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

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18

¹ Author contributions – JS, PS and DC designed the field protocols and collected the data, and corrected and amended successive draft versions. JZ, XL, JS and AM designed the study, JZ performed most analyses and wrote the first draft, and XL and AM provided guidance, supervised analyses, and extensively contributed to the redaction of the MS.

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
26 of double brooding in the population, ranging from 0 to 87%, was positively related to the
27 number of rodent prey stored at the nest. Females laying early in the season were more likely
28 to breed twice and the probability of double brooding increased with smaller initial brood
29 size, female age and the storage of wood mice at the nest early in the season. Fledglings from
30 first broods recruited more often (8.2%) than those from single broods (3.8%) or second
31 broods (3.3%) but this was primarily the consequence of laying dates, not brood type *per se*.
32 Females producing two broods within a year, at least once in their lifetime, had higher
33 lifetime reproductive success and produced more local recruits than females that did not (15.6
34 ± 8.1 vs. 6.1 ± 3.8 fledglings, 0.96 ± 1.2 vs. 0.24 ± 0.6 recruits). Our results suggests that the
35 benefits of double brooding exceed costs in terms of fitness, and that within-year variability in
36 double brooding is related to heterogeneity in individual/territory quality.

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38

39

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;
47 Béziers and Roulin 2016). Producing multiple broods is often a facultative strategy and its
48 frequency varies greatly among populations, but also among years within a given population
49 (Husby et al. 2009; Béziers and Roulin 2016; Jackson and Cresswell 2017). Such a variation
50 offers the opportunity to investigate the proximate factors underpinning the alternative
51 strategies and 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
56 Roulin 2016), Tengmalm's owl *Aegolius funereus* (Korpimäki et al. 2011), hoopoe *Upupa*
57 *epops* (Hoffmann et al. 2015), or black-throated blue warbler *Setophaga caerulescens* (Nagy
58 and Holmes 2005a). However, over an individual's lifetime, attempting double brooding may
59 be associated with costs that could cancel out the benefits of short-term increased breeding
60 success. Documented costs include reduced survival of multiple-brooding females (Verhulst
61 1998) and reduced body condition of fledglings from first broods due to maternal desertion
62 for the purpose of initiating a second brood (Béziers and Roulin 2016). Recruitment
63 probabilities of fledglings from females producing two or more broods could also be lowered
64 compared to fledglings from a single brood but this has been rarely assessed (but see

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

79 Variable availability of food resources has been shown to influence the frequency of
80 multiple brooding. In some cases, a relatively constant percentage of individuals produce two
81 broods each year, such as in the hoopoe (although different populations show different
82 average frequencies; Martín-Vivaldi et al. 1999, Hoffmann et al. 2015). In others cases, the
83 percentage of individuals double brooding can vary from zero to >80% in populations subject
84 to pulsed resources, such as in the black-throated blue warbler *Dendroica caerulescens* (Nagy
85 and 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
95 brooding (Baudvin 1986; Béziers and Roulin 2016). First, we measured the extent of among-
96 year variation in the frequency of double brooding at the population level and assessed
97 whether such variation was related to extrinsic factors such as food storage and climatic
98 conditions. Second, we investigated whether those extrinsic factors interacted with intrinsic
99 factors (laying date, brood size) to drive a female to breed twice in a year. Then, we compared
100 recruitment probabilities between fledglings originating from any of the three brood types
101 (single, first and second) to test whether brood type *per se* affected recruitment in addition to
102 laying date. Lastly, we assessed whether lifetime reproductive success (estimated as either the
103 number of fledglings or local recruits) of female barn owls having produced two broods in a
104 year at least once over 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
112 175 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 km². We installed more nest-boxes in 2006, resulting in a
115 total of 370 nesting-sites (295 nest-boxes and 75 alternative nesting sites) monitored annually,
116 with 2-4 visits per site. The first visit in March-April ascertained occupancy. We made
117 subsequent visits to sites where occupancy was suspected or recorded to assess clutch size and
118 ring nestlings just before fledging (May-July). We attempted to capture adults during all site
119 visits by placing a landing net at the entrance of the nest-boxes. We marked nestlings and
120 unmarked adults with alphanumeric aluminium bands (CRBPO - Museum National d'Histoire
121 Naturelle, Paris). We weighed chicks using a spring scale (Pesola © 500 g). We used nestling
122 age and weight to estimate nestling body condition (expressed as the deviation from predicted
123 body mass according to age and days since estimated hatching date in each year). We
124 revisited later in the season all sites deemed unoccupied on the first visit to detect second
125 clutches or late breeding attempts. The proportion of the barn owl population breeding in
126 monitored nesting-sites was unknown.

127 We defined laying date as the Julian week when the first egg was laid (week 1 = 1st week
128 of 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 ± 12 days of age. To
132 account for inter-annual variation in laying dates while comparing data over multiple years,
133 we centred laying dates to the average laying date recorded in each year and used relative
134 laying dates for the analyses. To characterise how clutches are distributed within a year, we
135 estimated the average laying date for each year using all the clutches detected, including
136 replacement clutches ($N = 93$) and those not assigned to any category (their characteristics
137 suggested replacement broods but we could not ascertain that [$N = 69$]). We assigned
138 breeding birds to two age classes (yearling vs. ≥ 2 years, hereafter called adult) based on

139 ringing, for birds ringed as chicks, or according to the moulting pattern otherwise (Taylor
140 1993).

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

162 *Proxies of prey abundance and weather conditions*

163 Barn owls typically prey on small mammals in Europe, primarily on microtine voles *Microtus*
164 *spp.* and wood mouse *Apodemus spp.* (Mikkola 1983; Chausson et al. 2014; Pavlůvčík et al.
165 2015), species that show high among-year variation in abundance. Surplus prey are
166 commonly stored at the nest (Taylor 2004), and we used the number of prey stored, recorded
167 during visits dedicated to chick ringing, as a proxy for prey abundance in the environment.
168 We therefore inspected nesting-sites and identified any prey items stored. We focused on
169 microtine voles (*M. arvalis/agrestis*) and wood mice (*A. sylvaticus/flavicollis*) which together
170 represent 86% of the prey items recorded (54% and 32% respectively, $N = 1961$, hereafter
171 *Microtus* and *Apodemus*). Visual inspection of prey was too cursory to reliably distinguish
172 *Microtus arvalis* from *M. agrestis* and *Apodemus sylvaticus* from *A. flavicollis*. However,
173 prey identification from pellet analysis revealed that *M. arvalis* was by far the most common
174 species preyed upon by barn owls in the study area ($N = 9792$ prey between 2004 and 2014;
175 JS, PS & DC unpublished data), making up 44% of prey items. *M. agrestis* represented only
176 7% of the *Microtus* prey. Regarding wood mice, *A. sylvaticus* was a slightly more common
177 prey than *A. flavicollis* (58 vs. 42%, $N = 770$ identified wood mice) and wood mice altogether
178 made 14% of prey items found in pellets. Other prey items found at nest included *Arvicola*
179 *terrestris* (7%), and *Rattus norvegicus*, *Glis glis*, *Myodes glareolus* and *Crocidura spp.*
180 accounting for <1% each. We investigated the temporal variation in the occurrence of both
181 *Microtus* and *Apodemus*, by modelling the arithmetic mean number of prey items stored
182 against Julian date, and found that the peak of *Apodemus* stored at nest occurred earlier during
183 the breeding season compared to the *Microtus* peak (Fig.1). We therefore defined five
184 different measures of prey abundance based on the mean number of prey stored at nest: 1-
185 total prey (*Microtus* + *Apodemus* over the whole season), 2- *Microtus* over the whole season,
186 3- *Microtus* at mid-season, 4- *Apodemus* over the whole season and 5- *Apodemus* in early
187 season (Fig. 1).

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

202

203 *Analytical and statistical procedures*

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

210 Second, at the individual level, we investigated the probability that a female produced a
211 second brood according to the influence of both intrinsic (relative laying date, brood size,

212 female age [yearling vs. adult]) and extrinsic factors (wNAO, prey stored at nest [presence or
213 not of *Microtus* stored at nest, and presence or not of *Apodemus* stored at nest]). To identify
214 the factors underpinning among-female variability in the number of broods raised within a
215 same year, we considered a dataset restricted to conditions under which double brooding was
216 recorded. Specifically, we only considered (1) broods from years in which the number of
217 second broods represented >5% of the number of first+single broods. Next, (2) to control for
218 changes in environmental conditions along the season, we discarded clutches laid later than
219 the latest first clutch recorded in the study area (May, 5th). Therefore, the restricted data set
220 only included clutches from years when double brooding was common and laid within the
221 range of dates in which we observed first clutches in these years, in order to ensure we detect
222 only relevant factors associated with double-brooding. We fitted generalised linear mixed
223 models (GLMM) to predict the likelihood of a female producing one or two broods using a
224 binomial distribution of error. We tested female identity, years, zones and female identity
225 nested within zones for the random structure.

226 Third, we evaluated the following individual characteristics as predictors of fledgling
227 recruitment probability: brood type (single, first, second), relative laying date and its quadratic
228 term to account for possible penalties for very early broods, rank (nestling order within
229 brood), chick body condition at ringing and brood size. In addition, we included extrinsic
230 factors related to environmental conditions experienced in the birth year: ratio of second
231 broods in the whole study area, arithmetic mean number of prey stored at the nest (*Microtus*,
232 *Apodemus*, *Microtus* + *Apodemus*), and the two NAO indices. To prevent bias in recruitment
233 rate estimates due to the possible influence of laying date, brood type or population density in
234 offspring dispersal (Altwegg et al. 2003; Huffeldt et al. 2012), prior to analyses we assessed
235 the correlation of post-natal dispersal distance (log transformed) with relative laying date
236 (linear and quadratic), brood type and number of nest-boxes occupied (as a proxy of

237 population size). Fledglings born during the last two years of the study were removed from
238 the analysis as the average age at first breeding was 1.75 yr (\pm 1.22 SD; median age = 1 yr).
239 We fitted GLMMs using a binomial distribution of error and female identity, years and zones
240 were tested for the random structure.

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

259 Finally, we investigated intergenerational effects by assessing whether female recruits
260 originating from different brood types showed differences in brood size during their first
261 breeding event and in lifetime reproductive success based on fledglings (data on recruits in

262 this case were too sparse to derive LRP but note that LFP was positively related to LRP; $\beta =$
263 0.113 ± 0.008 , $P < 0.001$, $N = 771$, $R^2 = 0.237$, Poisson GLM). We used centred brood sizes
264 as response variable, to control for among year variation in productivity, and fitted GLMMs
265 with Gaussian distribution of error with year and zones tested for the random structure. We
266 analysed variation in LFP or LRP using GLMs with a negative binomial distribution of error.

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

287

288 **Results**

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

290 Between 1998 and 2014, we recorded 2187 breeding events, among which 2012 were
291 classified as single ($N = 1529$), first ($N = 163$) or second broods ($N = 320$). Annual number of
292 breeding events greatly varied from year-to-year (mean = 124 ± 69 , from 261 in 2012 down to
293 4 in 2013). The ratio of double broods (number of second broods /number of single and first
294 broods) varied annually from zero (in four years) to 87% (in 2014; mean = $18 \pm 26\%$, Fig. 2).
295 The interval between the initiation of first and second broods was on average 98 ± 14 days
296 (range: 55-134, $N = 134$ instances with females identified on first and second broods).
297 Weather conditions in the preceding winter (wNAO) were unrelated to the ratio of double
298 broods. In contrast, several measures of prey stored at nest (annual arithmetic mean of
299 number of prey items stored at nest: *Microtus* [$\beta = 2.69 \pm 0.62$, $P < 0.001$], *Microtus* mid-
300 season [$\beta = 1.17 \pm 0.24$, $P < 0.001$], *Microtus* mid-season + *Apodemus* early-season [$\beta_{Microtus}$
301 = 1.21 ± 0.09 , $P < 0.001$, $\beta_{Apodemus} = 0.92 \pm 0.20$, $P < 0.001$], $N = 17$ in all cases) positively
302 correlated with the ratio of double broods (Fig. 3). However, annual ratio of double broods
303 did not correlate with numbers of *Microtus* stored at nest early in the season ($\beta_{Microtus} = 0.82 \pm$
304 0.74 , $P = 0.28$). Similar correlations were obtained when using only second broods for which
305 females were captured twice (*Microtus* mid-season + *Apodemus* early-season [$\beta_{Microtus} = 1.17$
306 ± 0.20 , $P < 0.001$; $\beta_{Apodemus} = 1.27 \pm 0.52$, $P = 0.03$]).

307 At the individual level, early breeding females were more likely to breed twice (Table 1,
308 Fig. 4). Females who produced larger broods had a reduced probability of double brooding as
309 well as yearling females. Regarding extrinsic factors, the occurrence of *Apodemus*
310 (presence/absence) stored at nest was associated with a slightly higher probability of double

311 brooding, while the presence of *Microtus* early in the season did not (Binomial GLMM; $\beta =$
312 0.15 ± 0.29 , $P = 0.61$). Controlling for laying date and brood size (fixed at their average
313 value), the probability of double brooding for a yearling female increased from 0.127 to 0.191
314 if it had at least one *Apodemus* stored in her first nest, while the same probabilities for an
315 adult female increased from 0.198 to 0.285, respectively. Note that these two effects were
316 only marginally significant ($P < 0.1$; Table 1). All the results are based on models including
317 only year as random factor (including female identity did not improve models).

318 *Fledgling recruitment probability*

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

336 compared to offspring from first broods: $\beta_{single} = 0.087 \pm 0.138$, $P = 0.53$, $\beta_{second} = 0.062 \pm$
337 0.184 , $P = 0.74$, $N = 208$) or annual number of nest-boxes occupied ($\beta = -0.041 \pm 0.066$, $P =$
338 0.54 , $N = 208$). Post-natal but not post-breeding dispersal of barn owl has been reported to
339 associate with coloration (van den Brink et al. 2012). We did not account for coloration and
340 that could influence our LRP estimates, yet post-natal dispersal distances in our study were
341 similar to these reported by van den Brink et al. (2012; 10.8 and 9.6 ± 0.6 km respectively)
342 suggesting we were able to detect recruits of both color morphs. In addition, as post-natal
343 dispersal distance was not correlated with laying date or brood type, it does not seem probable
344 that putative differences on dispersal associated to color are correlated with brood type and
345 influencing our results.

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

361 environmental conditions. By contrast, in years when prey stored in the nest were scarce,
362 females were much less likely to double brood. In addition offspring from early broods
363 (typically single broods) in low food years were less likely to recruit.

364 *Lifetime reproductive success of female barn owls*

365 Lifetime reproductive success of females with complete monitoring and estimate from the
366 count of fledglings (LFP) or recruits (LRP) were available for 771 females. The number of
367 breeding years over a female's lifetime averaged 1.60 ± 1.18 . Observed breeding lifespan was
368 significantly longer in females that double brooded at least once (2.5 ± 1.79) compared to
369 those that were never observed double brooding (1.45 ± 0.97 ; Poisson GLM: $\beta = 0.57 \pm 0.07$,
370 $P < 0.001$). Females that double brooded at least once in their lifetime produced on average
371 2.5 times more fledglings than those who did not (LFP: 15.6 vs. 6.2; Fig. 6a). This difference
372 was even more pronounced when considering the number of recruits (LRP: 0.96 vs. 0.24; Fig.
373 6b). Females with longer lifespans and that also experienced more favourable breeding
374 seasons had higher LFP and LRP. The differences observed between double- and single-
375 brooders remained highly significant even after controlling for lifespan and environmental
376 variability (Table 3). Post-breeding dispersal was correlated to the annual number of breeding
377 events detected. Females breeding in years with scarce breeding events recorded tended to
378 disperse further for the next breeding season (Gaussian GLMM for log transformed post-
379 breeding dispersal distance [+1 to avoid NAs] with female identity as random factor; $\beta = -$
380 1.78 ± 0.87 , $P = 0.043$, $N = 490$). However, the difference in mean predicted dispersal
381 distance between the years with lowest and highest number of breeding events recorded was $<$
382 20 metres (Fig. S3), suggesting the displacements respond rather to differences in availability
383 of alternative nest boxes within nesting sites than to breeding dispersal outside the area.

384 We found no evidence of a negative effect of double brooding on female return rate. Indeed,
385 the return rate of double-brooding females was significantly higher than of single-brooders

386 ones (Binomial GLMM with female identity nested in zone as random factor $\beta = 0.44 \pm 0.16$,
387 $P = 0.006$, $N = 1526$). Finally, our LFP and LRP estimates did not appear to be influenced by
388 our assignment of second broods based on laying date. We repeated the analyses classifying
389 as double brooding only these females captured twice in the same year and reclassifying as
390 single brooding these females captured only on what we considered to be their second brood,
391 and all reported differences in LFP and LRP were still significant (Table S1). To assess
392 whether these differences in LFP and LRP were only driven by extra offspring from second
393 broods, we repeated the analyses including only offspring from first and single broods.
394 Double brooding females tended to produce more fledglings even when considering only
395 offspring from first and single broods, compared to females never recorded as double
396 brooders, suggesting a difference in territory and/or individual quality between these two
397 categories. When accounting for females' breeding lifespan and environmental variability in
398 LFP, the best model retained double brooding as a predictor variable, although it was no
399 longer significant. When considering recruits however, females that double brooded at least
400 once during their lifetime produced more recruits (LRP) from their first/single broods than
401 other females, and this difference remained when accounting for females' breeding lifespan
402 and environmental variability (Table 3).

403 *Intergenerational effects*

404 Controlling for laying date, female recruits born from first broods produced 1.47 ± 0.49
405 additional fledglings during their first breeding attempt compared to females originating from
406 a single brood ($t = -4.52$, $P < 0.001$) and 1.76 ± 0.68 additional fledglings compared to a
407 female originating from a second brood ($t = -4.35$, $P < 0.001$; $N = 88$ female recruits from
408 single broods, 21 and 14 from first and second broods, respectively). When considering LFP
409 of those females, however, we did not find support for differences among brood types (AICc
410 $= 0.38$ unit higher than the null model) with a production of 9.4 ± 7.3 , 8.3 ± 5.6 and 6.6 ± 2.4

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

413

414 **Discussion**

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

428

429 *Proximate factors underpinning the occurrence of double brooding*

430 Double brooding was on average achieved by 18% of the female barn owls. However, there
431 was much among-year variation around this average, probably reflecting variation in prey
432 abundance. Over 17 years, four years had no record of double brooding and in three years
433 more than 60% and up to 87% of females bred twice, in line with other studies (Husby et al.
434 2009).

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

453 In years with higher mean numbers of prey stored at nest coinciding with the occurrence of
454 double brooding, the probability of a female undertaking a second brood decreased with first
455 brood laying date and brood size, yet increased marginally with the occurrence of *Apodemus*
456 stored at the nest and female age. The influence of laying date on the individual probability of
457 double brooding is recurrently reported across species (Taylor 2004; Nagy and Holmes
458 2005a; Hoffmann et al. 2015; Béziers and Roulin 2016). This pattern is related to obvious
459 temporal constraints for the breeding season to match the timing of resource availability

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

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

484 preferentially prey on *Apodemus* could benefit from the peak of this resource to start breeding
485 earlier. Unfortunately, we caught too few males to properly test this hypothesis.

486 Yearling females were slightly less likely to double brood compared to adults, under
487 similar environmental conditions (a difference of 4-6% in double brooding probability). This
488 adds to the abundant literature documenting the improvement of breeding success with age in
489 birds (Forslund and Pärt 1995). In contrast to our findings, most previous studies have found
490 no effect of brood size on the female probability of double brooding (Nagy and Holmes
491 2005a; Béziers and Roulin 2016; although the latter found an effect of brood size on male
492 probability of double brooding), or even positive effects (Hoffmann et al. 2015). A possible
493 explanation for such results is that females might be less reluctant to bequeath small broods to
494 their mates. The smaller the brood indeed, the easier for single males to cope with food
495 supply. It is noteworthy that small brood size has been identified as a cause of divorce
496 between successive years in this species (Dreiss and Roulin 2014).

497

498 *Fitness consequences of double brooding*

499 While using a different, arguably more relevant, metric we found no support for the
500 contention by Béziers and Roulin (2016) that double brooding in barn owls is traded-off with
501 offspring quality. These authors found that offspring from first broods have lower body
502 condition than offspring from single broods, a pattern also reported for jackdaws (*Corvus*
503 *monedula*; Verhulst et al. 1997). In our study population, fledglings reared in first broods
504 recruited with the same probability that offspring from single broods with the same laying
505 date, and their subsequent breeding performance and LFP was similar. Here we found no
506 evidence for intergenerational trade-offs. Moreover, from a breeding female perspective,
507 double brooding resulted in higher lifetime production of recruits. This is consistent with a

508 study on hoopoes, where double brooding females produced 2.6 times more recruits than
509 single-brooding females over their lifetime (Hoffmann et al. 2015). We found that double-
510 brooding female barn owls had longer breeding lifespans. They also produced more recruits
511 than single-brooding females, even after controlling for breeding lifespan and the number of
512 favourable breeding seasons experienced. Furthermore, this difference in the number of
513 recruits produced held when we considered only recruits from first and single broods. This
514 suggests that double brooding is highly rewarding in terms of fitness as we failed to find any
515 costs in terms of e.g. return rate and breeding lifespan. It is important to note here that the
516 uncertainty around the assignment of brood types did not affect our interpretations, as the
517 observed difference is in favour of the less detectable double-brooding event. Indeed, any
518 miss-assignment of first broods as single broods would result in smaller differences of fitness
519 parameters between brood types. Another bias in fitness estimate could arise if offspring of
520 different brood types, and single- or double-brooding females, differed in dispersal
521 propensity. Notwithstanding that we were unable to detect dispersal data outside our study
522 area, both its spatial scale and the fact that dispersal distances recorded within it did not differ
523 between the aforementioned categories, suggesting our estimate of lifetime recruit production
524 are unlikely to be strongly biased.

525 Most of the differences in individual probability of double brooding and in offspring
526 probability of recruitment arose from laying date with no detectable effect of brood type *per*
527 *se*, despite a slight penalization for very early broods (Fig. 5). This is in accordance with
528 observational and experimental results suggesting that the observed seasonal decline in fitness
529 is the result of laying date, with territory or parental identity/quality contributing little to the
530 covariance between laying date and recruitment (e.g. Van de Pol and Verhulst 2006, Pärt et al.
531 2017). An interesting question then arises: why do not all females double brood when
532 conditions are favourable? Although proximate causes of individual variation in laying date

533 are poorly known, a meta-analysis revealed that experimentally enhanced food provision in
534 birds mainly results in advanced laying dates, with increase in brood size showing smaller
535 effect size (Ruffino et al. 2014). Among-female variation in laying date might be related to
536 heterogeneity in individual and/or territory quality, and as a consequence may be a proxy of
537 quality itself. Male barn owls provide most of the food during the early breeding stages (from
538 courtship to early brooding) and male hunting skills provisioning rate might be an important
539 factor influencing laying date and probability of double-brooding (Taylor 2004; Durant et al.
540 2013). Unfortunately, low capture rates for adult males in our study did not allow us to
541 include male identity or characteristics in our analyses. Thus, females laying earlier broods
542 could be higher quality individuals or paired with higher quality males exploiting available
543 resources more efficiently and/or occupying territories with higher food abundance. We
544 predict that such females will be in better condition, be capable of starting breeding earlier,
545 and more capable of laying a second clutch, especially when, or if, *Microtus* abundance is
546 high.

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

554

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565

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681

682

683 **Table 1.** Results of the best binomial GLMM investigating the probability of a female barn
684 owl to breed twice in a year, considering only clutches laid before the 5th of May in years with
685 at least 5% of double broods ($N = 705$, marginal $R^2 = 0.14$, conditional $R^2 = 0.41$).
686 Explanatory variables retained in this model were relative laying date, female age (yearling or
687 ≥ 2 yr-old), occurrence (yes/no) of *Apodemus* stored at nest and brood size. Explanatory
688 variables were scaled such that effect sizes are comparable between each other. The model
689 included year as a random factor.

690

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

691

692

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

701

Explanatory variables	Estimate	SE	z	P_{02}
Intercept	-3.85	0.26	-14.82	<0.001 703
Brood Size	-0.25	0.06	-3.96	<0.001 704
Rel. laying date	-0.42	0.07	-6.15	<0.001
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_{PF}	0.45	0.07	6.60	<0.001
wNAO	0.32	0.05	6.182	<0.001

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

714

	Explanatory variables	Lifetime fledgling production				Lifetime recruit production			
		Estimate	se	z	P	Estimate	se	z	P
All offspring	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

715

716

717

718 **Figure 1.** Mean number of common vole (green circles) and wood mouse (blue circles) stored
719 at nest, as a proxy of prey abundance, according to barn owls' laying dates. Vertical dashed
720 lines indicate cut-offs between early, mid and late breeding season used in analyses. Size of
721 the circles are proportional to sample size (range: 1 – 225). Lines show values predicted by
722 the best model (linear, quadratic, exponential and logarithmic functional relationships were
723 tested for each prey species; negative binomial GLMMs assessed using year as random factor:
724 common vole quadratic function [min. $\Delta\text{AICc} = 6.4$]: $\beta = 2.05 \pm 0.63$, $P = 0.001$, $\beta_{\text{quad}} = -$
725 0.77 ± 0.25 , $P = 0.002$; *Apodemus* log function [min. $\Delta\text{AICc} = 0.3$]: $\beta = -1.80 \pm 0.19$, $P =$
726 0.001 , $N = 2221$).

727

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

732

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

737

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

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

746

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

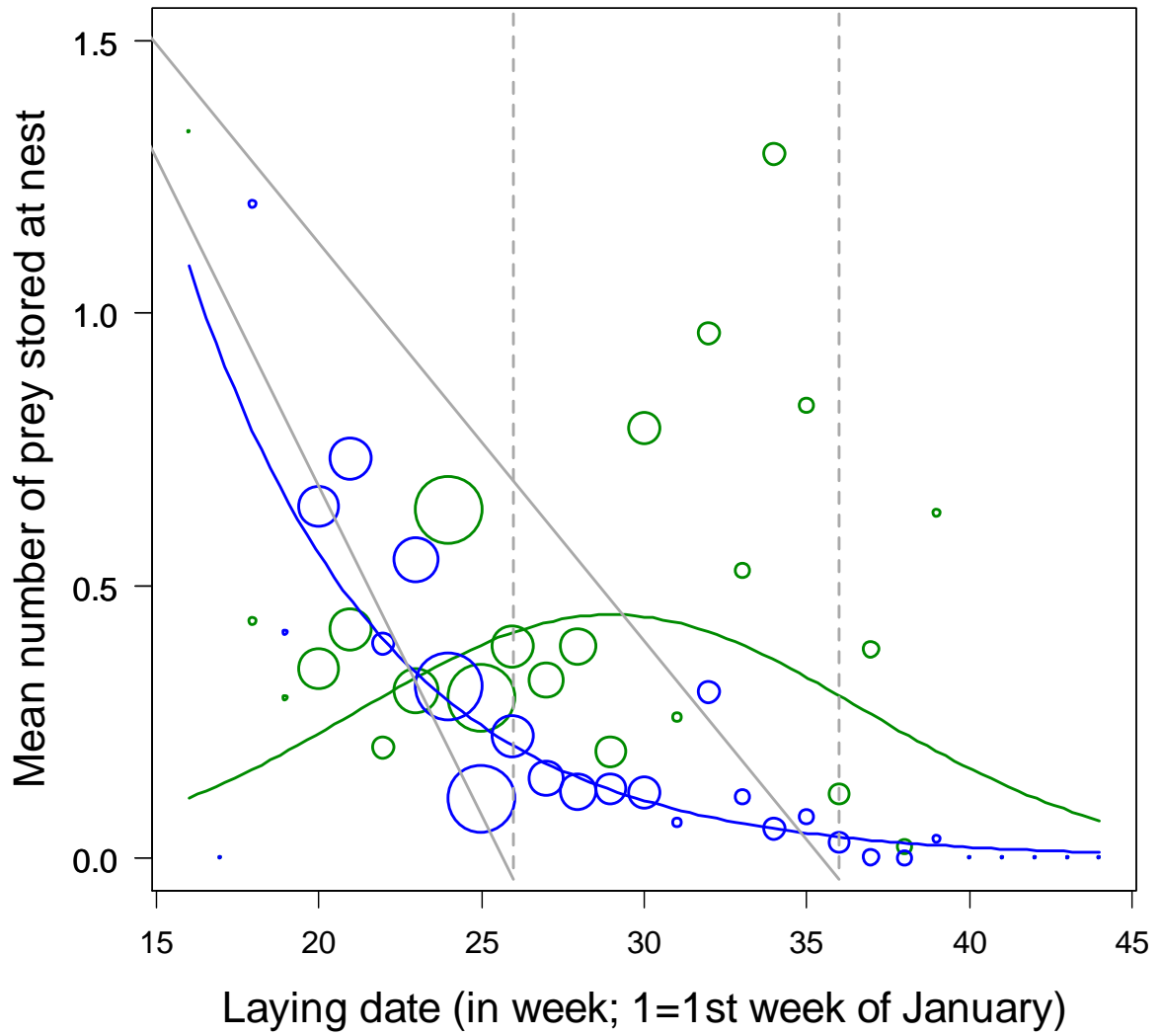
748 The solid line indicates mean probability from a model accounting for linear and quadratic
749 terms of laying date, brood size, *Microtus* abundance in mid-season, *Apodemus* abundance
750 early in the season, NAO_{PF} and $wNAO$. Values for these five explanatory variables were set at
751 their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

758

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

763

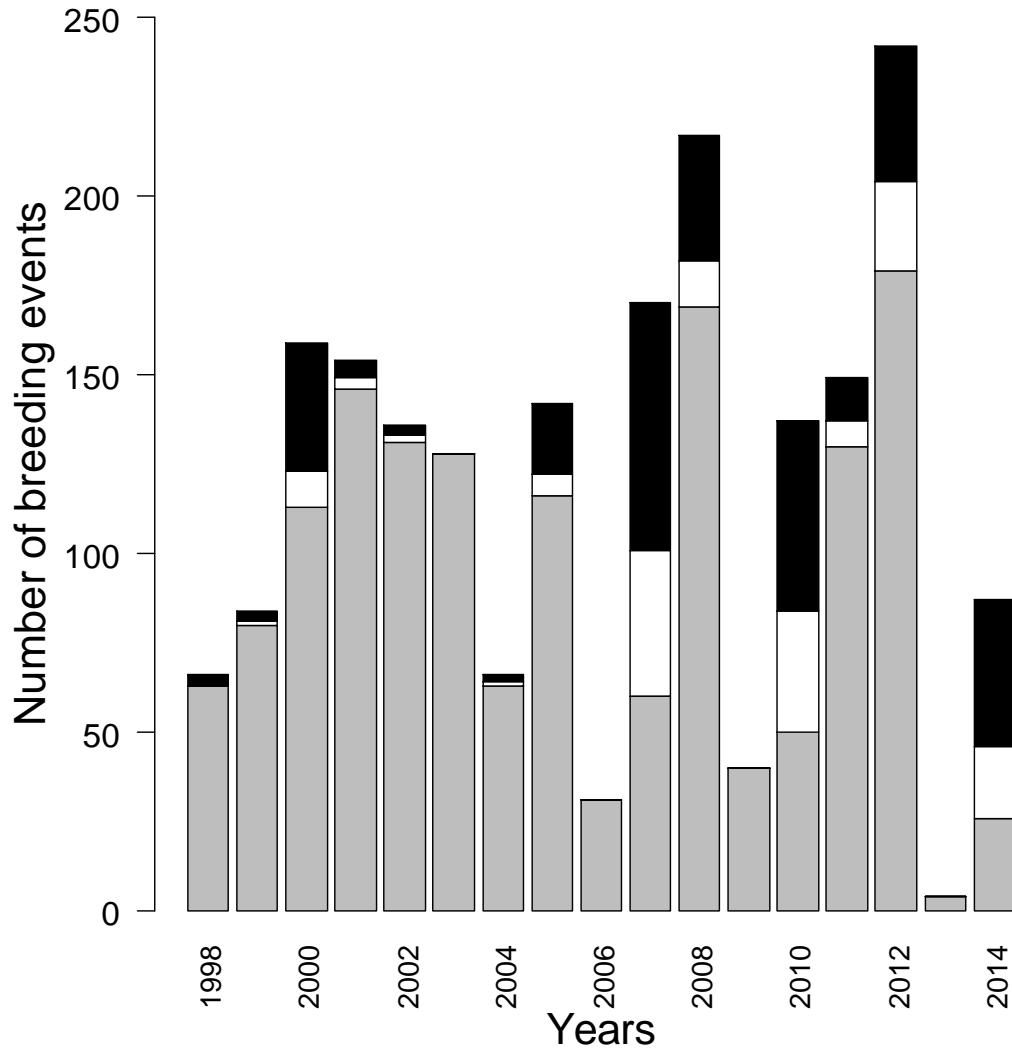
764 **Figure 1.**



765

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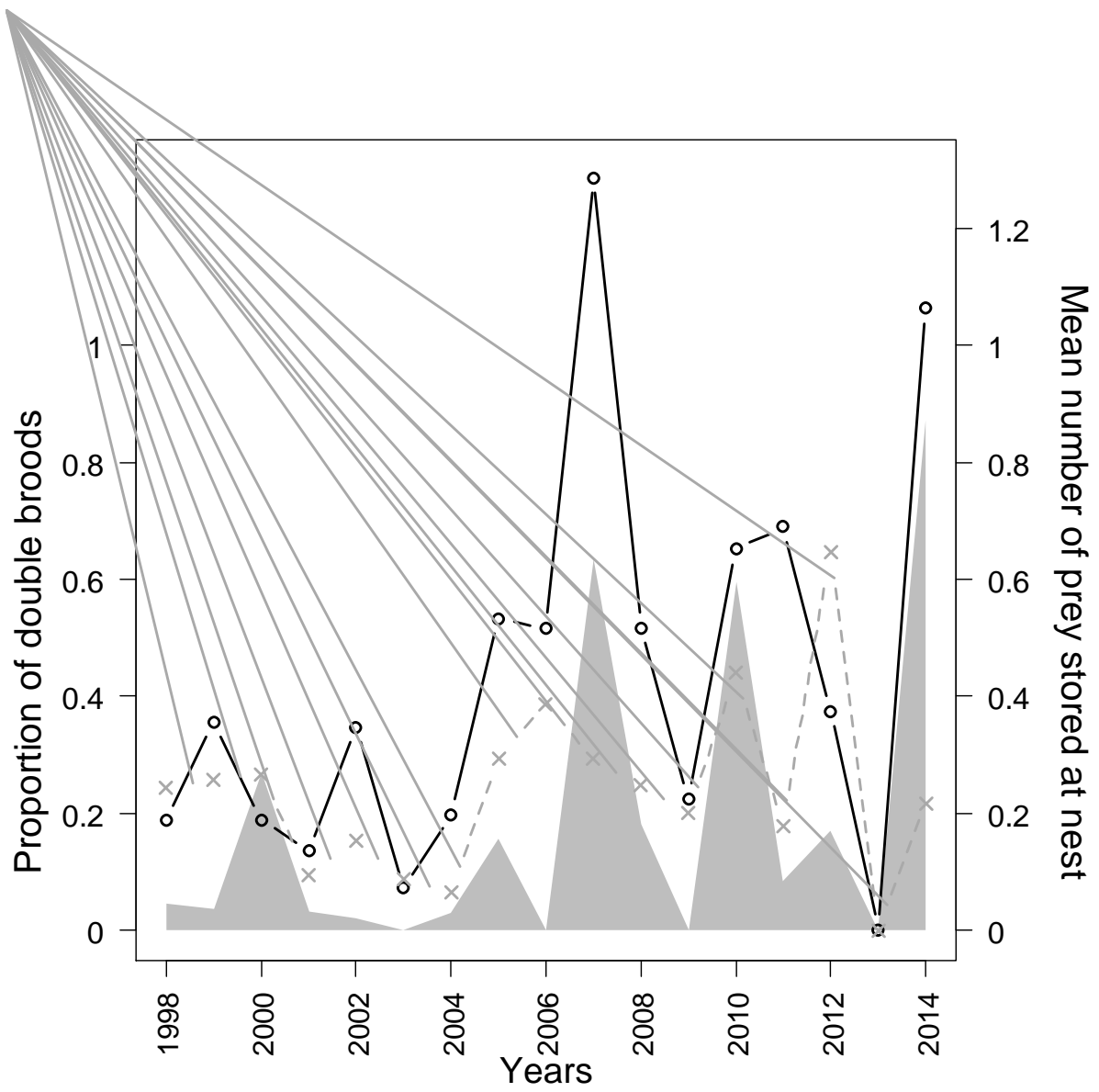
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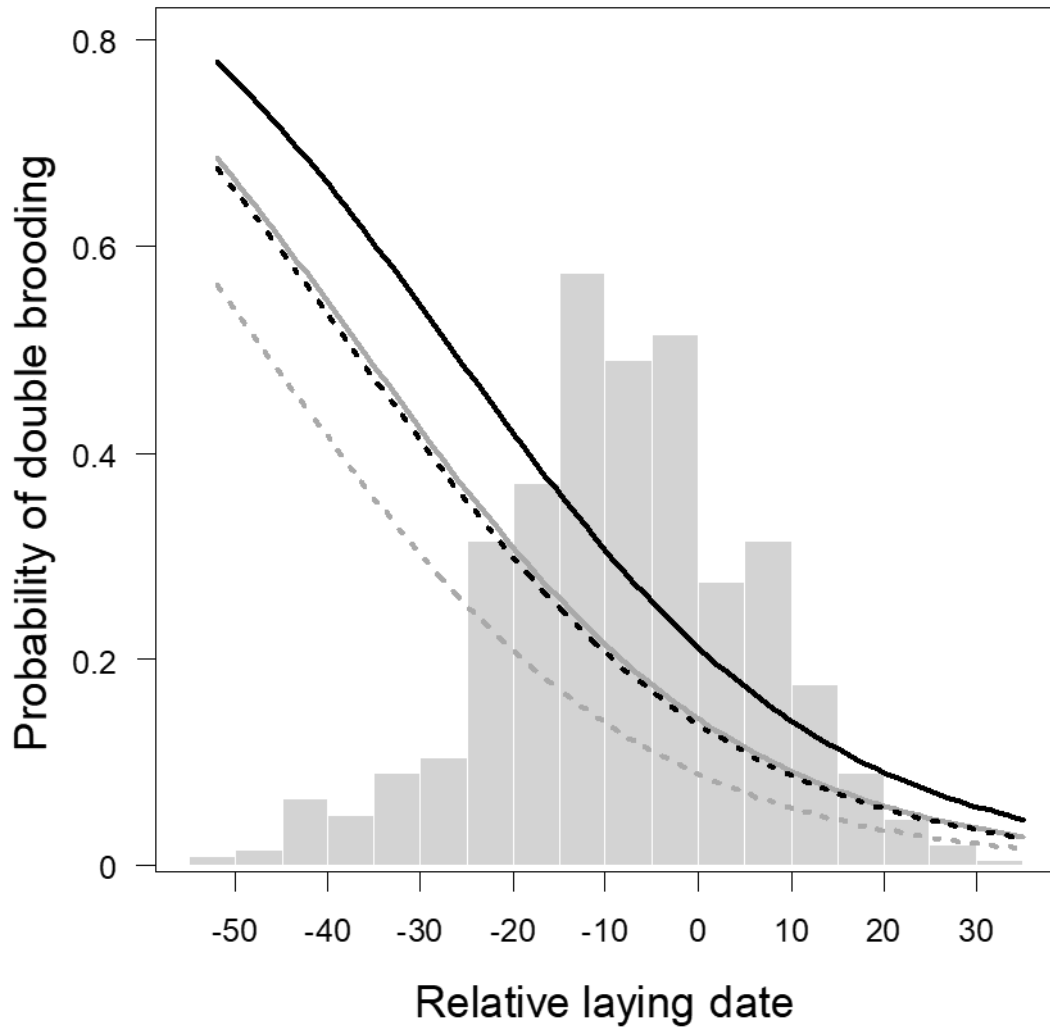
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773 **Figure 3.**



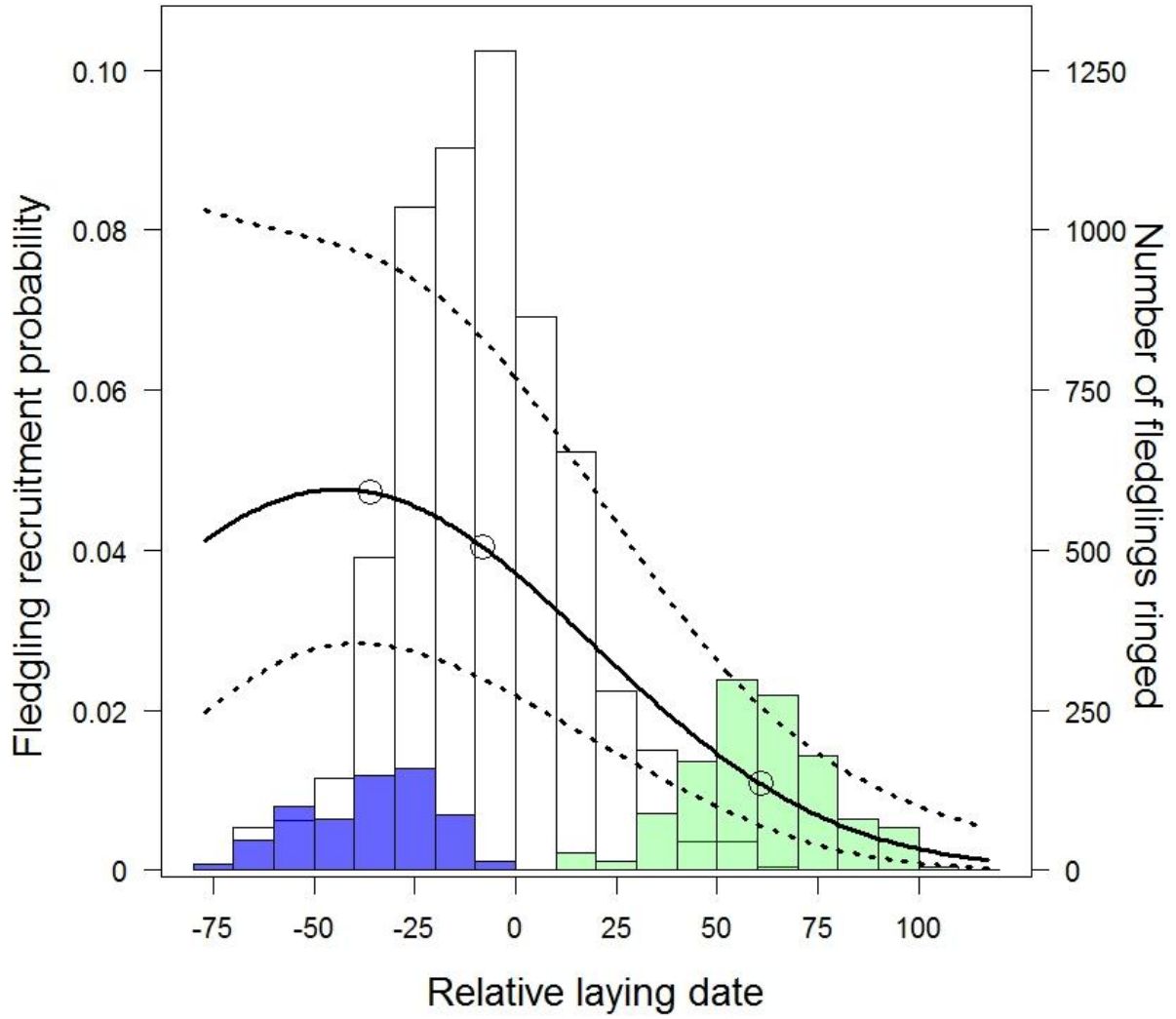
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