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The potential for climate change to intensify nest-site competition between two sympatric owl species

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Interspecific competition profoundly influences the ecology of species, and climate change is expected to alter the strength of interspecific interactions. Using long-term data from sympatric breeding populations of the Western Barn Owl *Tyto alba* (hereafter Barn Owl) and the Tawny Owl *Strix aluco* in southern Hungary, we explored the associations between the owl species' (i) breeding phenology (annual median laying dates) and regional weather components (daily precipitation, temperature minimum and maximum), (ii) temporal trends of median laying dates and the associated weather signals, and (iii) reproductive output (laying date, clutch size, fledgling number) and the co-occurence of the two species in the same nestbox during the same breeding season. In the Barn Owl, breeding onset was negatively associated with daily temperature maximum, and advanced by 2 weeks in the study period, while the Tawny Owl breeding onset did not change. We found that when the two species used the same nestbox, the breeding of Barn Owls (occurring after the Tawny Owl breeding) was delayed by a month, and they produced one more egg and owlet on average, but second clutches were practically absent, compared to cases when no interaction occurred in the same nestbox during the same breeding season. In contrast, when nesting in boxes later occuppied by Barn Owls, the Tawny Owl's breeding started a few days earlier with an increased clutch size, although with no difference in the number of fledglings. Our results suggest that climate change could heighten competition for nest-sites between the two owl species, as the Barn Owl's breeding season has shifted closer to the breeding season of the Tawny Owl through the study period in parallel with rising temperatures.

Keywords: Barn Owl, breeding, global warming, interspecific competition, laying date, nestbox, Tawny Owl.

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Human-induced global warming has increased the Earth's surface temperature by 1.1°C between the period of 1850–1900 and 2011–2020, and posed a significant threat to different ecosystems (IPCC 2023). Biological and ecological changes

caused by climate change affect many aspects of organisms and communities (McCarty 2002), such as range shifts (Parmesan *et al.* 1999, Chen *et al.* 2011), community composition (Lindström *et al.* 2013), timing and distance of migration (Jenni & Kéry 2003, Visser *et al.* 2009) and other fundamental ecological relationships such as interspecific competition (Samplonius & Both 2019).

Climate change can affect birds in numerous ways (Crick 2004). The effects of climate change are perhaps most strongly evidenced in its impact on phenology (Crick 2004), which can directly lead to a decline in the population of birds (Both *et al.* 2006). Among migratory birds, there is substantial evidence of earlier spring returns to breeding grounds (Hüppop & Hüppop 2003, Jonzén *et al.* 2006). Numerous bird species in diverse taxonomic groups have been shown to exhibit earlier breeding due to climate change (Dunn & Winkler 1999, Crick 2004, Dyrcz & Czyż 2018, Halupka *et al.* 2020, Laczi *et al.* 2024).

Interspecific competition influences the distribution and abundance of organisms. When multiple species utilize the same resources, interspecific competition can arise (Gause 1934). Birds are frequently used as a model group in field studies (Dhondt 2012) owing to their diverse species interactions and overlapping ecological niches, which often lead to competition for resources such as food (Ford 1979, Minot 1981) or nesting sites (e.g. Minot & Perrins 1986, Merilä & Wiggins 1995). The two types of interspecific competition, interference and exploitation, are well-known phenomena among birds, but there are far more examples of interference because exploitation is much more difficult to document (Maurer 1984). Several studies have shown that interspecific competition among different species pairs can lead to unsuccessful breeding and, in some cases, the dominance of one species results in the mortality of offspring or even adult individuals in the other (e.g. Gowaty 1984, Newton 1994, Merilä & Wiggins 1995, Mátics *et al.* 2008, Botero-Delgadillo *et al.* 2015).

For cavity-nesting birds, the availability of suitable nest-sites is one of the most important limiting factors for successful breeding (Newton 1994). A deeper understanding of interactions between cavity-nesting birds has become particularly important in recent decades, as invasive cavity-nesting bird species have appeared in many areas, capable of displacing native ones, including those with significant conservation value (Strubbe & Matthysen 2009, Charter *et al.* 2016, Yosef *et al.* 2016, Mori *et al.* 2017). Studies conducted on European passerines have clearly shown that global warming could affect interspecific interactions and competition (Ahola *et al.* 2007, Samplonius & Both 2019, Møller *et al.* 2020). Stenseth *et al.* (2015), in their study on Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*, demonstrated that long-term climate change could alter competitive interactions between the two species, and has the potential to disturb long-term coexistence. As a result of climate change, interspecific competition could indeed strengthen in certain situations (Samplonius & Both 2019). While interspecific competition for nest-sites and food is well known for cavity-nesting songbirds (e.g. Minot & Perrins 1986, Török & Tóth 1999, Møller *et al.* 2018), much less is known about this ecological relationship for non-passerines, including birds of prey such as owls.

Competition among owl species is well documented (e.g. Hakkarainen & Korpimäki 1996, Vrezec & Tome 2004, Suhonen *et al.* 2007, Wiens *et al.* 2014, Kajtoch *et al.* 2015), but in many cases it is not for nesting sites. Body-mass plays a role in interspecific competition among birds, becoming stronger where the body-mass of the two species is similar (Leyequién *et al.* 2007) and this seems to be the case for birds of prey (Hakkarainen & Korpimäki 1996). The two owl species we studied exhibit differences in body-mass, although their ranges overlap. For the Barn Owl *Tyto alba*, body-mass is in the range 241–380 g for males and 263–478 g for females (Roulin 2004). In the Tawny Owl *Strix aluco*, body-mass is in the range 335–482 g for males and 400–600 g for females (Martin 2022). Despite the larger size of the Tawny Owl, it is not clear which species is dominant, as interactions between them have been observed to result in different outcomes. Publications have described that in cases of competition, the Tawny Owl can displace the Barn Owl, but the Barn Owl can also kill Tawny Owl chicks. At the same time, there are also examples where both species used the same building for nesting, and no aggressive behaviour was observed (Zuberogoitia *et al.* 2005, Mátics *et al.* 2008).

Changes in breeding phenology resulting from climate change can differ significantly between competing bird species (Samplonius *et al.* 2018). Climate change can also affect the length of the reproductive period, shortening it for

single-brooded species yet extending it for multiple-brooded species (Møller *et al.* 2010, Halupka & Halupka 2017). This change can also have a significant impact on interspecific competition. Furthermore, owing to differing responses to climate change, reproductive output may vary differently between single-brooded and multiple-brooded species: it decreases or has no effect in single-brooded species, while it increases in multiple-brooded species (Halupka & Halupka 2017, Halupka *et al.* 2023). The Barn Owl is a multiple-brooded species (see, e.g., Taylor 1994, Béziers & Roulin 2016, Zabala *et al.* 2020), whereas the Tawny Owl is single-brooded (Szalai & Hegyi 2022). Therefore, climate change may affect their breeding differently, which could also alter the interspecific competition between the two species.

The habitat and nest-site preferences of the Barn Owl and Tawny Owl significantly differ from each other but sometimes they use the same nesting sites (Zuberogoitia *et al.* 2005, Mátics *et al.* 2008). The Barn Owl was originally a cavity-nesting bird, but due to human landscape transformation, its nesting is now primarily associated with buildings, especially in Europe (Taylor 1994). The Tawny Owl mostly nests in natural tree cavities, yet in the absence of such hollows it uses abandoned stick nests of other species, buildings and artificial nestboxes, and can even nest on the ground (Petty *et al.* 1994, Zuberogoitia *et al.* 2005). The breeding phenology of the two species also differs considerably. The Tawny Owl generally breeds much earlier than the Barn Owl (Taylor 1994, Chausson *et al.* 2014, Klein *et al.* 2022, Szalai & Hegyi 2022). Despite these differences, interspecific competition between the two owl species for nesting sites is known, particularly in cases where there are insufficient natural tree cavities available for the Tawny Owl (Zuberogoitia *et al.* 2005, Mátics *et al.* 2008). In light of the above, these two competing sympatric owl species serve as a good model system for studying the effects of global climate change on interspecific competition.

The aim of our research was (i) to investigate the potential effects of climate change on the sympatric owls' breeding phenology, (ii) to investigate the costs and consequences of nest-site competition between the two species, and (iii) to assess potential effects of climate change on the competitive relationship. We hypothesized that (i) breeding onset would advance as a response to climate change, and (ii) using the same nestbox one after another would be costly for both species. Regarding the second hyothesis, we expect a decrease in offspring number, but this effect could be asymmetrical. If climate change induces a shift in breeding phenology, it may intensify the competitive conflict for nest-sites. This would (indirectly) support the hypothesis that (iii) climate change could increase the costs of interspecific competition.

METHODS

Study site and breeding data

The research was carried out in Baranya County, in the southern part of Hungary (46°04′N, 18°14′E; see Fig. S1). The area covers 4430 km^2 with 301 settlements (villages and towns together). The area has a continental climate with a milder climate influence. This is evident in the greater number of sunny hours and milder winters compared to most of the other regions of the country. Based on data from 1991 to 2020, January is the coldest month and July is the warmest. Average annual precipitation is 673 mm; the least amount of rainfall occurs in January and March, while the wettest period occurs from May to June.

In the Barn Owl Conservation Program of the Baranya County Group of BirdLife Hungary, Barn Owl boxes have been provided since 1987; by 1995, 45 boxes had been installed, and by 2019, their number had reached 163 (Bank *et al.* 2019). The nestboxes were primarily placed in church towers, with a few of them in agricultural buildings. The dimensions of all the boxes were 100 × 50 × 50 cm, with a 15 × 15 cm entrance. Artificial nestboxes were typically installed in the eastern window of the church tower (since the prevailing wind direction is usually from the north or northwest, the southern direction might be too bright) in such a way that the bird could enter only the box but not the building. The first successful Barn Owl pair bred in 1988. Despite being initially designed for Barn Owls, the boxes – placed in buildings – also attracted Tawny Owls. Tawny Owls started breeding from 1992 onwards and its nesting also became regular. From 1998, sequential breedings – using the same box in the same year by both species – were documented: first the Tawny Owl starts its breeding in late winter or early spring, and then Barn Owl breeding

follows during spring or early summer. No cases were observed in which a Barn Owl bred first in a nestbox, followed by a Tawny Owl in the same box during the same breeding season.

For the analyses, we used three breeding parameters: clutch size (the number of eggs laid), fledgling number and laying date (the date the first egg was laid, calculated from characteristic laying intervals and hatching times characteristic for the species, and measured in days from 1 January). Nestboxes were checked at least five times during the breeding seasons, the first check being carried out usually between 1 and 15 April, or 8–10 days earlier after a mild winter. The date of the next visit was determined from the conditions observed on the first occasion (e.g. numbers of eggs, ages of chicks). In the case of occupied boxes, checks were carried out until the end of the second clutches (usually mid-October) (Bank *et al.* 2019). The data collectors checked the occupancy of the nestbox by lifting its lid and recorded their observations. In the case of nesting, they documented the observed number of eggs and chicks.

The Tawny Owl starts breeding significantly earlier than the Barn Owl (Chausson *et al.* 2014). In Hungary, the Tawny Owl typically begins nesting in February or March, although there are records of nesting as early as December (Szalai & Hegyi 2022). The Barn Owl starts breeding later, based on data from Hungary; egg-laying typically begins between March and May, although during mild winters egg-laying sometimes starts in February (Klein *et al.* 2022). A significant difference between the breeding biology of the two species is that the Barn Owl has a high proportion of second broods, which can be as high as 50% (Taylor 1994, Martínez & López 1999, Béziers & Roulin 2016). However, there was only one recorded case where a Barn Owl had two clutches after breeding in the same box as a Tawny Owl. Second broods are very rare in the Tawny Owl, even in years with high food availability (Southern 1954, Zuberogoitia *et al.* 2004). In our study area, we have observed only one case of a second breeding attempt by a Tawny Owl, but it was a replacement breeding, as the first attempt had failed. For the analysis, only data from the first broods were used. Because we have never observed the presence of the Tawny Owl following the first breeding of the Barn Owl, we assume that it no longer had an influence. We also excluded observations in the following cases: date of the laying of the first egg was uncertain; egg-laying was interrupted and the clutch was not completed (e.g. because of predation, desertion); or fledgling number was uncertain because the owlets were preyed upon, or had been abandoned by their parents.

As a consequence of our field data collection protocol, in most cases there was no chance to catch the breeding pairs. Hence, when two complete clutches of Barn Owl occurred in the same box during one breeding season, we considered these as a double breeding in our analyses.

Statistical methods

Association of breeding phenology with weather

We calculated the annual median laying dates to analyse the patterns of the temporal shifts of the breeding seasons of the two species, and their association with local weather components (i.e. temperatures and precipitation, see below in detail). We used the median rather than the mean to estimate the central tendency because the distribution of laying dates within most years was positively skewed. As we were especially interested in separating the effects of local weather on a long-term scale from potential confounding effects arising from interspecific competition, we calculated median laying dates for the Tawny Owls breeding with no Barn Owl following and Barn Owls breeding with no previous Tawny Owl breeding. For this, we excluded years that had only $n < 5$ data for a species; therefore, we considered the period of 2002–2019 for the Tawny Owl, and 1993–2019 for the Barn Owl. Weather predictors were available at a coarser spatial resolution than individual breeding observations. To ensure consistency in spatial scale, we chose to match the laying date with a broader, population-level measure of breeding onset too. Furthermore, as we aimed to analyse long-term trends of inter-annual variation, the population-level measure provided a robust estimate of how timing shifted over time. This approach reduces noise from within-year variation that may not be directly related to annual environmental conditions (e.g. local microhabitat effects, bird condition).

We acquired regional weather data from the E-OBS daily gridded dataset v.28.0e in $0.1° \times 0.1°$ spatial resolution (Haylock *et al.* 2008, Cornes *et al.* 2018) at the ECAD website (European Climate Assessment and Dataset, http://www.ecad.eu). We separated the gridcell

representing the study area by averaging the respective daily values of weather data extracted from the combinations of the relevant coordinates (i.e. combining each longitude coordinate with each latitude coordinate, 45.875N, 46.125N, and 17.875E, 18.125E, 18.375E, 18.625E). We extracted the following raw parameters: maximum temperature (°C), minimum temperature (°C), precipitation sum (mm; total amount of precipitation that falls within a 24-h period).

Studies on how biological traits respond to weather often use arbitrary time windows for choosing weather data (e.g. Goodenough *et al.* 2011, Laczi *et al.* 2019), which may fail to capture accurate biological responses as a result of misaligned or inappropriate time frames. Therefore, to avoid this potential limitation, we applied a sliding-window approach designed to deal with the aforementioned limitation by systematically testing all possible time windows within a biologically relevant period, thereby identifying the period that best explains variation in laying dates. (van de Pol *et al.* 2016).

We used the sliding-window approach with linear models, allowing linear effects between the given weather variable (predictor variable) and the median laying date, considering the sample size for each year as a weighting factor to account for variation in sample size across years. We searched for weather signals applying absolute time windows (i.e. the same window for all years, making the years comparable). The reference date was 1 April and 1 May in the Tawny Owl and Barn Owl, respectively, with a search range going back 150 days, using a daily resolution with respect to changing time-window lengths in sliding steps. For each of the three weather variables, the mean of the daily values corresponding to the actual time window was used in the sliding-window analyses (i.e. mean daily maximum temperature, mean daily minimum temperature and mean daily precipitation sum). In this method, each time window of a weather variable represents a different model, and each model is compared to the baseline model, which was in our case a null model with an intercept but no fixed effect.

We selected the best model by Akaike's information criterion corrected for small sample sizes (AICc; see Burnham & Anderson 2004). Using this method, we could select a window for a weather variable explaining the most variation in annual median breeding onset. Additionally, in each best model we calculated the Pc values, which, in essence, represent the probabilities of the model being observed by chance (van de Pol *et al.* 2016). To estimate the probability of a best model detected as a false positive, we generated a distribution of ΔAICc values in a dataset without a climate–response relationship. For this purpose, it is necessary to randomize the date variable in the dataset, and then perform a sliding-window analysis to obtain ΔAICc for the best model. In our case, this process (i.e. randomization between the median laying date and the year variables) was repeated 100 times to estimate the distribution of ΔAICc values from data without weather signals (ΔAICc_rand). Comparing ΔAICc_rand with observed ΔAICc yields the likelihood of a result occurring by chance, using the highly sensitive Pc metric developed by van de Pol *et al.* (2016) for such comparisons with a limited number of randomizations and sample sizes. Accordingly, we considered a weather parameter as an obvious (or verified) weather signal (i.e. which was therefore detected probably not the result of chance) if the relevant Pc metric was less than 0.05 (van de Pol *et al.* 2016).

Temporal trends of median laying dates and the associated weather signal(s)

For analysing temporal trends (i.e. change in a variable across years), median laying date and the weather signal(s) detected as obvious were used as response variables, and year as the predictor variable. In the case of the breeding phenology, the annual sample size was used as a weighting factor. The investigated time periods were 1993–2019 in the Barn Owl and 2002–2019 in the Tawny Owl (see below). In addition, in order to make the results more comparable between the two species, we also repeated this analysis on Barn Owls on a restricted time series taking into consideration the same time period covered for the Tawny Owl (i.e. 2002–2019, instead of the full Barn Owl period 1993–2019).

Shared temporal trends between variables could cause spurious correlations. Therefore before exploring the temporal trends, we checked for temporal autocorrelation of our response variables by Durbin–Watson tests. Based on these diagnostics, we had to correct for temporal autocorrelation in the median laying date variables (applying the following algorithm: $x(t) = x - (a + b \times x(t-1))$: $x(t)$ is the current value of the variable at time t;

$x(t-1)$ is the value at time $t-1$; a is a constant term that removes any overall trend or baseline shift from the series; b is an autocorrelation coefficient representing the direction and influence of the relationship between the current value and the previous value of the time series, where a and b were estimated from the data). Therefore, the first year of the corrected time series concerned was eliminated from the analyses.

Differences of breeding parameters between groups with different competitive situations

Considering the owls' status with regard to potential competitive situations, we performed comparisons of the breeding variables between the following contrasts: (1) Barn Owls breeding after Tawny Owls had bred in the same box vs in the absence of Tawny Owl breeding; and (2) Tawny Owls breeding in a box in which Barn Owls later bred vs in the absence of Barn Owl breeding. Importantly, before the comparisons we limited the years to those in which both species bred in the same box consecutively, mitigating the potential year effects due to climate change and different temporal coverage across years between the two species. We performed linear mixed models acquiring normal error, identity link function and Satterthwaite estimation for df, considering Type III error (because of the unbalanced sample sizes between groups). In these models, one of the breeding variables (clutch size, fledgling number, laying date) was used as a response variable, the status of the owls (Tawny owl vs Barn Owl in the presence/absence of breeding of the other species in the same nestbox; four groups) as a fixed effect, and we controlled for year and nestbox entering these variables as random effects. According to QQ-plots, model residuals were normally distributed, except in the case of median laying date. Hence, for median laying date, we applied Mann–Whitney–Wilcoxon tests. We applied Benjamini and Hochberg (1995) correction for false discovery rate.

Software and packages

We performed all analyses using R 4.2.1 (R Core Team 2022). For acquiring weather data, we used the 'ncdf4' R package (Pierce 2021). For sliding-window analyses, we applied the 'climwin' package (Bailey & van de Pol 2016, van de Pol *et al.* 2016). Analysing temporal trends, we applied the lm() function from R and the summary() function from the 'lmerTest' package (Kuznetsova *et al.* 2017). Temporal autocorrelations were tested by using the durbinWatsonTest() function from the 'car' package (Fox & Weisberg 2018). We compared groups of owls with the different competitive situations using the *lmer()* function from the 'lme4' package (Bates *et al.* 2015), the summary() function from the 'lmerTest' package (Kuznetsova *et al.* 2017), and the *wilcox.test()* function in R. We obtained standardized β values, Cliff's delta d values and their confidence intervals (CIs) using the 'effectsize' package (Ben-Shachar *et al.* 2020).

RESULTS

Association of owl breeding phenology with weather

The sliding-window analyses revealed no obvious weather signals in the case of the Tawny Owl (for mean temperature maximum: Pc = 0.66; mean temperature miminum: Pc = 0.74; mean daily rain sum: Pc = 0.42), yet for the Barn Owl, the daily temperature maximum was an obvious climatic signal (Pc < 0.001, best time window open/close day relative to May 01: 56/22, indicating 6 March–9 April, and hence essentially covering March; for more details, see Table S1). Daily temperature maximum was associated negatively with the median laying date of the Barn Owl in boxes with no previous Tawny Owl breeding (standardized β = −0.81, 95% CI [−0.91; −0.62], df = 1.25; Fig. 1a). After removing the temporal trend, the association between median laying date of the Barn Owl breeding with no previous Tawny Owl breeding and temperature remained strong (standardized β = −0.78, [−0.89; −0.57], df = 1.25). The best models of the other weather variables in the Barn Owl were not detected as obvious (mean temperature miminum: Pc = 0.11; mean daily rain sum: Pc = 0.066). For more details see Results S1.

Temporal trends of median laying dates and the associated weather signal(s)

The median Tawny Owl laying date in the absence of subsequent Barn Owl breeding showed no inter-annual linear trend (standardized β = 0.35, [−0.16; 0.71], df = 1.15; Fig. 1c). In contrast, Barn Owl laying date without previous Tawny

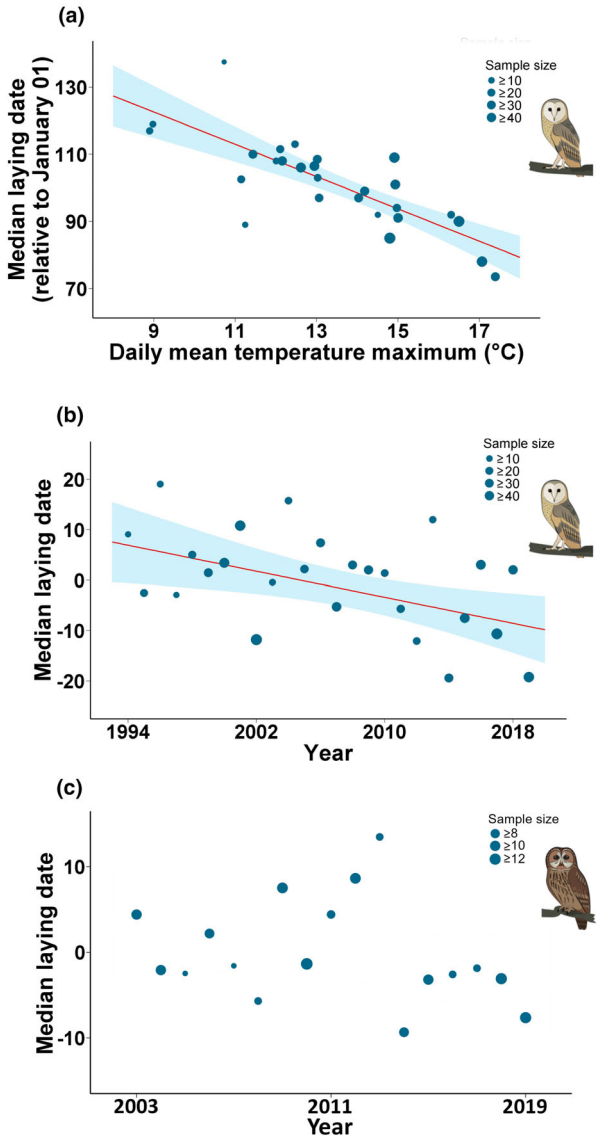

Figure 1. (a) The association between the annual median laying date of the Barn Owl and daily mean temperature maximum (only Barn Owl breeding events that were not preceded by Tawny Owl breeding were considered, temperatures were acquired from a time window that represented mainly March; details in the text) and temporal changes in (b) Temporal change of the barn owl annual median laying date (c) Temporal change of the tawny owl annual median laying date (corrected for temporal autocorrelation). Only Tawny Owl breeding events not followed by Barn Owl breeding were considered. Sample sizes refer to the number of breeding onsets in each year.

Owl breeding advanced through both the longer time period, 1994–2019 (standardized $\beta = -0.59$, [−0.79; −0.26], df = 1.25; Fig. 1b), and the restricted time period, i.e. 2003–2019 (standardized $\beta = -0.58$, [−0.83; −0.17], df = 1.15). In parallel with this, the mean daily temperature maximum of the relevant time window which was associated with Barn Owl breeding phenology (6 March–9 April based on sliding-window analysis) showed a significant increasing trend over the years (standardized $\beta = 0.48$, [0.12; 0.73], df = 1.25). For more details see Results S1.

Differences of breeding parameters between groups with different competitive situations

We found that in the Barn Owl nests with previous Tawny Owl breeding, egg-laying started later than in Barn Owl nests without previous Tawny Owl breeding (absolute median difference: 30.5 days, $d = -0.76$, [−0.82; −0.68]; Table 1). Clutch size was larger (standardized $\beta = 0.62$, [0.32; 0.92], df = 1607.39; Table 1), as was the number of fledglings (standardized $\beta = 0.47$, [0.18; 0.76], df = 1586.53; Table 1) based on mixed-effects models using Satterthwaite approximations for denominator df. We found that Tawny Owls whose breeding was followed by the breeding of a Barn Owl started egg-laying earlier (absolute median difference: 4.0 days, $d = 0.28$, [0.09, 0.46]; Table 1), and laid larger clutches (standardized $\beta = 0.74$, [0.23; 1.25], df = 199.67; Table 1). However, there were no differences in fledgling number (standardized $\beta = 0.22$, [−0.14; 0.58], df = 1162.80; Table 1) (Fig. 2). After correction for false discovery rate, the differences remained significant (Table 1). For more details on the test statistics results, see the Supporting Information (Results S2).

DISCUSSION

In this study, we investigated how climate change affects the breeding phenology and reproductive success of the sympatric Tawny Owl and Barn Owl competing for nesting sites. We found that Barn Owl breeding onset advanced by 2 weeks during the period 1993–2019, and was negatively associated with temperature conditions. When both species bred in the same nestbox within a year, Barn Owl breeding was delayed by more than 4 weeks, but they produced a slightly larger reproductive output, with no second clutches (Table 1). Tawny Owls, however, started breeding

Table 1. The breeding of Barn Owls and Tawny Owls breeding alone or in the case of sequential breeding (breeding of the two species in the same nestbox during the same year).

		Laying date			Clutch size			Fledgling number			Percentage performing a second brood
Species	Species interaction category	Median	IQR	*N*	Mean	SE	*N*	Mean	SE	*N*	
Barn Owl (BO), first breeding	BO after no TO	99.00	27.00	752	6.88	0.05	750	4.88	0.06	714	25.0
	BO after TO	129.50	36.50	48	7.79	0.25	47	5.63	0.29	48	2.1
Tawny Owl (TO)	TO before no BO	63.00	13.00	139	4.15	0.12	87	3.18	0.10	127	0
	TO before BO1	59.00	11.75	39	5.06	0.23	16	3.50	0.20	38	0

a few days earlier in such circumstances and also had larger clutches, but with no difference in fledgling numbers.

Sequential breedings (i.e. Tawny Owl followed by Barn Owl in the same box) were associated with different breeding outcomes for both species, clearly defining a competitive situation regarding nesting site. The nature of the competition between the two species may involve direct interactions (Mátics *et al.* 2008), which could perhaps be the result of a form of interference competition. However, the relatively later breeding by Barn Owls in nestboxes previously used by Tawny Owls is a result of that previous occupation. This could be a case of exploitative competition, whereby the Tawny Owl interacts indirectly with the Barn Owl by decreasing the availability of nest-sites. In addition, the competitive situation is probably asymmetric. Initially the Barn Owl faces greater disadvantages (e.g. the nesting sites preferred are more limited; the Tawny Owl is heavier and more aggressive; the absence of second broods leads to a significant decline in reproductive success) but as a response, Barn Owls might exert negative effects on the Tawny Owls too. Barn Owls may kill the Tawny Owl chicks (Mátics *et al.* 2008) and the presence of the Barn Owl during the breeding period of the Tawny Owl could represent a disturbance factor reducing fledging success. Our results, similar to studies conducted on several other bird species (Ahola *et al.* 2007, Samplonius & Both 2019, Møller *et al.* 2020), suggest that interspecific competition is most likely to intensify because the breeding onsets of the two species are getting closer to each other as a consequence the environmental pressure stemming from climate change.

It is known for numerous bird species that due to the direct or indirect effects of climate change, individuals start nesting earlier (Crick 2004, Dyrcz & Czyż 2018, Halupka *et al.* 2020). Regarding the breeding phenology of the Tawny Owl, long-term studies did not find significant shifts (Lehikoinen *et al.* 2011, Solonen 2014) and neither did our research. However, our results showed that the Barn Owl advanced its breeding by approximately 2 weeks in nearly three decades. As several studies have demonstrated, the length of the breeding season responds differently to climate change in single-brooded and multi-brooded species. In single-brooded species, the breeding season length tends to show a shortening, while in many multi-brooded species it has been extended (Møller *et al.* 2010, Halupka & Halupka 2017). Although this is not necessarily related to the advancement of the laying dates (Halupka & Halupka 2017), our findings also indicate that in the case of the multi-brooded Barn Owl, the earlier start of breeding has extended the breeding season, and late-season breeding has become increasingly common (pers. obs.). In contrast, this pattern was not observed in the single-brooded Tawny Owl.

We revealed that where the nesting of the Tawny Owl was followed by that of Barn Owls, the mean clutch size of Tawny Owls was higher, but this did not result in greater fledging success. It is not clear why the Tawny Owl laid more eggs in places where there is competition between the two species. Birds may use interspecific social cues too when selecting a nesting site or habitat (Kivelä *et al.* 2014, Jaakkonen *et al.* 2015, Szymkowiak *et al.* 2017, Morinay *et al.* 2020). This can also affect breeding parameters, such as laying date (Hromada *et al.* 2008) or offspring physical conditions (Hämäläinen *et al.* 2023). The Barn Owl may use the boxes for roosting in winter before the breeding season (pers. obs., Marti *et al.* 1979) and perhaps Barn Owl nest debris from the previous season could also serve as a signal to the

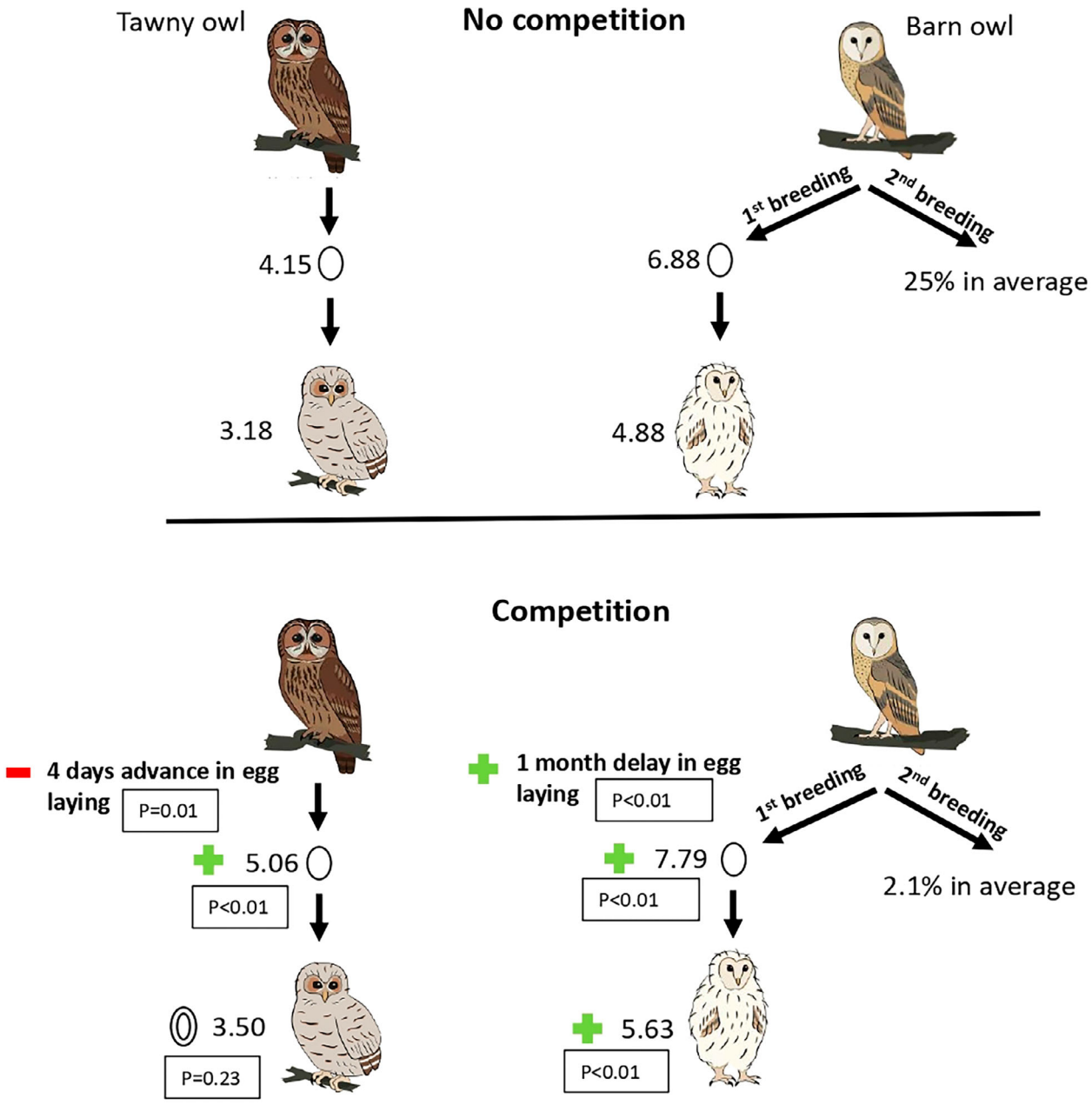

Figure 2. Differences in breeding parameters of two owl species that are (Competition) or are not (No competition) using the same nestbox for breeding within the same year. The plus and minus signs indicate the direction of significant changes in the breeding variables of the first brood (mean clutch size, mean fledgling numbers, median laying date), while the grey zero represents a non-significant change.

Tawny Owl (nestboxes are generally cleaned after only every fourth breeding attempt) that predicts competition, and the Tawny Owl thus compensates with a higher initial investment. It could also refer to the good quality of the breeding site. Another explanation could be that the larger clutch size simply results from higher food availability (Lehikoinen *et al.* 2011, Solonen *et al.* 2015) in those places where both species are present. However, it should be noted that there

are still significantly fewer data available on the described competitive interactions compared to when the two species breed independently (Table 1). Detecting subtle differences may not always be possible owing to the smaller sample size, and, therefore, further data collection is needed for a better understanding.

The reason why increased clutch size did not result in a higher reproductive output (fledgling number) in Tawny Owl has several possible explanations. This could simply be the result of a change in the quantity of food available throughout the breeding period (Brommer *et al.* 2002, Lehikoinen *et al.* 2011). It could also be because as the physiological development for breeding in the case of the Tawny Owl begins well before egg-laying, a potential high abundance of food during this period may be followed by reduced food availability during chick-rearing (Lehikoinen *et al.* 2011). As Mátics *et al.* (2008) demonstrated in this study site, the Barn Owl is capable of killing Tawny Owl chicks, suggesting a direct case of offspring loss affecting the whole brood. However, it is also possible that the Barn Owl does not directly destroy the nestlings or eggs but, rather, disturbs the Tawny Owl pair during hunting or incubation with its presence in a way that ultimately reduces the number of fledglings. The period of breeding when the Tawny Owl feeds the chicks coincides with the period when the Barn Owl male needs the putative nesting site to advertise it to the female, accumulate prey items as part of courtship, and other activities. All of these activities may represent a major disturbance to the Tawny Owl. Therefore, it is quite feasible that some degree of competition or disturbance may already be present from the beginning of the egg-laying period of the Tawny Owl.

This competition could be reduced in locations where the Tawny Owl starts laying a few days earlier, and the shift in laying date might be a response to the disturbance caused by competition from the Barn Owl. The response, however, may have negative side effects, because the timing of the Tawny Owl breeding is most probably not optimal. Earlier breeding is not necessarily advantageous if the colder weather makes it more costly (Lehikoinen *et al.* 2011) and it may lead to a mismatch between the available food source and breeding (Lehikoinen *et al.* 2011), leading to a negative impact on chick survival (Wann *et al.* 2019). However, Hromada *et al.* (2008) showed that heterospecific social information could influence the start of nesting among shrikes. It is possible that the observed nesting of the Barn Owl by the Tawny Owl in the previous breeding season or the presence of the Barn Owl during Tawny Owl nesting (see above) may indicate a high-quality nesting site, which could potentially result in an earlier start of nesting.

The consequences of within-season consecutive use of nestboxes are also evident for Barn Owls. Breeding pairs that follow the Tawny Owl nesting in the same nestbox in the same year start laying eggs a month later compared to the non-competitive situation. These pairs lay an average of one more egg, and fledging success is also significantly higher compared to pairs that nest in boxes with no Tawny Owl present. However, the chance of a second brood is negligible (Table 1), because the probability of a second clutch shows a positive correlation with the early timing of the first clutch in the Barn Owl (Taylor 1994, Béziers & Roulin 2016, Jackson & Cresswell 2017, Zabala *et al.* 2020). Accordingly, it is not surprising that, in the entire study, there was only one case where a Tawny Owl nesting was followed by a successful first and second brood of the Barn Owl.

Under non-competitive conditions (without presence of the Tawny Owl) the rate of second clutches was 25% for the full period investigated (1993–2019), and reached up to 59.5% (2014). This is similar to findings of other studies. For example, during a 7-year study by Martínez and López (1999), one-third of the Barn Owl females had a second clutch, and in one year this rate reached 60% (for other examples, see, e.g., Taylor 1994, Béziers & Roulin 2016, Zabala *et al.* 2020). Moreover, in addition to the early onset of breeding, the availability of food shows a positive correlation with the occurrence of second clutches (Jackson & Cresswell 2017, Zabala *et al.* 2020). Jackson and Cresswell (2017) found that Barn Owl pairs even with late first broods could produce a second brood during years with high prey (i.e. vole) abundance. A limitation of our study is that we do not have data on food availability, making further research necessary from this perspective.

It is known that second clutches are generally larger than first clutches in Barn Owls (Jackson & Cresswell 2017, Bank *et al.* 2019). Therefore, the observed increase in Barn Owl clutch size following Tawny Owl breeding may be a result of the

significant delay, similar to typical second clutches. Although it is possible that the Barn Owl begins a second (or first) clutch in another location (Béziers & Roulin 2016, Jackson & Cresswell 2017) that we were unable to detect, we consider that second clutches are unlikely because a second clutch is linked to the timing of the first clutch (Taylor 1994, Béziers & Roulin 2016, Jackson & Cresswell 2017). Therefore, as a result of the 1-month delay, the second breeding would be very late with accordingly low chances of chicks being fledged. Altogether, it seems that the lost chance of a second brood is a cost of the competitive situation for the Barn Owl: although the bigger first brood increases output, projected over the entire season the breeding performance becomes substantially lower, because second broods are very unlikely.

Our data supported that due to climate change, the starting point of breeding in the Barn Owl is advancing under non-competitive conditions, whereas in the Tawny Owl it remains unchanged. As a result, use of the nesting sites by the Barn Owl is getting closer to the period when Tawny Owls still use the nestbox. Therefore, interspecific competition between the two species may further intensify because of adaptation of the Barn Owl to climate change. It is especially important to consider this because the Barn Owl has shown significant local population declines in many areas (Colvin 1985, Taylor 1994, Martínez & Zuberogoitia 2004, Poprach 2010, Żmihorski *et al.* 2020), and potentially increased competition may worsen this situation.

As precise data on the actual population sizes of either the Barn Owl or the Tawny Owl are unavailable from Southern Hungary, we can only provide assumptions regarding the proportion of the population affected by this interspecific interaction. In many regions of Central Europe, the primary nesting sites for the Barn Owl remain church towers and artificial nestboxes in these buildings (Bank *et al.* 2019, Żmihorski *et al.* 2020, Klein *et al.* 2023). Given that a significant proportion of such buildings in Baranya County are accessible to owls (with Barn Owl nestboxes installed in every second settlement in Baranya County by 2019), we assume that a substantial and representative portion of the local population was included in this study. Additionally, because the number of Tawny Owl breeding pairs in these boxes continues to rise over time, we predict that the frequency of interactions will increase. This alone is unlikely to cause significant changes in the local Barn Owl population. However, considering the human-induced threats such as roadkill (Ramsden 2003, Grilo *et al.* 2014), rodenticide use (Newton *et al.* 1990, Salim *et al.* 2014, Spadetto *et al.* 2024) or agricultural intensification (Almasi *et al.* 2015), it may represent an additional, albeit mild, pressure on the local Barn Owl population. However, it is also worth noting that in multi-brooded species, such as the Barn Owl, the climate change-induced lengthening of the breeding season is expected to increase reproductive output (Halupka & Halupka 2017), which could serve as a compensation.

Because the greater number of available nestboxes decreases competition (Merilä & Wiggins 1995), it is worth considering that, as a conservation intervention, the installation of additional Barn Owl nestboxes in church towers and Tawny Owl nestboxes in nearby woodland patches would be advisable.

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AUTHOR CONTRIBUTIONS

Zoltán Schneider: Conceptualization; data curation; investigation; visualization; writing – original draft; writing – review and editing. **Erika Mátics:** Data curation; writing – review and editing. **Gyula Hoffmann:** Writing – review and editing. **Miklós Laczi:** Conceptualization; data curation; formal analysis; methodology; investigation; visualization; writing – review and editing; writing – original draft. **Gábor Herczeg:** Writing – review and editing; supervision. **Róbert Mátics:** Conceptualization; data curation; formal analysis; funding acquisition;

investigation; methodology; project administration; supervision; resources; writing – review and editing; writing – original draft.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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ETHICAL NOTE

Data collection complied with all relevant national, international, and institutional laws on nature conservation and animal welfare. This long-term study was conducted under permits issued by national and regional nature conservation authorities.

DATA AVAILABILITY STATEMENT

The primary data supporting the results of this study are available at https://doi.org/10.6084/m9.figshare.26354410.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. The location of Baranya County within Hungary. The zoomed-out map shows the placement of nesting boxes within the county.

Table S1. The first 20 models with the lowest negative ΔAICc values for the mean daily temperature maximum as the verified weather signal in connection to the annual median laying date of the Barn Owl. The reference date was 01/05 (1 May) for the time windows. Sample size was 27.