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Abstract

Multiple brooding, reproducing twice or more per year, is an important component of life-history strategies. However, what proximate factors drive the frequency of multiple brooding and its fitness consequences for parents and offspring remains poorly known. Using long-term longitudinal data, we investigated double brooding in a barn owl population in France. We assessed the effects of both extrinsic and intrinsic factors and the consequences of double brooding on fledgling recruitment and female lifetime reproductive success. The occurrence of double brooding in the population, ranging from 0 to 87%, was positively related to the number of rodent prey stored at the nest. Females laying early in the season were more likely to breed twice and the probability of double brooding increased with smaller initial brood size, female age and the storage of wood mice at the nest early in the season. Fledglings from first broods recruited more often (8.2%) than those from single broods (3.8%) or second broods (3.3%) but this was primarily the consequence of laying dates, not brood type *per se*. Females producing two broods within a year, at least once in their lifetime, had higher lifetime reproductive success and produced more local recruits than females that did not (15.6 ± 8.1 *vs*. 6.1 ± 3.8 fledglings, 0.96 ± 1.2 *vs*. 0.24 ± 0.6 recruits). Our results suggests that the benefits of double brooding exceed costs in terms of fitness, and that within-year variability in double brooding is related to heterogeneity in individual/territory quality.

Introduction

In order to maximize their fitness, individuals adopt alternative strategies for optimising the number of offspring that survive until reproduction. In seasonal environments where breeding occurs only during a restricted period of the year, individuals might nonetheless attempt to re-initiate reproduction following a first successful breeding event in the same year (Husby et al. 2009). Multiple brooding is a relatively common strategy in vertebrates with fast life histories, such as small mammals and passerine birds (Erb et al. 2001; Lambin and Yoccoz 2001; Béziers and Roulin 2016). Producing multiple broods is often a facultative strategy and its frequency varies greatly among populations, but also among years within a given population (Husby et al. 2009; Béziers and Roulin 2016; Jackson and Cresswell 2017). Such a variation offers the opportunity to investigate the proximate factors underpinning the alternative strategies and quantify their relative fitness.

Double brooding (*i.e.* producing a second brood after successfully completing one) is expected to be a rewarding strategy in terms of number of offspring produced annually. Individuals breeding twice in a year can expect producing almost twice as many offspring as individuals breeding only once, such as documented in barn owl *Tyto alba* (Béziers and Roulin 2016), Tengmalm's owl *Aegolius funereus* (Korpimäki et al. 2011), hoopoe *Upupa epops* (Hoffmann et al. 2015), or black-throated blue warbler *Setophaga caerulescens* (Nagy and Holmes 2005a). However, over an individual's lifetime, attempting double brooding may be associated with costs that could cancel out the benefits of short-term increased breeding success. Documented costs include reduced survival of multiple-brooding females (Verhulst 1998) and reduced body condition of fledglings from first broods due to maternal desertion for the purpose of initiating a second brood (Béziers and Roulin 2016). Recruitment probabilities of fledglings from females producing two or more broods could also be lowered compared to fledglings from a single brood but this has been rarely assessed (but see

Hoffmann et al. 2015). Altogether, these costs may reduce fitness gains for parents producing two broods in a year (Verhulst et al. 1997; Eldegard and Sonerud 2009; Husby et al. 2009). In a seasonal environment, the extent of the period during which resources are sufficiently abundant to allow individuals to reproduce is a key factor determining the frequency of multiple brooding. Indeed, the date of the onset of breeding has been repeatedly shown to alter breeding success, with later-breeding individuals having reduced breeding success (e.g. Verhulst and Nilsson 2008). This temporal decline in breeding success can be mainly attributed to 1) the date itself, *i.e.* the deterioration of the environment over the season, 2) the fact that late breeders are of poorer quality, or 3) the fact that late breeders are constrained to occupy low-quality territories. The date hypothesis has received most empirical support so far (Verboven and Verhulst 1996; Verhulst and Nilsson 2008; Pärt et al. 2017), although several processes may act together (Browne et al. 2007; Husby et al. 2009; Hoffmann et al. 2015). The timing of breeding is also relevant for multiple brooding, with early breeders being more likely to produce more than one brood per season (Béziers and Roulin 2016).

Variable availability of food resources has been shown to influence the frequency of multiple brooding. In some cases, a relatively constant percentage of individuals produce two broods each year, such as in the hoopoe (although different populations show different average frequencies; Martín-Vivaldi et al. 1999, Hoffmann et al. 2015). In others cases, the percentage of individuals double brooding can vary from zero to >80% in populations subject to pulsed resources, such as in the black-throated blue warbler *Dendroica caerulescens* (Nagy and Holmes 2005a) or the barn owl (Jackson and Cresswell 2017). Overall, how individual characteristics, the trade-offs between reproduction and survival (both intra- and inter-generation) and environmental conditions interact to determine the probability of double brooding remains poorly understood. Long-term longitudinal data offer the opportunity to i) investigate the factors associated with the occurrence of multiple brooding and ii) measure the consequences of double brooding for parents and offspring, which may shed light on the evolution and maintenance of multiple brooding.

Here we used 17 years of longitudinal data collected in a barn owl population of Burgundy (north-eastern France) to analyse both proximate factors and fitness consequences of double brooding. The barn owl is one of the few non-tropical raptors showing frequent double brooding (Baudvin 1986; Béziers and Roulin 2016). First, we measured the extent of among-year variation in the frequency of double brooding at the population level and assessed whether such variation was related to extrinsic factors such as food storage and climatic conditions. Second, we investigated whether those extrinsic factors interacted with intrinsic factors (laying date, brood size) to drive a female to breed twice in a year. Then, we compared recruitment probabilities between fledglings originating from any of the three brood types (single, first and second) to test whether brood type *per se* affected recruitment in addition to laying date. Lastly, we assessed whether lifetime reproductive success (estimated as either the number of fledglings or local recruits) of female barn owls having produced two broods in a year at least once over their lifetime was higher than that of females that have not.

Methods

Study species, zones & data collection

The barn owl is a medium-sized (ca. 240-350 g) nocturnal raptor whose breeding populations in the western Palearctic are mostly composed of resident individuals. Clutches contain 4-8 eggs (up to 13) and females can raise two broods a year, exceptionally three (Mikkola 1983). Between 1998 and 2006, we monitored an average of 280 nesting-sites annually, including 175 nest-boxes and 105 alternative nest-sites in buildings, in six neighbouring zones primarily across Burgundy and, to a lesser extent, Champagne (north-eastern France), over an approximated total area of 1675 km^2. We installed more nest-boxes in 2006, resulting in a total of 370 nesting-sites (295 nest-boxes and 75 alternative nesting sites) monitored annually, with 2-4 visits per site. The first visit in March-April ascertained occupancy. We made subsequent visits to sites where occupancy was suspected or recorded to assess clutch size and ring nestlings just before fledging (May-July). We attempted to capture adults during all site visits by placing a landing net at the entrance of the nest-boxes. We marked nestlings and unmarked adults with alphanumeric aluminium bands (CRBPO - Museum National d'Histoire Naturelle, Paris). We weighed chicks using a spring scale (Pesola © 500 g). We used nestling age and weight to estimate nestling body condition (expressed as the deviation from predicted body mass according to age and days since estimated hatching date in each year). We revisited later in the season all sites deemed unoccupied on the first visit to detect second clutches or late breeding attempts. The proportion of the barn owl population breeding in monitored nesting-sites was unknown.

We defined laying date as the Julian week when the first egg was laid (week 1 = 1st week of January), either deduced from the number of eggs when the clutch was observed before completion (assuming each egg was laid 2.5 days apart) or using back-calculation from chick wing length (following Taylor 1993 for age estimation and assuming 32 days of incubation; Bunn et al. 1982). On average we ringed nestlings when they were 38 ± 12 days of age. To account for inter-annual variation in laying dates while comparing data over multiple years, we centred laying dates to the average laying date recorded in each year and used relative laying dates for the analyses. To characterise how clutches are distributed within a year, we estimated the average laying date for each year using all the clutches detected, including replacement clutches (N = 93) and those not assigned to any category (their characteristics suggested replacement broods but we could not ascertain that [N = 69]). We assigned breeding birds to two age classes (yearling *vs*. ≥2 years, hereafter called adult) based on ringing, for birds ringed as chicks, or according to the moulting pattern otherwise (Taylor 1993).

We classified broods into four categories: (1) *First* broods were those laid by females caught on a brood and recaptured on another brood in the same year, either in the same nesting-site or in a different one; (2) *Second* broods included those raised by a female that had been previously captured on a different brood in the same year. Broods for which the female was not captured on a first breeding attempt but for which the laying date matched with identified second broods were also assigned as second broods based on the bimodal distribution observed in laying dates (Fig. 5, Fig. S1). In some rare cases, females captured during early incubation but late in the season showed distinctive marks of previous breeding in the same year (general aspect of the brood patch indicating a previous incubation in the same year); (3) *Replacement* broods were those raised by females that had been previously found breeding in the same year but failed in that breeding attempt; (4) *Single* broods included all broods that did not fall in one of the three aforementioned categories. We may have erroneously assigned some broods as singles in cases where subsequent reproduction of the female went unnoticed, which in turn would underestimate the ratio of double brooding. We also might have assigned some late single brood as seconds. We interpreted results with this uncertainty in mind, particularly those involving fitness differences between single and double brood females. Moreover for analyses that could be sensitive to mistaken assignment of brood type, we replicated the analyses using only data of females caught twice in the same year. We discarded from analyses the replacement clutches, as they were not genuine second broods, as well as clutches that could not be effectively assigned to any category based on the available information.

Proxies of prey abundance and weather conditions

Barn owls typically prey on small mammals in Europe, primarily on microtine voles *Microtus spp.* and wood mouse *Apodemus spp.* (Mikkola 1983; Chausson et al. 2014; Pavluvčík et al. 2015), species that show high among-year variation in abundance. Surplus prey are commonly stored at the nest (Taylor 2004), and we used the number of prey stored, recorded during visits dedicated to chick ringing, as a proxy for prey abundance in the environment. We therefore inspected nesting-sites and identified any prey items stored. We focused on microtine voles (*M. arvalis/agrestis*) and wood mice (*A. sylvaticus/flavicollis*) which together represent 86% of the prey items recorded (54% and 32% respectively, *N* = 1961, hereafter *Microtus* and *Apodemus*). Visual inspection of prey was too cursory to reliably distinguish *Microtus arvalis* from *M. agrestis* and *Apodemus sylvaticus* from *A. flavicollis*. However, prey identification from pellet analysis revealed that *M. arvalis* was by far the most common species preyed upon by barn owls in the study area (*N* = 9792 prey between 2004 and 2014; JS, PS & DC unpublished data), making up 44% of prey items. *M. agrestis* represented only 7% of the *Microtus* prey. Regarding wood mice, *A. sylvaticus* was a slightly more common prey than *A. flavicollis* (58 *vs.* 42%, N = 770 identified wood mice) and wood mice altogether made 14% of prey items found in pellets. Other prey items found at nest included *Arvicola terrestris* (7%), and *Rattus norvegicus*, *Glis glis*, *Myodes glareolus* and *Crocidura spp*. accounting for <1% each. We investigated the temporal variation in the occurrence of both *Microtus* and *Apodemus*, by modelling the arithmetic mean number of prey items stored against Julian date, and found that the peak of *Apodemus* stored at nest occurred earlier during the breeding season compared to the *Microtus* peak (Fig.1). We therefore defined five different measures of prey abundance based on the mean number of prey stored at nest: 1- total prey (*Microtus* + *Apodemus* over the whole season), 2- *Microtus* over the whole season, 3- *Microtus* at mid-season, 4- *Apodemus* over the whole season and 5- *Apodemus* in early season (Fig. 1).

Barn owl populations in Western Europe are sensitive to winter weather conditions (Altwegg et al. 2003). In Switzerland, winter harshness explained 17 and 49% of the inter-annual variation in juvenile and adult survival respectively, with extremely severe winters causing population crashes (Altwegg et al. 2006). In addition, fledglings may be sensitive to weather conditions, particularly at the end of parental care. We used the North Atlantic Oscillation index (NAO) as a proxy for climatic conditions. This index often better explains variation in ecological processes than covariates such as monthly temperature or precipitation (Hallett et al. 2004). We computed NAO index over two distinct periods: 1) winter (December to February, wNAO) and 2) during the month following the end of parental care (post-fledging NAO, NAO_{PF}), typically in June-August (from May to September). We calculated NAO_{PF} for each brood specifically according to its laying date. We determined the month of independence for each brood by adding 15 weeks to the estimated laying date (Bunn et al. 1982). In Burgundy, both summer and winter NAO indices negatively correlate with precipitation, whereas the correlations with temperature are close to zero (Bladé et al. 2012).

Analytical and statistical procedures

First, we evaluated whether the ratio of double broods at the population level was affected by extrinsic factors such as the mean number of prey stored at nest and weather conditions during the previous winter (wNAO). We ran generalised linear models (GLM) for proportion data, using a quasi-binomial distribution of error to account for over-dispersion observed in the data, fitted with no more than two explanatory variables at a time to account for the limited number of years available (N = 17).

Second, at the individual level, we investigated the probability that a female produced a second brood according to the influence of both intrinsic (relative laying date, brood size, female age [yearling *vs*. adult]) and extrinsic factors (wNAO, prey stored at nest [presence or not of *Microtus* stored at nest, and presence or not of *Apodemus* stored at nest]). To identify the factors underpinning among-female variability in the number of broods raised within a same year, we considered a dataset restricted to conditions under which double brooding was recorded. Specifically, we only considered (1) broods from years in which the number of second broods represented >5% of the number of first+single broods. Next, (2) to control for changes in environmental conditions along the season, we discarded clutches laid later than the latest first clutch recorded in the study area (May, 5^{th}). Therefore, the restricted data set only included clutches from years when double brooding was common and laid within the range of dates in which we observed first clutches in these years, in order to ensure we detect only relevant factors associated with double-brooding. We fitted generalised linear mixed models (GLMM) to predict the likelihood of a female producing one or two broods using a binomial distribution of error. We tested female identity, years, zones and female identity nested within zones for the random structure.

Third, we evaluated the following individual characteristics as predictors of fledgling recruitment probability: brood type (single, first, second), relative laying date and its quadratic term to account for possible penalties for very early broods, rank (nestling order within brood), chick body condition at ringing and brood size. In addition, we included extrinsic factors related to environmental conditions experienced in the birth year: ratio of second broods in the whole study area, arithmetic mean number of prey stored at the nest (*Microtus*, *Apodemus*, *Microtus* + *Apodemus*), and the two NAO indices. To prevent bias in recruitment rate estimates due to the possible influence of laying date, brood type or population density in offspring dispersal (Altwegg et al. 2003; Huffeldt et al. 2012), prior to analyses we assessed the correlation of post-natal dispersal distance (log transformed) with relative laying date (linear and quadratic), brood type and number of nest-boxes occupied (as a proxy of population size). Fledglings born during the last two years of the study were removed from the analysis as the average age at first breeding was 1.75 yr (± 1.22 SD; median age = 1 yr). We fitted GLMMs using a binomial distribution of error and female identity, years and zones were tested for the random structure.

Fourth, we calculated female lifetime reproductive success as the total number of fledglings (lifetime fledgling production, LFP), and total number of offspring recruited in the study area (LRP). We discarded females breeding before 1998 or still breeding in any of the last two years of the study as their LFP and LRP estimates could be incomplete, as well as breeders undetected in more than 33% of their known breeding lifespan (*i.e.* undetected in more than one year, assuming skipping reproduction for 2 years or more is unlikely given demographic parameters estimated from our data [mean breeding lifespan= 1.51 ± 1.04; see also Bunn et al. 1982]). To assess possible negative effects of double breeding on female survival, we compared next year return probabilities of single/double brooding females using binomial GLMMs with female identity and zone as random factor. Female fidelity to breeding sites among years is high (Mikkola 1983), yet to preclude biases in LFP and LRP estimates we assessed the influence of single/double brooding and annual number of breeding events detected (divided by the number of nesting sites monitored to account for changes in monitoring effort) on post-breeding dispersal (Altwegg et al. 2003). We assessed the influence of breeding lifespan (number of years from the first to the last breeding event recorded) and the number of years with ≥5% of double broods experienced by each female, the latter measuring environmental conditions experienced by females during their lifespan. We fitted GLMs using a negative binomial distribution of error.

Finally, we investigated intergenerational effects by assessing whether female recruits originating from different brood types showed differences in brood size during their first breeding event and in lifetime reproductive success based on fledglings (data on recruits in this case were too sparse to derive LRP but note that LFP was positively related to LRP; β = 0.113 ± 0.008, $P < 0.001$, $N = 771$, $R^2 = 0.237$, Poisson GLM). We used centred brood sizes as response variable, to control for among year variation in productivity, and fitted GLMMs with Gaussian distribution of error with year and zones tested for the random structure. We analysed variation in LFP or LRP using GLMs with a negative binomial distribution of error.

We ran statistical analyses in R 3.2.4 (R Development Core Team 2016) using the libraries *lme4* (Bates et al. 2015) and *nlme* (Pinheiro et al. 2016). We performed model selection for the fixed effects according to a stepwise procedure by deleting variables with the highest *p*-values, from the most complete model, until we achieved no reduction in AICc (Akaike Information criterion adjusted for small sample size; Burnham and Anderson 2002). When dealing with the ratio of double broods at the population level, we handled over-dispersion in the data using a quasi-binomial distribution of error, thus precluding the calculation of AICc. In this case, we took extra care when interpreting the results as sample size was low (N = 17 years) and only highly significant relationships were considered ($P < 0.001$; Crawley 2007). To select the best random effect model structure, we ran models with alternative random structures fitting the fixed-effect component with all covariates and selected the best one based on AICc (Zuur et al. 2009). We scaled explanatory covariates before analysis (except categorical ones) to compare their relative strength. We obtained the proportion of deviance explained by a model (R^2) using the *piecewiseSEM* package (Lefcheck 2015), which implements the approach developed by Nakagawa and Schielzeth (2013) to estimate R^2 for GLMs and GLMMs. Marginal R^2 describes the proportion of variance explained by the fixed factor component of the model alone, while conditional R^2 indicates the total variance explained by both the fixed and random components of the model together. We report both R^2 when appropriate. We present descriptive statistics as arithmetic mean ± 1 SD and modelled effect size (β) as mean ± 1 SE.

Results

Variation in the occurrence of double brooding at population and individual levels

Between 1998 and 2014, we recorded 2187 breeding events, among which 2012 were classified as single (N = 1529), first (N = 163) or second broods (N = 320). Annual number of breeding events greatly varied from year-to-year (mean = 124 ± 69, from 261 in 2012 down to 4 in 2013). The ratio of double broods (number of second broods /number of single and first broods) varied annually from zero (in four years) to 87% (in 2014; mean = 18 ± 26%, Fig. 2). The interval between the initiation of first and second broods was on average 98 ± 14 days (range: 55-134, N = 134 instances with females identified on first and second broods). Weather conditions in the preceding winter (wNAO) were unrelated to the ratio of double broods. In contrast, several measures of prey stored at nest (annual arithmetic mean of number of prey items stored at nest: *Microtus* [β = 2.69 ± 0.62, P < 0.001], *Microtus* mid-season [β = 1.17 ± 0.24, P < 0.001], *Microtus* mid-season + *Apodemus* early-season [$\beta_{Microtus}$ = 1.21 ± 0.09, P <0.001, $\beta_{Apodemus}$= 0.92 ± 0.20, P <0.001], N = 17 in all cases) positively correlated with the ratio of double broods (Fig. 3). However, annual ratio of double broods did not correlate with numbers of *Microtus* stored at nest early in the season ($\beta_{Microtus}$ = 0.82 ± 0.74, P = 0.28). Similar correlations were obtained when using only second broods for which females were captured twice (*Microtus* mid-season + *Apodemus* early-season [$\beta_{Microtus}$ = 1.17 ± 0.20, P < 0.001; $\beta_{Apodemus}$= 1.27 ± 0.52, P = 0.03]).

At the individual level, early breeding females were more likely to breed twice (Table 1, Fig. 4). Females who produced larger broods had a reduced probability of double brooding as well as yearling females. Regarding extrinsic factors, the occurrence of *Apodemus* (presence/absence) stored at nest was associated with a slightly higher probability of double brooding, while the presence of *Microtus* early in the season did not (Binomial GLMM; β = 0.15 ± 0.29, P = 0.61). Controlling for laying date and brood size (fixed at their average value), the probability of double brooding for a yearling female increased from 0.127 to 0.191 if it had at least one *Apodemus* stored in her first nest, while the same probabilities for an adult female increased from 0.198 to 0.285, respectively. Note that these two effects were only marginally significant (P < 0.1; Table 1). All the results are based on models including only year as random factor (including female identity did not improve models).

Fledgling recruitment probability

Out of 8157 offspring that fledged over the 17 years of study, 326, including males and female offspring (159 females, 162 males and 5 undetermined), were recruited in the study area (4 %). Fifty three of 644 (8.2%) fledglings from first broods recruited, compared to 233 of 6210 (3.8%) and 40 out of 1203 (3.3%) from single and second broods, respectively. Overall, fledglings from early broods in years with higher mean number of prey stored at nest and favourable weather conditions post-fledging were more likely to recruit. Brood type *per se* did not affect recruitment probability (β_{single} = -0.000 ± 0.190, P = 0.99: β_{second} = 0.702 ± 0.427, P = 0.10). However, as first broods were laid earlier, fledglings from first broods had higher recruitment probabilities as a consequence of earlier relative laying date (Fig. 5). While controlling for all the other covariates, by keeping them at their average value, the model predicted that offspring from clutches laid on the average laying date had a recruitment probability of 0.036 (± 0.016), while those from clutches laid 20 days before/after the average had recruitments probability of 0.043 (± 0.019) and 0.027 (± 0.012), respectively. Post-natal dispersal of recruits (10.8 ± 8.8 km, range: 0.49-52.6, N = 208) is unlikely to bias LFP and LRP calculation as it was not related to relative laying date (linear: β = 0.014 ± 0.054, P = 0.79, N = 208; quadratic β_1 = 0.020 ± 0.056, P = 0.724, β_2 = -0.028 ± 0.069, P = 0.69, N = 208), brood type (difference in dispersal of offspring from single and second broods compared to offspring from first broods: β_{single} = 0.087 ± 0.138, P = 0.53, β_{second} = 0.062 ± 0.184, P = 0.74, N = 208) or annual number of nest-boxes occupied (β = -0.041 ± 0.066, P = 0.54, N = 208). Post-natal but not post-breeding dispersal of barn owl has been reported to associate with coloration (van den Brink et al. 2012). We did not account for coloration and that could influence our LRP estimates, yet post-natal dispersal distances in our study were similar to these reported by van den Brink et al. (2012; 10.8 and 9.6 ± 0.6 km respectively) suggesting we were able to detect recruits of both color morphs. In addition, as post-natal dispersal distance was not correlated with laying date or brood type, it does not seem probable that putative differences on dispersal associated to color are correlated with brood type and influencing our results.

Regarding the other intrinsic factors, owls from large broods had a reduced recruitment probability, whereas rank and chick body condition had no effect. For extrinsic factors, weather conditions experienced during the first months of life had a positive effect on recruitment, with a stronger effect of NAO_{PF} compared to wNAO. This indicates that survival of juvenile barn owls was favoured by comparatively drier weather conditions in the month of independence, typically between June and August, and during the following winter. Prey stored at nest also positively affected recruitment probabilities. We found positive effects of the number of stored *Microtus* recorded at mid-season and, to a lesser extent, of stored *Apodemus* early in the season (Table 2). When the number of *Microtus* increased from 0.59 (mean) to 1.03 (mean + 1 SD), average recruitment probability increased from 0.033 to 0.055, while at a *Microtus* abundance of 0.15 (mean − 1 SD), recruitment probability went down to 0.019. As mean number of *Microtus* stored at the nest was also related to the probability of double brooding, it accounted for part of the difference in recruitment between first and single broods. Indeed, in years with relatively high numbers of stored prey items, double brooding females and fledglings from early broods (typically first broods) experienced favourable environmental conditions. By contrast, in years when prey stored in the nest were scarce, females were much less likely to double brood. In addition offspring from early broods (typically single broods) in low food years were less likely to recruit.

Lifetime reproductive success of female barn owls

Lifetime reproductive success of females with complete monitoring and estimate from the count of fledglings (LFP) or recruits (LRP) were available for 771 females. The number of breeding years over a female's lifetime averaged 1.60 ± 1.18. Observed breeding lifespan was significantly longer in females that double brooded at least once (2.5 ± 1.79) compared to those that were never observed double brooding (1.45 ± 0.97; Poisson GLM: $\beta = 0.57 \pm 0.07$, $P < 0.001$). Females that double brooded at least once in their lifetime produced on average 2.5 times more fledglings than those who did not (LFP: 15.6 *vs.* 6.2; Fig. 6a). This difference was even more pronounced when considering the number of recruits (LRP: 0.96 *vs.* 0.24; Fig. 6b). Females with longer lifespans and that also experienced more favourable breeding seasons had higher LFP and LRP. The differences observed between double- and single-brooders remained highly significant even after controlling for lifespan and environmental variability (Table 3). Post-breeding dispersal was correlated to the annual number of breeding events detected. Females breeding in years with scarce breeding events recorded tended to disperse further for the next breeding season (Gaussian GLMM for log transformed post-breeding dispersal distance [+1 to avoid NAs] with female identity as random factor; $\beta = -1.78 \pm 0.87$, $P = 0.043$, $N = 490$). However, the difference in mean predicted dispersal distance between the years with lowest and highest number of breeding events recorded was < 20 metres (Fig. S3), suggesting the displacements respond rather to differences in availability of alternative nest boxes within nesting sites than to breeding dispersal outside the area.

We found no evidence of a negative effect of double brooding on female return rate. Indeed, the return rate of double-brooding females was significantly higher than of single-brooders ones (Binomial GLMM with female identity nested in zone as random factor $\beta = 0.44 \pm 0.16$, $P = 0.006$, $N = 1526$). Finally, our LFP and LRP estimates did not appear to be influenced by our assignment of second broods based on laying date. We repeated the analyses classifying as double brooding only these females captured twice in the same year and reclassifying as single brooding these females captured only on what we considered to be their second brood, and all reported differences in LFP and LRP were still significant (Table S1). To assess whether these differences in LFP and LRP were only driven by extra offspring from second broods, we repeated the analyses including only offspring from first and single broods. Double brooding females tended to produce more fledglings even when considering only offspring from first and single broods, compared to females never recorded as double brooders, suggesting a difference in territory and/or individual quality between these two categories. When accounting for females' breeding lifespan and environmental variability in LFP, the best model retained double brooding as a predictor variable, although it was no longer significant. When considering recruits however, females that double brooded at least once during their lifetime produced more recruits (LRP) from their first/single broods than other females, and this difference remained when accounting for females' breeding lifespan and environmental variability (Table 3).

Intergenerational effects

Controlling for laying date, female recruits born from first broods produced 1.47 ± 0.49 additional fledglings during their first breeding attempt compared to females originating from a single brood ($t = -4.52$, $P < 0.001$) and 1.76 ± 0.68 additional fledglings compared to a female originating from a second brood ($t = -4.35$, $P < 0.001$; $N = 88$ female recruits from single broods, 21 and 14 from first and second broods, respectively). When considering LFP of those females, however, we did not find support for differences among brood types (AICc = 0.38 unit higher than the null model) with a production of 9.4 ± 7.3, 8.3 ± 5.6 and 6.6 ± 2.4

fledglings respectively for females originating from single, first and second broods. Data were too scarce to conduct the analysis based on LRP.

Discussion

We documented a large among-year variation in the occurrence of double brooding in a barn owl population of north-eastern France. The ratio of double-brooding events in a year was positively related to the mean number of prey stored at the nest, possibly related to prey abundance in the field. In years with double brooding events, early-laying females were more likely to undertake a second brood, possibly reflecting their mate’s ability to exploit wood mice as alternative prey earlier in the breeding season. Fledglings born from first broods had on average a higher recruitment probability compared to fledglings from single or second broods. This difference, however, mainly arose as a consequence of variation in laying date as fledglings born at a similar date in the same year recruited with a similar probability irrespective of brood type. Overall, female barn owls that managed to double brood at least once over their lifetime produced more than twice as many fledglings and recruits compared to females that did not. We did not detect any evidence of cost of double-brooding for breeding females nor for their offspring.

Proximate factors underpinning the occurrence of double brooding

Double brooding was on average achieved by 18% of the female barn owls. However, there was much among-year variation around this average, probably reflecting variation in prey abundance. Over 17 years, four years had no record of double brooding and in three years more than 60% and up to 87% of females bred twice, in line with other studies (Husby et al. 2009).

At the population level, the annual mean number of *Microtus* voles stored at the nest was the main factor explaining inter-annual variation. Double brooding was more common in years when the mean number of voles stored at the nest peaked. Years with the highest ratio of double broods (≥ 60% in 2007, 2010, 2014) did not coincide with the highest number of breeding pairs. The latter is further limited by winter harshness affecting owl survival, as well as breeding success (and thus cohort size) in the two preceding years (Altwegg et al. 2003). Interestingly, these three years coincided with the highest densities and breeding success by a another vole predator, the Montagu's harrier *Circus pygargus* survey in Champagne (Millon et al. 2002; A. Millon unpublished data). This migratory raptor is known to exhibit a direct numerical response to the abundance of common voles in French cereal landscapes (Millon and Bretagnolle 2008). The number of prey stored at nest, averaged across all nests within a year, could be viewed as a proxy of prey abundance in the field, although it is likely also affected by e.g. the timing of nest visits during the day, brood size and the age of chicks. To assess the assumed relationship, we correlated the annual mean number of voles stored at nest with an index of common vole abundance derived from a survey of 30 grasslands across the study area monitored between 2009 and 2018 (authors' unpublished data, following methods described by Lambin et al. 2000). We found a positive, though marginally non-significant, relationship (β = 0.033± 0.017, T value = 1.965, df = 8, P = 0.085, R^2= 0.33, N = 10).

In years with higher mean numbers of prey stored at nest coinciding with the occurrence of double brooding, the probability of a female undertaking a second brood decreased with first brood laying date and brood size, yet increased marginally with the occurrence of *Apodemus* stored at the nest and female age. The influence of laying date on the individual probability of double brooding is recurrently reported across species (Taylor 2004; Nagy and Holmes 2005a; Hoffmann et al. 2015; Béziers and Roulin 2016). This pattern is related to obvious temporal constraints for the breeding season to match the timing of resource availability

(Husby et al. 2009). However, while the resource availability constraint is clear for species preying on insects with marked seasonality (Nagy and Holmes 2005b; Husby et al. 2009), *Microtus* can still be available in high quantities during autumn (Delattre et al. 1999) and *Apodemus* densities typically increase from August to November, with an overwinter plateau (Montgomery 1989). However, post-harvesting ploughing of annual crops (wheat, barley, rapeseed) early in the summer may drastically reduce the availability of voles for predators such as barn owls.

Marked seasonal declines of food may not be the only reason for the temporal limit to second broods in the barn owl. Barn owls fledging late in the season certainly suffer from a reduced period to develop hunting skills before facing harsher weather and competition with conspecifics to secure a territory. In years of high mean numbers of vole stored at nest, females that had *Apodemus* prey stored at their nest were slightly more likely to breed twice in that year (an increase of 4-6% in double brooding probability compared to females that did not). *Apodemus* usually reach their peak in abundance in late autumn, decrease in spring, and remain low during summer (Montgomery 1989). This suggests that females breeding in territories with higher prey diversity might be able to lay earlier and therefore were more likely to undertake a second reproduction. Moreover, at least in high vole years, females that started breeding early experienced higher food abundance at mid-season when their first breeding cycle ended (Fig. 1), facilitating the initiation of a second brood. This can be achieved with the same male after the completion of the first brood, or following nest (and mate) desertion and starting a second brood with a different mate in another nest-site (Eldegard and Sonerud 2009; Béziers and Roulin 2016). Colour dimorphism in the barn owl has been associated with different morphology and prey preference (*Microtus* vs. *Apodemus*; Roulin 2004, Charter et al. 2014). In that context, females paired with males that preferentially prey on *Apodemus* could benefit from the peak of this resource to start breeding earlier. Unfortunately, we caught too few males to properly test this hypothesis.

Yearling females were slightly less likely to double brood compared to adults, under similar environmental conditions (a difference of 4-6% in double brooding probability). This adds to the abundant literature documenting the improvement of breeding success with age in birds (Forslund and Pärt 1995). In contrast to our findings, most previous studies have found no effect of brood size on the female probability of double brooding (Nagy and Holmes 2005a; Béziers and Roulin 2016; altough the latter found an effecto of brood size on male probability of doible brooding), or even positive effects (Hoffmann et al. 2015). A possible explanation for such results is that females might be less reluctant to bequeath small broods to their mates. The smaller the brood indeed, the easier for single males to cope with food supply. It is noteworthy that small brood size has been identified as a cause of divorce between successive years in this species (Dreiss and Roulin 2014).

Fitness consequences of double brooding

While using a different, arguably more relevant, metric we found no support for the contention by Béziers and Roulin (2016) that double brooding in barn owls is traded-off with offspring quality. These authors found that offspring from first broods have lower body condition than offspring from single broods, a pattern also reported for jackdaws (*Corvus monedula*; Verhulst et al. 1997). In our study population, fledglings reared in first broods recruited with the same probability that offspring from single broods with the same laying date, and their subsequent breeding performance and LFP was similar. Here we found no evidence for intergenerational trade-offs. Moreover, from a breeding female perspective, double brooding resulted in higher lifetime production of recruits. This is consistent with a study on hoopoes, where double brooding females produced 2.6 times more recruits than single-brooding females over their lifetime (Hoffmann et al. 2015). We found that double-brooding female barn owls had longer breeding lifespans. They also produced more recruits than single-brooding females, even after controlling for breeding lifespan and the number of favourable breeding seasons experienced. Furthermore, this difference in the number of recruits produced held when we considered only recruits from first and single broods. This suggests that double brooding is highly rewarding in terms of fitness as we failed to find any costs in terms of e.g. return rate and breeding lifespan. It is important to note here that the uncertainty around the assignment of brood types did not affect our interpretations, as the observed difference is in favour of the less detectable double-brooding event. Indeed, any miss-assignment of first broods as single broods would result in smaller differences of fitness parameters between brood types. Another bias in fitness estimate could arise if offspring of different brood types, and single- or double-brooding females, differed in dispersal propensity. Notwithstanding that we were unable to detect dispersal data outside our study area, both its spatial scale and the fact that dispersal distances recorded within it did not differ between the aforementioned categories, suggesting our estimate of lifetime recruit production are unlikely to be strongly biased.

Most of the differences in individual probability of double brooding and in offspring probability of recruitment arose from laying date with no detectable effect of brood type *per se*, despite a slight penalization for very early broods (Fig. 5). This is in accordance with observational and experimental results suggesting that the observed seasonal decline in fitness is the result of laying date, with territory or parental identity/quality contributing little to the covariance between laying date and recruitment (e.g. Van de Pol and Verhulst 2006, Pärt et al. 2017). An interesting question then arises: why do not all females double brood when conditions are favourable? Although proximate causes of individual variation in laying date are poorly known, a meta-analysis revealed that experimentally enhanced food provision in birds mainly results in advanced laying dates, with increase in brood size showing smaller effect size (Ruffino et al. 2014). Among-female variation in laying date might be related to heterogeneity in individual and/or territory quality, and as a consequence may be a proxy of quality itself. Male barn owls provide most of the food during the early breeding stages (from courtship to early brooding) and male hunting skills provisioning rate might be an important factor influencing laying date and probability of double-brooding (Taylor 2004; Durant et al. 2013). Unfortunately, low capture rates for adult males in our study did not allow us to include male identity or characteristics in our analyses. Thus, females laying earlier broods could be higher quality individuals or paired with higher quality males exploiting available resources more efficiently and/or occupying territories with higher food abundance. We predict that such females will be in better condition, be capable of starting breeding earlier, and more capable of laying a second clutch, especially when, or if, *Microtus* abundance is high.

In conclusion, we do not consider single- and double-brooding females as displaying genuine alternative breeding strategies. In the case of barn owls, both the fact that double-brooding females enjoyed much higher fitness than single-brooded ones, with no evidence for costs to parents or their offspring, and that in years of high prey abundance the proportion of double-brooding exceeded 50%, suggest that all females have the potential to breed twice in a year. Environmental conditions, and prey abundance particularly, are driving breeding decisions in a predator, such as the barn owl, showing high reproductive rates.

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Table 1. Results of the best binomial GLMM investigating the probability of a female barn owl to breed twice in a year, considering only clutches laid before the 5th of May in years with at least 5% of double broods (*N* = 705, marginal R^2 = 0.14, conditional R^2 = 0.41). Explanatory variables retained in this model were relative laying date, female age (yearling or ≥ 2yr-old), occurrence (yes/no) of *Apodemus* stored at nest and brood size. Explanatory variables were scaled such that effect sizes are comparable between each other. The model included year as a random factor.

Explanatory variables	Estimate	SE	*z*	*P*
Intercept	-1.40	0.46	-3.03	0.002
Rel. laying date	-0.69	0.12	-5.61	< 0.001
Age (yearling)	-0.53	0.28	-1.88	0.060
Apodemus (yes)	0.48	0.26	1.83	0.067
Brood size	-0.29	0.11	-2.58	0.010

Table 2. Results of the best binomial GLMM investigating variation in the recruitment probability of fledgling (N = 8157; R^2_{marg} = 0.15; R^2_{cond} = 0.231). Explanatory variables retained were relative laying date, quadratic term of relative laying date, mean number of *Microtus* stored at nest in mid-season (*Microtus*-mid), mean number of *Apodemus* stored at nest early in the season (*Apodemus*-early), NAO index for the first month post-fledging (NAO_{PF}) and NAO index of the following winter (wNAO). Explanatory variables were scaled. The model included zone nested in year as random effects. Rel. laying date stands for relative laying date

Explanatory variables	Estimate	SE	*z*	*P*
Intercept	-3.85	0.26	-14.82	<0.001
Brood Size	-0.25	0.06	-3.96	<0.001
Rel. laying date	-0.42	0.07	-6.15	<0.001
Rel. laying date Quad.	-0.24	0.09	-2.76	0.006
Microtus-mid	0.55	0.07	8.16	<0.001
Apodemus-early	0.14	0.06	2.30	0.021
NAO_{PF}	0.45	0.07	6.60	<0.001
wNAO	0.32	0.05	6.182	<0.001

Table 3. Results of the best negative binomial GLM comparing female lifetime reproductive success, based on count of offspring (LFP) or recruits (LRP), between females detected to breed twice in a year at least once in their lifetime (DB) *vs.* those that were never detected to do so (N = 771 females; 110 of them categorised as DB). Explanatory variables also retained in these model were breeding lifespan, *i.e.* the number of years between first and last detected breeding (Lifespan), and the number of favourable breeding seasons in lifespan (*i.e.* years in which the ratio of double broods exceeded 5%; Fav. breed. Season). Outputs of two distinct models are presented here: one considering offspring from any brood type and one considering only offspring form first and single broods. Explanatory variables were scaled.

	Explanatory variables	**Lifetime fledgling production**				**Lifetime recruit production**			
All offspring		Estimate	se	*z*	*P*	Estimate	se	*z*	*P*
	Intercept	1.82	0.02	107.26	<0.001	-1.47	0.09	-16.68	<0.001
	DB	0.54	0.04	13.80	<0.001	0.83	0.18	4.55	<0.001
	Lifespan	0.30	0.01	20.87	<0.001	0.34	0.07	4.98	<0.001
	Fav. breed. season	0.04	0.02	2.28	0.023	0.17	0.08	2.04	0.042
Only first/single broods									
	Intercept	1.34	0.02	57.42	<0.001	-1.44	0.09	-16.60	<0.001
	DB	0.07	0.04	1.59	0.113	0.41	0.19	2.13	0.034
	Lifespan	0.27	0.01	23.79	<0.001	0.37	0.07	5.47	<0.001
	Fav. breed. season	0.05	0.02	2.54	0.011	0.170	0.08	2.09	0.037

Figure 1. Mean number of common vole (green circles) and wood mouse (blue circles) stored at nest, as a proxy of prey abundance, according to barn owls' laying dates. Vertical dashed lines indicate cut-offs between early, mid and late breeding season used in analyses. Size of the circles are proportional to sample size (range: 1 – 225). Lines show values predicted by the best model (linear, quadratic, exponential and logarithmic functional relationships were tested for each prey species; negative binomial GLMMs assessed using year as random factor: common vole quadratic function [min. ΔAICc = 6.4]: β = 2.05 ± 0.63, P = 0.001, β_{quad}= -0.77 ± 0.25, P = 0.002; *Apodemus* log function [min. ΔAICc = 0.3]: β = -1.80 ± 0.19, P = 0.001, N = 2221).

Figure 2. Temporal variation in the number of breeding events of barn owls per brood category (single: grey bars, first: white bars, second: black bars). Note that the second brood of a female can be identified without the observation of the first one, based on laying dates (see Methods).

Figure 3. Time-series for the ratio of double brooding events in the barn owl (grey polygon, number of second brood / [number of first + single broods]) and the mean number of prey items stored at nest (*Microtus*: solid black line & open dots; *Apodemus*: grey dotted line and crosses).

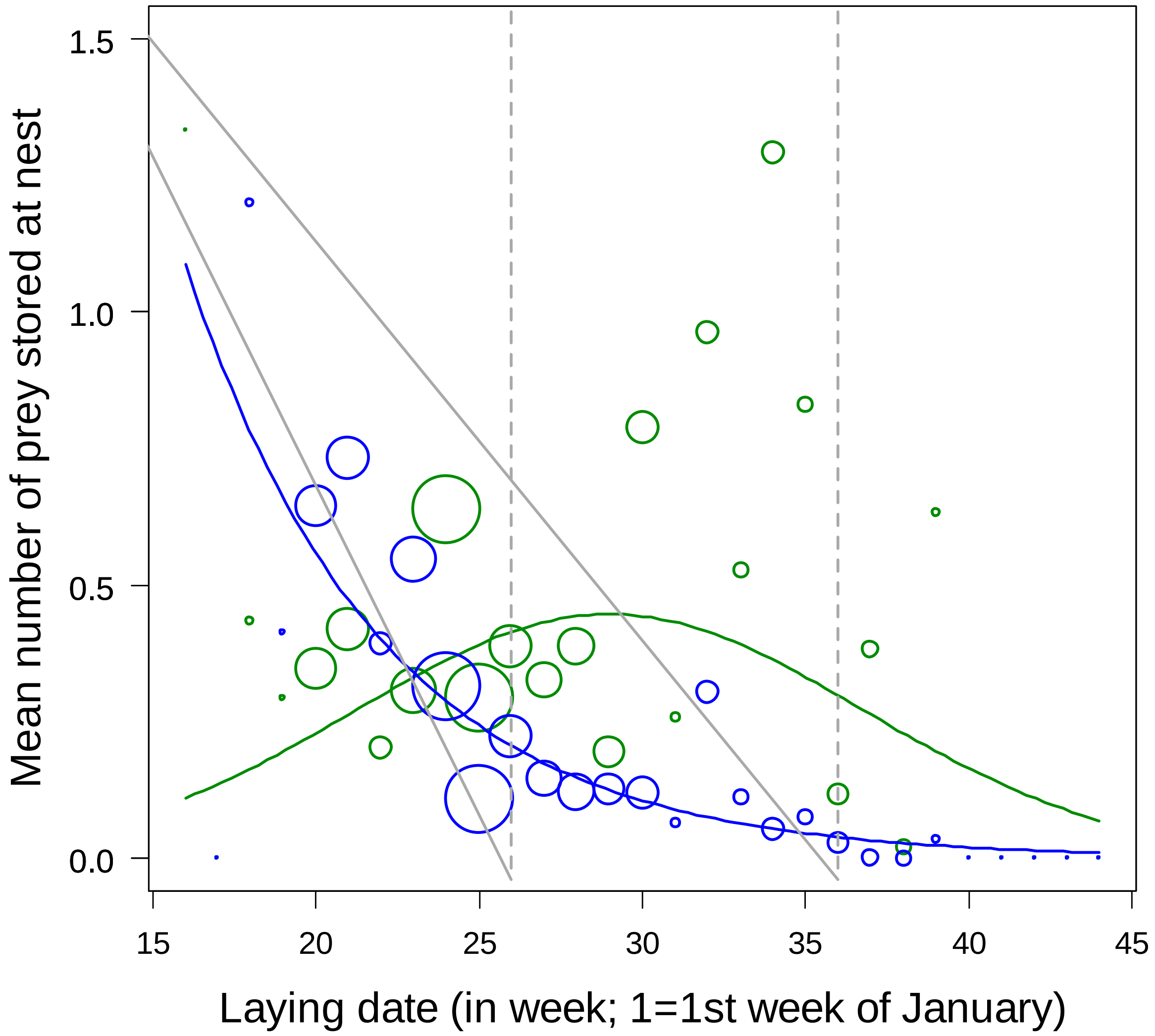
Figure 4. Probability of double brooding for female barn owls in Burgundy according to relative laying date. The analysis was based on a dataset restricted to females laying not later than May 5th, *i.e.* the latest date recorded for a first brood, and to years with ≥ 5% of second broods recorded. Black and grey lines are for females having at least one or no *Apodemus*

stored at their nest, respectively. Solid and dotted lines are for adult (≥2 yr-old) and yearling females, respectively. Histogram shows the distribution of relative laying dates, pooled over the whole period. Mean probability of double brooding was 0.20 ± 0.19. The highest bar represents 115 breeding attempts.

Figure 5. Recruitment probability of barn owl's fledglings according to relative laying date. The solid line indicates mean probability from a model accounting for linear and quadratic terms of laying date, brood size, *Microtus* abundance in mid-season, *Apodemus* abundance early in the season, NAO_{PF} and wNAO. Values for these five explanatory variables were set at their average values. 95% confidence intervals are represented with dotted lines. Open circles indicate recruitment probabilities for fledglings with a relative laying date matching the average for, from left to right, first (0.059), single (0.050) and second (0.013) broods. Histogram shows the distribution of relative laying dates for first (purple), single (white) and second (green) broods. Figure is based on model fitted values, in which probability for each fledgling is calculated considering also its particular values for all the other covariates and with zone as random factor.

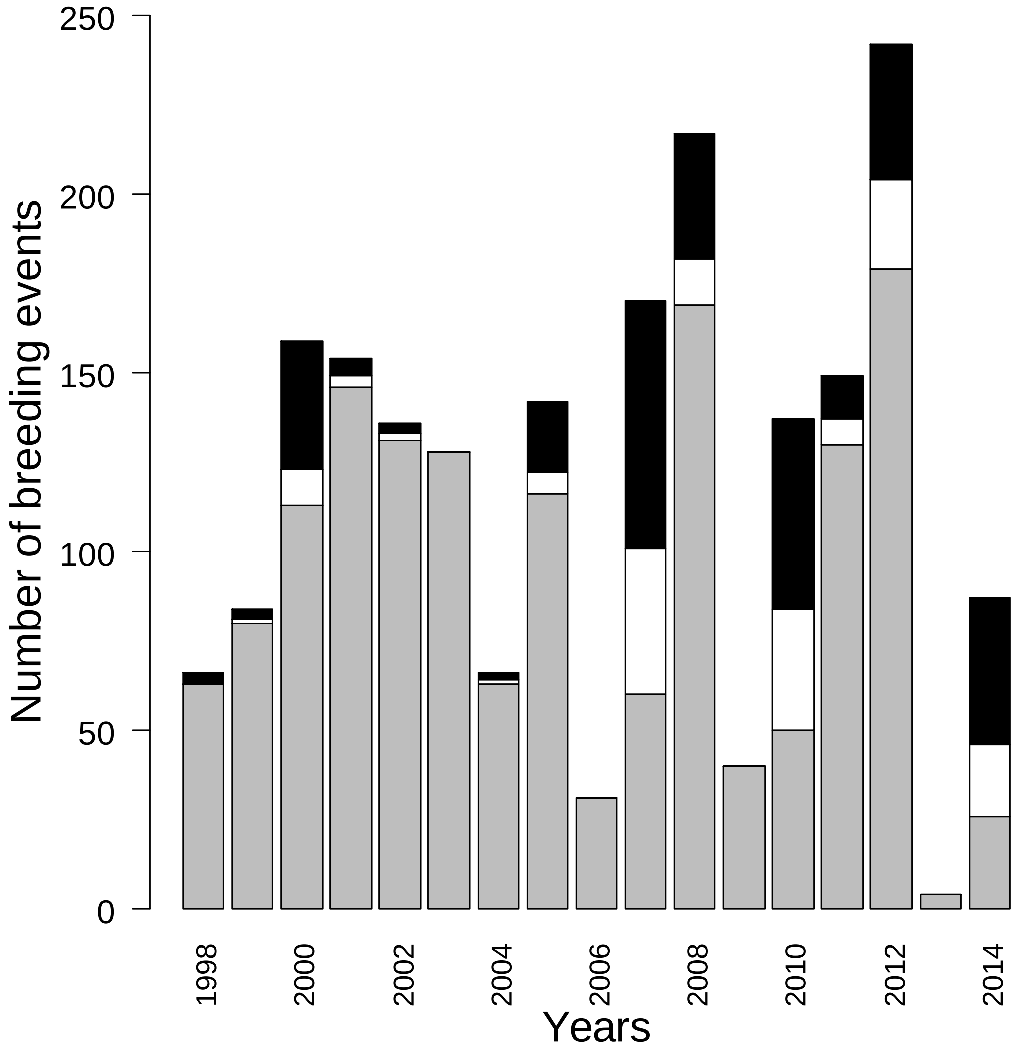
Figure 6. a) Lifetime reproductive success of female barn owls as inferred from the number of fledglings and b) the number of recruits (± SD) according to whether female barn owls have been recorded to breed twice in a year at least once over their lifetime. Hatched area indicate the contribution of first/single broods for double brooding females.

Figure 1.

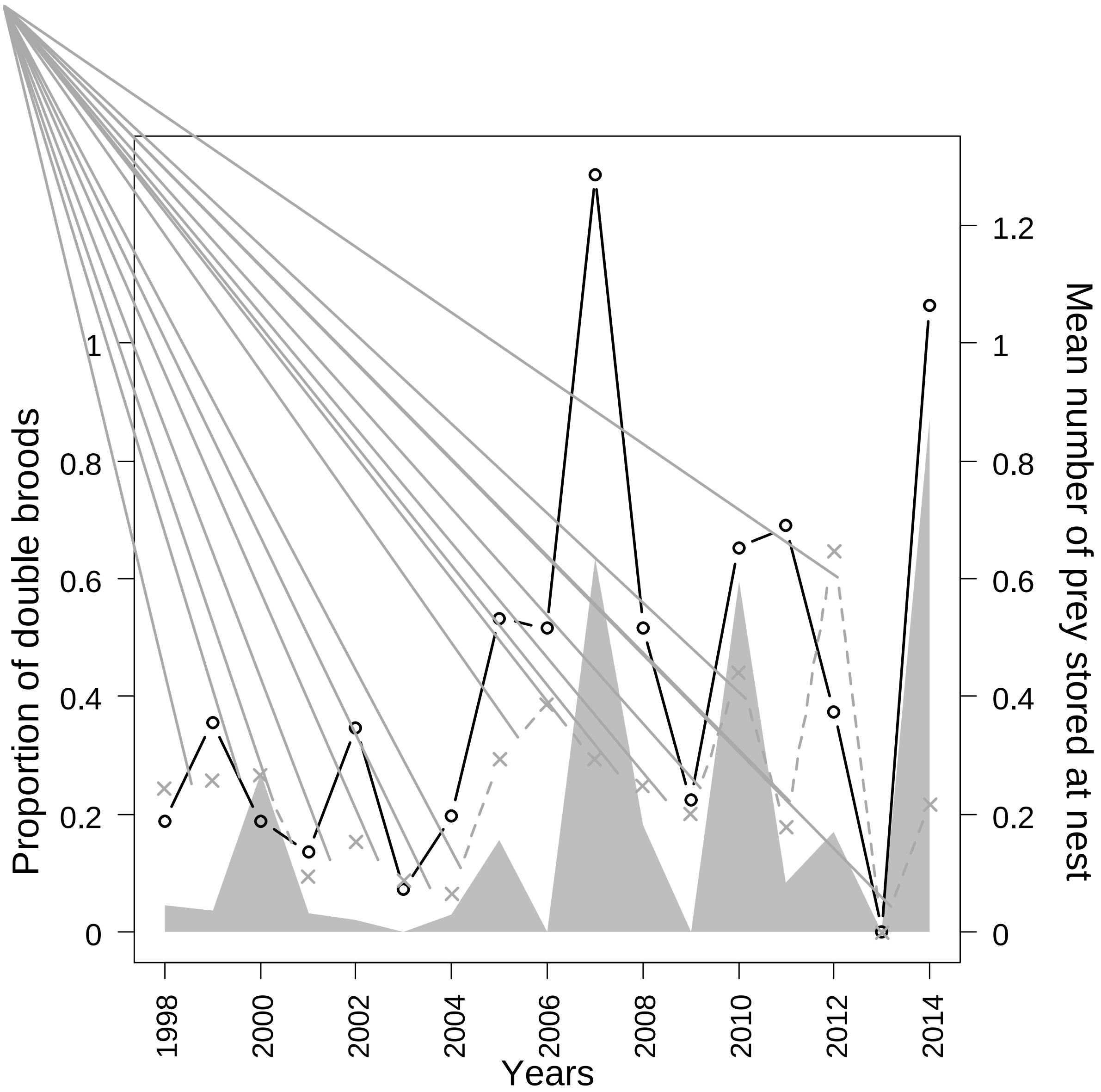


1.5
1.0
0.5
0.0
Mean number of prey stored at nest
15
20
25
30
35
40
45
Laying date (in week; 1=1st week of January)

Figure 2.


250
200
150
100
50
0
Number of breeding events
1998
2000
2002
2004
2006
2008
2010
2012
2014
Years

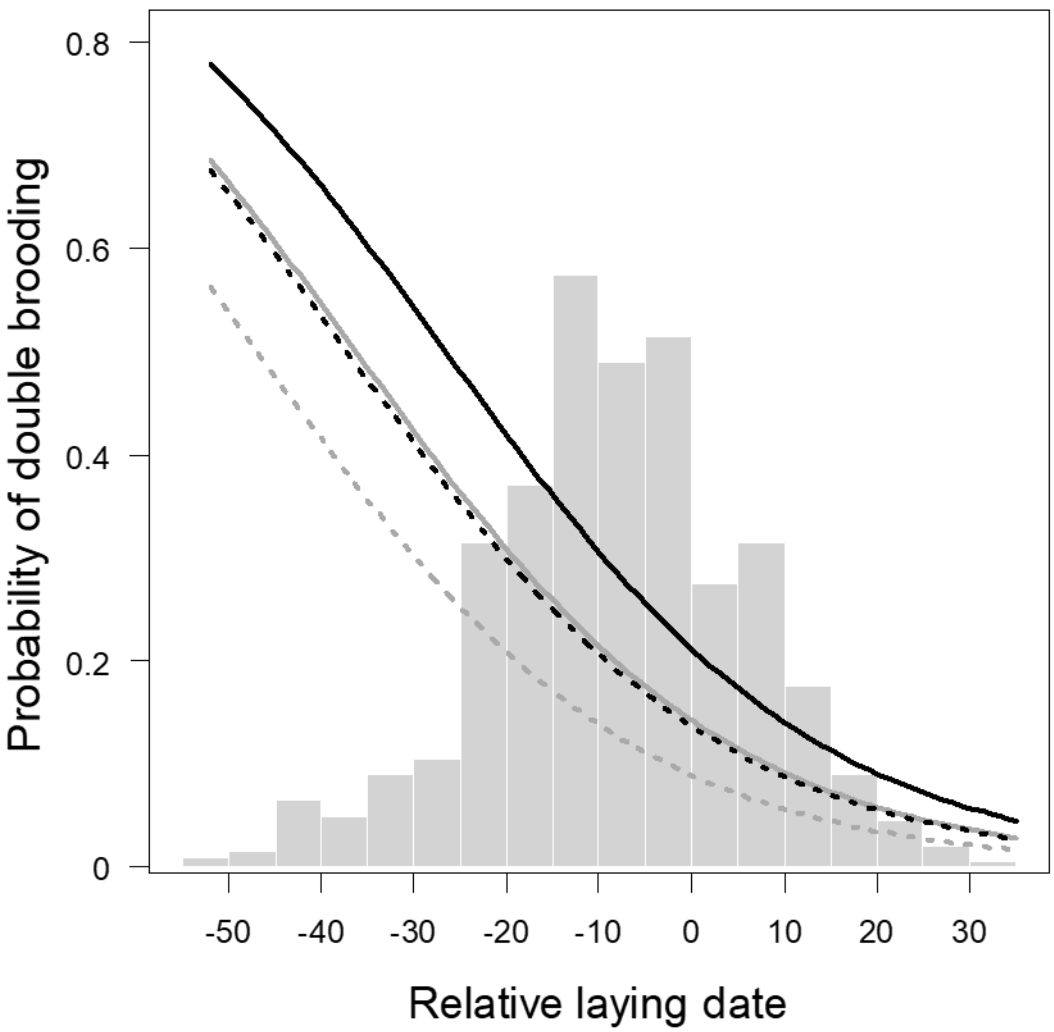
773 **Figure 3.**



774

775

Figure 4.



Probability of double brooding
0.8
0.6
0.4
0.2
0
-50
-40
-30
-20
-10
0
10
20
30
Relative laying date

Figure 5.

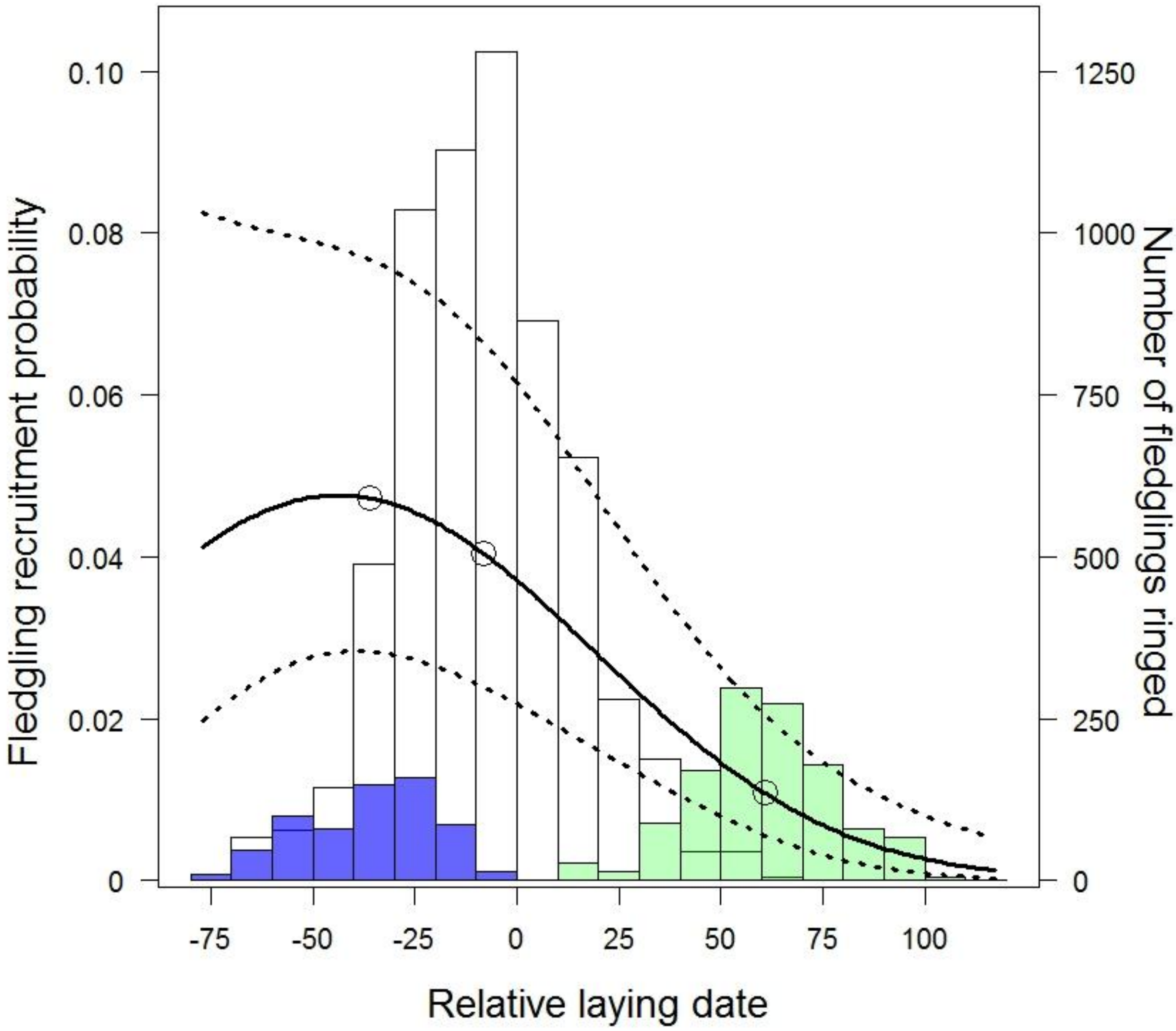
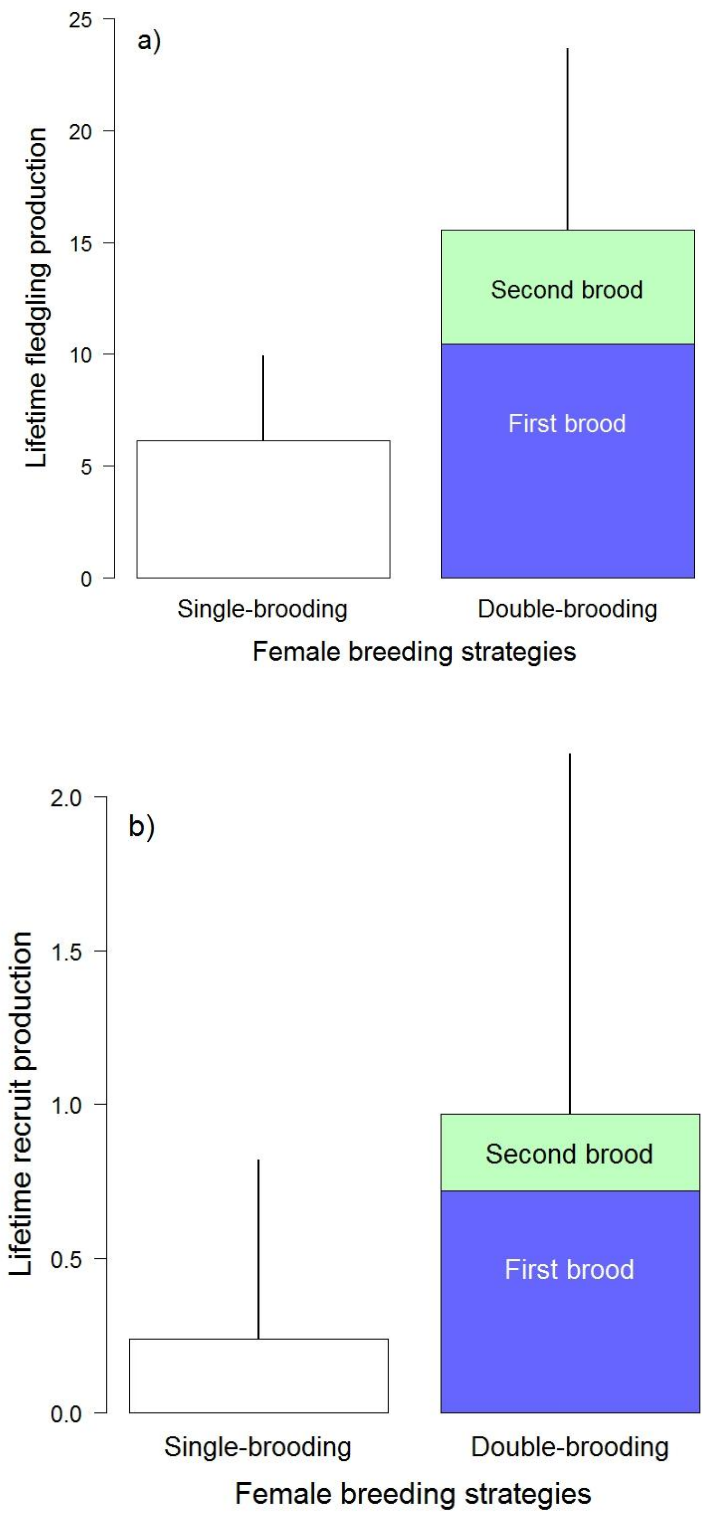

Fledgling recruitment probability
0.10
0.08
0.06
0.04
0.02
0
Number of fledglings ringed
1250
1000
750
500
250
0
-75
-50
-25
0
25
50
75
100
Relative laying date

Figure 6.



a)
Lifetime fledgling production
25
20
15
10
5
0
Second brood
First brood
Single-brooding
Double-brooding
Female breeding strategies
b)
Lifetime recruit production
2.0
1.5
1.0
0.5
0.0
Second brood
First brood
Single-brooding
Double-brooding
Female breeding strategies