



Factors influencing double brooding in Eurasian Hoopoes *Upupa epops*

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Double brooding may be a good strategy for short-lived species to maximize annual and lifetime reproductive success (ARS and LRS, respectively). Nevertheless, there is typically individual variation in the probability of producing a second clutch. Here we evaluate factors that influence the decision to double brood in the Eurasian Hoopoe *Upupa epops*. Analyses of an 11-year dataset showed that 36% of the females and 21% of the males produced a second clutch after successfully raising a first clutch. Double-brooded females had higher ARS (9.1 ± 1.9 fledglings; mean \pm se) and LRS (0.93 ± 0.08 recruits) than single-brooded females (ARS: 4.5 ± 2.1 fledglings; LRS: 0.36 ± 0.03 recruits). This suggests that double brooding is adaptive in Hoopoes, and raises the question of why most individuals only produce one clutch per season. The probability of double brooding varied only slightly between years, suggesting that it is influenced by individual characteristics rather than by external, population-level environmental factors. In both sexes, the probability of double brooding increased with earlier timing of the first clutch, and the timing of reproduction was the most important factor influencing reproductive success. The latter is likely to be mediated by changes in resources during the season. The probability of double brooding also increased slightly with female age, due to differences in intrinsic quality among females rather than to a gain in experience. In contrast to many other studies, the probability of double brooding increased with an increasing number of fledglings from the first clutch, suggesting that it is a strategy of individuals of high quality. Taken together, we show that the individual quality of the breeder and the timing of their first clutches are key factors influencing the decision to double brood, and thereby that they are important determinants of reproductive performance in Eurasian Hoopoes.

Keywords: density-dependence, lifetime reproduction, multiple breeding, recruitment, seasonal decline.

The trade-off between reproduction and survival leads to different reproductive strategies (Drent & Daan 1980, Roff 1992, Stearns 1992). Species experiencing low extrinsic mortality risk are predicted to allocate resources to their own survival, and hence their future reproduction, at the cost of their current breeding attempt. On the other hand, short-lived species facing high extrinsic mortality risks have a small chance of survival to the

next breeding season. They may have no further possibility to reproduce and they are therefore expected to invest more in their current breeding attempt.

One strategy to maximize annual breeding success is to produce more than one clutch in the same season, known as multiple brooding. For example, the annual breeding success of double-brooding Louisiana Waterthrushes *Seiurus motacilla* was twice as high as that of conspecifics that bred only once per breeding season (Mulvihill *et al.* 2009). On the other hand, multiple brooding

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is energy-consuming and may affect the future survival of the parents. Indeed, experimental removal of the second clutch in Common House Martins *Delichon urbicum* (Bryant 1979) and Great Tits *Parus major* (Verhulst 1998) resulted in higher adult survival. Furthermore, there can be consequences for the quality and survival of the fledglings from a second clutch. For example, survival of Snow Bunting *Plectrophenax nivalis* chicks reared in first clutches was 12% higher than that of chicks from second clutches, and the survival of chicks from first clutches was higher when no second clutch followed (Smith & Marquiss 1995). Such differences in quality and recruitment between fledglings from first and second clutches may be the result of differential parental care (Grüebler & Naef-Daenzer 2010).

The maximum number of successful breeding attempts per breeding season is constrained by the time needed to raise a clutch relative to the length of the breeding season. Indeed, many studies have shown that the timing of the first clutch is the most important factor determining double brooding, with the incidence of second clutches generally declining the later the first clutch (Geupel & DeSante 1990, Verboven *et al.* 2001, Brinkhof *et al.* 2002, Parejo & Danchin 2006, Husby *et al.* 2009, O'Brien & Dawson 2012). This decline may result from differences among early and late brooding individuals in terms of their own quality or the quality of their territory (quality hypothesis). Alternatively, it may be the result of a gradual change in the environment that affects all individuals in the same way (date hypothesis) (Verboven & Verhulst 1996). Experiments that have tried to distinguish between these hypotheses have revealed that Great Tits do not differ in their intrinsic ability to produce and raise a second clutch but that only individuals that started their first clutch early produced a second clutch (Verboven & Verhulst 1996).

Other factors that affect the incidence of double brooding include the size of the first clutch, body condition and age of the parents, and territory quality. The fact that the probability of double brooding usually declines with increasing size of the first clutch (Verboven & Verhulst 1996, Nagy & Holmes 2005a) suggests constraints on the amount of energy that can be allocated to first and second clutches. Furthermore, some studies have found a positive association between double brooding and body condition or age (Winkel &

Winkel 1995), although others found no relationship (Odgen & Stutchbury 1996, Nagy & Holmes 2005b).

Finally, environmental factors such as food availability and weather can influence multiple brooding (Verboven *et al.* 2001, Nagy & Holmes 2005b, Husby *et al.* 2009, O'Brien & Dawson 2012). For example, in Black-throated Blue Warblers *Setophaga caerulescens* double brooding varied between 0% in years with low food availability and 87% in years with high food availability (Nagy & Holmes 2005b). The frequency of double brooding can also be subject to negative density-dependence (Kluyver 1951).

In this study we examined the reproductive performance of Eurasian Hoopoes *Upupa epops*, a facultative double brooder. Documented rates of double brooding range from 19% in Spain (Martín-Vivaldi *et al.* 1999a) to 30–57% in Germany (Oehlschlaeger & Ryslavý 2002, Stange & Havelka 2003). Reproductive output is an important driver of Hoopoe population dynamics (Schaub *et al.* 2012), and second clutches are presumably an important component of overall reproductive output. Variation in the frequency of double brooding therefore has the potential to contribute significantly to Hoopoe population dynamics.

Earlier studies of double brooding by Hoopoes have found positive effects of laying date and strophe length of male songs on the probability of producing a second clutch (Martín-Vivaldi *et al.* 1999a,b) but no difference in the number of fledglings in first and second clutches (Martín-Vivaldi *et al.* 1999a, Oehlschlaeger & Ryslavý 2002). However, although multiple brooding has been reported repeatedly in Hoopoes, a detailed study of its causes and consequences is lacking.

We use individual-based longitudinal data over 11 years from the largest Hoopoe population in Switzerland to assess whether intrinsic factors (age, body size, hatching date of first clutch, number of fledglings in the first clutch) and extrinsic factors (quality of the territory where the first clutch is raised, population density) were associated with the decision of the individuals to nest twice in a season. We then assess whether any seasonal decline in reproductive performance was due to a gradual change in the environment (date hypothesis) or to individual differences (quality hypothesis). Although experiments are needed to distinguish conclusively between these two

hypotheses (e.g. Verboven & Verhulst 1996), double brooding can be seen as a natural experiment (Hochachka 1990). If the date hypothesis is true, the seasonal decline in reproductive performance should be the same in first and second clutches and there should be no difference between first and second clutches, apart from the date. In contrast, if the quality hypothesis is true, the seasonal decline in first and second clutches may have a similar slope but the intercepts will differ because individuals that perform better in fledging a first clutch will perform consistently better with their second clutch, too (Hochachka 1990). To evaluate the consequences for fledglings of being reared in the single clutch of single-brooding females or in a first or second clutch of double-brooding females, we compared the number of fledglings and their recruitment probability in these three types of clutches. Finally, we assessed whether lifetime production of fledglings and lifetime reproductive success, measured as the number of offspring recruiting into the breeding population, were linked to the frequency of double brooding to infer fitness consequences of double brooding.

METHODS

Study species

The Eurasian Hoopoe is a long-distance migratory bird that overwinters in sub-Saharan Africa (Bächler *et al.* 2010). In our study area, Hoopoes arrive on the breeding grounds by the end of March, where they start breeding at the end of April. They are secondary cavity breeders that depend on relatively large cavities. The annual survival probability of adults is about 0.4 (Schaub *et al.* 2012), making the Hoopoe a relatively short-lived species. Although both parents contribute to raising the brood, only females incubate the eggs and distribute the food collected by males. Males feed brooding females and the young until they are independent (Bussmann 1950, Martín-Vivaldi *et al.* 1999a). Only when the nestlings are older than about 10 days do females stop brooding and start hunting for prey. Females may leave the brood before the chicks fledge to start a second clutch, often with a new partner (43% within-season mate-switching in our study area). Second clutches are often laid at a different place from the first clutch, and within-season breeding dispersal is thus common (Bötsch *et al.* 2012).

Study area and data collection

The study was carried out on the plain of the upper Rhône valley between Sierre and Vernayaz (Valais, Switzerland, 46°14'N, 7°22'E) from 2002 to 2012. Intensive agriculture, consisting mainly of fruit trees, vegetable plantations and vineyards, characterize the 64-km² study area. Since 2002, about 700 nestboxes have been placed in pairs at 350 locations in the study area (Arlettaz *et al.* 2010a,b). Due to a lack of natural nesting cavities, Hoopoes breed almost exclusively in these nestboxes. After a rapid increase, the population has remained fairly constant at about 80 breeding pairs over the last 8 years.

In each of the 11 study years, all nestboxes were checked every 2 weeks from the end of April to the beginning of August. Occupied nestboxes were checked every third day to record clutch size, hatching date, and number of nestlings and fledglings. All fledglings were ringed between day 15 and 18 after hatching. Adults were captured no earlier than 4 days after hatching of the nestlings, either with mist-nets or clap-traps, or they were taken directly from the nestbox by hand. Capture efficiency was very high, with > 90% of adults with hatchlings being caught. Adults were classified as in their first year (second calendar year) or older based on moult (P. Mosimann-Kampe unpubl. data) and sexed by the size of the uropygial gland (Martín-Vivaldi *et al.* 2009), and their tarsus length was measured. We used the occupation frequency of each nestbox over all 11 years as a measure of territory quality (Tschumi *et al.* 2014). The number of first clutches per year was taken as a measure of population density, and the number of ringed fledglings as a measure of the success of a brood. The annual breeding success is the total number of fledglings produced by an individual per breeding season. The lifetime production of fledglings is the total number of fledglings produced by an individual over its lifetime. Lifetime reproductive success of an individual was defined as the total number of recruits (i.e. fledglings that returned to the study site to breed and were recaptured) that it produced.

Data analysis

A first clutch was defined as the first clutch of an individual in a given breeding season. A second clutch was defined as a clutch following a

successful first clutch (i.e. that produced at least one fledgling) in the same breeding season, regardless of whether the second brood was successful. If the first clutch was unsuccessful (i.e. produced no fledglings), the new clutch was termed a replacement clutch. The hatching dates of first (mean \pm sd, 150.17 ± 19.67 , $n = 452$) and replacement broods (mean \pm sd, 145.89 ± 19.78 , $n = 37$) did not differ (t -test, $t = 1.27$, $df = 42$, $P = 0.21$). Replacement clutches (< 2% of all clutches) were therefore treated as first clutches. In 1 year an individual may be single brooded, and in another double brooded. Due to the high rate of within-season mate-switching, a clutch could be the first clutch of the male, but the second clutch of the female or vice versa. To avoid inconsistent definitions of clutches, we therefore performed most analyses using the individual as the replicate rather than the clutch, and conducted analyses separately for females and males.

Estimation and modelling of the probability of double brooding is often challenging because it requires capturing all adults at their first and possible second clutch (Cornulier *et al.* 2009). Complete capture incorporates the detection of the clutch and the capture or at least the identification of the adults. Imperfect capture typically results in an underestimation of the probability of double brooding. In our study, there were almost no other breeding locations than the nestboxes (Arlettaz *et al.* 2010b) and thus the risk of missing broods is very low. Nevertheless, the capture probability of single- and double-brooded adults is around 0.9 in the study site (Schaub *et al.* 2012) and some breeders remained undetected because the brood failed before the nestlings hatched. Therefore, the true probability of double brooding is slightly underestimated.

We used generalized linear mixed models (GLMMs) to evaluate the impact of explanatory variables on the causes and consequences of double brooding. Individual identification number (ID) was included as a random effect in all models to account for pseudo-replication as some individuals appear several times (in different years) in the dataset. Furthermore, year was included as a random effect to account for differences in the frequency of double brooding among years. All analyses were performed with R (R Development Core Team 2004) using libraries lme4 (mixed models), arm and sim (both for computing se) and MuMIn (model selection). For each analysis a

global model was defined including all explanatory variables. We then fitted all possible nested models, ranked them according their AIC_c value (small sample size-adjusted Akaike's information criterion, Burnham & Anderson 2002) and calculated predictions under each model. We then averaged these predictions based on AIC weights across the best (Δ AIC_c of < 4) models. Confidence intervals for predictions were calculated from 1000 simulations using the package sim (Gelman & Hill 2007).

Whether an individual produced a second clutch (no: 0; yes: 1) in a season was modelled with a binomial error structure and a logit link function. Fixed effects included individual traits (age and tarsus length of the parent), characteristics of the first brood (hatching date, number of fledglings, territory quality) and population density in the respective year. The pair-wise correlations between the continuous variables fledgling number, hatchling number, territory quality and tarsus length were between -0.26 and 0.12 , so there was no indication of problems due to collinearity.

To study the fitness consequences of double brooding we evaluated whether the number of fledglings and their recruitment probability differed between single-brooded individuals and the first and second clutches of double-brooded individuals. The number of fledglings was modelled with a GLMM with a Poisson error structure and a log link function, and the recruitment probability was analysed with a GLMM with a binomial error structure and a logit link function. The classification of whether fledglings belonged to a single, first or second clutch was based on the identification of the female. Therefore, only clutches for which the female was identified were included. As adults that failed before the hatching were not captured, these results are an overestimation of success. For each analysis, the global model contained the main effects clutch status, hatching date, territory quality, population density, and the interaction between hatching date and clutch status. The interaction was included to evaluate whether the change in the number of fledglings or their recruitment probability with hatching date was different in single, first and second clutches. Individual ID and year were again included as random factors. For the analysis of the recruitment probability, clutches from 2012 were not included, as recruitment data are incomplete for these offspring.

We estimated lifetime production of fledglings (LF) as the total number of fledglings that an individual raised over its lifetime in the study area and lifetime reproductive success (LRS) as the total number of fledglings that were caught at least once in a later year in the study area across an individual's lifetime. Both were related to the proportion of second clutches produced by this individual. LRS is likely to be more strongly correlated with fitness than LF because the former captures additional variation originating from differential survival. However, previous work has shown that only about half of the surviving fledglings settle in the study area (Schaub *et al.* 2012), and thus LRS as estimated here is underestimated. Yet, provided double brooding does not impact natal dispersal, this will not lead to incorrect inferences. Sample sizes differ between analyses because data for certain covariates were missing in some individuals.

RESULTS

Our dataset comprised 1323 clutches, and from 1121 of these at least one adult was known (both adults were known for 861 clutches, only the female for 207 and only the male for 53). The total number of adults was 1049 (555 females; 494 males). Overall, 36% (269 of 758 clutches) of females and 21% (147 of 688 clutches) of males produced a second clutch. The mean hatching date of single-brooded females was 30 May (sd: 19.7 days, $n = 489$), whereas first and second clutches of double-brooded females hatched on average on 11 May (sd: 10.1 days, $n = 269$) and 23 June (sd: 11.9, $n = 269$, Fig. 1), respectively. As indicated by these standard deviations, the variance in hatching date of single-brooded females was much higher than that of double-brooded females. As a consequence, there was a large fraction of single-brooded females that hatched their clutches at the same time as the first clutches of double-brooded individuals (Fig. 1).

Factors affecting probability of double brooding

The ranking of the 64 candidate models for the probability of female and male double brooding identified eight and 12 models that had a $\Delta AIC_c < 4$, respectively (Table 1), giving a cumulative weight of 0.84 and 0.90, respectively. Hatching date of the first clutch and the number

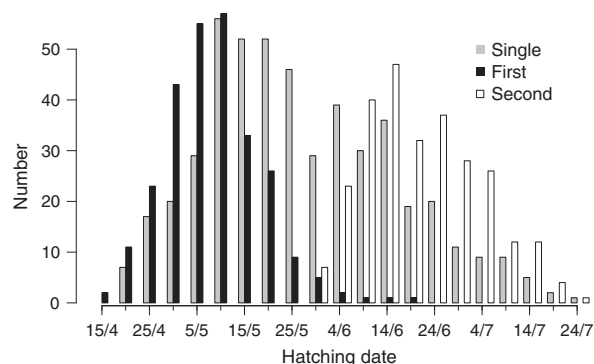


Figure 1. Frequency distribution of hatching dates of single-brooded female Hoopoes ($n = 489$) and of the first and second clutches in double-brooded females ($n = 269$).

of fledglings of the first clutch were the most important factors associated with double brooding in both sexes, as they were included in all top models. The model-averaged probability of laying a second clutch increased with the number of fledglings in the first clutch (Fig. 2a) but was lower for later hatching date of the first clutch (Fig. 2b). Females whose clutches hatched before 20 May had a probability higher than 0.5 of initiating a second clutch, whereas females whose first clutch hatched after 31 May rarely started a second clutch. Additionally, female age was present in all but one of the top models, with the probability of double brooding being higher in older females. Male age had little effect (Fig. 2). Territory quality and population density were present in many of the top models, but their effects were relatively small. The probability of double brooding increased slightly with territory quality and declined with increasing population density (Fig. 2c,d). Tarsus length was absent in most top models for either sex, and parameter estimates were all close to zero, suggesting this was of negligible importance in shaping variation in double brooding. The temporal variance of the probability of double brooding was 0.061 in females and 0.000 in males. For older females this means that the probability of producing a second clutch varied little over the 11 study years from 0.29 (se: 0.09) in 2012 to 0.40 (se: 0.11) in 2006.

The effect of female age on the probability of double brooding may be due to increasing experience with age, or to individuals of higher intrinsic quality being more likely to live beyond their second calendar year. To evaluate which is the more likely explanation, we analysed a reduced dataset

Table 1. Parameter estimates and standard error (parentheses) from the best GLMMs explaining variation in the probability of double brooding in female ($n = 705$) and male ($n = 656$) Hoopoes. The models are ordered by their support from the data, with the best model at the top for each sex. The number of estimated parameters (np), the model deviance, the difference in the AIC_c between the current and the best model (ΔAIC_c), and the AIC_c weights (ω_i) are given for each model. The intercept refers to second-year birds and the age to the difference between second-year and after second-year birds. Individual ring number and year were included as random factors in all models. Shown are the top models ($\Delta\text{AIC}_c < 4$) of the 64 candidate models of each sex. See Supporting Information Tables S1 and S2 for the ranking of all 64 candidate models.

Intercept	Age	Fledglings	Hatching date	Territory quality	Population density	Tarsus	np	Deviance	ΔAIC_c	ω_i
<i>Females</i>										
-1.247 (0.170)	0.486 (0.204)	0.300 (0.103)	-1.624 (0.166)	0.209 (0.106)	-0.236 (0.124)		8	-352.651	0.000	0.288
-1.199 (0.169)	0.460 (0.203)	0.318 (0.103)	-1.565 (0.161)	0.227 (0.105)			7	-354.416	1.484	0.137
-1.257 (0.169)	0.511 (0.202)	0.311 (0.102)	-1.655 (0.165)		-0.259 (0.123)		7	-354.528	1.709	0.123
-1.247 (0.170)	0.487 (0.204)	0.301 (0.103)	-1.624 (0.166)	0.209 (0.106)	-0.237 (0.124)	-0.018 (0.102)	9	-352.636	2.022	0.105
-1.058 (0.151)		0.276 (0.103)	-1.710 (0.167)	0.228 (0.106)	-0.228 (0.129)		7	-355.307	3.267	0.056
-1.198 (0.169)	0.461 (0.203)	0.319 (0.103)	-1.565 (0.161)	0.226 (0.105)		-0.018 (0.102)	8	-354.401	3.500	0.050
-1.257 (0.169)	0.512 (0.202)	0.312 (0.102)	-1.654 (0.165)		-0.260 (0.123)	-0.022 (0.101)	8	-354.507	3.712	0.045
-1.202 (0.170)	0.483 (0.201)	0.332 (0.101)	-1.595 (0.160)				6	-356.673	3.957	0.040
<i>Males</i>										
-1.908 (0.156)		0.357 (0.116)	-1.385 (0.179)	0.244 (0.120)			6	-275.761	0.000	0.194
-1.925 (0.158)		0.332 (0.119)	-1.424 (0.184)	0.228 (0.122)	-0.133 (0.115)		7	-275.111	0.742	0.134
-1.915 (0.157)		0.361 (0.117)	-1.382 (0.180)	0.240 (0.121)		0.092 (0.110)	7	-275.415	1.351	0.099
-1.853 (0.182)	-0.135 (0.227)	0.368 (0.118)	-1.404 (0.183)	0.252 (0.121)			7	-275.587	1.694	0.083
-1.916 (0.157)		0.385 (0.116)	-1.445 (0.180)			0.087 (0.111)	5	-277.857	2.154	0.066
-1.932 (0.159)		0.336 (0.119)	-1.420 (0.185)	0.225 (0.122)	-0.129 (0.115)		8	-274.810	2.190	0.065
-1.935 (0.159)		0.352 (0.118)	-1.487 (0.185)		-0.163 (0.114)		6	-276.881	2.239	0.063
-1.878 (0.185)	-0.114 (0.229)	0.341 (0.120)	-1.438 (0.187)	0.235 (0.123)	-0.129 (0.116)		8	-274.989	2.548	0.054
-1.856 (0.183)	-0.144 (0.228)	0.373 (0.119)	-1.402 (0.183)	0.248 (0.121)		0.095 (0.110)	8	-275.218	3.006	0.043
-1.924 (0.158)		0.389 (0.117)	-1.441 (0.181)			0.103 (0.110)	6	-277.430	3.338	0.037
-1.942 (0.160)		0.357 (0.119)	-1.482 (0.185)		-0.157 (0.115)	0.094 (0.111)	7	-276.526	3.572	0.033
-1.880 (0.185)	-0.123 (0.229)	0.347 (0.121)	-1.435 (0.187)	0.232 (0.123)	-0.124 (0.116)	0.089 (0.111)	9	-274.669	3.964	0.027

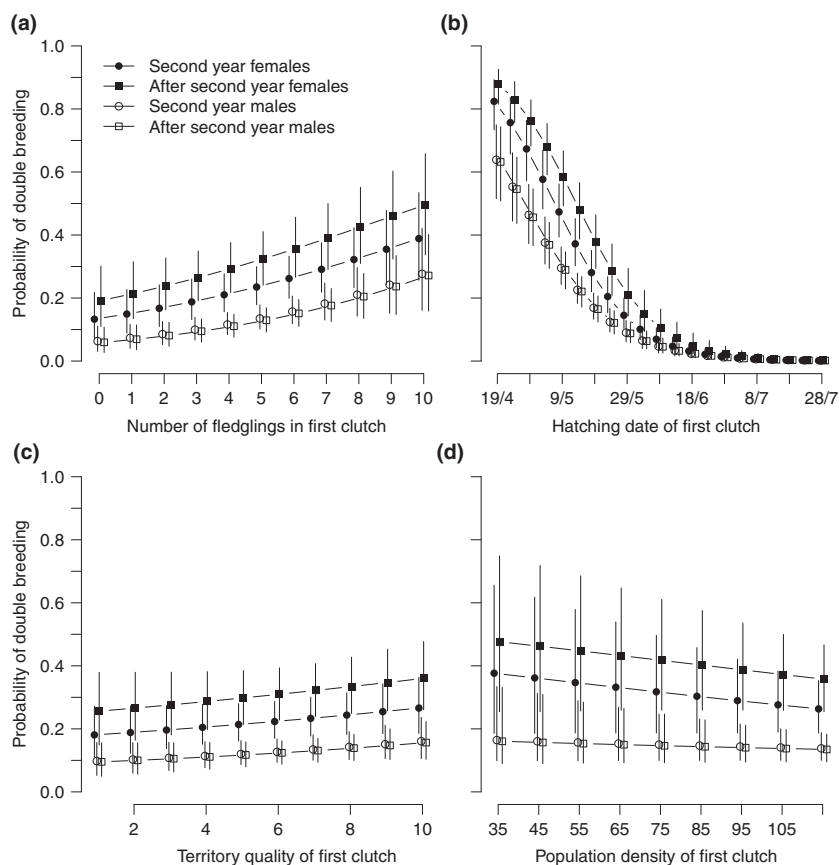


Figure 2. Model-averaged, predicted relationships between the probability of double brooding in Hoopoes and number of fledglings in the first clutch (a), hatching date of the first clutch (b), territory quality of the first clutch (c) and population density (d). The symbols show the model-averaged predictions across the top models for each sex and age class (Table 1). The vertical lines indicate the 95% confidence intervals.

of females that were captured in their second year of life and at least in one further year. We fitted the structurally identical model as the best one from Table 1 and an additional model without an age effect to these data. The latter model was preferred (ΔAIC_c : 1.68, evidence ratio = 5.37, $n = 248$), indicating that age was of little importance when considering only females that became at least 3 years old. The mean probability of double brooding in these females was 0.37 (se: 0.05). Overall, this suggests that the observed age effect in the complete dataset was induced by differential intrinsic quality rather than by a gain in experience.

Consequences of double brooding

Fledging success

Double-brooded females produced on average 9.1 (se: 1.9, $n = 269$) fledglings per year. They raised

more fledglings in their first (mean \pm se, 5.41 ± 1.96 , $n = 269$) than in their second clutch (3.69 ± 1.77 , $n = 269$). Single-brooded females produced an intermediate number of fledglings (4.46 ± 2.10 , $n = 489$). The difference between the number of fledglings from the first clutch of single- and double-brooded birds may be due in part to a seasonal decline in fledgling numbers (Arlettaz *et al.* 2010a). Yet, even if only clutches are included that hatched around the same time as the first clutch of double-brooded females (before 30 May), the number of fledglings of single-brooded females was lower (4.77 ± 2.25 , $n = 270$) than that of double-brooded females (5.43 ± 1.97 , $n = 258$).

The ranking of the 20 candidate models for the number of fledglings resulted in six models with $\Delta AIC_c < 4$ (Table 2). These models had a cumulative weight of 0.97. Hatching date and population density were included in all of these top models, indicating that their effects were strongly

Table 2. Parameter estimates and standard error (parentheses) from the best models explaining variation in the number of Hoopoe fledglings using GLMMs with Poisson error structure ($n = 1027$). Shown are the best models ($\Delta AIC_c < 4$) of the 20 candidate models. The number of estimated parameters (np), the model deviance, the difference in the AIC_c between the current and the best model (ΔAIC_c) and the AIC_c weights (ω_i) are given for each model. The intercept refers to single clutches, clutch status (1) to the difference between single and first clutches, and clutch status (2) to the difference between single and second clutches. Individual ring number and year are included as random factors in all models. See Table S3 for the ranking of all 20 candidate models.

Intercept	Clutch status (1)	Clutch status (2)	Hatching date	Territory quality	Population density	Hatching date × clutch status (1)	Hatching date × clutch status (2)	np	Deviance	ΔAIC_c	ω_i
1.478 (0.028)	0.087 (0.065)	0.121 (0.070)	-0.128 (0.025)	0.025 (0.015)	-0.069 (0.019)	0.002 (0.064)	-0.170 (0.066)	10	-537.731	0.000	0.354
1.475 (0.028)	0.086 (0.065)	0.121 (0.070)	-0.130 (0.025)		-0.071 (0.019)	-0.006 (0.065)	-0.164 (0.066)	9	-539.101	0.701	0.250
1.487 (0.022)			-0.173 (0.015)	0.024 (0.015)	-0.073 (0.019)			6	-542.934	2.270	0.114
1.474 (0.027)	0.069 (0.038)	-0.020 (0.046)	-0.150 (0.022)	0.022 (0.015)	-0.070 (0.019)			8	-541.158	2.778	0.088
1.487 (0.022)			-0.175 (0.015)		-0.075 (0.019)			5	-544.272	2.923	0.082
1.471 (0.027)	0.075 (0.038)	-0.015 (0.046)	-0.152 (0.022)		-0.072 (0.019)			7	-542.256	2.943	0.081

supported by the data. Clutch status, the interaction between hatching date and clutch status, and territory quality were included in the overall best model but appeared only in half of the top models, indicating that they were less strongly supported by the data than hatching date and population density.

The number of fledglings declined with hatching date and was inversely related to population density (Fig. 3a,c). The number of fledglings

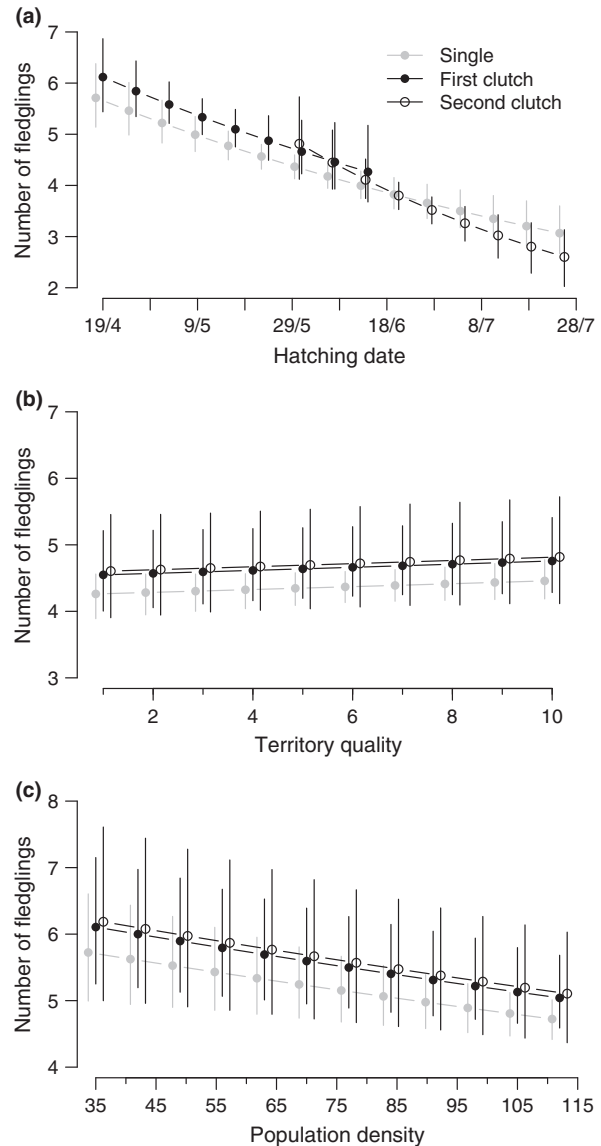


Figure 3. Model-averaged number of Hoopoe fledglings from clutches of single-brooded females and from first and second clutches of double-brooded females in relation to hatching date (a), territory quality (b) and population density (c, $n = 1027$). The vertical lines indicate the 95% confidence intervals.

tended to be higher in first clutches of double-brooded females than in clutches of single-brooded females; however, the difference was small and the confidence intervals overlapped. The interaction between hatching date and clutch status was weak but indicated that the seasonal decline in the number of fledglings was strongest in second clutches (Fig. 3a). The number of fledglings increased only slightly with territory quality (Fig. 3b).

Recruitment

Mean recruitment probability was 0.087 (se: 0.006, *n* = 391) for fledglings of single-brooded females, 0.106 (se: 0.008, *n* = 248) for fledglings from first clutches of double-brooded females and 0.067 (se: 0.008, *n* = 229) for fledglings of second clutches. If only early clutches (hatching date before May 30) are included, recruitment of fledglings from single-brooded females was virtually identical (mean ± se: 0.100 ± 0.009, *n* = 211) to that of double-brooded females (0.102 ± 0.008, *n* = 237).

Ten of the 20 candidate models appeared as top models ($\Delta AIC_c < 4$) and had a cumulative weight of 0.96 (Table 3). Hatching date was included in all top models, while the clutch status appeared in six and the interaction between hatching date and clutch status in four of the top models. Population density appeared in the best model but it had low relative importance over all top models. Similarly, although territory quality was present in four models, it had low relative importance.

The recruitment probability of the fledglings declined with hatching date (Fig. 4a). This seasonal decline was almost identical in the three types of clutches. Recruitment probability also tended to decline slightly with increasing population density (Fig. 4c) and to increase with increasing territory quality (Fig. 4b). All these trends were small and the confidence intervals wide, suggesting that they were of relatively little importance.

The total number of fledglings (LF) and of local recruits (LRS) that an individual produced over its lifetime correlated positively with the proportion of its clutches that were second clutches (female LF: correlation coefficient = 0.53, *P* < 0.001, *n* = 550; female LRS: correlation coefficient = 0.31, *P* < 0.001, *n* = 550; male LF: correlation coefficient = 0.54, *P* < 0.001, *n* = 482; male

Table 3. Parameter estimates and standard error (parentheses) from the best models of variation in recruitment probability of Hoopoe fledglings, using GLMMs with binomial error structure (*n* = 868). Shown are the top models ($\Delta AIC_c < 4$) of the 20 candidate models. The number of estimated parameters (np), the model deviance, the difference in the *AIC_c* between the current and the best model (ΔAIC_c), and the *AIC_c* weights (ω_i) are given. The intercept refers to single clutches, clutch status (1) to the difference between single and first clutches, and clutch status (2) to the difference between single and second clutches. Individual ring number and year were included as random factors in all models. See Table S4 for the ranking of all 20 candidate models.

Intercept	Clutch status (1)	Clutch status (2)	Hatching date	Territory quality	Population density	Hatching date × clutch status (1)	Hatching date × clutch status (2)	np	Deviance	ΔAIC_c	ω_i
-2.716 (0.297)			-0.276 (0.063)		-0.340 (0.230)			5	-394.680	0.000	0.218
-2.607 (0.320)			-0.273 (0.063)					4	-395.692	0.000	0.218
-2.607 (0.319)			-0.263 (0.064)	0.067 (0.059)				5	-395.033	0.706	0.153
-2.715 (0.297)			-0.266 (0.064)	0.066 (0.059)	-0.335 (0.230)			6	-394.049	0.766	0.149
-2.613 (0.320)	0.261 (0.220)	0.445 (0.287)	-0.250 (0.107)			0.240 (0.235)	-0.506 (0.301)	8	-393.272	3.283	0.042
-2.720 (0.300)	0.254 (0.220)	0.448 (0.287)	-0.254 (0.108)		-0.330 (0.227)	0.235 (0.234)	-0.505 (0.301)	9	-392.292	3.364	0.041
-2.605 (0.319)	0.270 (0.219)	0.447 (0.287)	-0.240 (0.107)	0.082 (0.060)		0.270 (0.234)	-0.528 (0.302)	9	-392.332	3.444	0.039
-2.710 (0.300)	0.263 (0.219)	0.450 (0.287)	-0.243 (0.107)	0.080 (0.060)	-0.322 (0.227)	0.264 (0.234)	-0.527 (0.302)	10	-391.392	3.611	0.036
-2.621 (0.326)	0.041 (0.138)	0.011 (0.191)	-0.264 (0.092)					6	-395.647	3.962	0.030
-2.730 (0.304)	0.039 (0.138)	0.016 (0.191)	-0.268 (0.092)		-0.339 (0.230)			7	-394.639	3.978	0.030

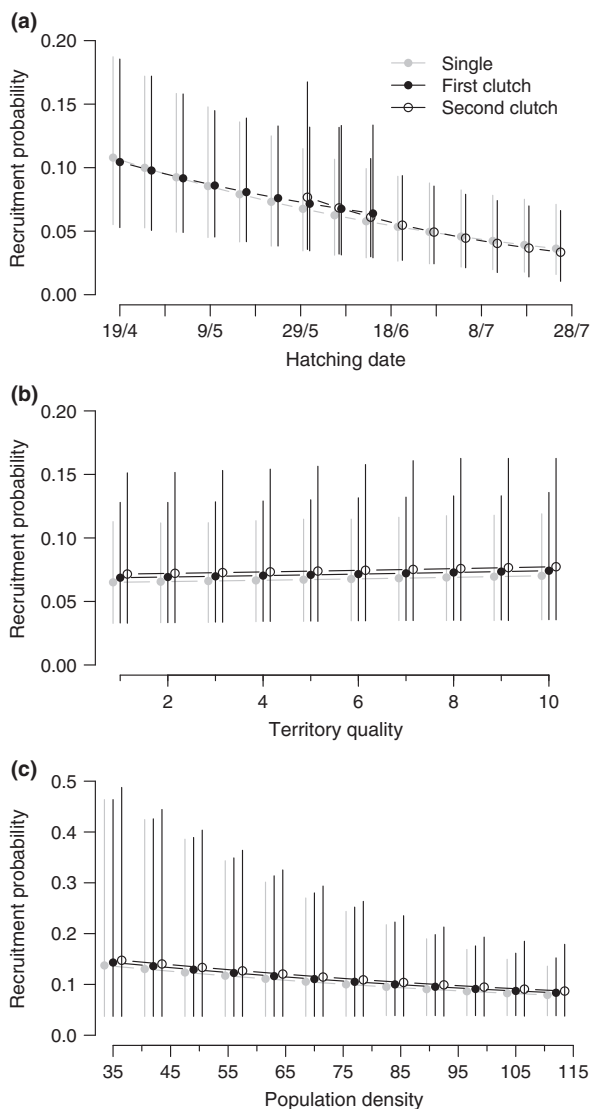


Figure 4. Model-averaged recruitment probability of Hoopoe fledglings from clutches of single-brooded females and from first and second clutches of double-brooded females in relation to hatching date (a), territory quality (b) and population density (c, $n = 868$). The vertical lines indicate the 95% confidence intervals.

LRS: correlation coefficient = 0.30, $P < 0.001$, $n = 482$). Females that never had two clutches in a season produced on average 5.01 fledglings (sd: 2.90) resulting in 0.36 local recruits (sd: 0.64; male LF: 5.84 (sd: 3.97), male LRS: 0.45 (sd: 0.75)), whereas females that initiated second clutches every year produced 11.07 (sd: 5.70) fledglings resulting in 0.93 local recruits (sd: 1.25; males LF: 11.08 (sd: 4.90), male LRS: 0.78 (sd:

1.00)) on average. From a total of 4627 fledglings that females raised, 992 (21%) fledged from second clutches. Females raised in total 370 local recruits, of which 62 (17%) fledged from second clutches. Males raised 4006 fledglings (610 (15%) from second clutches), of which 334 recruited locally (40 (12%) originated from second clutches).

DISCUSSION

Double brooding was common in our study population: in a given breeding season, approximately one-third of the females and one-fifth of the males produced second clutches, and these proportions were fairly constant across years. The most important factors associated with whether Hoopoes lay a second clutch are the timing of and the number of fledglings in their first clutch: the earlier the first clutch and the more fledglings it produced, the higher the probability of a second clutch. Although the number of fledglings declined seasonally, double-brooded individuals produced more fledglings. The recruitment probability of fledglings did not differ between single- and double-brooded females, or between first and second clutches, but showed a tendency to decline seasonally. On the whole, this resulted in individuals that produced more second clutches having a higher lifetime production of fledglings and higher lifetime reproductive success.

Factors influencing double brooding

The timing of the first clutch was the most important predictor of double brooding. The earlier in the year a first clutch was laid, the higher the probability of a second clutch. This finding accords with results from many previous studies (Stouffer 1991, Odgen & Stutchbury 1996, Verboven & Verhulst 1996, Verboven *et al.* 2001, Brinkhof *et al.* 2002, Parejo & Danchin 2006, Husby *et al.* 2009, O'Brien & Dawson 2012), including a study of a Spanish Hoopoe population (Martín-Vivaldi *et al.* 1999a). The importance of timing is most likely an effect of seasonally changing food availability (Grüebler *et al.* 2008, Husby *et al.* 2009, Wilson *et al.* 2013). However, although the timing of the first clutch was the most important factor affecting the probability of double brooding, a substantial number of individuals that produced their first clutch early did not have a second clutch.

This suggests that in addition to time, other factors must be involved, for example variation in phenotypic (e.g. foraging ability) or environmental quality (e.g. food availability in territories).

In migratory species such as the Eurasian Hoopoe, early breeding is only possible for individuals that arrive early on the breeding grounds. The arrival date on the breeding grounds depends on both the timing of departure from the wintering grounds and the speed of migration. These may depend on environmental conditions such as food supply and weather. Individuals in good condition (e.g. healthy, low parasite loads, large fat deposits) can travel faster and are more successful at withstanding harsher environmental conditions early in the breeding season (Francis & Cooke 1986, Møller *et al.* 2004, Sergio *et al.* 2007). This suggests that effects experienced in the wintering grounds or on migration may carry over to the annual reproductive output via timing of reproduction and the initiation of second clutches. Studies that link migration trajectories of individuals (Bächler *et al.* 2010) with their reproductive performance are needed to test this hypothesis.

The second most important factor determining double brooding was the number of fledglings from the first clutch. Previous studies either found a negative relationship between the number of fledglings in the first clutch and the probability of double brooding (Stouffer 1991, Verboven & Verhulst 1996, Nagy & Holmes 2005a, Parejo & Danchin 2006) or found no relationship (Odgen & Stutchbury 1996, Brinkhof *et al.* 2002). A decline in the probability of double brooding with increasing size of the first clutch has been explained by the elongation of the inter-clutch interval with increasing number of fledglings in the first clutch (Drent & Daan 1980, Verboven & Verhulst 1996). A higher number of fledglings increases the energy demand on the parents through a higher food provisioning rate and a longer period of post-fledging parental care. Thus, raising more young in the first clutch is often associated with costs that influence whether a second clutch can be raised. However, we found a contrasting pattern in this Swiss Hoopoe population. The larger the size of the first brood, the more likely it was that Hoopoes started a second clutch. This result is not an artefact due to the timing of the clutches, as the timing of the clutch was accounted for in the models.

Although the inter-clutch interval increased with brood size in a Spanish Hoopoe population

(Martín-Vivaldi *et al.* 1999a), in our study population the relationship between a female's inter-clutch interval and the size of her first brood was weak and negative (linear regression model; slope \pm se: -0.008 ± 0.005 , $P = 0.08$, $n = 270$). Because individual fledglings of large broods would be expected to receive less care until independence than fledglings of small broods, one might expect fledglings from large broods to be of lower quality. Yet fledglings from first clutches of double-brooded individuals had the same recruitment probability as fledglings from first clutches of single-brooded individuals. We consider that the positive relationship between number of fledglings in the first clutch and probability of double brooding suggests differences in phenotypic or environmental quality between single- and double-brooded individuals. This conclusion is supported by strong individual differences in adrenocortical stress response in female Hoopoes from the same population (Schmid *et al.* 2013). Females with low reproductive success showed a higher adrenocortical stress response than those with high reproductive success. Moreover, the age effect on the probability of double brooding appears to be due to differences in individual quality in females. Finally, the length of song strophes in males, a measure of individual quality, was positively related with the frequency of double brooding in a Spanish Hoopoe population (Martín-Vivaldi *et al.* 1999b). It appears therefore that high-quality individuals (or those that are present in a high-quality territory) are able to raise larger broods without compromising the quality of their offspring and are still able to produce a second clutch compared with individuals of lower quality (or inhabiting a lower quality territory) that raise a brood at the same time.

The probability of double brooding was inversely related to population density. However, the effect was weak and perhaps not ecologically relevant. Furthermore, territory occupancy, our measure of territory quality, had a positive effect on the incidence of double brooding (Tschumi *et al.* 2014), but the effect was again relatively weak. Finally, although the probability of raising a second clutch often varies strongly in facultative double brooders between years (Verboven & Verhulst 1996, Brinkhof *et al.* 2002) in response to variable food availability (Nagy & Holmes 2005a, O'Brien & Dawson 2012), the temporal variation in the probability of double brooding was low in

Hoopoes. This suggests that either the relevant environmental factors (such as weather, temperature and food availability) varied little between years, or that individual rather than environmental factors affected the decision to double brood.

The difference in the probability of double brooding between females and males could be an artefact of the slightly lower recapture rate of males than of females (Schaub *et al.* 2012), resulting in the probability of double brooding in males being underestimated. However, the difference in the recapture rate was small and therefore it is unlikely to be the sole explanation. Alternatively, it could originate from a biased sex ratio in the population. If there are more males than females, there is stronger competition among males for females, which would result in a reduced probability of double brooding in males. However, although male-biased population sex ratios have been found frequently in other species (Donald 2007), the sex ratio of fledgling Hoopoes is even (Schaub *et al.* 2012) and the apparent survival probabilities are very similar in both sexes (Schaub *et al.* 2012).

Quality vs. date hypothesis

A seasonal decline of clutch size and other components of reproductive performance (including double brooding) is very common in birds (Klomp 1970, Hochachka 1990). Hence it is unsurprising that the probability of producing a second clutch, as well as the number of Hoopoe fledglings per brood and their recruitment probability, declined during the season. This decline may be caused by population-level effects, where seasonal trends in food availability affect all individuals in the same way (date hypothesis), or by differences in quality of the individuals or in the territory they occupy (quality hypothesis, Hochachka 1990, Verhulst *et al.* 1995). In our study, the number of fledglings and the recruitment probability of first and second clutches declined with hatching date at almost the same rate (Figs 3 & 4), supporting the date hypothesis. Moreover, the seasonal decline of recruitment probability of fledglings from single-brooded individuals was also identical to that of double-brooded individuals, again supporting the date hypothesis. However, the number of fledglings from single-brooded individuals was lower than that of double-brooded individuals, so there is some evidence in support of both hypotheses.

Costs and benefits of double brooding

Double-brooded Hoopoes achieved higher numbers of fledglings and of recruits compared with conspecifics that bred only once in a breeding season. The fact that, despite its benefits in terms of reproductive success, not all individuals produce second clutches suggests that double brooding is costly and that only some individuals can afford these costs. Indeed, reduced survival of fledglings from the first clutch (Smith & Marquiss 1995), reduced survival of parents (Bryant 1979, Verhulst 1998) and lower reproductive success of the parents in the next breeding season (Hamel *et al.* 2009) are known costs of double brooding in other species. However, here we found no evidence for a reduced success of first clutches followed by a second clutch. Furthermore, survival is positively correlated with annual number of raised fledglings (Bötsch *et al.* 2012), such that individuals that were double brooded had on average higher survival than single-brooded individuals. Such positive relationships between reproduction and survival are rare and could indicate a seasonal matching between quality of the individual and quality of the habitat (Gunnarsson *et al.* 2005).

CONCLUSION

Timing of reproduction was a major determinant of individual reproductive performance of Eurasian Hoopoes. Most of the seasonal decline in reproductive performance was probably caused by seasonal changes in resources to which all individuals are similarly sensitive. Further studies should test which resources change seasonally and how the timing of reproduction is affected by the timing and conditions of migration. Despite significant advantages of double brooding, not all Hoopoes produced a second clutch after a successful first clutch, even if they had enough time to do so. This suggests differences in phenotypic or environmental quality. As found in other studies (Hochachka 1990, Verhulst *et al.* 1995), we conclude that reproduction of Hoopoes is affected by both the date and individual quality.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Parameter estimates and standard error (parentheses) from all 64 candidate models explaining variation in the probability of double brooding in Hoopoe females ($n = 705$, Binomial GLMM).

Table S2. Parameter estimates and standard error (parentheses) from all 64 candidate models explaining variation in the probability of double brooding in Hoopoe males ($n = 656$, Binomial GLMM).

Table S3. Parameter estimates and standard error (parentheses) of the 20 candidate models explaining variation in the number of Hoopoe fledglings with a GLMM with Poisson error structure ($n = 1027$).

Table S4. Parameter estimates and standard error (parentheses) of the 20 candidate models explaining variation in recruitment probability of Hoopoe fledglings with a GLMM with Binomial error structure ($n = 868$).