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Breeding performance of the White-throated Dipper (*Cinclus cinclus*) under different temperature conditions

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Many bird species breeding under optimal temperature conditions show higher reproductive success. However, less information can be found about how the reproductive output differs within one population and one breeding season. To find inter and intra-seasonal differences in several aspects of breeding ecology and breeding output we monitored 223 breedings of the White-throated Dippers within the three river basins of northern Slovakia (Central Europe) in 2010–2018. We registered the beginning of egg laying, clutch size, nest success and the proportion of second clutches. There were significant differences in egg-laying commencement between breeding seasons. The mean February and March temperature significantly influenced the first egg day (20 February–18 March), median laying date (8 March–6 April), the interval between the first and the last first egg in all clutches in one breeding season (37–50 days) and the proportion of second clutches (0.77%–0.95%). However, the differences were found not only between different seasons. The egg-laying initiation of individual nests within each season was considerable affected by the altitude and the proportion of second clutches of particular nests was significantly influenced by their timing of egg laying.

Introduction

The temperature is one of the major factors affecting the breeding of birds. Rising temperatures accelerate the start of breeding by various species of birds, and this trend can be seen among migrating as well as sedentary species (Crick & Sparks 1999, Weidinger & Král 2007, Visser *et al.* 2009). The effects of earlier egg-laying have been demonstrated in several species, namely larger clutch size or increased number of clutches in the year (Klomp 1970, Verhulst *et al*. 1995, Skwarska *et al.* 2012).

With regard to the White-throated Dipper (*Cinclus cinclus*), which is one of the sedentary species in Europe, frequently inhabiting its territory even during the winter months (Glutz von Blotzheim & Bauer 1985, Tyler & Ormerod 1994), the influence of temperature on the beginning of breeding and egg-laying has been similarly demonstrated (Boitier 2004, Hegelbach 2013). As a species breeding relatively early in spring, it is influenced by temperatures at the end of winter, whereby yearly differences in temperature can lead to time shifts of up to 30 days in the commencement of egg-laying (Hrčková *et al*. 2014). It is influenced not only by inter-seasonal variations in temperature but also by different temperature conditions in particular breeding areas (D´Amico *et al.* 2003). As a result, within one season there may be delays in the start of breeding by pairs in the same population (but in different altitude) amounting to as much as several weeks.

It has been found in the case of the White-throated Dipper, as with several other species of birds, that the timing of breeding has an additional impact on their overall reproductive success, expressed as the number of breedings (clutches) in one season. The proportion of pairs achieving two clutches in one season has been shown to be noticeably higher in years with higher temperatures in early spring than when that period of the year is colder (Hegelbach 2013, Hrčková *et al.* 2014). It can be assumed that the overall reproductive success of pairs which start breeding earlier in the year will be higher compared to that of later-breeding pairs.

The aim of this study was therefore to find the impact of the temperature effect on breeding of the White-throated Dipper. We monitored the influence of differing spring temperatures on the beginning of breeding, clutch size, nest success and the number of clutches per year during nine breeding seasons. We focused on three points: (i) yearly differences in egg laying dates, clutch size and proportion of second clutches and their dependence on the regional average temperature in late winter and early spring; (ii) intra-seasonal differences in order to different altitudes and temperatures; (iii) the influence of the onset of egg-laying on the proportion of second clutches.

2. Materials and methods

2.1. Study area

The breeding of White-throated Dippers was monitored on highland and sub-highland rivers in the north of Slovakia (Fig. 1) during the breeding seasons 2010–2018. This is an area with predominantly limestone bedrock and the rivers have stony to gravelly/sandy beds, so the dipper is a characteristic species here (Karaska 2002).

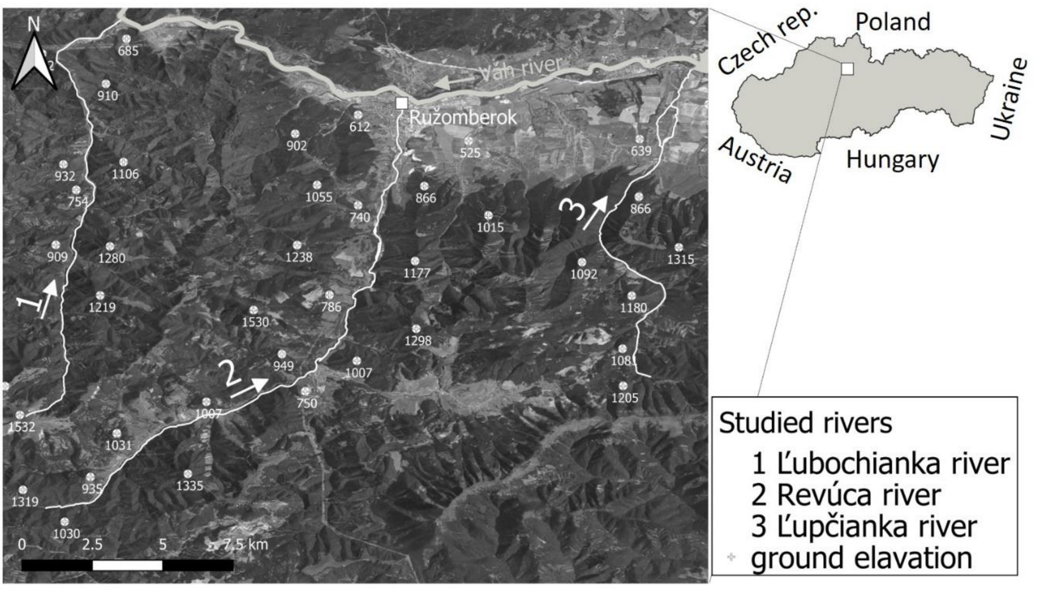

Fig. 1. The study area in northern Slovakia with three rivers with the White-throated Dipper´s nest boxes.

Its average breeding density along these rivers is roughly one pair per kilometre (Baláž *et al*. 2015).

We selected a river network with a total stream length of approx. 65 km, with average flow rates ranging from less than one to more than six m^3 per second. The region is characterized by relatively cool and moist conditions, with an average annual temperature of 4–7 °C and average total precipitation of 700–1200 mm (Miklós 2002).

Average monthly temperatures were provided by the Slovak Hydrometeorological Institute at the closest measuring station. Temperature changes linked with increasing altitude were recorded by means of dataloggers exposed for a period of seven days in one breeding season. For each increase of 100 m in altitude there was an average drop of 0.59 °C ($F = 43.587$, $p = 0.003$). According to this relationship we used the altitude of every nest site (as a characteristic associated with the temperature) in analyses.

We recorded considerable temperature differences between individual years, both in February ($F = 15.160$, $p < 0.001$) and in March ($F = 8.312$, $p < 0.001$). The average temperature in February ranged from –6 to 2.5 °C, in March between 0.0 and 5.5 °C.

2.2. Breeding data

White-throated Dipper breeding was monitored in nest-boxes (n = 46) placed for the most part beneath bridges at the altitude range from 450 up to 1000 m a.s.l. In nine breeding seasons we recorded 223 first clutches. The start of breeding was marked as first egg day (FED), the Julian calendar date of this date (1=1 January) and the median laying day (MLD), the median of all first eggs from all first clutches in one season. The scatter of breeding commencement dates was, defined as the number of days between the laying of the first egg in the first clutch to the first egg in the last clutch in one season.

The nest-site with FED was marked as day 1, and the other nest-sites in the same breeding season were numbered according to the number of days by which the laying of their first egg was delayed (hereafter – laying order). The laying order was assigned to all nest-sites in each breeding season and it was used in further analyses across the whole study period.

The nests success was evaluated as a proportion of successful nests (nests from which at least one nestling fledged) from all nests where the laying eggs was begun.

2.3. Statistical methods

The impact of the temperature on the egg laying initiation and the proportion of the second clutches was demonstrated using the average temperature values. The influence of average February and March temperature on of the commencement of breeding, clutch size, nest success and proportion of second clutches were tested by means of linear regression. For yearly comparisons of temperatures, one-way ANOVA was used. The variation of laying dates was tested using nonparametric Kruskal-Wallis test.

As the FED was highly correlated with laying order within individual years, to avoid multicollinearity we always used only one predictor (FED or laying order) in the analysis. We used a generalised linear model (GLM) to analyse variation of the FED (or laying order) in relation to elevation (set as continuous predictors) and year (set as categorical predictor). Similarly, GLM was used to analyse variation of clutch size and nest success. Only first clutches were taken into consideration. Substitute and second clutches were excluded from the analyses.

To find the factors influencing the second clutch presence we used generalized linear mixed model with binomial error distribution and logit link function. Presence of the second clutch was set as a response. All analyses were carried out using the Statistica program (Statsoft).

3. Results

There were considerable yearly differences in the dates of commencement of egg-laying (Fig. 2). The earliest FED was recorded on 20 February 2014, whereas the latest FED was at 18 March 2013 ($F = 16.322$; $p < 0.001$). MLD varied from year to year between 8 March and 6 April (Table 1). The timing of breeding correlated significantly with the average February temperature in each year, and this was true for the FED (R^2 = 0.53; p = 0.02) as well as for the MLD for all clutches in each specific season (R^2 = 0.61; p = 0.01).

There were not only yearly differences in FEDs, but also differences within particular breeding seasons. The interval between the first and last egg laid varied from 37 to 50 days. This interval also correlated significantly with the average February temperature (R^2 = 0.53; p = 0.03).

The timing of egg-laying in specific nests within the same season (laying order) was clearly influenced by altitude of the nest site (Table 2), with pairs breeding at lower altitudes starting egg-laying earlier than pairs breeding in higher areas (Fig. 3).

The clutch size varied between 5.1 and 5.7 eggs per one clutch and the nest success between 77% and 95% (Table 1). We have found no inter-seasonal significant variation in the clutch size and the nest success and no relationship between the temperature and the clutch size (R^2 = 0.04; p = 0.59) and nest success (R^2 = 0.03; p = 0.18), as well as no dependence of the clutch size and nest success on altitude and FED in any season (Table 2).

Temperature at the beginning of the breeding season was identified as a joint factor influencing the reproductive success. In years with higher February temperatures and earlier FEDs dippers had higher proportions of second clutches (R^2 = 0.63; p = 0.02). The same was also true for the laying order correlated positively with the proportion of second clutches (F = 33.806; p < 0.001; Fig. 4) across whole study period.

4. Discussion

Although there are many studies describing the correlation between the temperature fluctuation and beginning

Table 1. First egg day (FED), median laying day (MLD), clutch size (CS), nest success (NS) and the proportion of second clutches (2nd clutch) of the White-throated Dipper in study area during 2010–2018. (n = number of nests)

	FED	MLD	CS	NS	2nd clutch	n
2010	78	82	5.5	0.95	0.58	12
2011	69	89	5.5	0.89	0.50	18
2012	76	93	5.7	0.77	0.44	13
2013	76	97	5.5	0.79	0.50	18
2014	51	68	5.1	0.83	0.68	22
2015	74	87	5.5	0.84	0.53	19
2016	55	79	5.5	0.83	0.56	23
2017	63	79	5.1	0.86	0.75	32
2018	76	92	5.2	0.81	0.46	26

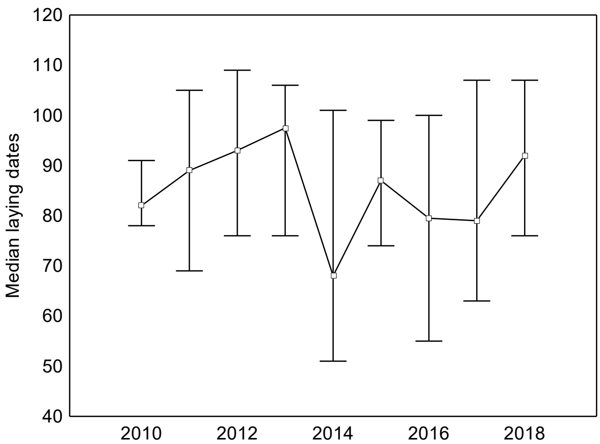

Fig. 2. The variation of the egg laying dates in first clutches (median laying dates with the minimal and maximal values; in Julian dates) of the White-throated Dipper in study area during 2010–2018.

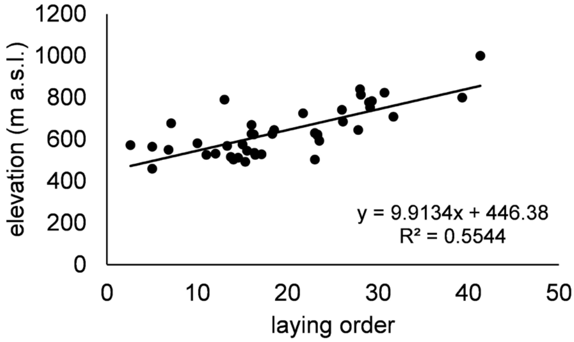

Fig. 3. Laying order (in Julian days) of the White-throated Dippers influenced by the altitudes.

of egg laying in many migrating bird species (Crick & Sparks 1999, Weidinger & Král 2007, Hušek & Adamík 2008), we know also sedentary species that are able to adjust egg laying to spring temperature (Visser *et al*. 2009, Wesolowski *et al.* 2016).

The White-throated Dipper belongs among the species which remain in their territory outside of the breeding period, often during winter as well (Glutz von Blotzheim & Bauer 1985, Tyler & Ormerod 1994). It is a food specialist concentrating on macrozoobenthic life, whose availability is affected by water temperature (Bruno *et al.* 2010, Hill & Hawkins 2014), and the maximum food availability is in late spring (Armitage *et al.* 2001, Pliūraitė 2007). Since yearly fluctuations in water temperature in highland streams are smaller than the changes in air temperature, the availability of the dippers' food is affected by changing temperature to a lesser degree than that of other species living on insects growing in terrestrial (non-aquatic) biotopes (e. g., Both & Visser 2001).

In contrast to our study, Gamelon *et al.* (2018), reporting on a 35-year study monitoring more than 700 nests, found that the beginning of dippers' egg-laying was under stabilizing selection and that the timing of breeding had no effect on the survival of their young. In spite of these expectations, we found distinct yearly differences in the commencement of breeding and significant influence of temperature on the initiation of egg-laying, similarly as in other studies of this type (Tyler & Ormerod 1985, D´Amico *et al.* 2003, Boitier 2004, Hegelbach 2013).

The results of our study show not only that temperature influences the differences in the start of egg-laying between individual seasons, but that a similar time interval was also found when comparing nests at lower and higher altitudes above sea level (both within particular seasons and over the whole study period). In addition, we found positive correlation between temperature and the time interval between the initiation of breeding in the first and last clutch in a given season. This means that temperature positively influences the beginning of dippers' egg-laying, whereby the pairs which are most influenced are those breeding at lower altitude, that is in an optimal environment in terms of temperature.

Table 2. Variation of first egg day (FED) and laying order (LO) in relation to elevation and year as well as relationship between clutch size (CS), nest success (NS) and second clutch presence (2C) in relation to elevation and laying order and year. *df* – degrees of freedom, *F* and *p* – values and significance for predictor variables used in generalized linear model and Wald Stat. used in generalized linear mixed model with binomial error distribution.

		df	*F*	*p*-values
FED	Intercept	1	214.560	< 0.001
	elevation	1	104.502	**< 0.001**
	year	8	16.322	**< 0.001**
LO	Intercept	1	22.946	< 0.001
	elevation	1	104.502	**< 0.001**
	year	8	4.534	**< 0.001**
CS	Intercept	1	170.243	< 0.001
	elevation	1	0.897	0.346
	laying order	1	1.803	0.128
	year	8	1.031	0.417
NS	Intercept	1	36.730	< 0.001
	elevation	1	0.000	0.988
	laying order	1	0.146	0.703
	year	8	0.542	0.824
		df	Wald Stat.	p
2C	Intercept	1	2.169	0.141
	elevation	1	0.714	0.398
	laying order	1	20.439	**< 0.001**
	year	7	9.643	0.210

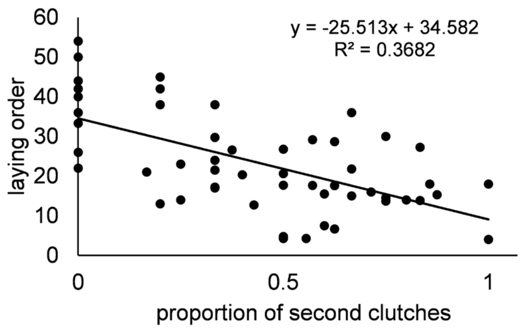

Fig. 4. The proportion of second clutches of the White-throated Dippers influenced by the laying order.

In this way dippers may be stimulated directly into breeding, not so much by the availability of food but by means of internal processes dependent on temperature.

An earlier start of breeding is also linked with higher reproductive potential in several species of birds, expressed as a greater number of eggs laid: pairs breeding earlier in warm spring seasons tend to have larger clutches (Verhulst *et al*. 1995, Skwarska *et al.* 2012). The White-throated Dipper is a species whose clutch size is relatively uniform (Gamelon *et al.* 2018), and we did not find any differences between individual breeding seasons either. Nor did we find any influence of start of breeding on the number of eggs in any clutch. That is well-known of course, mainly in bird species breeding just once in the season (Klomp 1970). Dippers however are birds which are capable in favourable conditions of breeding twice (producing two clutches) in one season, thus making the proportion of double breeding itself a suitable indicator of reproductive potential. The probability of double breeding seems moreover to be strongly influenced by spring temperatures in particular, represented by the onset of egg-laying in the first clutch (Hegelbach 2013, Hrčková *et al*. 2014).

This means that altitude of the nest location does not merely influence the timing of the start of breeding, but also affects the probability of a second clutch in the same season, thereby also affecting the overall reproductive potential. The conclusion is that areas with higher average temperature can be considered as the optimum ones, and areas at higher altitudes as suboptimum for the White-throated Dipper, and on the basis of this it is possible to expect that with rising temperature the breeding success rate and thus also the overall incidence of dippers in the monitored areas will increase, similarly as on the rivers in Scandinavia (Nilsson *et al.* 2011). On the other hand, this positive effect of global climatic changes may be eliminated by the local impact of conditions in highland streams, where reduction in the amounts of water flowing in them may produce an environment less suitable for macrozoobenthic life and consequently also for the dippers living on it (Chen & Wang 2010, Hong *et al.* 2019).

Lämpötilan vaikutus koskikaran lisääntymismenestykseen

Monien lajien lisääntymismenestys on suurempi optimaalisissa ympäristöolosuhteissa. Lajinsisäisestä vaihtelusta lisääntymismenestyksessä vuosien välillä ja kauden sisällä on rajoitetummin tietoa, erityisesti vaikeammin seurattavilla lajeilla. Tutkimme vuosien välistä ja sisäistä vaihtelua koskikaran lisääntymisen ajoittumisessa ja menestyksessä (223 pesintää) Pohjois-Slovakiassa vuosina 2010–2018. Keräsimme aineistoa muninnan ajoituksesta, munaluvusta, pesimämenestyksestä ja uusintapesintöjen määrästä. Muninnan ajoittumisessa havaittiin vuosien välillä vaihtelua. Helmi-maaliskuun lämpötila oli yhteydessä muninnan aloitukseen, keskimääräisen munintapäivään, ensimmäisen ja viimeisen munan väliseen ajanjaksoon, sekä uusintapesintöjen määrään. Pesimäkauden sisällä yksittäisen pesän munintapäivään vaikutti korkeus merenpinnasta. Munintapäivä taas vaikutti uusintapesintöjen määrään.

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