbura² · Adam Kaliński¹ · Marcin Markowski¹ · Joanna Skwarska¹ · Jarosław Wawrzyniak¹ · Piotr Zieliński³ · Jerzy Bańbura¹

Received: 30 September 2019 / Revised: 17 December 2019 / Accepted: 21 December 2019 / Published online: 8 January 2020
© The Author(s) 2020

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 (Charmantier et al. 2008; Pipoly et al. 2013; Charmantier 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

✉ Michał Gładalski
michal.gladalski@biol.uni.lodz.pl

¹ Department of Experimental Zoology and Evolutionary Biology, Faculty of Biology and Environmental Protection, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland

² Museum of Natural History, Faculty of Biology and Environmental Protection, University of Łódź, Kilińskiego 101, 90-011 Łódź, Poland

³ Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland

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, Whitehouse 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 passerines, 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 abnormally colder year, but a sudden drop of temperatures for several days – a cold snap – during the laying–early incubating period in Polish populations of the great tit (*Parus major*) caused a marked hatching delay (Gładalski et al. 2018a). That harsh period was followed by completely opposite, warm and invariable breeding season of 2018. In this paper, we report on response of breeding parameters (hatching success, fledging success, physiological condition of nestlings) of great tits to extreme laying–early incubating temperature variation between 2017 and 2018. We predict that birds that came across the large temperature drop in 2017 should have a lower fledging success and hatching success than birds in 2018. We also predict that nestlings from 2017 should have a lower concentration of hemoglobin than nestlings from 2018. Hemoglobin concentration, as a physiological condition indicator of nestling altricial birds (Campbell 1995; Lill et al. 2013; Minias 2015; Johnstone et al. 2017; Kaliński et al. 2017, 2019), is currently eagerly used in experimental and field studies of birds (Lill et al. 2013; Podlaszczuk et al. 2017; Gładalski et al. 2018b, 2019). Studies on tits (Paridae) at our study areas in central Poland suggest that a higher level of hemoglobin is positively related to good physiological condition of nestlings (Kaliński et al. 2017, 2019; Gładalski et al. 2018b).

Materials and methods

This study was carried out as a part of long-term research project concerning the breeding biology of secondary hole-nesting birds occupying nest boxes near Łódź, central Poland (51°47' N, 19°28' E) (Wawrzyniak et al. 2015). The forest study area (51°50' N, 19°29' E) and the urban parkland study area (51°45' N, 19°24' E) are located in two, structurally and floristically contrasting habitats (10 km apart). The urban parkland site (about 80 ha) consists of the botanical garden (about 64 ha) and the zoological garden (about 16 ha). Both gardens are considered as the biggest entertainment and recreation areas in Łódź. The vegetation of the parkland area consists of a mix of tree and shrub species including exotic species (Marciniak et al. 2007). The forest area is about 130 ha area in the center of large, mature mixed deciduous forest (1250 ha in total), bordering on the NE suburbia of the city of Łódź. Oaks (*Quercus robur* and *Q. petraea*) are predominating tree species in the Łagiewniki Forest.

The forest study area and the urban parkland study area were supplied with standard wooden nest boxes (Lambrechts et al. 2010). About 200 nest boxes were placed in the parkland and about 300 nest boxes were placed in the forest. All the nest boxes were set on trees at a height of about 3 m. All the distances between neighboring nest boxes were about 50 m. A total of 94 first clutches of great tits were studied in 2017 (blood samples were taken from nestlings from 80 clutches), and a total of 67 first clutches of great tits were studied in 2018 (blood samples were taken from nestlings from 62 clutches). The great tit nestlings were banded with individually numbered metal rings, and wing length was measured (to the nearest 1 mm) 13–14 days after the hatching. The number of fledglings is an equivalent to the number of fledglings in a brood (1284 fledglings in 2017 and 1263 fledglings in 2018).

The large temperature drop in 2017 was also recorded in many tit populations (and other bird populations, Shitikov et al. 2019) all over the Europe: in Belgium, England, France, Germany, Hungary, the Netherlands, Poland (Figs. 1, 2), Sweden, and others (see Gładalski et al. 2018a). The critical period of the temperature drop during the laying–incubating period in April of 2017 lasted for about 5 days. The mean ambient temperature dropped to about 2–3 °C (Fig. 2). Following Altwegg et al. (2017) and van de Pol et al. (2017), we define this sudden drop in ambient temperature for a period of time during laying–early incubating period as an extreme weather event that caused the biological response to be in the 5% of most extreme values of the biological response variable (hatching delay). The local temperatures for Łódź were obtained from TuTiempo.net climate database (<https://en.tutiempo.net/climate/ws-121055.html> and <http://www.tutiempo.net/en/Climate/LODZ/124650.htm>).

Fig. 1 Laying–early incubating warmth sums, as the sum of the mean daily temperatures for the 7 days starting in the 4th day since the first egg date in great tits in the forest study area and in the urban parkland study area (2002–2018)



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, Gładalski 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).

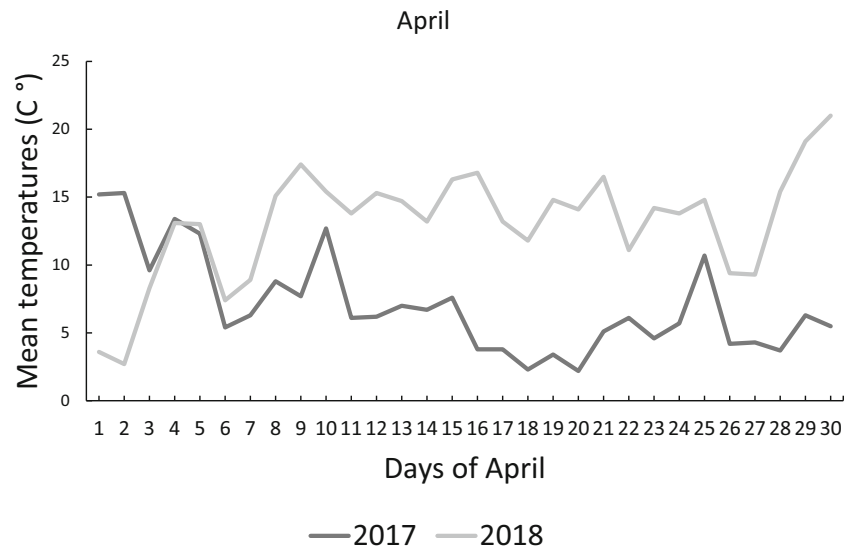
The individual nestling values of hemoglobin concentration were treated as unit records and analyzed using mixed linear models, brood ID being included as a random factor to control for clustering; degrees of freedom were approximated by the Satterthwaite method (Heck et al. 2010). Effects of year and 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).

Fig. 2 Mean temperatures of April in 2017 and 2018 in Łódź



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 ($b = 0.41 \pm 0.10$ SE; Wald $\chi^2 = 17.13$, $P < 0.001$), while the relation was negative in 2018 ($b = -0.33 \pm 0.10$ 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 (est = -4.61 , $t = -5.51$, $df = 358.86$, $P < 0.001$), while the relation was negative in 2018 (est = -1.30 , $t = -2.52$, $df = 284.22$, $P = 0.012$).

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.

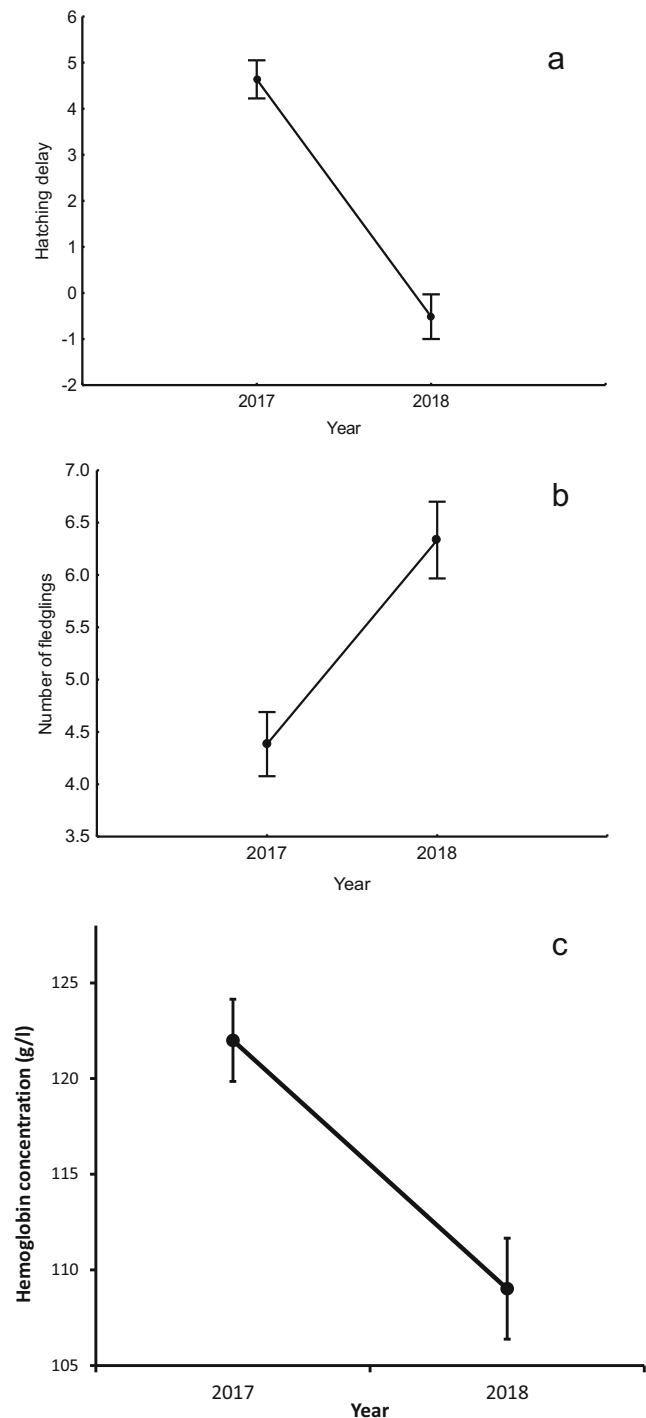


Fig. 3 (A) Mean hatching delay in the great tit in extreme years of 2017 and 2018. Mean laying dates are represented as averages $\pm 95\%$ confidence intervals. (B) Mean number of fledglings in the extreme years of 2017 and 2018. Mean level of fledglings is presented as averages \pm standard error. (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 \pm standard error

Visser et al. (2006) suggested that quantifying food resources is essential to establishing an understanding of

Table 1 Summary of a generalized linear models with binomial error distribution, logit link function, and Wald Chi-squared test statistics examining variation in great tits fledging success and hatching success in terms of year, study area, and hatching delay

Factor	b ± SE	Wald chi-square	Df	P
Fledging success				
Intercept	1.2 ± 0.1	33.4	1	< 0.001
Year	-1.1 ± 0.2	36.5	1	< 0.001
Study area	-0.2 ± 0.1	3.1	1	0.079
Hatching delay	-0.3 ± 0.1	6.2	1	0.013
Year*hatching Delay	0.4 ± 0.1	17.1	1	< 0.001
Hatching success				
Intercept	2.4 ± 0.2	313.4	1	< 0.001
Year	-0.8 ± 0.2	11.1	1	0.001
Study area	-0.3 ± 0.2	5.0	1	0.025
Hatching delay	0.01 ± 0.03	0.2	1	0.680

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

Table 2 Summary of a linear mixed model analysis for hemoglobin concentration in the blood of the great tit nestlings

Factor	b ± SE	Df	F	P
Intercept	50.4 ± 9.8	1; 390.6	81.3	< 0.001
Year	41.3 ± 6.6	1; 259.3	38.6	< 0.001
Study area	3.8 ± 2.9	1; 124.7	1.7	0.195
Wing length (cov)	0.7 ± 0.2	1; 397.7	13.2	< 0.001
No. of fledglings (cov)	4.8 ± 0.7	1; 191.5	20.9	< 0.001
Hatching delay (cov)	-1.3 ± 0.5	1; 284.2	6.4	0.012
Year*No. of fledglings	-4.6 ± 0.8	1; 358.9	30.4	< 0.001

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. Tomás (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 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.

Acknowledgments All procedures were approved by the Local Ethical Committee and the State Office for Environment Protection. We thank A. Jaksa, M. Winsche, D. Mańkowska, and J. Białek for their help and consent to conducting research in the areas under their administration. We are very grateful to three anonymous referees and the field editor for critical comments and constructive suggestions on the previous draft of the manuscript.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Altwegg R, Visser V, Bailey LD, Erni B (2017) Learning from single extreme events. *Philos Trans R Soc B* 372:20160141. <https://doi.org/10.1098/rstb.2016.0141>
- Bailey LD, van de Pol M (2016) Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *J Anim Ecol* 85:85–96
- Bańbura J, Bańbura M, Gładalski M, Kaliński A, Marciniak B, Markowski M, Michalski M, Nadolski J, Skwarska J, Wawrzyniak J, Zieliński P (2013) Consequences of experimental changes in the rearing conditions of blue tit *Cyanistes caeruleus* and great tit *Parus major* nestlings. *Acta Ornithol* 48:129–139
- Bonamour S, Chevin L-M, Charmantier A, Teplitsky C (2019) Phenotypic plasticity in response to climate change: the importance of cue variation. *Philos Trans R Soc B* 374:20180178. <https://doi.org/10.1098/rstb.2018.0178>
- Campbell TW (1995) Avian hematology and cytology, 2nd edn. Iowa University Press, Ames
- Chamberlain D, Pearce-Higgins J (2013) Impacts of climate change on upland birds: complex interactions, compensatory mechanisms and the need for long-term data. *Ibis* 155:451–455
- Charmantier A, Gienapp P (2014) Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evol Appl* 7:15–28
- Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LE, Sheldon BC (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320:800–803
- Chevin L-M, Hoffmann AA (2017) Evolution of phenotypic plasticity in extreme environments. *Philos Trans R Soc B* 372:20160138. <https://doi.org/10.1098/rstb.2016.0138>
- Crawley MJ (2002) Statistical computing: an introduction to data analysis using S-plus. Wiley, Chichester
- Fargallo IA, Merino S (1999) Brood size manipulation modifies the intensity of infection by Haematozoa in female blue tits *Parus caeruleus*. *Ardea* 87:261–268
- García-Navas V, Sanz JJ (2011) Short-term alterations in songbird breeding schedule lead to better synchronization with food availability. *Auk* 128:146–155
- Gładalski M, Bańbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J (2014) Extreme weather event in spring 2013 delayed breeding time of great tit and blue tit. *Int J Biometeorol* 58:2169–2173. <https://doi.org/10.1007/s00484-014-0816-6>
- Gładalski M, Bańbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J (2016) Effects of extreme thermal conditions on plasticity in breeding phenology and double-bloodedness of great tits and blue tits in Central Poland in 2013 and 2014. *Int J Biometeorol* 60:1795–1800
- Gładalski M, Bańbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J (2018a) Hatching delays in great tits and blue tits in response to an extreme cold spell: a long term study. *Int J Biometeorol* 62:1437–1445. <https://doi.org/10.1007/s00484-018-1541-3>
- Gładalski M, Bańbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Cyżewska I, Bańbura J (2017) Differences in the breeding success of blue tits (*Cyanistes caeruleus*) between a forest and an urban area: along-term study. *Acta Ornithol* 52:59–68
- Gładalski M, Cyżewska I, Bańbura M, Kaliński A, Markowski M, Skwarska J, Wawrzyniak J, Bańbura J (2019) Influence of habitat composition on nestling body condition and breeding success in European pied flycatchers (*Ficedula hypoleuca*). *Avian Biol Res* 12:67–72. <https://doi.org/10.1177/1758155919834466>
- Gładalski M, Kaliński A, Wawrzyniak J, Bańbura M, Markowski M, Skwarska J, Bańbura J (2018b) Physiological condition of nestling great tits *Parus major* in response to experimental reduction in nest micro- and macro-parasites. *Conserv Physiol* 6:coy062. <https://doi.org/10.1093/conphys/coy062>
- Haftom S (1988) Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scand* 19:97–110
- Hale HP (1933) The freezing point of yolk and white egg. *Proc R Soc B Biol Sci* 112:473–477

- Heck RH, Thomas SL, Tabata LN (2010) Multilevel and longitudinal modeling with IBM SPSS. Routledge, New York
- Heck RH, Thomas SL, Tabata LN (2012) Multilevel modeling of categorical outcomes using IBM SPSS. Routledge, New York
- Indykiewicz P (2015) Egg losses caused by cold snap in the black-headed gull, *Chroicocephalus ridibundus* L. Pol J Ecol 63:460–466
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374
- Johnstone CP, Lill A, Reina RD (2017) Use of erythrocyte indicators of health and condition in vertebrate ecophysiology: a review and appraisal. Biol Rev 92:150–168. <https://doi.org/10.1111/brv.12219>
- Kaliński A, Bańbura M, Gładalski M, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J (2017) Nestling physiological performance in great tits *Parus major* and blue tits *Cyanistes caeruleus* in relation to brood fledging success. Acta Ornithol 52: 141–148
- Kaliński A, Bańbura M, Gładalski M, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J (2019) Physiological condition of nestling great tits (*Parus major*) declines with the date of brood initiation: a long term study of first clutches. Sci Rep 9:9843. <https://doi.org/10.1038/s41598-019-46263-z>
- Kaliński A, Bańbura M, Gładalski M, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Cyżewska I, Bańbura J (2015) Long-term variation in haemoglobin concentration in nestling great tits *Parus major*. Comp Biochem Physiol A 185:9–15
- Kluen E, de Heij ME, Brommer JE (2011) Adjusting the timing of hatching to changing environmental conditions has fitness costs in blue tits. Behav Ecol Sociobiol 65:2091–2103
- Lambrechts M, Adriaenssens F, Ardia DR, Artemyev AV, Atiénzar F, Bańbura J, Barba E, Bouvier J-C, Camprodon J et al (2010) The design of artificial nest boxes for the study of secondary hole nesting birds: a review of methodological inconsistencies and potential biases. Acta Ornithol 45:1–26
- Lee JK, Lima SL (2017) Egg viability as a determinant of clutch size in birds: a basic analysis. Avian Biol Res 10:98–206
- Lill A, Rajchl K, Yachou-Wos L, Johnstone CP (2013) Are haematocrit and haemoglobin concentration reliable body condition indicators in nestlings: the welcome swallow as a case study. Avian Biol Res 6: 57–66
- Mainwaring MC, Barber I, Deeming DC, Pike DA, Roznik EA, Hartley IR (2017) Climate change and nesting behaviour in vertebrates: a review of the ecological effects and potential for adaptive responses. Biol Rev 92:1991–2002. <https://doi.org/10.1111/brv.12317>
- Mainwaring MC, Hartley IR (2016) Local weather conditions have complex effects on the growth of blue tit nestlings. J Therm Biol 60:12–19
- Marciniak B, Nadolski J, Nowakowska M, Loga B, Bańbura J (2007) Habitat and annual variation in arthropod abundance affects blue tit *Cyanistes caeruleus* reproduction. Acta Ornithol 42:53–62
- Marrot P, Garant D, Charmantier A (2017) Multiple extreme climatic events strengthen selection for earlier breeding in a wild passerine. Philos Trans R Soc B 372:20160372. <https://doi.org/10.1098/rstb.2016.0372>
- Minias P (2015) The use of haemoglobin concentrations to assess physiological condition in birds: a review. Conserv Physiol 3:cov007. <https://doi.org/10.1093/conphys/cov007>
- Musselman TE (1939) The effects of cold snaps upon the nesting of the eastern bluebird (*Sialia sialis*). Bird-Banding 10:33–35
- Neuenschwander S, Brinkhof MWG, Kolliker M, Richner H (2003) Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). Behav Ecol 14:457–462
- Perrins CM (1991) Tits and their caterpillar food supply. Ibis 133:49–54
- Pipoly I, Bókony V, Seress G, Szabó K, Liker A (2013) Effects of extreme weather on reproductive success in a temperate-breeding songbird. PLoS One 8:e80033
- Podlaszczuk P, Włodarczyk R, Janiszewski T, Kaczmarek K, Minias P (2017) When moult overlaps migration: moult-related changes in plasma biochemistry of migrating common snipe. PeerJ 5:e3057. <https://doi.org/10.7717/peerj.3057>
- Radchuk V, Reed T, Teplitsky R, van de Pol M, Charmantier A et al (2019) Adaptive responses of animals to climate change are most likely insufficient. Nature Comm 10:3109. <https://doi.org/10.1038/s41467-019-10924-4>
- Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol 82:131–144
- Shitikov D, Samsonov S, Makarova T (2019) Cold weather events provoke egg ejection behaviour in open-nesting passerines. Ibis 161: 441–446. <https://doi.org/10.1111/ibi.12695>
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Theimer TC, Sogge MK, Cardinal SN, Durst SL, Paxton EH (2018) Extreme drought alters frequency and reproductive success of floaters in willow flycatchers. Auk 135:647–656. <https://doi.org/10.1642/AUK-17-206.1>
- Tobolka M, Zolnierowicz KM, Reeve NF (2015) The effect of extreme weather events on breeding parameters of the white stork *Ciconia ciconia*. Bird Study 62:377–385
- Tomás G (2015) Hatching date vs laying date: what should we look at to study avian optimal timing of reproduction? J Avian Biol 46:107–112
- van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Philos Trans R Soc B 372: 20160134
- Verboven N, Visser ME (1998) Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81:511–524
- Verhulst S, van Balen JH, Tinbergen JM (1995) Seasonal decline in reproductive success of the great tit: variation in time or quality? Ecology 76:2392–2403
- Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172. <https://doi.org/10.1007/s00442-005-0299-6>
- Wawrzyniak J, Kaliński A, Gładalski M, Bańbura M, Markowski M, Skwarska J, Zieliński P, Cyżewska I, Bańbura J (2015) Long-term variation in laying date and clutch size of the great tit *Parus major* in Central Poland: a comparison between urban parkland and deciduous forest. Ardeola 62:311–322
- Wesołowski T, Cholewa M, Hebda G, Maziarz M, Rowiński P (2016) Immense plasticity of timing of breeding in a sedentary forest passerine, *Poecile palustris*. J Avian Biol 47:129–133. <https://doi.org/10.1111/jav.00733>
- Wingfield JC, Pérez JH, Krause JS, Word KR, González-Gómez PL, Lisovski S, Chmura HE (2017) How birds cope physiologically and behaviourally with extreme climatic events. Philos Trans R Soc B. <https://doi.org/10.1098/rstb.2016.0140>
- Whitehouse MJ, Harrison NM, Mackenzie J, Hinsley SA (2013) Preferred habitat of breeding birds may be compromised by climate change: unexpected effects of an exceptionally cold, wet spring. PLoS One 8:e75536