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RESEARCH PAPER

Low breeding synchrony of great reed warbler hosts in warmer springs does not increase their susceptibility to common cuckoo parasitism

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Abstract. Breeding simultaneously with other members of a population can be induced socially or by the seasonality of climatic conditions or availability of resources. Simultaneous breeding has several fitness benefits, including mate choice, food acquisition or protection against nest predators or brood parasites. In this study, we investigate how spring temperatures at a breeding site affect breeding synchrony and brood parasitism in a great reed warbler (*Acrocephalus arundinaceus*) population heavily parasitised by the common cuckoo (*Cuculus canorus*). We predict that in colder springs, the hosts will start breeding later and, thus, their nest attempts will be more synchronised, resulting in a lower proportion of parasitised nests than in warmer springs. Our results confirmed that the hosts started to breed significantly later in colder springs and were more synchronised than in warmer springs. Nevertheless, we found no significant effect of host breeding synchrony on the proportion of parasitised nests. This finding challenges the widely accepted scenario that synchronised breeding leads to a lower proportion of parasitised nests in a host population. It is possible that in strongly parasitised host populations, the high parasite density makes the host breeding synchrony less effective in mitigating the negative impact of brood parasitism. Further research is needed to explore the potential influence of parasite density on the effectiveness of host breeding synchrony as an antiparasitic defence.

Key words: antiparasitic defence, egg-laying synchronisation, nest protection, pre-breeding temperature

Introduction

Birds commonly exhibit breeding synchrony, a phenomenon in which individuals within a population breed simultaneously (Ims 1990a, b). This synchronisation may result from various factors. In seasonal environments, individuals often synchronise their breeding in response to the variability in climatic conditions (Both et al. 2005, Bulluck et al. 2013, Fernández et al. 2020) or availability of resources (Cresswell & McCleery 2003, Vatka et al. 2011). Alternatively, breeding synchrony may arise in response to seasonal time constraints: when the season is short or starts late (such as in high latitudes), breeding may be more synchronised than when the season is long or starts early (Spottiswoode & Møller 2004, Smith et al. 2010, Burr et al. 2016). Finally, breeding synchrony may be stimulated socially, especially in group-living birds (Brown & Brown 2001, Evans et al. 2009).

Synchronous breeding may be associated with several fitness benefits. Simultaneously breeding birds may, for example, have better chances to select

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the best mate and more opportunities for communal foraging (Ims 1990a, b, Spottiswoode & Møller 2004). Further, breeding synchrony may also effectively mitigate the negative impact of nest predation on parental fitness (Ims 1990a). Accordingly, birds breeding simultaneously may profit from active nest defence via corporate vigilance and joint aggression (Westneat 1992, Murphy & Schauer 1996). On the other hand, breeding synchrony often offers a more straightforward benefit: passive nest protection due to dilution of nest predation risk through predator confusion or swamping (Ims 1990b, Descamps 2019).

Apart from nest predation, interspecific brood parasitism is another factor that adversely affects the fitness of parental birds. Interspecific brood parasites lay eggs in the nests of other species (hosts) that care for the parasitic offspring at the expense of their own progeny or survival (Davies 2000). In response to this selection, hosts have evolved specific antiparasitic adaptations, such as breeding far away from the vantage points, nest concealment, aggressive nest defence and rejection of parasite eggs or nestlings (Soler 2017). Nevertheless, host breeding synchrony is considered an important anti-parasite adaptation in this context (Martínez et al. 1996). Previous studies have shown that hosts breeding simultaneously with each other had a lower probability of being parasitised than asynchronously breeding hosts (Martínez et al. 1996, Massoni & Reboreda 2001, Jelínek et al. 2014). The proposed mechanisms are likely similar to those involved in nest predation. They include the inability of the brood parasite to exploit a surplus of nests at once (Martínez et al. 1996, Jelínek et al. 2014) and the parasite's inability to resist collective host nest defence (Massoni & Reboreda 2001).

One of the best-studied brood parasites worldwide is the common cuckoo (*Cuculus canorus*; hereafter cuckoo), parasitising more than 100 host species (Davies 2000). Like other brood parasites, cuckoo females inspect or visit host nests before parasitism (Honza et al. 2002) to synchronise their laying with the hosts (Moskát et al. 2006). Adopting these behaviours, the females reduce the risk of committing laying errors (Honza et al. 2020), which occur when their eggs are laid outside the host egg-laying period. Such errors may have far-reaching consequences for cuckoo fitness, as they affect the hatching success or survival of cuckoo nestlings and increase the probability that the host would reject the mistakenly laid cuckoo egg. However, the above-described synchronisation of cuckoo and host egg laying provides a relatively narrow time window in which a host can be parasitised. Furthermore, cuckoo females are limited to laying one egg per nest and only on alternate days (Davies 2000). All these factors reduce the number of host nests that can be parasitised by the female over the breeding season. In addition, if the hosts breed simultaneously, the time window in which the cuckoo can lay is even narrower.

The great reed warbler (*Acrocephalus arundinaceus*) is an important cuckoo host. Across its breeding range, it faces parasitism rates ranging from 0% to 90% (Moskát et al. 2002, Campobello & Sealy 2009, Honza et al. 2022). Like many other cuckoo hosts, this species is insectivorous and migrates long distances to winter in sub-Saharan Africa (Koleček et al. 2016). Its breeding phenology is thus primarily affected by migration phenology, which can be advanced or delayed depending on conditions encountered on wintering grounds or *en route* (Brlík et al. 2020). However, conditions on breeding grounds, particularly spring temperature and precipitation (via their effect on the development of vegetation and insects), may also play a crucial role in host breeding phenology (Dyrcz & Halupka 2009, Mérő et al. 2015, Hauber et al. 2021). Low spring temperatures, for example, may delay the start of host egg laying, a consistent pattern observed in populations of many avian species breeding in the temperate zone (reviewed in Dunn 2004). Consequently, the late onset of breeding may result in the hosts breeding more synchronously within a population. This synchronisation may pose a challenge for the cuckoo, which has limited options for egg-laying (see above). Yet, simultaneous breeding may benefit the hosts by increasing their chances of escaping brood parasitism (Jelínek et al. 2014).

In this study, we explore the relationship between the spring temperatures at a breeding site, host breeding synchrony and brood parasitism in a great reed warbler population heavily parasitised by the cuckoo. We predict that 1) in colder springs, the great reed warblers will start breeding later and thus will be more synchronised than in warmer springs and that 2) this will result in a lower proportion of parasitised nests in colder springs than in warmer springs.

Material and Methods

Breeding data

We collected breeding data in 2009-2021 at ponds between Hodonín (48°51′ N, 17°07′ E) and Mutěnice (48°54′ N, 17°02′ E), Czech Republic, as part of a long-term study of host-brood parasite interactions

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Table 1. Clutch initiation dates (CID), percentage of parasitism and number of first nests per season in the studied host population.

Year	Mean CID ± SE	First CID[1]	Last CID[2]	Parasitism (%)	Number of first nests
2009	24 May ± 1.0	02 May	29 June	38.7	99
2010	25 May ± 1.1	04 May	25 June	47.1	74
2011	27 May ± 1.3	10 May	05 July	39.7	80
2012	26 May ± 1.5	04 May	08 July	55.1	79
2013	22 May ± 1.0	09 May	19 June	54.7	83
2014	24 May ± 1.0	05 May	16 June	70.4	78
2015	23 May ± 1.4	03 May	30 June	83.6	69
2016	26 May ± 1.5	08 May	27 June	73.9	47
2017	24 May ± 1.4	12 May	23 June	92.3	43
2018	23 May ± 1.8	26 April	19 June	94.7	38
2019	24 May ± 1.1	08 May	15 June	74.5	47
2020	26 May ± 1.5	07 May	17 June	78.3	46
2021	29 May ± 1.2	18 May	18 June	62.5	35

[1] Initiation date of the first clutch in a season.
[2] Initiation date of the last clutch in a season.

between great reed warblers and cuckoos (Jelínek et al. 2014, Koleček et al. 2015, Honza et al. 2022). The host population in that period experienced heavy parasitism (Table 1). Each season, we started the fieldwork at the end of April, when we monitored the occupancy of territories by arriving males and recorded male territorial behaviour. At this time, we captured and colour-ringed males or re-sighted them if they were marked in previous years. Once the males were paired, we colour-ringed or re-sighted also the females and searched for their nests in the territories. In this way, we found the vast majority of nests during the building stage or at the beginning of egg laying and checked them daily until clutch completion to determine clutch size and to detect brood parasitism. During these checks, we numbered each newly laid host and cuckoo (if present) egg with a waterproof pen according to its laying order.

In the nests found at the early breeding stages, we determined the clutch initiation date as the date when the first host egg was laid. In the nests found at later stages, we estimated the clutch initiation date by floating the eggs to determine for how long they had been incubated (analogically to Hays & LeCroy 1971) by back-dating from the hatching date of host or cuckoo nestlings, or based on nestling age (in case of host nestlings, we used the age of the oldest nestling). We used the description of nestling developmental stages in a closely related Eurasian reed warbler (*Acrocephalus scirpaceus*; Hałupka et al. 2018), which we adjusted to the about one-day-slower pace of development of the great reed warbler nestlings. For cuckoo nestlings, we used our own developmental data collected to study cuckoo growth performance (Požgayová et al. 2018).

Following clutch completion, we checked the nests less often (approximately every 3-4 days) to record possible cases of late parasitism (Honza et al. 2020). This procedure, however, did not apply to the parasitised nests, which were checked daily for the next five days after parasitism (and then less intensively) to determine host response to parasite eggs. Around the estimated hatching date, the nest checks were again intensified to minimise the bias in determining nestling age.

We considered a nest parasitised if it contained a cuckoo egg or nestling or if there were yolk remnants on otherwise intact host eggs, the latter being a good indicator of host egg-ejection behaviour (our unpublished data from video recordings collected within the study of Jelínek et al. 2021). We considered a nest non-parasitised if it contained a clutch of four or five host eggs with no cuckoo egg and/or traces of yolk. In other instances, we assigned the nest an unknown parasitism status.

Temperature data

We used the temperature data from the weather station in Tuřany (49°9′ N, 16°41′ E, 241 m a.s.l.) that were available for free via the website of the Czech Hydrometeorological Institute (https://www.chmi.

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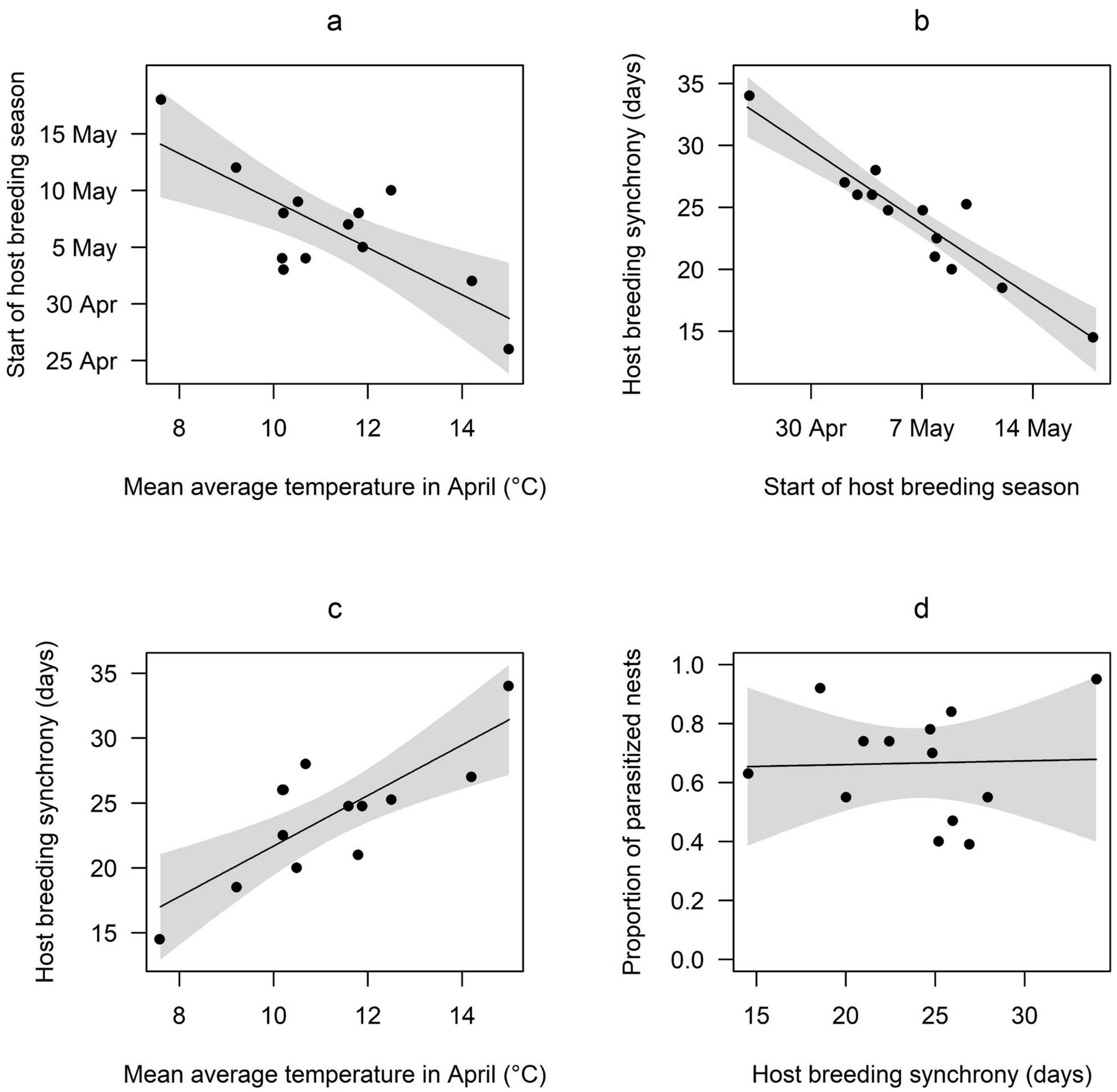

Fig. 1. Relationships between a) the start of the host breeding season and mean average temperature in April, b) host breeding synchrony and the start of host breeding season, c) host breeding synchrony and mean average temperature in April, and d) proportion of parasitised nests and host breeding synchrony (data from 2009-2021). The start of the host breeding season was expressed as the initiation date of the first clutch in a particular season. Host breeding synchrony was expressed as the time elapsed from laying the first clutch in a season to laying the clutch that constituted the 75 percentile of host clutches. Lower values of this variable indicate more synchronised breeding and vice versa. Grey shading depicts 95% confidence bands.

cz/historicka-data/pocasi/denni-data/data-ze-stanic-site-RBCN). The station is 41 km northeast of our study site, and we chose it because it was the nearest weather station with complete data comprising daily measurements of average temperatures (other stations had incomplete data). We calculated mean values of average temperatures for April and May, from these measurements. Mean monthly temperatures at Tuřany were highly correlated ($r \geq 0.94$) with mean monthly temperatures at two weather stations that are closer to our study site, Kobylí (48°56′ N, 16°52′ E, 175 m a.s.l.; 14 km west from our study site) and Strážnice (48°54′ N, 17°20′ E, 176 m a.s.l.; 19 km east from our study site). This correlation indicates that the temperature measured at the more distant weather station corresponds well to the local temperature. Thus, using the values from Tuřany should not bias the results of our study.

Statistical analyses

We converted clutch initiation dates to numerical values such that day 1 represents the 1st of April. Because great reed warbler females often build their replacement (or second) nests within the same male

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territory or elsewhere in the study area, we conducted the analyses only on the first nests to maintain independence in the data (Table 1). As a measure of host breeding synchrony, we used the interval (in days) between the initiation date of the first clutch in a given season and 75%-quantile of clutch initiation dates (see Williams et al. 2015 for the same metrics). This approach allowed us to cover the time interval when the first 75% of clutches were initiated and to exclude the clutches that were laid late, as these may be replacement or second clutches of females arriving from other sites. We quantified breeding synchrony separately for each year.

We conducted all statistical analyses in R 4.1.2 (R Core Team 2021). Overall, we fitted four general linear models with Gaussian error distribution. In the first model, we explored how the spring temperature on the breeding site (continuous predictor) influences the initiation of the host breeding season (i.e. initiation date of the first clutch in a season; response variable). In the second model, we examined how the timing of the initiation of host breeding season (continuous predictor) affects host breeding synchrony (response). The third model explained the effect of spring temperature (predictor) on host breeding synchrony (response), and the fourth model the relationship between host breeding synchrony (predictor) and the proportion of parasitised nests (response). We fitted the models with the mean average daily temperatures in April and May, yet we present only the results with April temperatures. We decided to do so because the great reed warblers at our study site usually start to breed at the beginning of May (Table 1), which is the period that may be most immediately affected by the temperatures from the preceding month. The results with May temperatures were, however, qualitatively the same. All response variables in the models conformed to the assumptions of normality, and model residuals did not exhibit any unusual patterns. For data and R code, see Supplementary online material.

Results

The start of the host breeding season (i.e. initiation date of the first clutch in a season) varied significantly with mean average daily temperatures in April, indicating that in colder springs, the hosts began breeding later than in warmer springs (Table 2a, Fig. 1a). Host breeding synchrony was strongly dependent on the start of the season: the breeding was more synchronised in years when it started late and less synchronised in years when it commenced early (Table 2b, Fig. 1b).

Host breeding synchrony also significantly varied with mean average daily temperatures in April (Table 2c, Fig. 1c): the interval when 75% clutches were initiated increased with increasing mean average daily temperatures in April, indicating that host breeding became less synchronised as April temperatures increased. However, host breeding synchrony did not affect the proportion of parasitised host nests (Table 2d, Fig. 1d).

Discussion

In this study, we explored how spring temperatures at a breeding site affected host breeding synchrony and, consequently, brood parasitism in a great reed warbler population heavily parasitised by the cuckoo. We expected that the hosts would start breeding later in colder springs and, as a result, would breed

Table 2. Results of four general linear models explaining the relationships between a) start of host breeding season and mean average temperature in April, b) host breeding synchrony and the start of host breeding season, c) host breeding synchrony and mean average temperature in April, and d) proportion of parasitised nests and host breeding synchrony. Start of host breeding season – initiation date of the first clutch in a season, host breeding synchrony – time interval (in days) during which the first 75% of host clutches were initiated.

Model	Variable	Estimate	SE	t	*P*
a)	Start of host breeding season ~				
	Intercept	29.86	5.95		
	Mean average temperature in April	–2.08	0.52	–3.96	0.002
b)	Host breeding synchrony ~				
	Intercept	29.67	0.78		
	Start of host breeding season	–0.85	0.09	–9.15	< 0.001
c)	Host breeding synchrony ~				
	Intercept	2.22	5.15		
	Mean average temperature in April	1.95	0.45	4.29	0.001
d)	Proportion of parasitised nests ~				
	Intercept	0.64	0.28		
	Host breeding synchrony	0.00	0.01	0.11	0.916

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more synchronously than in warmer springs. This outcome, in turn, was anticipated to lead to a lower proportion of parasitised nests in colder springs than in warmer springs. Indeed, we found that the great reed warblers started to breed significantly later in cold springs and were more synchronised than in warmer springs. Nevertheless, we found no effect of host breeding synchrony on the proportion of nests parasitised by the cuckoo.

The negative relationship between the spring temperatures at breeding sites and the timing of breeding is well documented in birds (see e.g. Dunn 2004). In this respect, our results align with this general pattern. However, the relationship between spring temperatures and breeding synchrony may be obscure. Host breeding was more synchronised in springs with low temperatures compared to springs with high temperatures (Both et al. 2005, Bulluck et al. 2013). This finding may be attributed to the fact that under low spring temperatures, the start of the breeding season is shifted to later dates when the breeding conditions become more favourable. The delayed start of breeding may then lead to a shortened breeding season, forcing individual breeders to reproduce simultaneously. The relatively synchronised breeding in colder springs may, thus, arise in response to this time constraint, a phenomenon typical for long-distance migrants breeding in higher latitudes (Spottiswoode & Møller 2004, Smith et al. 2010, Burr et al. 2016). In this context, our results corroborate the findings of the studies mentioned above. However, they contradict Nol et al. (1997), who found that the most synchronous breeding occurred in the warmest year. The authors explained this by noting that, in that particular year, the breeding conditions were so good in terms of prey availability that any effect on the timing of breeding was negligible, which would otherwise be more pronounced due to the differences in breeders' quality.

The proportion of parasitised nests in a host population is often negatively correlated with the degree of host breeding synchrony (Martínez et al. 1996, Massoni & Reboreda 2001, Jelínek et al. 2014). When hosts breed synchronously, many nests become available for parasitism simultaneously. The surplus of nests may swamp the brood parasite because there are more nests than the parasite can physically utilise (Martínez et al. 1996, Jelínek et al. 2014). This swamping effect may be further enhanced by collective vigilance and/or aggressive nest defence, typical of hosts breeding in groups or aggregations (Massoni & Reboreda 2001). However, our results contradict the widely accepted scenario that synchronised host breeding leads to a lower proportion of parasitised nests and support the findings of several other studies. In one of these studies, Woolfenden et al. (2004) did not detect any relationship between parasitism and host breeding synchrony in either communally or solitarily breeding hosts. Similarly, Moskát et al. (2006) found that the cuckoo parasitism rate was consistently high, irrespective of whether the great reed warbler hosts bred synchronously or asynchronously with each other. More importantly, the temporal pattern of parasitism correlated tightly with the temporal pattern of host breeding (Moskát et al. 2006). As the great reed warbler population in the latter study is, like ours, heavily parasitised, it may be the high parasite density which makes the host breeding synchrony less effective in mitigating the negative impact of brood parasitism (see also Strausberger 1998 for similar results). Perhaps if the number of cuckoo females at our study site were significantly lower than it currently is (i.e. 13-15; see Koleček et al. 2021), we would observe some relationship between host breeding synchrony and the proportion of parasitised nests. Regardless, to thoroughly explore this issue, host breeding synchrony in populations subjected to various parasite densities should be considered in future studies.

To conclude, our study supported the established knowledge that avian breeding phenology (specifically, initiation and synchrony of breeding) is strongly affected by pre-breeding spring temperatures at breeding sites. Nevertheless, we found no association between the breeding synchrony of a host population under intense brood parasitism pressure and the proportion of parasitised nests in this population. Although the hosts may escape brood parasitism when they breed in synchrony (as discussed above), there are indications that the parasite may also take advantage of this. Simultaneously breeding hosts may enable it to improve egg mimicry (Møller et al. 2011), or, more specifically, egg-spot matching (Li et al. 2016), as it has more options to select which nest to parasitise. That the parasite can adjust its nest-searching strategy according to the availability of host nests, being selective when there is a surplus of nests and non-selective when the nests are in shortage, was already indicated by Jelínek et al. (2014). Nevertheless, this parasite behaviour certainly deserves further attention.

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Author Contributions

M. Požgayová analysed the data and wrote the paper; P. Procházka designed the study and supervised the analyses; M. Honza and P. Procházka ensured funding and commented on the manuscript. All authors conducted the fieldwork.

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Supplementary online material

Table S1. Raw breeding, parasitism, and spring temperature data that were used to fit general linear models presented in the manuscript.

Appendix S1. R code used to fit the general linear models presented in the manuscript.

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