18/08/2025 13:11:00Seasonal, environmental and individual determinants of double-brooding in the White-throated Dipper *Cinclus cinclus*

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Acknowledgements

We would like to thank the local landowners and the Yorkshire Dales National Park for providing access and continuous support to the project. Special appreciation goes to the many students and volunteers who helped with fieldwork, in particular Flora Whitehead, Lucy Magoolagan and Tess Moore; and Duncan Whyatt and Albert Bertolero Badenes for their support and comments which helped to improve this manuscript. We also thank the three anonymous reviewers and editor, Prof. Jeremy Wilson, for their extremely helpful suggestions. The project was funded by the Faculty of Science and Technology, Lancaster University.

Author contribution

Noelia D. Álvarez: conceptualisation, methodology, formal analysis and writing - original draft. Peter Mawby: methodology, writing - review and editing. Stuart P. Sharp: conceptualisation, methodology, writing - review and editing, project administration and supervision.

Conflict of interest

The authors declare no conflicts of interest.

Data availability statement

Data supporting the findings of this study are available on request from the authors.

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In many birds, productivity can be boosted by producing more than one brood during the breeding season. This multi-brooding strategy may become more common as a response to environmental change, especially in those species for which the timing of breeding is advancing or the breeding season is lengthening. Understanding the factors affecting the likelihood and outcome of multi-brooding is therefore crucial for predicting population change. Here, we investigate double-brooding in a declining river bird species, the White-throated Dipper *Cinclus cinclus*. Using data collected between 2013 and 2021 from a long-term study population in the UK, we found that double-brooding was common, with an average of 29% of pairs per year having a second brood, and that reproductive output was significantly higher in double-brooded pairs than single-brooded pairs. The best predictor of double-brooding was the timing of breeding for the first brood; the earlier this occurred, the higher the likelihood of having a second brood. This suggests that seasonal changes in environmental conditions and food resources may determine opportunities for breeding. The probability of double-brooding was also higher in older males, indicating that individual quality likely plays a role too, although there was no effect of female age. Clutch size and the number of chicks fledged were lower in second broods than first broods, and the best predictor of breeding success in second broods was nestbox use. The probability of young fledging was almost twice as high in boxes, suggesting that nestbox provision may be an important conservation measure. Together, these results provide evidence that double-brooding is driven by favourable environmental conditions, but further work is needed to better understand individual and adaptative variation in this response.

Keywords: multi-brooding, *Cinclus cinclus*, time of breeding, age, nestbox.

Multi-brooding is an important adaptation that can significantly increase the reproductive output of birds within a breeding season, thereby providing substantial fitness benefits and allowing individuals to capitalise on favourable conditions and boost offspring production (Verhulst 1998, Hoffmann *et al*. 2015, Trnka & Samas 2024). Many studies have shown that reproductive success is higher in multi-brooded than single-brooded individuals, measured either annually (Nagy & Holmes 2005a, Smith & Marquiss 2008, Naef-Daenzer *et al.* 2011, Béziers & Roulin 2016) or across the lifetime (Hoffmann *et al.* 2015). However, some have suggested that breeding success is lower in second broods and may contribute less to parental fitness (Smith & Marquiss 2008, Hoffmann *et al.*, 2015, Béziers & Roulin, 2016), which given the costs of reproduction, raises questions about the value of second broods

(Béziers & Roulin 2016). Any increase in breeding success resulting from multiple broods must offset the associated costs, which may include lower survival and future fecundity (Stearns 1976, Smith & Marquiss 2008), and a decrease in the condition or survival of offspring from the first brood, for example through a reduction in post-fledging parental care (Bennett & Owens 2002, Grüebler & Naef-Daenzer 2008a, Naef-Daenzer *et al.* 2011). Understanding the conditions which favour multi-brooding and investigating the fitness consequences therefore remain key goals in avian ecology.

Multi-brooding is relatively common in passerines, although its prevalence can vary across years (Verboven & Verhulst 1996, Trnka & Samas 2024), latitudes and different habitats (Cooper *et al*. 2005, Lambrechts *et al*. 2008), both intra- and interspecifically (Brinkhof *et al*. 2002, Hoffmann *et al*. 2015, Béziers & Roulin 2016). Among species, it is associated with several ecological and life-history traits. For example, it is thought to be more common in shorter-lived species, which are less able to trade off current and future survival and reproduction, and are therefore expected to invest more in the current breeding season (Husby *et al.* 2009, Bleu *et al*. 2016, Trnka & Samas, 2024). Polygamous mating systems and sex-specific parental care strategies may limit the potential for multi-brooding (Kempenaers 2022), and the length of the reproductive window has also been suggested as an important influence (Halupka & Halupka 2017). For example, dietary generalists have a longer reproductive window as they are not tied to the seasonal peak in a specific food source (Svensson 1995, Nagy & Holmes 2005a, Weggler 2006), and residents and short-distance migrants have extended breeding seasons compared with long-distance migrants, increasing the opportunities for raising multiple broods (Halupka & Halupka 2017).

In many species, only a proportion of the population attempts to raise a second brood in any one year (Nagy & Holmes 2005a). The most widely cited predictor of whether or not a pair will do so is the timing of breeding for the first brood, with the likelihood of second-brooding decreasing as the season progresses (Verboven & Verhulst 1996, Hoffmann *et al.* 2015, Beziers & Roulin 2016). Two hypotheses have been put forward to explain this. First, the *date hypothesis* suggests environmental conditions become less favourable as the breeding season advances, and all individuals are affected equally (Verboven & Verhulst 1996, Marcel *et al*. 2003, Hoffmann *et al.* 2015). Second, under the *individual quality hypothesis*, individuals breeding earlier possess higher phenotypic qualities, including better body condition and more experience, or hold better quality breeding territories (Verboven & Verhulst 1996, Marcel *et al.* 2003, Hoffmann *et al.* 2015). Several experimental studies have found support for these hypotheses (Verboven & Verhulst 1996, O'Brien & Dawson 2013), although they are not mutually exclusive and may interact (Verboven & Verhulst 1996, Brinkhof *et al.* 2002, O'Brien & Dawson, 2013). Furthermore, recent evidence suggests that the duration and end date of the breeeding season may have similar influence to the start in determining the likelihood of multi-brooding (Lv *et al*. 2020, Halupka *et al*. 2021). Further research is required to understand these processes in more detail.

With climate change, average values of temperature and rainfall as well as the frequency and severity of extreme weather events are predicted to increase significantly (Jentsch & Beierkuhnlein 2008, IPCC 2023). A well-established effect of recent temperature increases is the advancing of lay date in temperate birds (Crick & Sparks 1999, Martin 2007, Shipley *et al*. 2020). Some multi-brooded species are breeding earlier and extending their reproductive season in order to exploit prolonged favourable conditions (Halupka & Halupka 2017, Halupka *et al*., 2021), and temperature-related lengthening of the season is positively associated with the frequency of multiple broods (Townsend *et al.* 2013, Halupka *et al*. 2021). By contrast, the breeding season can become shorter if birds do not advance their timing of breeding sufficiently to match changes in peak food availability, and conditions deteriorate earlier (Jankowiak *et al*. 2014, Halupka & Halupka 2017). Indeed, several studies have linked this to a decline in multi-brooding (Husby *et al.* 2009, Townsend *et al.* 2013).

Weather conditions tend to become more extreme with elevation and as a result food availability is reduced or the seasonal peak in food abundance delayed (Bears *et al.* 2009). These conditions often cause birds to start breeding later and to have a shorter reproductive season which can ultimately restrict the probability of having multiple broods (Bears *et al.* 2009, Jankowiak *et al*. 2014, Hoffmann *et al.* 2015). However, only a few studies have investigated the effect of elevation on multi-brooding (Martin & Wiebe 2004, Bears *et al.* 2009, Camfield *et al*. 2010). For example, Bears *et al.* (2009) found that Dark-eyed Juncos *Junco hyemalis* were single-brooded at high elevations (2000 m) and multi-brooded at low elevations (1000 m). Similarly, Lu *et al*. (2010) observed that White-bellied Redstarts *Luscinia phaenicuroides* breeding at high elevations (4300 m) had a nesting period extended by nine days compared to individuals at lower elevations (< 1300 m), making multi-brooding unviable.

Finally, individuals of higher quality may be more likely to attempt to raise multiple broods (O'Brien and Dawson 2013, Nomi *et al*. 2018). For example, De Laet & Dhondt (1987) observed that female Great Tits *Parus major* which lost less body weight during their first brood were more likely to initiate a second brood. Several studies have also suggested that high quality individuals defend better breeding territories leading to a higher probability of multi-brooding (Béziers & Roulin 2016, Nomi *et al*. 2018, Lv *et al*. 2020). Reproductive performance can also improve with age due to individuals gaining experience or access to better resources, at least until reaching middle or old age when senescence occurs (Nol & Smith 1987, Bennet & Owens 2002, Balbontín *et al.* 2007). However, only a few studies have investigated the effect of age on having multiple broods. Two studies, one of Song

Sparrows *Melospiza melodia* and another of Black-throated Blue Warblers *Setophaga caerulescens*, found that older birds produced more broods per year (Nol & Smith 1987, Holme *et al.* 1992), but more research is needed on how individual quality and age impact multi-brooding.

Here, we provide the first detailed investigation of the factors affecting the likelihood and outcome of double-brooding in the White-throated Dipper *Cinclus cinclus* (hereafter 'Dipper'), an ideal model system for several reasons. The Dipper is a riverine species, currently amber-listed under the British Birds of Conservation Concern (Stanbury *et al*. 2021), with the UK population declining by 39% between 1995 and 2020 (Massimino *et al*. 2022). Dippers start breeding earlier than most European passerines, typically in the late winter, and have a relatively long breeding season lasting until early summer (Tyler & Ormerod 1994). One of the major changes in the life-history traits of this species is an advance in the timing of breeding, likely due to rising temperatures (Nilsson *et al*. 2019, Massimino *et al*. 2022). Dippers are facultatively double-brooded species, with the proportion of a population attempting to raise a second brood varying between years and regions according to environmental conditions (Tyler & Ormerod 1994); two records from Germany are the only documented cases of a third brood being raised (Grunwald 1973 and Fuchs 1970 as cited in Tyler & Ormerod 1994).

Ormerod and Tyler (1993) suggested that Dippers having two broods achieve a reproductive success and recruitment rate that is almost as high as those having one brood later in the breeding season. This indicates that the contribution of second broods to overall productivity may be low (Ormerod & Tyler 1993). However, double-brooding could become more common or more successful in response to the effects of climate change, which may even mitigate population declines (Halupka *et al*. 2008). Further analyses are therefore important for predicting future demographic change. In this study, we conduct a detailed analysis of double-brooding in a long-term study population of Dippers in the Yorkshire Dales National Park, UK. Our main aims were to investigate: (1) the frequency of double-brooding and the difference in breeding parameters between first and second broods; (2) the factors affecting the likelihood of double-brooding, in particular the timing of breeding and age; and (3) the factors affecting breeding success in second broods.

METHODS

Study site

Data collection was undertaken in the Yorkshire Dales National Park, in the River Lune catchment within an 8 km radius of the town of Sedbergh, Cumbria, UK (54°19'N, 2°31'W). The catchment includes the rivers Lune, Rawthey, Clough and Dee, together with their many tributaries. Here, an individually marked breeding population of 30 - 50 pairs is the subject of an intensive long-term monitoring project. For the present study, the data were collected between 2013 and 2021. Nestlings were fitted with a British Trust for Ornithology (BTO) metal ring and a unique combination of three colour rings (under BTO licence), and the following biometrics were recorded: body mass (to 0.1 g) using an electronic balance, and tarsus length or 'maximum tarsus' (to 0.1 mm), defined as the length of the tarsometatarsus, using dial callipers. Adults not ringed as nestlings within the study site (i.e., immigrants) were captured in mist-nets or hand nets and fitted with a metal ring and three colour rings, using the same method as for nestlings. The same biometrics were taken as for nestlings, with the addition of maximum wing length (to 1.0 mm), measured using a capped wing ruler. All biometrics were recorded by the same person. Most individuals ringed as nestlings that recruited into the breeding population were recaptured as adults, so their sex could be determined from their wing length and their age determined as first-year or older according to the presence or absence of retained juvenile wing coverts (Demongin 2016).

Most nests in the study site are built in natural sites (the riverbank, overhanging trees, etc.), bridges or culverts, but a variable number of nestboxes are also used each year. Therefore, we differentiate two types of nest; nestboxes and natural nests (i.e., all nests excluding those in nestboxes). The nestboxes are no. 19 Schwegler boxes (Schwegler Ltd., Germany), with a bottom opening, specifically designed for breeding Dippers and wagtails. Between 11 and 16 boxes were in place each year, with some being moved between years; annual occupancy varies, although boxes in some locations are used almost every year.

Nest monitoring

Breeding attempts of all pairs were monitored every year between 2013 and 2021, from the start of nest-building in February through to failure or fledging; the earliest laying date recorded during the study period was 1 March, and the latest ever nest fledged on 11 July. Nest location and elevation were recorded with a Garmin eTrex H Global Positioning System (GPS) device (Garmin Ltd., Switzerland); nest elevations ranged from 70 to 520 metres above sea level (hereafter given in m). Nests were found by observing individuals carrying nest material or by checking known nesting sites from previous years, and then visited weekly until laying was imminent. Once a pair was observed carrying leaves (or dry grass at high elevations), or these materials were found in the lining, the nest was checked every two to three days to determine lay date, normally in the afternoon to minimise the risk of disturbing females during laying. Lay date was defined as the date on which the first egg of the clutch was laid. Dippers generally lay one egg per day and incubation starts when the clutch is complete (Tyler & Ormerod 1994, Ferguson-Lees *et al.* 2011); if eggs were first detected when cold, lay date could be determined by back calculation. Clutch size was recorded by counting the number of eggs a week after incubation started. The incubation period in Dippers, on average, takes 16 days, with a range of 15 - 18 days (Tyler & Ormerod 1994, Ferguson-Lees *et al.* 201118/08/2025 13:11:00). Nests were checked daily at the end of incubation to confirm hatch date (i.e., the date on which at least one chick had hatched); if hatch date was missed by a day or two, nestling age could be determined reliably by assessing the size of the birds and the development of the feather tracts (S. P. Sharp, *pers comm*).

In most cases, nestlings were ringed when they were nine days old (hatch date = day 0). On those occasions when ringing could not take place on day 9 due to problems with nest access (e.g., flooding), nestlings were ringed on day 13; more rarely, they were ringed on other days (7 - 21) for logistical reasons. Brood size was recorded at the time of ringing. Young spend around 20 - 24 days in the nest before fledging (Tyler & Ormerod 1994, Ferguson-Lees *et al*. 2011), so nests were checked daily from day 20 to determine fledge date (i.e., the date on which the chicks leave the nest) until young were seen leaving the nest or the nest was empty. The number of fledged chicks was assumed to be the same as brood size at ringing unless dead chicks were found in the nest or the immediate vicinity. After a successful first brood, from which at least one chick fledged, or a failed first brood, nest sites were re-visited regularly to determine the lay date of 'second broods' or replacement clutches, respectively. In most cases, the nest for the first brood was re-lined and used again, but ocassionally a new nest was built nearby. Second broods were defined as breeding attempts (that reached at least the laying stage) by a pair which had already fledged at least one chick in that season. Nests were classified based on the identity of the female, so a female who fledged one brood and then switched partners before producing another clutch was considered to have a second brood. This was uncommon, and occurred on six occasions (11%) during the study period. Pairs having one or more replacement clutches in our study site never progressed to having a second brood, and no pair was ever recorded having a replacement clutch following a failed second brood. Percentage recruitment from both first and second broods was obtained by counting the number of young successfully fledged that were found as adult breeders in subsequent years, usually the following year because Dippers typically reach reproductive maturity one year after being born (Tyler & Ormerod 1994).

Weather data

Daily mean, minimum and maximum temperatures, and total daily rainfall were obtained from Shap Weather Station (Met Office 2022), located in Shap, Cumbria, UK (54°31'N, 2°40'E), at 255 m elevation. This is approximately 30 km from the study site and is the closest weather station with complete annual records covering the study period. For each first brood in the dataset, the means of the daily mean, minimum and maximum temperatures were calculated for the 12-day period following fledging; this corresponds with the average interbrood interval in our study site, defined as the mean number of days between first brood fledging date and second brood lay date. Cumulative total daily rainfall was also calculated for this 12-day period.

Statistical analyses

Analyses were carried out in R, Version 1.4.1103 (R Core Team, 2021). Comparisons of clutch size and number of chicks fledged from first and second broods (by the same pair in a given year) were made using a paired t-test. Two Mann-Whitney tests were performed to compare the number of eggs laid and chicks fledged from single and double-brooded pairs, and a third was used to test for differences between the number of chicks fledged from double broods using nestboxes and natural nests. In all cases, the mean number of chicks fledged was calculated by averaging across unsuccessful and successful nests. All descriptive statistics are given as means ± SD. All other analyses were carried out using generalised linear mixed-effects models (GLMMs). First, a series of GLMMs with a binomial error distribution and logit link function were fitted to model the probability of pairs having second broods; for these, the response variable was a binary indicator of whether or not a breeding pair which had fledged one brood had a second brood (0 = no, 1 = yes), hereafter 'second brood probability'. Second, to analyse the reproductive success of second broods, hurdle mixed models were fitted with two components, a binomial error distribution with a logit link function and a truncated Poisson distribution with a log link function, to account for zero-inflation. In the binomial part, the response variable was a binary indicator of whether or not a pair fledged at least one chick (0 = no chicks, 1 = at least one chick) in a second brood, hereafter 'second brood fledging success'. For the truncated Poisson part, restricted to successful second broods, the response variable was the number of chicks fledged (> 0), hereafter 'second brood fledgling number'.

For the analysis of second brood probability, the explanatory variables included in the models were first brood lay date, first brood fledgling number (defined as the number of chicks fledged in the first brood), male age (in years, 1 - 8), female age (in years, 1 - 8), elevation (first brood nest elevation in m), interbrood total rainfall, interbrood mean temperature, interbrood minimum temperature and interbrood maximum temperature. In addition, a binary indicator of whether the nest was in a nestbox (N = 41) or a natural nest (N = 149) was included, hereafter 'nest type'. Nest type was a variable of interest as there is an extensive literature about the benefits of providing nestboxes in other passerine species, including greater opportunities for breeding and a higher breeding success (e.g., Walseng & Jerstad 2014). Female (N = 119) and male (N = 115) identities were included as random effects to control for repeated measures of individuals breeding in successive years. Analysis was restricted to those breeding attempts that had a corresponding successful first brood (N = 190). Replacement clutches were excluded to avoid biasing the sample towards later lay dates of first broods. Models were fitted using the *lme4* package (Bates *et al*. 2015). Collinearity was tested using correlation plots and Variance Inflation Factors (VIFs) following Zuur *et al.* (2009). First brood lay date was strongly positively correlated with interbrood mean temperature, interbrood minimum temperature and interbrood maximum temperature ($r = 0.653$, $r = 0.681$ and $r = 0.567$, respectively), so the interbrood temperature variables were removed from the model. Lay date was selected over interbrood temperatures because, based on previous studies, it was considered more likely to be an important predictor of second brood probability. The rest of the variables had low correlations ($r < 0.4$) and VIF values (< 3), and so were included in the models.

For second brood breeding success, hurdle mixed models were fitted using the *glmmTMB* package (Brooks *et al*. 2017). The explanatory variables tested were the same as in the model of second brood probability, but first brood lay date was substituted by second brood lay date. Nest type was again included (nestbox , N = 11; natural nest, N = 41). Female (N = 38) and male (N = 36) identities were included as random effects. A total of 52 attempted second broods were included in the analyses. Collinearity was again tested using collinearity plots and VIFs (Zuur *et al.* 2009). Interbrood mean temperature, interbrood minimum temperature and interbrood maximum temperature were highly positive correlated with each other ($r > 0.5$), so only interbrood maximum temperature was retained. Interbrood maximum temperature was retained because extremes of high temperatures are likely to have a greater impact on prey availability, and therefore on breeding success in Dippers (Tyler & Ormerod 1994). For all other variables, correlations were low ($r < 0.4$) and VIF values were small (< 3), so they were included in the models.

All dates were transformed to Julian Dates (JD, day 1 = 1 January) for analyses. Before running the models, all numerical variables were centred and standardised in order to facilitate comparison between the fixed effects in the model results (Zuur *et al.*, 2009, Schielzeth, 2010). The best-fitting models were selected with a backward stepwise exclusion approach, using the *stepAIC* function from the *MASS* package, based on the Akaike's Information Criterion (AIC) (Venables & Ripley 2002), and random effects were selected using the *stepcAIC* function from the *cAIC4* package, based on the conditional Akaike's Information Criterion (AICc) (Säfken *et al*. 2021). The *p* values of the fixed effects were calculated using the *lmerTest* package following the Satterthwaite's method (Kuznetsova *et al*. 2017). The R^2 of the GLMM model was estimated using the *r.squaredGLMM* function from the *MuMIn* package (Nakagawa & Schielzeth 2013), and for the hurdle model, the *r2* function from the *Performance* package (Lüdecke *et al*. 2021). GLMMs were validated by plotting the distribution of the residuals and the scaled simulated residuals against the expected values using the *plotResiduals* and the *plotQQunif* functions from the *DHARMa* package (Hartig 2022) and for the hurdle model, the *check_model* function from the *patchwork* package (Pedersen 2024). Overdispersion was checked using the *testDispersion* function from the *DHARMa* package (Hartig 2022).

RESULTS

Second brood probability

Between 2013 and 2021, a total of 307 first brood attempts were monitored of which 190 (62%) were successful, fledging at least one chick. Of those successful breeding attempts, 52 (27%) were followed by a second breeding attempt. On average, 20 ± 8% of the total nesting attempts per year were second broods with the lowest proportion of 8% being in 2018, and the maximum value being 30% in 2019. The mean proportion of pairs attempting a second brood per year was 29%, ranging from 8% to 43% in 2018 and 2019, respectively. Around 77% of the females and 76% of males (30 females and 28 males) had a second brood only once, although some individuals double-brooded more than once in the nine-year study period: 15% (6) of females and 14% (5) of males double-brooded twice, 5% (2) of females and males double-brooded three times, and 3% (1) of females and 5% (2) of males double-brooded four times. Of those individuals double-brooding twice or more in their lifetime, 75% of both males and females did so with the same partner each time.

The best-fitting model of second brood probability contained first brood lay date, male age, elevation and interbrood total rainfall. Variables excluded from the best-fitting model were first brood fledgling number, female age and nest type. Second brood probability was best explained by first brood lay date ($P < 0.001$; Table 1, Fig. 1A), with the probability decreasing as first broods were laid later in the breeding season (mean lay date of first broods = 19 March ± 9 in double-brooded females and 6 April ± 14 in single-brooded females). No second brood attempts occured when the first brood was laid after the 12 April. The earliest second brood lay date was 20 April and the latest 4 June (mean second brood lay date = 12 May ± 9). There was a significant positive correlation ($P < 0.05$) between second brood probability and male age (Table 1, Fig. 1B; mean age of double-brooded males = 3.3 ± 1.8 and single-brooded males = 2.2 ± 1.5). The elevation of nest sites was negatively correlated ($P < 0.05$) with second brood probability (Table 1, Fig. 1C), with no second broods occurring at elevations higher than 190 m. Interbrood total rainfall was also positively correlated with second brood probability ($P < 0.05$; Table 1), although the confidence interval was wide when interbrood total rainfall was high (Fig. 1D), and results must be interpreted with caution.

Second brood breeding success

The number of successful second brood attempts between 2013 and 2021 was 30 (56%). Second broods contributed 9% to the total number of all successful breeding attempts and 11% to the total number of young fledged. First and second brood fledging success were almost identical (56% and 57%, respectively). However, mean clutch size in second broods (4.3 ± 0.7) was significantly smaller than in corresponding first broods (4.8 ± 0.5; t = 3.987; df = 46; $P < 0.001$). Likewise, the mean number of chicks fledged in second broods (3.2 ± 1.3) was also significantly smaller than in first broods (4.0 ± 1.0; t = 6.820; df = 51; $P < 0.001$). The number of chicks fledged from second broods in the period 2013 to 2020 (and could therefore have been recorded as breeders in the years 2014 to 2021) was 78, of which only six individuals (7.7%), two females and four males (all from different broods), recruited into the breeding population in the following year. Recruitment was higher in first broods; of the 654 chicks that fledged from first broods during the same period, 80 (12.2%) recruited. Therefore, there was a higher production of eggs, fledglings and young recruiting into the breeding population in first broods than in second broods. Overall, double-brooded parents produced significantly more eggs and fledglings in total than single-brooded parents, with 8.7 ± 1.8 and 4.5 ± 1.1 eggs (U = 348, $P < 0.001$), and 5.8 ± 2.1 and 3.7 ± 0.9 fledglings (U = 1381, $P < 0.001$), respectively.

The best-fitting hurdle mixed model of the second brood breeding success included nest type, first brood fledgling number and second brood lay date. Second brood fledging success was best explained by nest type ($P < 0.05$; Table 2), with 90% breeding success in nestboxes and 47% in natural nests (Fig. 2). Similar results have been found for first broods in the population, with 77% breeding success in nest boxes and 51% in natural nests (S. P. Sharp, unpublished data). There was no significant difference in clutch size between pairs using nestboxes or natural nests (4.2 ± 0.6 eggs in nest boxes, 4.3 ± 0.7 eggs in natural nests; U = 202; $P > 0.05$), but the mean number of chicks fledged, averaged across successful and unsuccessful nests, was 3.2 ± 1.6 in nest boxes, significantly higher than in natural nests, 1.5 ± 1.8 (U = 104.500; $P < 0.01$). Second brood fledging success was not significantly correlated with first brood fledgling number and second brood lay date ($P > 0.05$; Table 2). In contrast, second brood fledgling number was best predicted by second brood lay date ($P < 0.05$; Table 2), with a smaller number of fledglings produced in later second broods (Fig. 3). Nest type and first brood fledgling number had no significant effect on the second brood fledgling number ($P > 0.05$; Table 2).

DISCUSSION

Double-brooding occurred frequently in our study with, on average, 29% of successful first breeding attempts in a season being followed by an attempted second brood (27% when measured across all 190 successful first broods). This is slightly higher than in previous studies of Dippers in Wales (19.3%

of 325 successful first breeding attempts followed by a second, study period 1978 - 1983; Tyler & Ormerod 1985) and Scotland (19.3% of 296 successful first breeding attempts followed by a second, study period 1979 - 1986 and 1990 - 1991; Wilson 1996). Elsewhere in Europe, the percentage of pairs having a second brood is more variable ranging from 49% in Germany to 5.3% in Sweden (Tyler & Ormerod 1995), although in Scandinavia the breeding season is shorter and subject to snow and ice cover (Nilsson *et al.* 2019, 2020b). We found the annual proportion of pairs having second broods varied from only 8% to 43%, compared with up to 90% in a Welsh population (Tyler & Ormerod 1994). This annual variation is likely related to changes in food abundance (Zabala *et al*. 2020) and weather conditions, with warmer springs inducing early breeding and allowing more time to rear a second brood (Nilsson *et al*. 2019).

The most important predictor associated with the probability of double-brooding was the timing of the first brood. The probability of double-brooding was higher when first brood lay date occurred earlier, and decreased as the season progressed, with no second broods taking place when the first brood was laid after the 12 April. Similar findings were observed in other studies on multi-brooding in birds (e.g., Verboven & Verhulst 1996, Hoffmann *et al*. 2015, Béziers & Roulin 2016) and support the *date hypothesis*. The main prey of Dippers, the larvae of aquatic invertebrates (Tyler & Ormerod 1994), declines in availability with metamorphosis and emergence of adults, and this occurs as the season advances, triggered by environmental cues such as changes in hydrology and increases of temperature (Woods *et al*. 2022). The effect of temperature was not included in the analyses due to its correlation with timing of breeding, but is likely to be important via its effects on invertebrate availability (Durance & Ormerod 2007, Pearce-Higgins & Morris 2022).

The timing of breeding in birds typically coincides with a seasonal peak in food availability, and this has also been shown to be important for the likelihood of double-brooding (Svensson 1995, Nagy & Holmes 2005b, Townsend *et al.* 2013). For example, in an experimental study of Black-throated Blue Warblers, females that were supplemented daily with food after laying a first clutch were more likely to double-brood compared with control females (Nagy & Holmes 2005b). Higher food availability was suggested to improve female condition and to decrease the energy spent in finding food for the young (Nagy & Holmes 2005a). In Dippers, if the emergence of invertebrates occurs before or at the time of initiating a second brood, food availability may be reduced during the nestling period of the second brood and thereby act as a limiting factor. Some studies have shown an advance in the emergence of freshwater invertebrates due to the effects of climate change on flow conditions and temperature (Harper & Peckarsky 2006, Everall *et al*. 2015, Anderson *et al*. 2019). This may at least partly explain the strong effect of timing of breeding on the probability of having a second brood, although it was not directly tested in our study. Very few studies have provided results on the seasonal changes in the abundance of aquatic invertebrate larvae, so future research on this may be valuable for further understanding the timing of breeding and double-brooding in river birds.

According to the *date hypothesis*, all individuals that start breeding early should be able to produce a second brood (Verboven & Verhulst 1996). However, we found that 52% of pairs that produced a successful first brood before our threshold date for second broods did not attempt a second brood. Single-brooded pairs started breeding on average 18 days later than double-brooded pairs. Although this fits with the *date hypothesis*, as initiating a second brood late is unlikely to outweigh the associated costs (Grüebler & Naef-Daezer 2008b), the question of why individuals do not attempt a second brood given the optimum timing remains unanswered. The *individual quality hypothesis* may provide an explanation (Verboven & Verhulst 1996, Hoffmann *et al.* 2015), with early breeders having greater phenotypic attributes (i.e., better condition or foraging success) or holding a territory of higher quality (Verboven & Verhulst 1996, Grüebler & Naef-Daenzer 2008b). For example, studies have shown that females that lose less body mass during the first brood may be also more likely to initiate a second brood (De Laet & Dhondt 1987, Martin 1987). In our population, birds that defend a territory throughout the winter breed earlier (i.e., in the same territory; Crowther *et al*. 2018), which is advantageous for double-brooding. The fact that, in our study, three quarters of all the double-brooded individuals had a second brood only once, is perhaps indicative of the costs associated with this life-history strategy, and highlights the need to investigate the net fitness consequences of double-brooding for a more comprehensive picture. Additionally, it may be that only individuals of high quality doube-brood multiple times (Geupel & DeSante 1990, Hoffmann *et al*. 2015). Most of the birds that double-brooded more than once in our study site were paired with the same partner in consecutive years, suggesting pair bonding and experience is also likely to improve the probability of double-brooding, as has been found in other species (Adkins-Regan & Tomaszycki 2007, Hatch & Westneat 2008). Again, this requires further, longer term study.

We found that older males had a higher probability of having a second brood, further suggesting an effect of individual quality. While the effect of age on reproductive success is well-researched in birds, few studies have investigated how the probability of multi-brooding varies with age (Balbontín *et al*. 2007, Steenhof & Heath 2009, Genovart *et al*. 2022), but similar mechanisms are likely to be involved. For example, Nagy and Holmes (2005a) found that older male Black-throated Blue Warblers held territories with higher food abundance, and females were therefore more likely to double-brood when paired with them. Geupel & DeSante (1990) also found an increase in double-brooding with age in male and female Wrentits *Chamaea fasciata*, and this was linked to a combination of individual quality and experience. Breeding experience increases with age and can help to optimise performance, for example through knowledge of good feeding sites or safe nesting places (Curio 1983, Forslund & Pärt 1995, Genovart *et al*. 2022). Reproductive success typically increases up to a peak age before senescence occurs (Vleck *et al.* 2007, Zhang *et al.* 2015, Genovart *et al*. 2022). Our results show an increase to a maximum probability of double-brooding at three years of age, however there was no clear evidence of senescence thereafter. Selective disappearance could be masking any declines (Bouwhuis *et al*., 2009, Rebke *et al*. 2010) which may explain our wide confidence interval at older ages.

Elevation was negatively correlated with double-brooding. This result is not surprising as elevation has been found to influence breeding success of Dippers (Nilsson *et al*., 2020a), and perhaps the same processes are associated with the low probability of double-brooding. Timing of breeding of first broods in Dippers occurs later at higher elevations due to harsher weather conditions (Wilkinson 2019, Nilsson *et al*. 2020b), so breeding seasons are generally shorter, giving less time to raise a second brood. Despite the elevational variation being lower (range 70 - 520 m) than that of other studies (Bears *et al*., 2009), we found a clear effect, with double-brooding absent at elevations greater than 190 m. Additionally, smaller streams at high elevations have generally lower densities of food and a poorer capacity to cope with flow variations (Chiu *et al*., 2008, Nilsson *et al*. 2020a). Therefore, higher elevation breeding sites may be of suboptimal suitability and be occupied by lower quality or less experienced birds (Smith & Marquiss 2008, Bears *et al*. 2009, Nilsson *et al*. 2020a). Our sample size of nests above 190 m was small (N = 22) due to the low density of pairs breeding there, hence further research is required to consolidate these ideas.

The positive correlation between second brood probability and rainfall is likely due to the rain-dependence of river flow conditions and the effects on aquatic invertebrates (Kakouei *et al*. 2018). Dry spells are associated with changes in stream invertebrate communities and can cause species to decline with only moderate decreases in flow, in particular specialist (Kakouei *et al*. 2018) and large-bodied species, including species in the orders Ephemeroptera, Plecoptera and Trichoptera (Extence 1981, Aspin *et al*. 2019), which are the main prey of Dippers (Ormerod & Tyler 1994). Heavy rains can produce a similar effect, whereby invertebrates get washed away by a severe increase in river flow, reducing their abundance and diversity not only momentarily but also long-term (Chiu *et al*. 2008, Hong *et al*. 2018, Lv *et al*. 2020). Therefore, care must be taken interpreting our results; as rainfall increases, the probability of double-brooding becomes more variable. With climate change, extreme events are becoming more common, and so how rainfall is distributed over time (i.e., dry spells, mild showers or heavy storms) can have either positive or negative effects on invertebrate communities

(Lv *et al*. 2020), and consequently, on the likelihood of double-brooding. Future research looking directly at the impact of rain patterns or river flow changes would be beneficial.

Double-brooded pairs produced on average more offspring per year than single-brooded pairs. Our results are in accordance with studies of other species which have shown that double-brooding increases reproductive output (i.e. Carro *et al*. 2014, Béziers & Roulin 2016, Cornell & Williams 2016). However, fledging success was almost identical in first and second broods (~ 56%), and this differs from the findings in a Welsh population where second broods had lower success, with higher incidence of desertion and predation (Tyler & Ormerod 1994). It may be that, in our population, there is little difference between broods in predation pressure, perhaps because the timing of the breeding season is slightly different (Tyler & Ormerod 1994). Second broods produced fewer eggs, fledglings and recruits, so reproductive value may be lower compared with first broods (Ormerod & Tyler 1993, Husby *et al.* 2009), and there is likely a trade-off between having a single brood with young of greater fitness and two broods comprising more chicks but of inferior condition (Verboven & Verhulst 1996).

Nest type was the main predictor of second brood breeding success, with nestboxes having almost twice the fledging probability of natural nests. This is perhaps unsurprising as several studies have highlighted the benefits of nest boxes, including protection against predators and adverse weather (Purcell *et al*. 1997, Fargallo *et al*. 2001, Libois *et al*. 2012). In Dippers, on average, natural nests are built at less than 3 m over water (Tyler & Ormerod 1994), so nestboxes can also provide protection against flash flooding. However, this result must be interpreted with caution as our sample size was small. On the contrary, we found no effect of nest type on the number of fledglings, and this may be explained by other overriding factors such as the seasonal decline of conditions and resources (Verboven & Verhulst 1996). Indeed, this may be the main driver of the negative correlation found between the timing of breeding and fledgling number in second broods, with similar patterns reported in other species (Brinkhof *et al.* 2002, Grüebler & Naef-Daezer 2008b, Hoffmann *et al*. 2015). Overall, our results provide evidence supporting the benefits of providing nestboxes for Dippers, an approach that may benefit their conservation.

Conclusion

Double-brooding in Dippers is common and can significantly boost annual reproductive output and potentially lifetime breeding success. Our results fit with the *date hypothesis*, whereby the decline of double-brooding and number of fledglings is driven primarily by the seasonal deterioration of breeding conditions rather than the quality of the individuals. However, the finding that some pairs breeding earlier and older males are more likely to double-brood indicates that the mechanisms described by the *individual quality hypothesis* may also be operating. Only half of all pairs had a second brood in apparently suitable conditions within the appropriate timing, suggesting that double-brooding may not be purely an opportunistic response to a favourable environment. Further research is needed to better understand the relative effects of seasonal changes in food availability, individual variation and the costs associated with double-brooding, for instance adult survival or future fecundity. Finally, double-brooding may become more common as a response to the advance of the timing of breeding in this declining species, which could have positive consequences for population dynamics. Long-term studies such as this offer exceptional opportunities for monitoring and understanding these processes especially in light of ongoing climate change.

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Tables

Table 1. Results of the best-fitting GLMM of factors affecting second brood probability (N = 190). Values shown correspond with the model estimates, standard error and p values of significance. Significant effects are highlighted in bold (*P* ≤ 0.05). Variance of random effects and R^2 are also included.

Fixed effects	*Estimate*	*SE*	*P*
Intercept	-2.407	0.506	**<0.001**
First brood lay date	-2.169	0.489	**<0.001**
Elevation	-0.971	0.489	**<0.05**
Interbrood total rainfall	0.599	0.295	**<0.05**
Male age	0.508	0.238	**<0.05**
Random effects	*Variance σ2*		
Female identity	4.533e-1		
Male identity	8.126e-6		
Marginal R2/Conditional R2	0.633 / 0.678		

Table 2. Results of the best-fitting hurdle mixed model of factors affecting second brood fledging success (zero-inflation model) (N = 52) and second brood fledgling number (conditional model) (N = 30). Values shown correspond with the model estimates, standard error and p values of significance. Significant effects are highlighted in bold ($P \leq 0.05$). Variance of random effects and R^2 are also included.

	Zero-inflation model			**Conditional model**		
Fixed effects	** Estimate*	*SE*	*p*	*Estimate*	*SE*	*P*
Intercept	0.025	0.387	0.949	1.055	0.146	5.690e-13
Nest type (nest box)	-2.737	1.268	**<0.05**	0.125	0.243	0.606
First brood fledgling number	0.596	0.359	0.097	0.123	0.112	0.272
Second brood lay date	0.060	0.323	0.853	-0.204	0.106	**<0.05**
Random effects	*Variance σ2*			*Variance σ2*		
Female identity	1.188e-8			5.089e-12		
Male identity	1.710e-1			5.138e-12		
Marginal R2/Conditional R2	0.184/0.184					

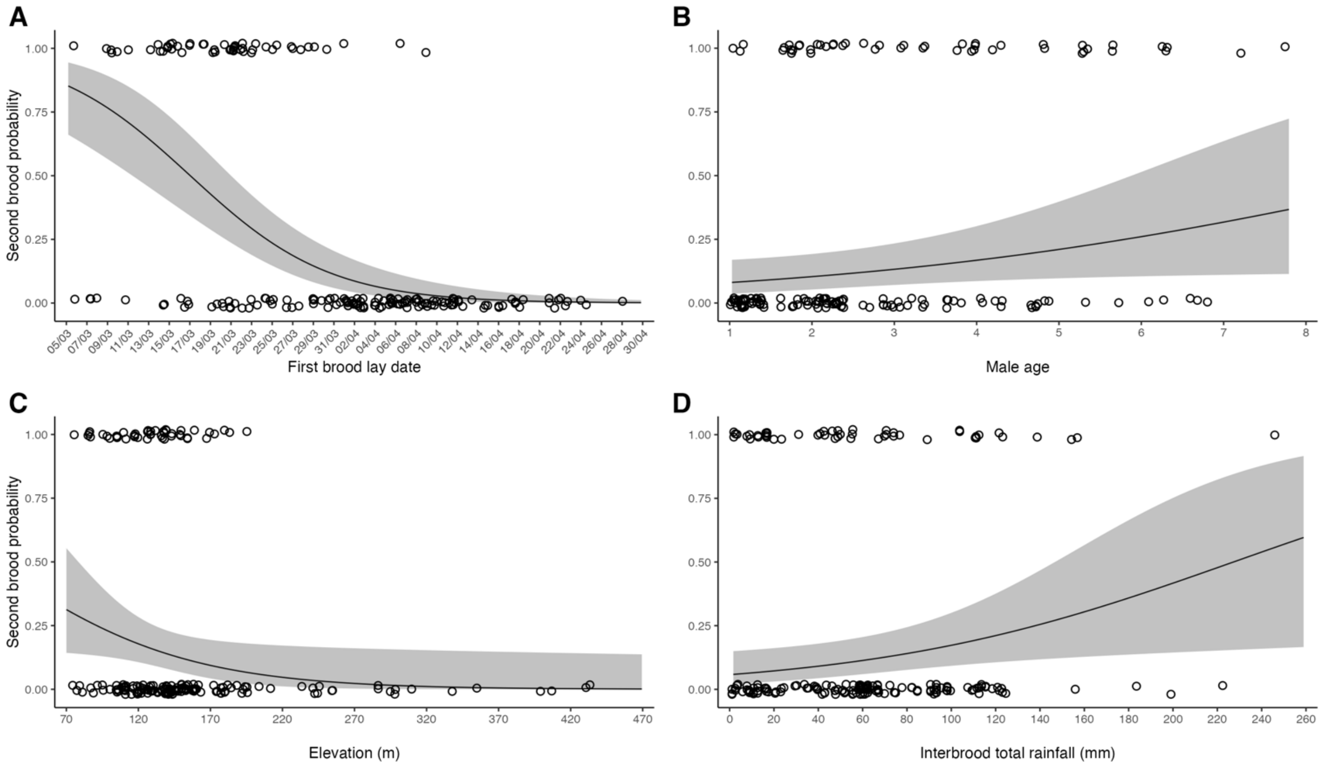
* Note in the zero-inflation component, modelling is based on the zeros (non-event), hence the estimates need to be read with opposite sign.

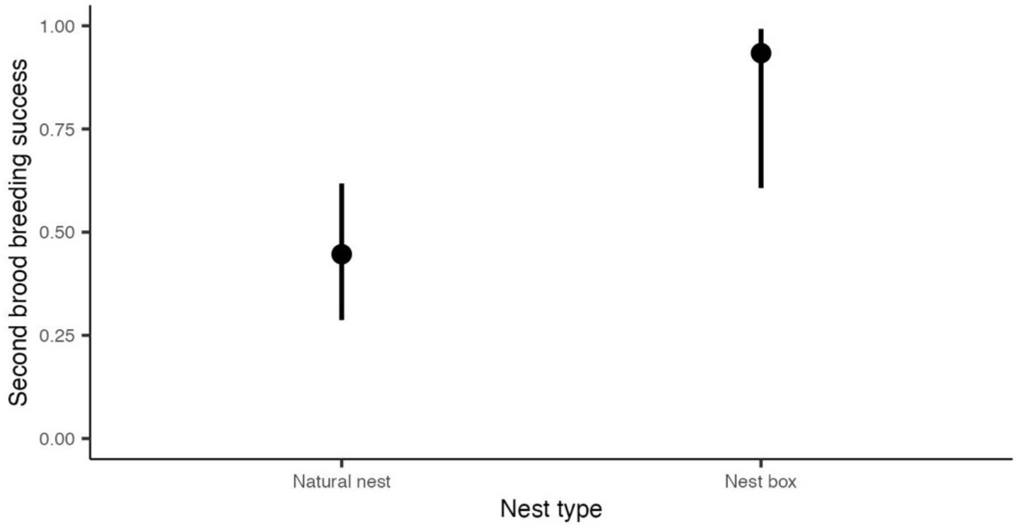
Figures

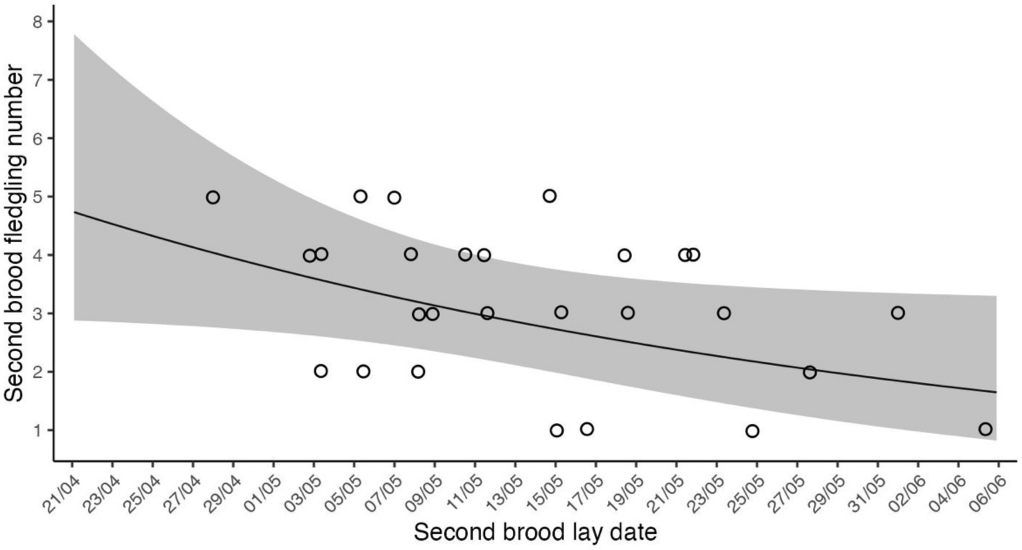
Figure 1. The best-fitting model with predicted relationships between the probability of double-brooding in Dippers and lay date of first broods (A), male age (B), elevation (C) and the interbrood total rainfall (D). The lines show the predicted relationship from a GLMM and the circles show the raw data; shaded areas show the 95% confidence intervals.

Figure 2. The probability of second brood fledging success in natural nests and nestboxes in Dippers. Points show the predicted means, and upper and lower whiskers show the 95% confidence intervals from a GLMM hurdle model (zero-inflation model).

Figure 3. The relationship between the second brood lay date and the second brood fledgling number in Dippers. The line shows the predicted relationship from a GLMM hurdle model (conditional model), and the circles show the raw data; shaded areas illustrate the 95% confidence intervals.


A
B
C
D
Second brood probability
1.00
0.75
0.50
0.25
0.00
05/03
07/03
09/03
11/03
13/03
15/03
17/03
19/03
21/03
23/03
25/03
27/03
29/03
31/03
02/04
04/04
06/04
08/04
10/04
12/04
14/04
16/04
18/04
20/04
22/04
24/04
26/04
28/04
30/04
First brood lay date
1
2
3
4
5
6
7
8
Male age
70
120
170
220
270
320
370
420
470
Elevation (m)
0
20
40
60
80
100
120
140
160
180
200
220
240
260
Interbrood total rainfall (mm)


Second brood breeding success
1.00
0.75
0.50
0.25
0.00
Natural nest
Nest box
Nest type


Second brood fledgling number
8
7
6
5
4
3
2
1
21/04
23/04
25/04
27/04
29/04
01/05
03/05
05/05
07/05
09/05
11/05
13/05
15/05
17/05
19/05
21/05
23/05
25/05
27/05
29/05
31/05
02/06
04/06
06/06
Second brood lay date