

1 **Proximate causes and fitness consequences of double brooding in**  
2 **female barn owls**

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19 **Abstract**

20 Multiple brooding, reproducing twice or more per year, is an important component of life-  
21 history strategies. However, what proximate factors drive the frequency of multiple brooding  
22 and its fitness consequences for parents and offspring remains poorly known. Using long-term  
23 longitudinal data, we investigated double brooding in a barn owl population in France. We  
24 assessed the effects of both extrinsic and intrinsic factors and the consequences of double  
25 brooding on fledgling recruitment and female lifetime reproductive success. The occurrence of  
26 double brooding in the population, ranging from 0 to 87%, was positively related to the number  
27 of rodent prey stored at the nest. Females laying early in the season were more likely to breed  
28 twice and the probability of double brooding increased with smaller initial brood size, female  
29 age and the storage of wood mice at the nest early in the season. Fledglings from first broods  
30 recruited more often (8.2%) than those from single broods (3.8%) or second broods (3.3%) but  
31 this was primarily the consequence of laying dates, not brood type *per se*. Females producing  
32 two broods within a year, at least once in their lifetime, had higher lifetime reproductive success  
33 and produced more local recruits than females that did not ( $15.6 \pm 8.1$  vs.  $6.1 \pm 3.8$  fledglings,  
34  $0.96 \pm 1.2$  vs.  $0.24 \pm 0.6$  recruits). Our results suggests that the benefits of double brooding  
35 exceed costs in terms of fitness, and that within-year variability in double brooding is related to  
36 heterogeneity in individual/territory quality.

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## 40 **Introduction**

41 In order to maximize their fitness, individuals adopt alternative strategies for optimising the  
42 number of offspring that survive until reproduction. In seasonal environments where breeding  
43 occurs only during a restricted period of the year, individuals might nonetheless attempt to re-  
44 initiate reproduction following a first successful breeding event in the same year (Husby et al.  
45 2009). Multiple brooding is a relatively common strategy in vertebrates with fast life histories,  
46 such as small mammals and passerine birds (Erb et al. 2001; Lambin and Yoccoz 2001; Béziers  
47 and Roulin 2016). Producing multiple broods is often a facultative strategy and its frequency  
48 varies greatly among populations, but also among years within a given population (Husby et al.  
49 2009; Béziers and Roulin 2016; Jackson and Cresswell 2017). Such a variation offers the  
50 opportunity to investigate the proximate factors underpinning the alternative strategies and  
51 quantify their relative fitness.

52 Double brooding (*i.e.* producing a second brood after successfully completing one) is  
53 expected to be a rewarding strategy in terms of number of offspring produced annually.  
54 Individuals breeding twice in a year can expect producing almost twice as many offspring as  
55 individuals breeding only once, such as documented in barn owl *Tyto alba* (Béziers and Roulin  
56 2016), Tengmalm's owl *Aegolius funereus* (Korpimäki et al. 2011), hoopoe *Upupa epops*  
57 (Hoffmann et al. 2015), or black-throated blue warbler *Setophaga caerulescens* (Nagy and  
58 Holmes 2005a). However, over an individual's lifetime, attempting double brooding may be  
59 associated with costs that could cancel out the benefits of short-term increased breeding success.  
60 Documented costs include reduced survival of multiple-brooding females (Verhulst 1998) and  
61 reduced body condition of fledglings from first broods due to maternal desertion for the purpose  
62 of initiating a second brood (Béziers and Roulin 2016). Recruitment probabilities of fledglings  
63 from females producing two or more broods could also be lowered compared to fledglings from  
64 a single brood but this has been rarely assessed (but see Hoffmann et al. 2015). Altogether,

65 these costs may reduce fitness gains for parents producing two broods in a year (Verhulst et al.  
66 1997; Eldegard and Sonerud 2009; Husby et al. 2009). In a seasonal environment, the extent of  
67 the period during which resources are sufficiently abundant to allow individuals to reproduce  
68 is a key factor determining the frequency of multiple brooding. Indeed, the date of the onset of  
69 breeding has been repeatedly shown to alter breeding success, with later-breeding individuals  
70 having reduced breeding success (e.g. Verhulst and Nilsson 2008). This temporal decline in  
71 breeding success can be mainly attributed to 1) the date itself, *i.e.* the deterioration of the  
72 environment over the season, 2) the fact that late breeders are of poorer quality, or 3) the fact  
73 that late breeders are constrained to occupy low-quality territories. The date hypothesis has  
74 received most empirical support so far (Verboven and Verhulst 1996; Verhulst and Nilsson  
75 2008; Pärt et al. 2017), although several processes may act together (Browne et al. 2007; Husby  
76 et al. 2009; Hoffmann et al. 2015). The timing of breeding is also relevant for multiple brooding,  
77 with early breeders being more likely to produce more than one brood per season (Béziers and  
78 Roulin 2016).

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

90 consequences of double brooding for parents and offspring, which may shed light on the  
91 evolution and maintenance of multiple brooding.

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

105

## 106 **Methods**

### 107 *Study species, zones & data collection*

108 The barn owl is a medium-sized (ca. 240-350 g) nocturnal raptor whose breeding populations  
109 in the western Palearctic are mostly composed of resident individuals. Clutches contain 4-8  
110 eggs (up to 13) and females can raise two broods a year, exceptionally three (Mikkola 1983).  
111 Between 1998 and 2006, we monitored an average of 280 nesting-sites annually, including 175  
112 nest-boxes and 105 alternative nest-sites in buildings, in six neighbouring zones primarily  
113 across Burgundy and, to a lesser extent, Champagne (north-eastern France), over an

114 approximated total area of 1675 km<sup>2</sup>. We installed more nest-boxes in 2006, resulting in a total  
115 of 370 nesting-sites (295 nest-boxes and 75 alternative nesting sites) monitored annually, with  
116 2-4 visits per site. The first visit in March-April ascertained occupancy. We made subsequent  
117 visits to sites where occupancy was suspected or recorded to assess clutch size and ring  
118 nestlings just before fledging (May-July). We attempted to capture adults during all site visits  
119 by placing a landing net at the entrance of the nest-boxes. We marked nestlings and unmarked  
120 adults with alphanumeric aluminium bands (CRBPO - Museum National d'Histoire Naturelle,  
121 Paris). We weighed chicks using a spring scale (Pesola © 500 g). We used nestling age and  
122 weight to estimate nestling body condition (expressed as the deviation from predicted body  
123 mass according to age and days since estimated hatching date in each year). We revisited later  
124 in the season all sites deemed unoccupied on the first visit to detect second clutches or late  
125 breeding attempts. The proportion of the barn owl population breeding in monitored nesting-  
126 sites was unknown.

127 We defined laying date as the Julian week when the first egg was laid (week 1 = 1<sup>st</sup> week of  
128 January), either deduced from the number of eggs when the clutch was observed before  
129 completion (assuming each egg was laid 2.5 days apart) or using back-calculation from chick  
130 wing length (following Taylor 1993 for age estimation and assuming 32 days of incubation;  
131 Bunn et al. 1982). On average we ringed nestlings when they were  $38 \pm 12$  days of age. To  
132 account for inter-annual variation in laying dates while comparing data over multiple years, we  
133 centred laying dates to the average laying date recorded in each year and used relative laying  
134 dates for the analyses. To characterise how clutches are distributed within a year, we estimated  
135 the average laying date for each year using all the clutches detected, including replacement  
136 clutches ( $N = 93$ ) and those not assigned to any category (their characteristics suggested  
137 replacement broods but we could not ascertain that [ $N = 69$ ]). We assigned breeding birds to

138 two age classes (yearling *vs.*  $\geq 2$  years, hereafter called adult) based on ringing, for birds ringed  
139 as chicks, or according to the moulting pattern otherwise (Taylor 1993).

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

#### 160 *Proxies of prey abundance and weather conditions*

161 Barn owls typically prey on small mammals in Europe, primarily on microtine voles *Microtus*  
162 *spp.* and wood mouse *Apodemus spp.* (Mikkola 1983; Chausson et al. 2014; Pavlůvčík 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



188 population crashes (Altwegg et al. 2006). In addition, fledglings may be sensitive to weather  
189 conditions, particularly at the end of parental care. We used the North Atlantic Oscillation index  
190 (NAO) as a proxy for climatic conditions. This index often better explains variation in  
191 ecological processes than covariates such as monthly temperature or precipitation (Hallett et al.  
192 2004). We computed NAO index over two distinct periods: 1) winter (December to February,  
193 wNAO) and 2) during the month following the end of parental care (post-fledging NAO,  
194 NAO<sub>PF</sub>), typically in June-August (from May to September). We calculated NAO<sub>PF</sub> for each  
195 brood specifically according to its laying date. We determined the month of independence for  
196 each brood by adding 15 weeks to the estimated laying date (Bunn et al. 1982). In Burgundy,  
197 both summer and winter NAO indices negatively correlate with precipitation, whereas the  
198 correlations with temperature are close to zero (Bladé et al. 2012).

199

#### 200 *Analytical and statistical procedures*

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

207 Second, at the individual level, we investigated the probability that a female produced a  
208 second brood according to the influence of both intrinsic (relative laying date, brood size,  
209 female age [yearling vs. adult]) and extrinsic factors (wNAO, prey stored at nest [presence or  
210 not of *Microtus* stored at nest, and presence or not of *Apodemus* stored at nest]). To identify the  
211 factors underpinning among-female variability in the number of broods raised within a same

212 year, we considered a dataset restricted to conditions under which double brooding was  
213 recorded. Specifically, we only considered (1) broods from years in which the number of second  
214 broods represented >5% of the number of first+single broods. Next, (2) to control for changes  
215 in environmental conditions along the season, we discarded clutches laid later than the latest  
216 first clutch recorded in the study area (May, 5<sup>th</sup>). Therefore, the restricted data set only included  
217 clutches from years when double brooding was common and laid within the range of dates in  
218 which we observed first clutches in these years, in order to ensure we detect only relevant  
219 factors associated with double-brooding. We fitted generalised linear mixed models (GLMM)  
220 to predict the likelihood of a female producing one or two broods using a binomial distribution  
221 of error. We tested female identity, years, zones and female identity nested within zones for the  
222 random structure.

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

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

255 Finally, we investigated intergenerational effects by assessing whether female recruits  
256 originating from different brood types showed differences in brood size during their first  
257 breeding event and in lifetime reproductive success based on fledglings (data on recruits in this  
258 case were too sparse to derive LRP but note that LFP was positively related to LRP;  $\beta = 0.113$   
259  $\pm 0.008$ ,  $P < 0.001$ ,  $N = 771$ ,  $R^2 = 0.237$ , Poisson GLM). We used centred brood sizes as  
260 response variable, to control for among year variation in productivity, and fitted GLMMs with

261 Gaussian distribution of error with year and zones tested for the random structure. We analysed  
262 variation in LFP or LRP using GLMs with a negative binomial distribution of error.

263 We ran statistical analyses in R 3.2.4 (R Development Core Team 2016) using the libraries  
264 *lme4* (Bates et al. 2015) and *nlme* (Pinheiro et al. 2016). We performed model selection for the  
265 fixed effects according to a stepwise procedure by deleting variables with the highest *p*-values,  
266 from the most complete model, until we achieved no reduction in AICc (Akaike Information  
267 criterion adjusted for small sample size; Burnham and Anderson 2002). When dealing with the  
268 ratio of double broods at the population level, we handled over-dispersion in the data using a  
269 quasi-binomial distribution of error, thus precluding the calculation of AICc. In this case, we  
270 took extra care when interpreting the results as sample size was low ( $N = 17$  years) and only  
271 highly significant relationships were considered ( $P < 0.001$ ; Crawley 2007). To select the best  
272 random effect model structure, we ran models with alternative random structures fitting the  
273 fixed-effect component with all covariates and selected the best one based on AICc (Zuur et al.  
274 2009). We scaled explanatory covariates before analysis (except categorical ones) to compare  
275 their relative strength. We obtained the proportion of deviance explained by a model ( $R^2$ ) using  
276 the *piecewiseSEM* package (Lefcheck 2015), which implements the approach developed by  
277 Nakagawa and Schielzeth (2013) to estimate  $R^2$  for GLMs and GLMMs. Marginal  $R^2$  describes  
278 the proportion of variance explained by the fixed factor component of the model alone, while  
279 conditional  $R^2$  indicates the total variance explained by both the fixed and random components  
280 of the model together. We report both  $R^2$  when appropriate. We present descriptive statistics as  
281 arithmetic mean  $\pm$  1 SD and modelled effect size ( $\beta$ ) as mean  $\pm$  1 SE.

282

## 283 **Results**

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

285 Between 1998 and 2014, we recorded 2187 breeding events, among which 2012 were classified  
286 as single ( $N = 1529$ ), first ( $N = 163$ ) or second broods ( $N = 320$ ). Annual number of breeding  
287 events greatly varied from year-to-year (mean =  $124 \pm 69$ , from 261 in 2012 down to 4 in 2013).  
288 The ratio of double broods (number of second broods /number of single and first broods) varied  
289 annually from zero (in four years) to 87% (in 2014; mean =  $18 \pm 26\%$ , Fig. 2). The interval  
290 between the initiation of first and second broods was on average  $98 \pm 14$  days (range: 55-134,  
291  $N = 134$  instances with females identified on first and second broods). Weather conditions in  
292 the preceding winter (wNAO) were unrelated to the ratio of double broods. In contrast, several  
293 measures of prey stored at nest (annual arithmetic mean of number of prey items stored at nest:  
294 *Microtus* [ $\beta = 2.69 \pm 0.62$ ,  $P < 0.001$ ], *Microtus* mid-season [ $\beta = 1.17 \pm 0.24$ ,  $P < 0.001$ ],  
295 *Microtus* mid-season + *Apodemus* early-season [ $\beta_{Microtus} = 1.21 \pm 0.09$ ,  $P < 0.001$ ,  $\beta_{Apodemus} =$   
296  $0.92 \pm 0.20$ ,  $P < 0.001$ ],  $N = 17$  in all cases) positively correlated with the ratio of double broods  
297 (Fig. 3). However, annual ratio of double broods did not correlate with numbers of *Microtus*  
298 stored at nest early in the season ( $\beta_{Microtus} = 0.82 \pm 0.74$ ,  $P = 0.28$ ). Similar correlations were  
299 obtained when using only second broods for which females were captured twice (*Microtus* mid-  
300 season + *Apodemus* early-season [ $\beta_{Microtus} = 1.17 \pm 0.20$ ,  $P < 0.001$ ;  $\beta_{Apodemus} = 1.27 \pm 0.52$ ,  $P =$   
301  $0.03$ ]).

302 At the individual level, early breeding females were more likely to breed twice (Table 1, Fig.  
303 4). Females who produced larger broods had a reduced probability of double brooding as well  
304 as yearling females. Regarding extrinsic factors, the occurrence of *Apodemus*  
305 (presence/absence) stored at nest was associated with a slightly higher probability of double  
306 brooding, while the presence of *Microtus* early in the season did not (Binomial GLMM;  $\beta =$   
307  $0.15 \pm 0.29$ ,  $P = 0.61$ ). Controlling for laying date and brood size (fixed at their average value),  
308 the probability of double brooding for a yearling female increased from 0.127 to 0.191 if it had  
309 at least one *Apodemus* stored in her first nest, while the same probabilities for an adult female

310 increased from 0.198 to 0.285, respectively. Note that these two effects were only marginally  
311 significant ( $P < 0.1$ ; Table 1). All the results are based on models including only year as random  
312 factor (including female identity did not improve models).

### 313 *Fledgling recruitment probability*

314 Out of 8157 offspring that fledged over the 17 years of study, 326, including males and female  
315 offspring (159 females, 162 males and 5 undetermined), were recruited in the study area (4 %).  
316 Fifty three of 644 (8.2%) fledglings from first broods recruited, compared to 233 of 6210 (3.8%)  
317 and 40 out of 1203 (3.3%) from single and second broods, respectively. Overall, fledglings  
318 from early broods in years with higher mean number of prey stored at nest and favourable  
319 weather conditions post-fledging were more likely to recruit. Brood type *per se* did not affect  
320 recruitment probability ( $\beta_{single} = -0.000 \pm 0.190$ ,  $P = 0.99$ ;  $\beta_{second} = 0.702 \pm 0.427$ ,  $P = 0.10$ ).  
321 However, as first broods were laid earlier, fledglings from first broods had higher recruitment  
322 probabilities as a consequence of earlier relative laying date (Fig. 5). While controlling for all  
323 the other covariates, by keeping them at their average value, the model predicted that offspring  
324 from clutches laid on the average laying date had a recruitment probability of  $0.036 (\pm 0.016)$ ,  
325 while those from clutches laid 20 days before/after the average had recruitments probability of  
326  $0.043 (\pm 0.019)$  and  $0.027 (\pm 0.012)$ , respectively. Post-natal dispersal of recruits ( $10.8 \pm 8.8$   
327 km, range: 0.49-52.6,  $N = 208$ ) is unlikely to bias LFP and LRP calculation as it was not related  
328 to relative laying date (linear:  $\beta = 0.014 \pm 0.054$ ,  $P = 0.79$ ,  $N = 208$ ; quadratic  $\beta_1 = 0.020 \pm$   
329  $0.056$ ,  $P = 0.724$ ,  $\beta_2 = -0.028 \pm 0.069$ ,  $P = 0.69$ ,  $N = 208$ ), brood type (difference in dispersal  
330 of offspring from single and second broods compared to offspring from first broods:  $\beta_{single} =$   
331  $0.087 \pm 0.138$ ,  $P = 0.53$ ,  $\beta_{second} = 0.062 \pm 0.184$ ,  $P = 0.74$ ,  $N = 208$ ) or annual number of nest-  
332 boxes occupied ( $\beta = -0.041 \pm 0.066$ ,  $P = 0.54$ ,  $N = 208$ ). Post-natal but not post-breeding  
333 dispersal of barn owl has been reported to associate with coloration (van den Brink et al. 2012).  
334 We did not account for coloration and that could influence our LRP estimates, yet post-natal

335 dispersal distances in our study were similar to these reported by van den Brink et al. (2012;  
336 10.8 and  $9.6 \pm 0.6$  km respectively) suggesting we were able to detect recruits of both color  
337 morphs. In addition, as post-natal dispersal distance was not correlated with laying date or brood  
338 type, it does not seem probable that putative differences on dispersal associated to color are  
339 correlated with brood type and influencing our results.

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

358 *Lifetime reproductive success of female barn owls*

359 Lifetime reproductive success of females with complete monitoring and estimate from the count  
360 of fledglings (LFP) or recruits (LRP) were available for 771 females. The number of breeding  
361 years over a female's lifetime averaged  $1.60 \pm 1.18$ . Observed breeding lifespan was  
362 significantly longer in females that double brooded at least once ( $2.5 \pm 1.79$ ) compared to those  
363 that were never observed double brooding ( $1.45 \pm 0.97$ ; Poisson GLM:  $\beta = 0.57 \pm 0.07$ ,  $P <$   
364  $0.001$ ). Females that double brooded at least once in their lifetime produced on average 2.5  
365 times more fledglings than those who did not (LFP: 15.6 vs. 6.2; Fig. 6a). This difference was  
366 even more pronounced when considering the number of recruits (LRP: 0.96 vs. 0.24; Fig. 6b).  
367 Females with longer lifespans and that also experienced more favourable breeding seasons had  
368 higher LFP and LRP. The differences observed between double- and single-brooders remained  
369 highly significant even after controlling for lifespan and environmental variability (Table 3).  
370 Post-breeding dispersal was correlated to the annual number of breeding events detected.  
371 Females breeding in years with scarce breeding events recorded tended to disperse further for  
372 the next breeding season (Gaussian GLMM for log transformed post-breeding dispersal  
373 distance [+1 to avoid NAs] with female identity as random factor;  $\beta = -1.78 \pm 0.87$ ,  $P = 0.043$ ,  
374  $N = 490$ ). However, the difference in mean predicted dispersal distance between the years with  
375 lowest and highest number of breeding events recorded was  $< 20$  metres (Fig. S3), suggesting  
376 the displacements respond rather to differences in availability of alternative nest boxes within  
377 nesting sites than to breeding dispersal outside the area.

378 We found no evidence of a negative effect of double brooding on female return rate. Indeed,  
379 the return rate of double-brooding females was significantly higher than of single-brooders ones  
380 (Binomial GLMM with female identity nested in zone as random factor  $\beta = 0.44 \pm 0.16$ ,  $P =$   
381  $0.006$ ,  $N = 1526$ ). Finally, our LFP and LRP estimates did not appear to be influenced by our  
382 assignment of second broods based on laying date. We repeated the analyses classifying as  
383 double brooding only these females captured twice in the same year and reclassifying as single



384 brooding these females captured only on what we considered to be their second brood, and all  
385 reported differences in LFP and LRP were still significant (Table S1). To assess whether these  
386 differences in LFP and LRP were only driven by extra offspring from second broods, we  
387 repeated the analyses including only offspring from first and single broods. Double brooding  
388 females tended to produce more fledglings even when considering only offspring from first and  
389 single broods, compared to females never recorded as double brooders, suggesting a difference  
390 in territory and/or individual quality between these two categories. When accounting for  
391 females' breeding lifespan and environmental variability in LFP, the best model retained double  
392 brooding as a predictor variable, although it was no longer significant. When considering  
393 recruits however, females that double brooded at least once during their lifetime produced more  
394 recruits (LRP) from their first/single broods than other females, and this difference remained  
395 when accounting for females' breeding lifespan and environmental variability (Table 3).

#### 396 *Intergenerational effects*

397 Controlling for laying date, female recruits born from first broods produced  $1.47 \pm 0.49$   
398 additional fledglings during their first breeding attempt compared to females originating from  
399 a single brood ( $t = -4.52$ ,  $P < 0.001$ ) and  $1.76 \pm 0.68$  additional fledglings compared to a female  
400 originating from a second brood ( $t = -4.35$ ,  $P < 0.001$ ;  $N = 88$  female recruits from single broods,  
401 21 and 14 from first and second broods, respectively). When considering LFP of those females,  
402 however, we did not find support for differences among brood types (AICc = 0.38 unit higher  
403 than the null model) with a production of  $9.4 \pm 7.3$ ,  $8.3 \pm 5.6$  and  $6.6 \pm 2.4$  fledglings  
404 respectively for females originating from single, first and second broods. Data were too scarce  
405 to conduct the analysis based on LRP.

406

#### 407 **Discussion**

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

421

#### 422 *Proximate factors underpinning the occurrence of double brooding*

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

427 At the population level, the annual mean number of *Microtus* voles stored at the nest was  
428 the main factor explaining inter-annual variation. Double brooding was more common in years  
429 when the mean number of voles stored at the nest peaked. Years with the highest ratio of double  
430 broods ( $\geq 60\%$  in 2007, 2010, 2014) did not coincide with the highest number of breeding pairs.  
431 The latter is further limited by winter harshness affecting owl survival, as well as breeding

432 success (and thus cohort size) in the two preceding years (Altwegg et al. 2003). Interestingly,  
433 these three years coincided with the highest densities and breeding success by a another vole  
434 predator, the Montagu's harrier *Circus pygargus* survey in Champagne (Millon et al. 2002; A.  
435 Millon unpublished data). This migratory raptor is known to exhibit a direct numerical response  
436 to the abundance of common voles in French cereal landscapes (Millon and Bretagnolle 2008).  
437 The number of prey stored at nest, averaged across all nests within a year, could be viewed as  
438 a proxy of prey abundance in the field, although it is likely also affected by e.g. the timing of  
439 nest visits during the day, brood size and the age of chicks. To assess the assumed relationship,  
440 we correlated the annual mean number of voles stored at nest with an index of common vole  
441 abundance derived from a survey of 30 grasslands across the study area monitored between  
442 2009 and 2018 (authors' unpublished data, following methods described by Lambin et al. 2000).  
443 We found a positive, though marginally non-significant, relationship ( $\beta = 0.033 \pm 0.017$ , T value  
444 = 1.965,  $df = 8$ ,  $P = 0.085$ ,  $R^2 = 0.33$ ,  $N = 10$ ).

445 In years with higher mean numbers of prey stored at nest coinciding with the occurrence of  
446 double brooding, the probability of a female undertaking a second brood decreased with first  
447 brood laying date and brood size, yet increased marginally with the occurrence of *Apodemus*  
448 stored at the nest and female age. The influence of laying date on the individual probability of  
449 double brooding is recurrently reported across species (Taylor 2004; Nagy and Holmes 2005a;  
450 Hoffmann et al. 2015; Béziers and Roulin 2016). This pattern is related to obvious temporal  
451 constraints for the breeding season to match the timing of resource availability (Husby et al.  
452 2009). However, while the resource availability constraint is clear for species preying on insects  
453 with marked seasonality (Nagy and Holmes 2005b; Husby et al. 2009), *Microtus* can still be  
454 available in high quantities during autumn (Delattre et al. 1999) and *Apodemus* densities  
455 typically increase from August to November, with an overwinter plateau (Montgomery 1989).

456 However, post-harvesting ploughing of annual crops (wheat, barley, rapeseed) early in the  
457 summer may drastically reduce the availability of voles for predators such as barn owls.

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

477 Yearling females were slightly less likely to double brood compared to adults, under similar  
478 environmental conditions (a difference of 4-6% in double brooding probability). This adds to  
479 the abundant literature documenting the improvement of breeding success with age in birds  
480 (Forslund and Pärt 1995). In contrast to our findings, most previous studies have found no effect

481 of brood size on the female probability of double brooding (Nagy and Holmes 2005a; Béziers  
482 and Roulin 2016; although the latter found an effect of brood size on male probability of double  
483 brooding), or even positive effects (Hoffmann et al. 2015). A possible explanation for such  
484 results is that females might be less reluctant to bequeath small broods to their mates. The  
485 smaller the brood indeed, the easier for single males to cope with food supply. It is noteworthy  
486 that small brood size has been identified as a cause of divorce between successive years in this  
487 species (Dreiss and Roulin 2014).

488

#### 489 *Fitness consequences of double brooding*

490 While using a different, arguably more relevant, metric we found no support for the contention  
491 by Béziers and Roulin (2016) that double brooding in barn owls is traded-off with offspring  
492 quality. These authors found that offspring from first broods have lower body condition than  
493 offspring from single broods, a pattern also reported for jackdaws (*Corvus monedula*; Verhulst  
494 et al. 1997). In our study population, fledglings reared in first broods recruited with the same  
495 probability that offspring from single broods with the same laying date, and their subsequent  
496 breeding performance and LFP was similar. Here we found no evidence for intergenerational  
497 trade-offs. Moreover, from a breeding female perspective, double brooding resulted in higher  
498 lifetime production of recruits. This is consistent with a study on hoopoes, where double  
499 brooding females produced 2.6 times more recruits than single-brooding females over their  
500 lifetime (Hoffmann et al. 2015). We found that double-brooding female barn owls had longer  
501 breeding lifespans. They also produced more recruits than single-brooding females, even after  
502 controlling for breeding lifespan and the number of favourable breeding seasons experienced.  
503 Furthermore, this difference in the number of recruits produced held when we considered only  
504 recruits from first and single broods. This suggests that double brooding is highly rewarding in  
505 terms of fitness as we failed to find any costs in terms of e.g. return rate and breeding lifespan.

506 It is important to note here that the uncertainty around the assignment of brood types did not  
507 affect our interpretations, as the observed difference is in favour of the less detectable double-  
508 brooding event. Indeed, any miss-assignment of first broods as single broods would result in  
509 smaller differences of fitness parameters between brood types. Another bias in fitness estimate  
510 could arise if offspring of different brood types, and single- or double-brooding females,  
511 differed in dispersal propensity. Notwithstanding that we were unable to detect dispersal data  
512 outside our study area, both its spatial scale and the fact that dispersal distances recorded within  
513 it did not differ between the aforementioned categories, suggesting our estimate of lifetime  
514 recruit production are unlikely to be strongly biased.

515 Most of the differences in individual probability of double brooding and in offspring  
516 probability of recruitment arose from laying date with no detectable effect of brood type *per se*,  
517 despite a slight penalization for very early broods (Fig. 5). This is in accordance with  
518 observational and experimental results suggesting that the observed seasonal decline in fitness  
519 is the result of laying date, with territory or parental identity/quality contributing little to the  
520 covariance between laying date and recruitment (e.g. Van de Pol and Verhulst 2006, Pärt et al.  
521 2017). An interesting question then arises: why do not all females double brood when  
522 conditions are favourable? Although proximate causes of individual variation in laying date are  
523 poorly known, a meta-analysis revealed that experimentally enhanced food provision in birds  
524 mainly results in advanced laying dates, with increase in brood size showing smaller effect size  
525 (Ruffino et al. 2014). Among-female variation in laying date might be related to heterogeneity  
526 in individual and/or territory quality, and as a consequence may be a proxy of quality itself.  
527 Male barn owls provide most of the food during the early breeding stages (from courtship to  
528 early brooding) and male hunting skills provisioning rate might be an important factor  
529 influencing laying date and probability of double-brooding (Taylor 2004; Durant et al. 2013).  
530 Unfortunately, low capture rates for adult males in our study did not allow us to include male

531 identity or characteristics in our analyses. Thus, females laying earlier broods could be higher  
532 quality individuals or paired with higher quality males exploiting available resources more  
533 efficiently and/or occupying territories with higher food abundance. We predict that such  
534 females will be in better condition, be capable of starting breeding earlier, and more capable of  
535 laying a second clutch, especially when, or if, *Microtus* abundance is high.

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

543

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554

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671

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

679

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
<i>Apodemus</i> (yes)	0.48	0.26	1.83	0.067
Brood size	-0.29	0.11	-2.58	0.010

680

681

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

689

Explanatory variables	Estimate	SE	<i>z</i>	<i>P</i> <sub>690</sub>
Intercept	-3.85	0.26	-14.82	<0.001 691
Brood Size	-0.25	0.06	-3.96	<0.001
Rel. laying date	-0.42	0.07	-6.15	<0.001 692
Rel. laying date Quad.	-0.24	0.09	-2.76	0.006
<i>Microtus</i> -mid	0.55	0.07	8.16	<0.001
<i>Apodemus</i> -early	0.14	0.06	2.30	0.021
NAO <sub>PF</sub>	0.45	0.07	6.60	<0.001
wNAO	0.32	0.05	6.182	<0.001

693 **Table 3.** Results of the best negative binomial GLM comparing female lifetime reproductive  
694 success, based on count of offspring (LFP) or recruits (LRP), between females detected to breed  
695 twice in a year at least once in their lifetime (DB) vs. those that were never detected to do so ( $N$   
696 = 771 females; 110 of them categorised as DB). Explanatory variables also retained in these  
697 model were breeding lifespan, *i.e.* the number of years between first and last detected breeding  
698 (Lifespan), and the number of favourable breeding seasons in lifespan (*i.e.* years in which the  
699 ratio of double broods exceeded 5%; Fav. breed. Season). Outputs of two distinct models are  
700 presented here: one considering offspring from any brood type and one considering only  
701 offspring from first and single broods. Explanatory variables were scaled.

702

	Explanatory variables	Lifetime fledgling production				Lifetime recruit production			
		Estimate	se	$z$	$P$	Estimate	se	$z$	$P$
<b>All offspring</b>	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
<b>Only first/single broods</b>	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

703

704

705

706 **Figure 1.** Mean number of common vole (green circles) and wood mouse (blue circles) stored  
707 at nest, as a proxy of prey abundance, according to barn owls' laying dates. Vertical dashed  
708 lines indicate cut-offs between early, mid and late breeding season used in analyses. Size of  
709 the circles are proportional to sample size (range: 1 – 225). Lines show values predicted by  
710 the best model (linear, quadratic, exponential and logarithmic functional relationships were  
711 tested for each prey species; negative binomial GLMMs assessed using year as random factor:  
712 common vole quadratic function [min.  $\Delta\text{AICc} = 6.4$ ]:  $\beta = 2.05 \pm 0.63$ ,  $P = 0.001$ ,  $\beta_{\text{quad}} = -$   
713  $0.77 \pm 0.25$ ,  $P = 0.002$ ; *Apodemus* log function [min.  $\Delta\text{AICc} = 0.3$ ]:  $\beta = -1.80 \pm 0.19$ ,  $P =$   
714  $0.001$ ,  $N = 2221$ ).

715

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

720

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

725

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



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

734

735 **Figure 5.** Recruitment probability of barn owl's fledglings according to relative laying date.

736 The solid line indicates mean probability from a model accounting for linear and quadratic  
737 terms of laying date, brood size, *Microtus* abundance in mid-season, *Apodemus* abundance  
738 early in the season,  $NAO_{PF}$  and  $wNAO$ . Values for these five explanatory variables were set at  
739 their average values. 95% confidence intervals are represented with dotted lines. Open circles  
740 indicate recruitment probabilities for fledglings with a relative laying date matching the  
741 average for, from left to right, first (0.059), single (0.050) and second (0.013) broods.

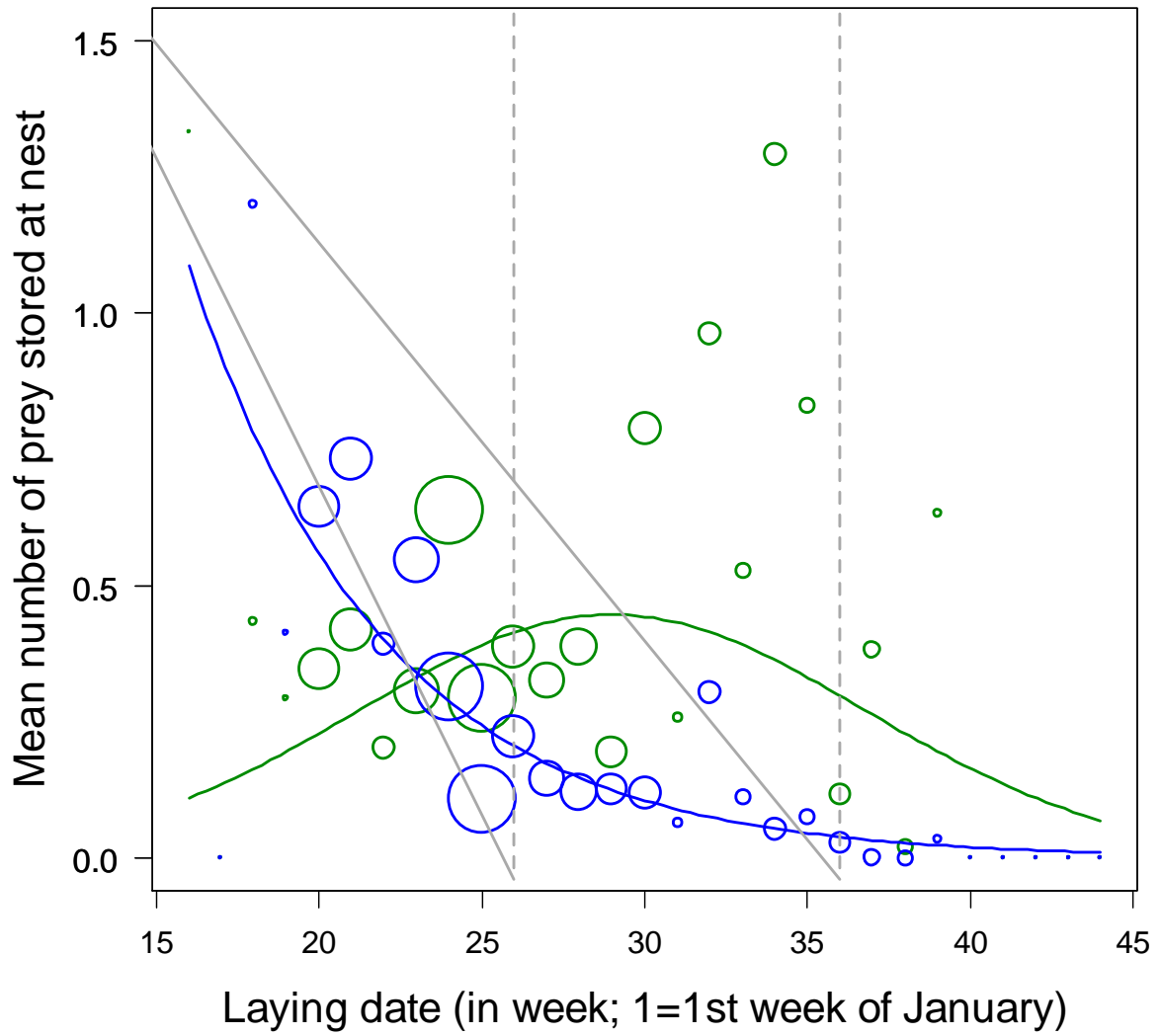
742 Histogram shows the distribution of relative laying dates for first (purple), single (white) and  
743 second (green) broods. Figure is based on model fitted values, in which probability for each  
744 fledgling is calculated considering also its particular values for all the other covariates and  
745 with zone as random factor.

746

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

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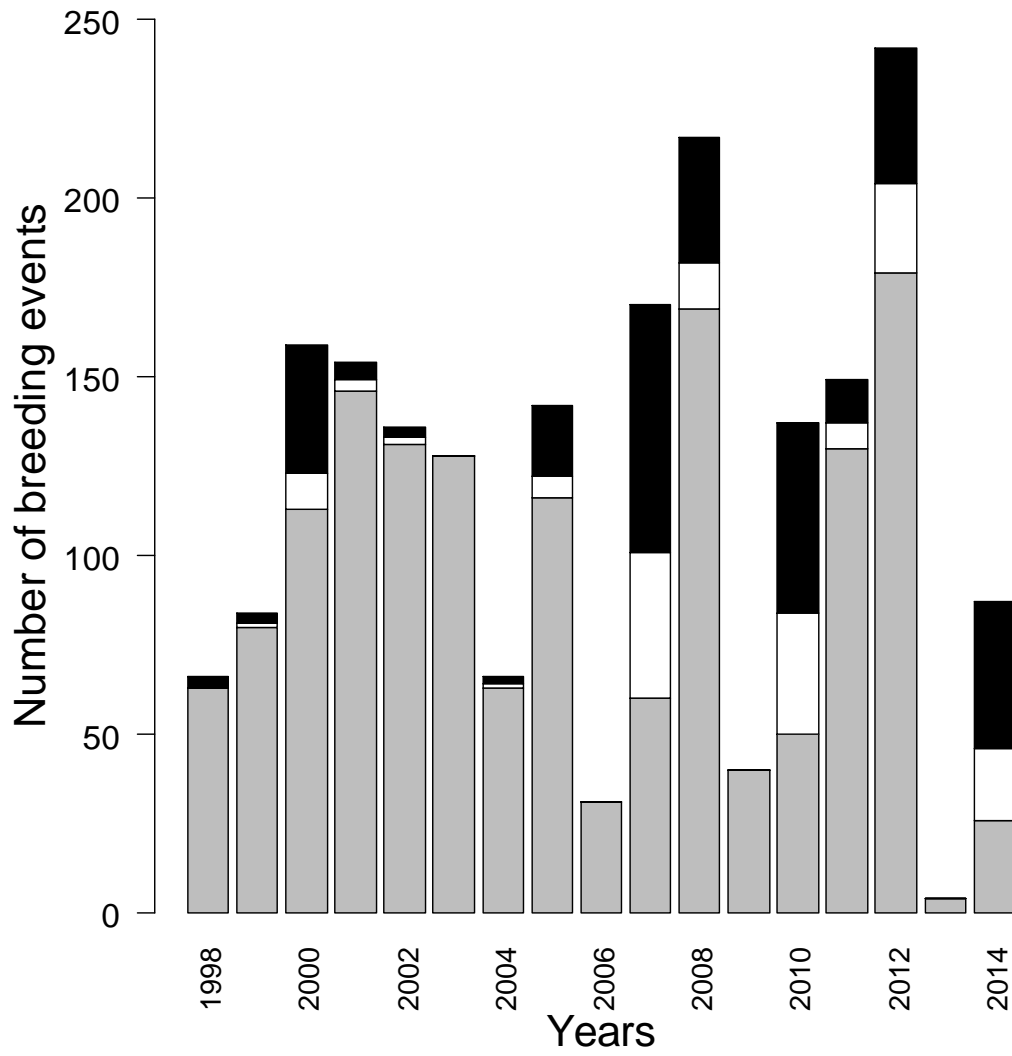
752 **Figure 1.**



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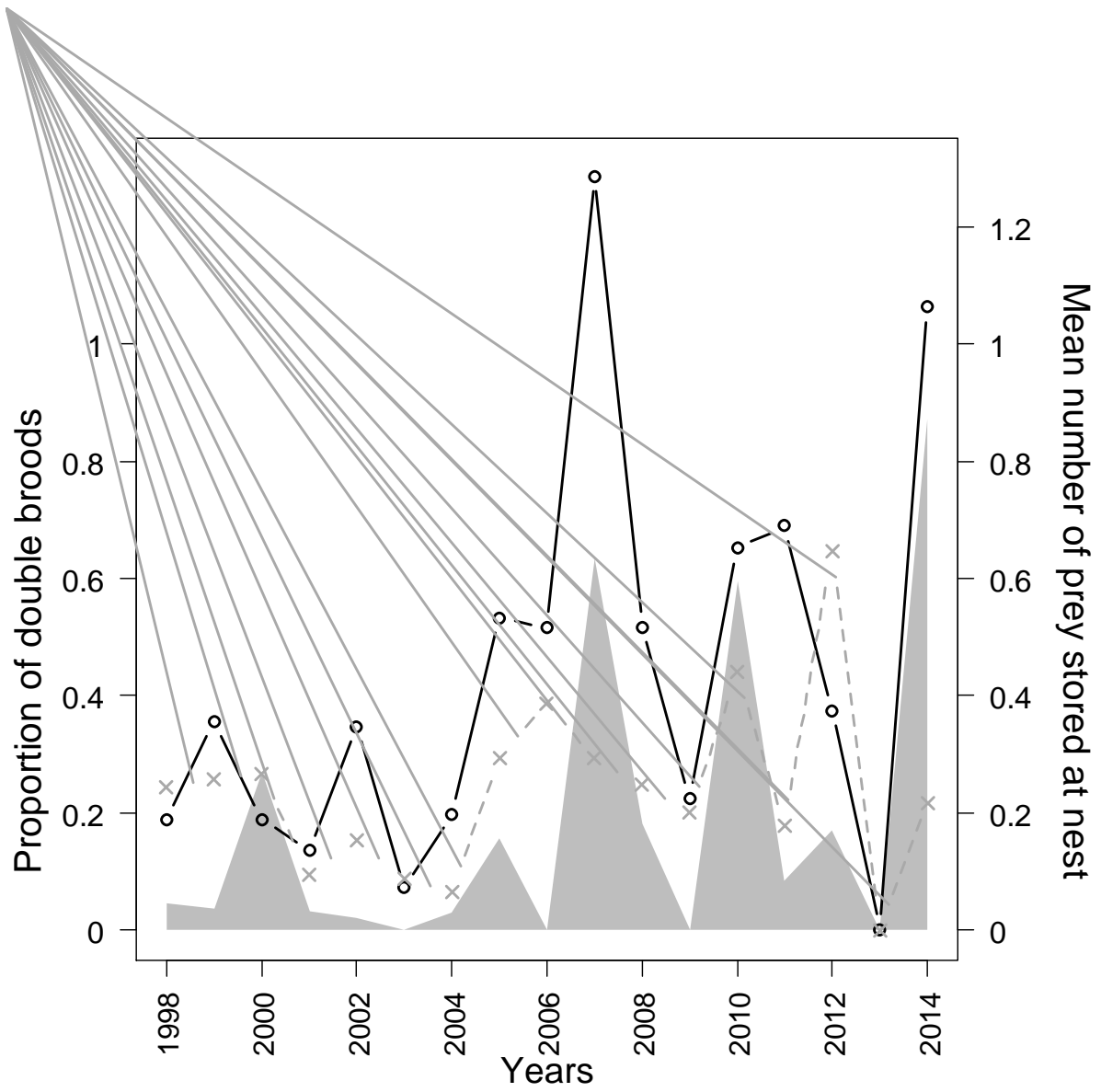
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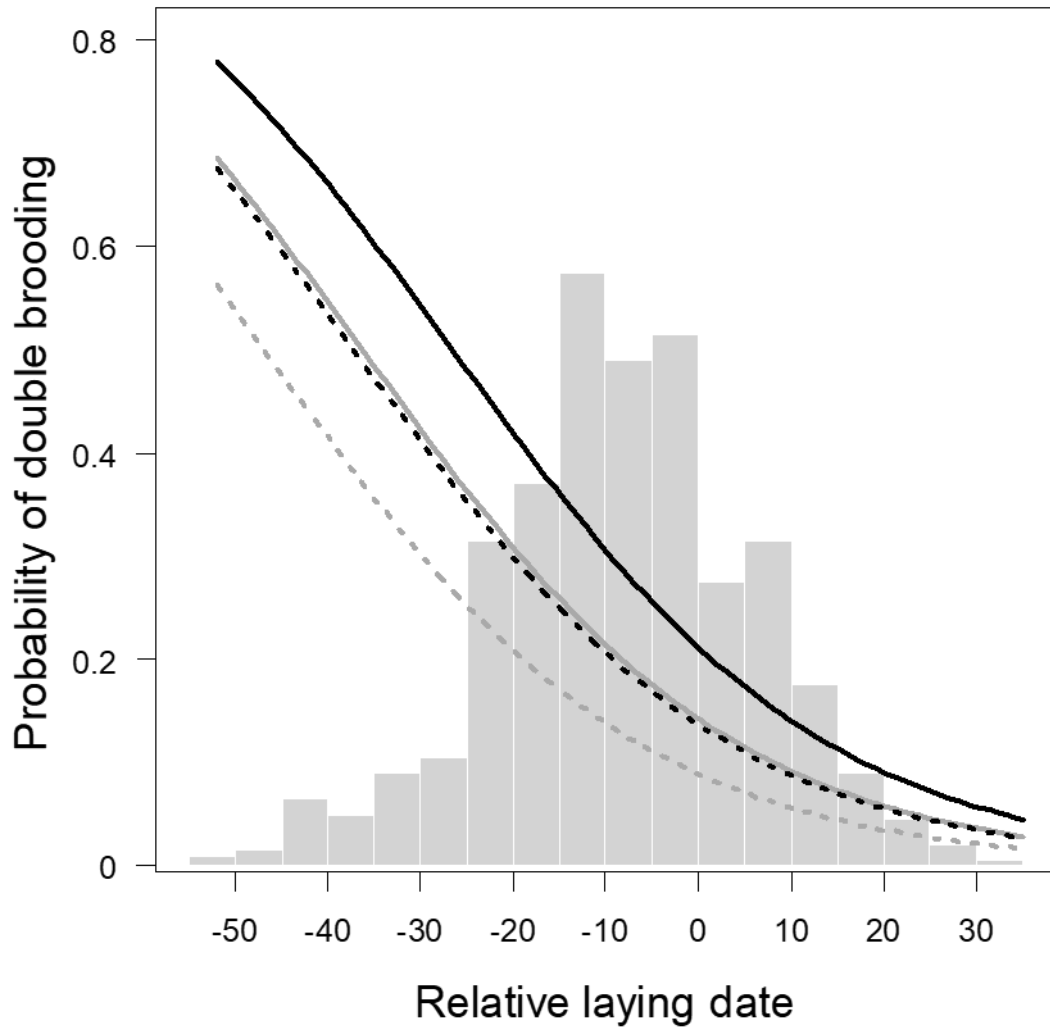
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761 **Figure 3.**

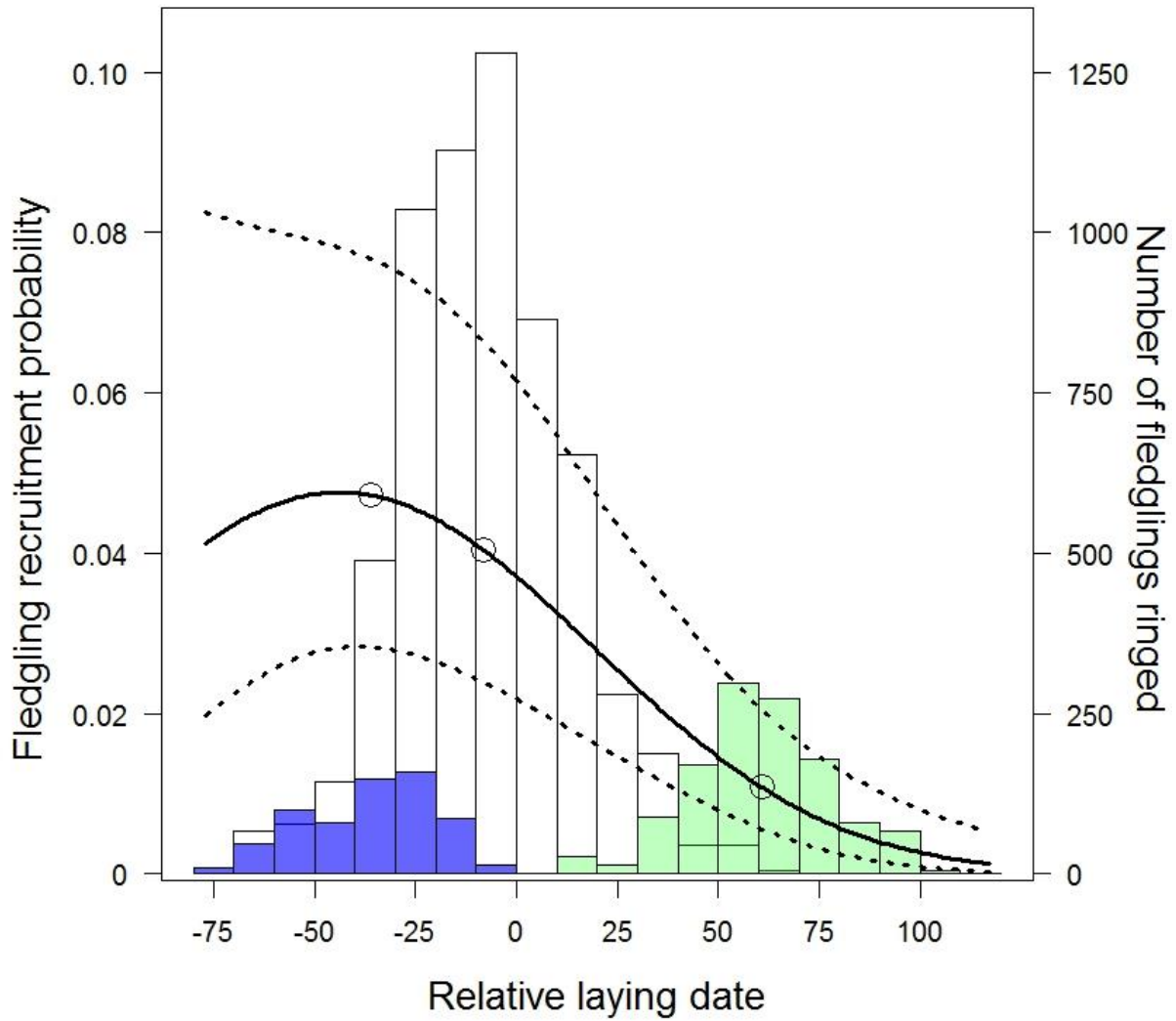


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767 **Figure 5.**



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770 **Figure 6.**

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