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POPULATION ECOLOGY – ORIGINAL RESEARCH

Hoopoe males experience intra-seasonal while females experience inter-seasonal reproductive costs

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Abstract

Reproductive and survival costs due to reproductive investment are a central element for the evolution of life histories. Both intra- (reduction of reproductive performance of second brood due to investment in first brood) and inter-seasonal costs (reduction of reproductive performance or annual survival due to reproductive investment in preceding year) may appear in multiple breeding species. Knowledge about how trade-offs within and between seasons shape individual trajectories and influence fitness are crucial in life-history evolution, yet intra- and inter-seasonal reproductive costs are rarely analysed simultaneously. We investigated sex-specific differences in intra- and inter-seasonal reproductive and survival costs in response to previous reproductive effort in a monogamous, double-brooding bird, the hoopoe (*Upupa epops*), accounting for heterogeneity in individual and annual quality. Intra-seasonal reproductive costs were detected in males and inter-seasonal reproductive and survival costs were detected in females. In males, the probability of being a successful double breeder was negatively correlated with the number of hatchlings produced in the first brood. In females, the number of fledglings raised in the first brood was negatively correlated with the reproductive effort in the preceding season. Female annual survival was also negatively influenced by the number of broods produced in the previous reproductive season. Most of these reproductive costs were detected only in years with low productivity, suggesting that costs become evident when environmental conditions are harsh. Our results illustrate how different investment in current vs. future reproduction and survival shape different life-history strategies in males and females of a monogamous bird species.

Keywords Double-breeding · Environmental conditions · Individual quality · Trade-off · *Upupa epops*

Introduction

Individuals have to allocate the energy they obtain from food resources between different activities such as maintenance, growth and reproduction (Cody 1966). As a consequence, a high reproductive expenditure in a given year is expected to negatively influence survival or reproductive success in the following years (Williams 1966; Drent and Daan 1980). Within a given year, some species have the possibility to increase their annual reproductive success by having successive reproductive attempts (Holmes et al. 1992). The success of a second attempt may be negatively influenced by the reproductive effort made in the first reproduction of the season (intra-seasonal costs Tinbergen 1987; Grüebler and Naer-Daenzer 2008) but also by the reproductive effort made in the preceding reproductive season (inter-seasonal costs Nur 1988; Festa-Bianchet et al. 1998). Intra- and inter-seasonal costs are often analysed independently. However,

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intra-seasonal costs can mask inter-seasonal costs and thus both costs need to be investigated together.

The decision of investing in a second reproductive attempt depends on the reproductive value of this second attempt relative to future ones (Hamilton 1966; Andersson et al. 1980). The magnitude of intra-seasonal costs should decrease with the relative reproductive value of the current reproductive season. If the current reproductive value is high, reproductive costs can be delayed and influence individual performance in the following reproductive season or can also accumulate and influence late-life reproduction and/or survival (Kirkwood and Rose 1991). Nevertheless, intra- and inter-seasonal costs can occur together for an optimal allocation of energy to each demanding activity. Their relative magnitude may depend on life-history tactics, individual quality and resource limitation.

The occurrence of both intra- and inter-seasonal costs has been demonstrated experimentally but mostly independently from each other. The probability of being a double-breeder decreased in great tits (Parus major) when the first brood had been enlarged (Tinbergen 1987). Inter-seasonal costs have also been found in this species with higher reproductive success in the year following the experimental removal of the second brood (Verhulst 1998). However, evidence from unmanipulated field experiments is mixed (Roff 1992; Stearns 1992; Parejo and Danchin 2006).

Ambiguous results likely occurred because the expressions of reproductive costs may depend on environmental conditions and may vary according to individual quality (Santos and Nakagawa 2012; Bleu et al. 2016). If the environmental conditions are favorable, reproductive costs may be absent because individuals can accumulate enough energy to cover them in successive years. Trade-offs may thus become observable when the environment becomes rapidly unfavorable (Hamel et al. 2010; Tavecchia et al. 2005). When per-capita resources are scarce and the gathered energy has to be shared between survival and reproduction or between successive reproductive attempts, reproductive costs may appear. Furthermore, individuals differ in quality. van Noordwijk and de Jong (1986) showed how variable individual assimilation of resources can result in variable amount of energy available to different individuals. High-quality individuals can allocate more energy to reproduction and survival than low-quality individuals. If variability in individual quality is large, positive correlations between current and future reproduction or survival are typically found (Bérubé et al. 1999; Weladji et al. 2008).

Patterns of reproductive costs are also expected to differ between sexes (Bleu et al. 2016). In polygynous species, males often suffer higher reproductive cost on survival than females as a consequence of sexual selection (Clutton-Brock and Isvaran 2007; Michener and Locklear 1990). In monogamous species with bi-parental care, the energy allocated by each sex is rarely known but different reproductive efforts are also expected to occur (Kokko and Jennions 2008). While females invest energy to produce eggs, males can invest energy in sperm competition (Monaghan and Nager 1997; Birkhead and Møller 1998) and territory defence to avoid extra-pair paternities which are common in many monogamous species (Griffith et al. 2002). In great tits and Eastern blue birds (*Sialia sialis*) for instance, annual survival of females only is reduced when the first brood has been enlarged (Verhulst 1998; Siefferman and Hill 2008). Sex-specific patterns of intra-seasonal costs on physiological condition have also been evidenced (Williams and Fowler 2015). However, because intra-seasonal cost are often analysed for a given pair, sex-specific intra-seasonal costs on the success of next reproductive attempts (second brood for instance) have rarely been investigated.

There is a need to understand how the interactions between individual quality, sex and environment influence intra- and inter-seasonal reproductive costs on next reproductive success and on survival (Santos and Nakagawa 2012; Lemaître et al. 2015; Bleu et al. 2016). We investigated sex-specific differences in reproductive costs in a monogamous, double brooding bird, the hoopoe (*Upupa epops*). This correlative analysis was performed while accounting for individual and annual quality. It is sometimes argued that reproductive costs are particularly difficult to observe using correlative traits because females adapt their clutch size to environmental conditions and resource availability (Nur 1988). However, reproductive costs can still be detected in correlative studies in males and, in females in the common situation when they cannot perfectly predict environmental conditions. Moreover, some individuals can take the risk of having larger clutches and cost may emerge in poor environments (Festa-Bianchet et al. 1998).

We tested the presence of an interaction between annual quality, individual quality and reproductive effort in each sex to understand how these factors influence brood success and adult survival. We defined individual quality as the fixed covariation between life-history traits that is positively linked to fitness (Wilson and Nussey 2010). As a measure of individual quality, we used the positive covariation between six morphological traits that is known to positively correlate with male and female reproductive success in hoopoes (Plard et al. 2017). Annual quality was defined as the mean annual productivity per individual. Because the reproductive success of first and second broods are highly correlated in hoopoes (Hoffmann et al. 2015), we expected to find stronger inter-seasonal reproductive costs on reproductive success and on subsequent survival than intra-seasonal reproductive costs. However, the study of Hoffmann et al. (2015) could hardly evidence reproductive costs because it did not take account of individual and annual quality. We nonetheless expected the reproductive costs to be evidenced

in low-quality individuals and in unfavorable years. Because more females than males are double-breeders (Hoffmann et al. 2015), we expected to find higher inter-seasonal reproductive costs in females than in males.

Materials and methods

Studied population

The hoopoe is a long-distance migrant that breeds in Europe from April to August. Hoopoes lay 6 (1–12) eggs per clutch, on average and can have two (exceptionally three) successful broods per season with different partners. This study was carried out in 2002–2016 on the plain of the Upper Rhône Valley (Central Valais, south-western Swiss Alps; 46°140N, 7°22E, 460–520 m altitude, 64 km^2). High-intensity farming had caused a dramatic decline of natural cavities that served as breeding sites for hoopoes, massively impacting population size. Since the late 1990s, however, the hoopoe population uses almost exclusively the hundreds of nestboxes that have been placed in the study area (Arlettaz et al. 2010b). These nestboxes were checked every second week during the breeding season from the end of April to the beginning of August. Nestboxes containing hoopoe broods were additionally checked every third to fifth day to record brood size, hatching date and numbers of hatchlings and fledglings. Adults were captured after hatching of the nestlings, ringed, aged [first-year breeder (1 year old) vs. adult (older than 1 year)] based on moult, sexed based on the size of the uropygial gland, and six morphological traits were measured (bill length, tarsus length, wing length, feathered crest length and lengths of the central tail feather and of the fifth primary feather). Appropriate ethical approval and licences were obtained each year from the Swiss Federal Office for the Environment.

Dependent variables potentially affected by reproductive costs

We investigated possible intra- and inter-seasonal costs of reproductive effort on reproductive success as well as cost of reproductive effort on parental survival. Intra-seasonal reproductive costs are defined as a decline of the reproductive success of the second brood with increasing effort in the first successful brood in the same breeding season. Inter-seasonal reproductive costs are defined as a decline of the current reproductive success with increasing reproductive effort in the previous breeding season. Finally, costs in terms of survival are defined as a decline in following annual parental survival with increasing reproductive effort.

Annual reproductive success is the total number of fledglings that a female or a male raised during a reproductive season. To investigate both intra- and inter-seasonal costs, we decomposed the annual reproductive success into two variables: the number of fledglings of the first brood and the number of fledglings of a potential (see below) second brood. To avoid any confusion between a replacement clutch and a second brood, the probability of raising a second brood is conditional on having a first successful brood. The number of fledglings of the second brood was 0 if the second brood was not successful or if no second brood was initiated. We defined the first brood either as the first successful brood of an individual or as the only breeding attempt of an individual. We assumed that all broods were conducted in nestboxes in our study area. Given the high recapture probability [0.86 (95% credible interval: 0.78; 0.91) and 0.86 (0.79; 0.92) for the analysis on males and females, respectively] and that there are hardly any suitable natural cavities in the study for hoopoe broods, we are confident that most birds breed in the nestboxes (Arlettaz et al. 2010b).

Independent variables used to study reproductive costs

The reproductive effort of a breeding attempt is often difficult to measure. In hoopoes, hatching is asynchronous so that one egg hatched per day, on average (Hildebrandt and Schaub 2017). Nestlings of a brood differ in size and thus have differential competitive abilities. When the delivered food is scarce, strong nestlings are never completely full and out-compete the weaker siblings, with the result that the latter may die, which is known as brood reduction strategy (Ricklefs 1965). Therefore, the loss of nestlings is likely to be linked to energetic constraints faced by provisioning parents. Nest predation hardly occurs in hoopoes in our study area because hoopoe produced a foul-smelling fluid that they use as a defence against mammalian nest predator (Martín-Vivaldi et al. 1999). Thus, for a given reproductive event we defined the number of hatchlings instead of the number of fledglings as an index of projected reproductive effort because the former corresponds to the minimal number of eggs that a female has produced and incubated, and represents the maximum number of nestlings the parents may feed. We used the number of hatchlings instead of the number of eggs because we expected that the effort to feed an additional hatchling is higher than the effort needed to incubate one more egg. As control, we also performed the same analyses in which the number of hatchlings had been replaced by the number of fledglings. The results were similar but effect sizes greater with the former, which justifies our choice. Thus, to study intra-seasonal costs, we used the number of hatchlings of the first successful brood to characterize reproductive effort.

To study inter-seasonal reproductive costs, we used the number of broods raised and the mean number of

hatchlings per brood in a given breeding season as two measures of reproductive effort. We did not use the total annual number of hatchlings because it does not account for the difference in reproductive effort made while raising one or several broods. Each supplemental brood requires for the male to defend a territory and to feed the female during incubation, and for the female to incubate the eggs. We used the mean number of hatchlings per brood to avoid collinearity with the number of broods. The number of broods raised also included the failed broods to account for the possible cost of laying a replacement clutch.

As a measure of individual heterogeneity in quality we used a principal component analysis on the above fixed morphological traits: bill length, tarsus length, wing length, feathered crest length and lengths of the central tail feather and of the fifth primary feather. As these six traits were strongly correlated, the first axis (PC1) explained 61% of the variation (Plard et al. 2017). PC1 is a good indicator of the overall size of an individual and is positively linked with male and female reproductive performance and with male annual survival (Plard et al. 2017). Individuals of each sex were allocated to two groups (small and large individuals). The separation was based on the median PC1 value for each sex. We did not use individual identity as a random effect as most individuals appeared only once or twice in each model (as the hoopoe is a short-lived species) and individual random effect explained only up to 5% of the variation in the number of fledglings of the first brood in both sexes.

We used the mean annual individual productivity estimated as the average annual number of fledglings produced per individual to measure annual quality. Mean annual individual productivity decreased by 30% since 2002 (Fig. S1). This decline in annual productivity was followed by a decline of the population size from 2006 onwards (Fig. S1). Thus, the decline in annual productivity was probably not caused by density-dependent mechanisms. Its reason remains unknown but it may have been caused by changes in the natural environment, human or even research activities. For illustrative purpose, we used the first and the third quartile of the distribution of mean annual individual productivity to predict effect sizes in years of "low" and "high" productivity, respectively.

Statistical analysis

65% of male and female partners changed between the first and second broods within a breeding season and 95% of partners change between breeding seasons, respectively. Annual reproductive successes of males and females that share one brood are thus often different. This allowed us to perform the analysis for each sex separately.

Costs on reproductive success

The numbers of fledglings of first and second broods were modelled with zero-inflated Poisson models (Table 1) in a frequentist framework using R (R Core Team 2014), the package pscl and the function zeroinfl(). The zero-inflated Poisson model is a mixture model including the product of a binomial and a Poisson variable. The binomial variable models the probability for the brood to be unsuccessful and the Poisson variable models the number of fledglings produced conditional on the success of the brood. For first

Table 1 Models and variables used to investigate reproductive costs

Y	Model		Test of reproductive costs		Other variables		Individuals
			Intra	Inter	Interaction	Simple effect	
Brood 1	Zero-inflated poisson	$Y = B \times P$					
First successful brood or only breeding attempt	Probability of not being successful	$B\sim$		$(\#Brood_{t-1} + \#\bar{ha}_{t-1})$	$* PC1 * Prod_{t-1}$	+ age+ hd1	$N_{♀} = 273$ $N_{♂} = 274$
	# of fledglings produced	$P\sim$		$(\#brood_{t-1} + \#\bar{ha}_{t-1})$	$* PC1 * Prod_{t-1}$	+ age+ hd1	
Brood 2	Zero-inflated poisson	$Y = B \times P$					
Potential brood following a first successful brood	Probability of not being a double breeder	$B\sim$	$(\#ha_{b1} +$	$\#Brood_{t-1} + \#\bar{ha}_{t-1})$	$* PC1 * Prod_{t/t-1}$	+ age+ hd1	$N_{♀} = 258$ $N_{♂} = 262$
	# of fledglings produced	$P\sim$	$(\#ha_{b1} +$	$\#Brood_{t-1} + \#\bar{ha}_{t-1})$	$* PC1 * Prod_{t/t-1}$	+ age+ hd1	
Survival	CMR probability of survival	$B\sim$		$\#\bar{ha}_{t-1}$	$* PC1 * Prod_{t-1}$	+age	$N_{♀} = 592$ $N_{♂} = 534$
				$\#Brood_{t-1}$	$* PC1 * Prod_{t-1}$	+age	

Y variable to explain, *B* binomial variable, *P* Poisson variable, $\#ha_{b1}$ number of hatchlings of a first successful brood, $\#brood_{t-1}$ number of broods produced in the previous year; $\#\bar{ha}_{t-1}$ mean number of hatchlings per brood raised in the previous years, *PC1* first axis of a principal component analysis on six morphological traits (individual quality), $Prod_t$ mean annual individual productivity (annual quality), *age* 2-year-old vs. older than 2-year- old, *hd1* hatching date of the first brood, $N_{♀}$, $N_{♂}$ numbers of hoopoe females and males used in each analysis

broods, the binomial model is the probability for a given individual to have no successful brood, while for second broods, it is defined as the probability for an individual of not being a successful second breeder. All individuals with data on two successive years were included in the analysis of the number of fledglings of first broods. Because, by definition, a bird must have had a first successful brood to become a double-breeder, we included only individuals with a first successful brood in the analysis of the number of fledglings of potential second broods (Table 1).

To investigate inter-seasonal costs, we tested the influence of the mean number of hatchlings per brood and of the number of broods in year $t-1$ in 3-way interactions with individual PC1 and mean individual productivity in year $t-1$, on the number of fledglings produced in first and second broods in year t. To investigate intra-seasonal costs, we tested the influence of the number of hatchlings of the first successful brood in a 3-way interaction with individual PC1 and mean individual productivity in year t, on the number of fledglings of the second brood. In the model explaining the number of fledglings of the second brood, intra- and inter-seasonal costs were investigated simultaneously (Table 1). We tested if the estimated regression coefficients of each interaction or simple effect including variables characterizing the reproductive effort were different from 0 using z-scores. If their p value was higher than 0.10, we removed the corresponding effect/interaction to simplify the model. We began by testing the 3-way interactions between reproductive effort, individual PC1 value and mean annual productivity, and simplified the model progressively by testing subsequently lower level interactions. To avoid missing any effects, we report and discuss the effect size of all effects with p value lower than 0.10 in addition to the simple effects of individual and annual quality, age and hatching date. We included age (second year, $N = 275$ vs. > second year $N = 272$) and hatching date of the first brood in these analyses because age and timing of breeding are known to influence reproductive success in birds (Sydeman and Eddy 1995; Black and Owen 1995).

Costs on survival

We used Cormack–Jolly–Seber models (Kéry and Schaub 2012) to analyse capture–recapture data (Table 1). We modelled apparent survival using the following continuous explanatory variables: mean number of hatchlings per brood and number of broods in two separated analyses with 3-way interactions with individual PC1, and mean annual productivity. Age (second year vs. after second year) was also included as a simple effect. When missing (3 values in total), the mean number of hatchlings per brood or the number of broods were simulated in the model, following King et al. (2009). Based on previous survival analyses of this population (Schaub et al. 2012; Plard et al. 2017), we modelled a constant recapture probability. We performed a Bayesian analysis using JAGS (Plummer 2003) that was run from R (R Core Team 2014) via package jagsUI (Kellner 2015) as this allows a straightforward inclusion of missing co-variables. We provided vague prior distributions with normal distribution of mean 0 and variance 10^2. We generated 3 chains of length 75,000 and used the first 30,000 as burn-in. Convergence of models was assessed using the Gelman and Rubin convergence diagnostic ($R < 1.01$, Gelman and Rubin 1992). If an interaction or a simple effect including variables characterizing the reproductive effort had a 90% credible interval that included 0, we removed it to simplify the model. We report and discuss the effect size of all variables whose 90% credible interval did not include 0 in addition to the simple effects of individual and annual quality, and age.

Results

Intra-seasonal reproductive costs on second broods

We found evidence of intra-seasonal reproductive costs in males, but not in females (Fig. 1, Table S2). The interaction between the number of fledglings in the first brood and mean annual individual productivity influenced the probability of double brooding of males (Table S2, binomial variable of the zero-inflated Poisson model, Fig. 1a) but had no residual effect on the number of fledglings of a successful second brood (Poisson variable of the zero-inflated Poisson model, Fig. 1b, Table S1). In years of low mean individual productivity, a male that had raised 3 hatchlings in the first brood had a probability of 0.52 (95% confidence interval) (0.33–0.69) to conduct a second brood while it was only 0.18 (0.09–0.35) in a male that had raised 9 fledglings, on average. In years of high productivity, no intra-seasonal reproductive costs were apparent (Fig. 1a, b). The probability of being a successful double-breeder was higher in males older than 2 years [0.75 (0.66–0.83)] than in 2-year-old males [0.62 (0.53–0.70)]. The success of the second brood decreased with hatching date of the first brood in both sexes (Table S2).

No intra-seasonal costs were apparent in females, but the probability of double brooding and the number of fledglings of a second successful brood were higher in years of high productivity (Fig. 1c, d, Table S2). Moreover, the second brood was influenced by the reproductive effort of the previous year.

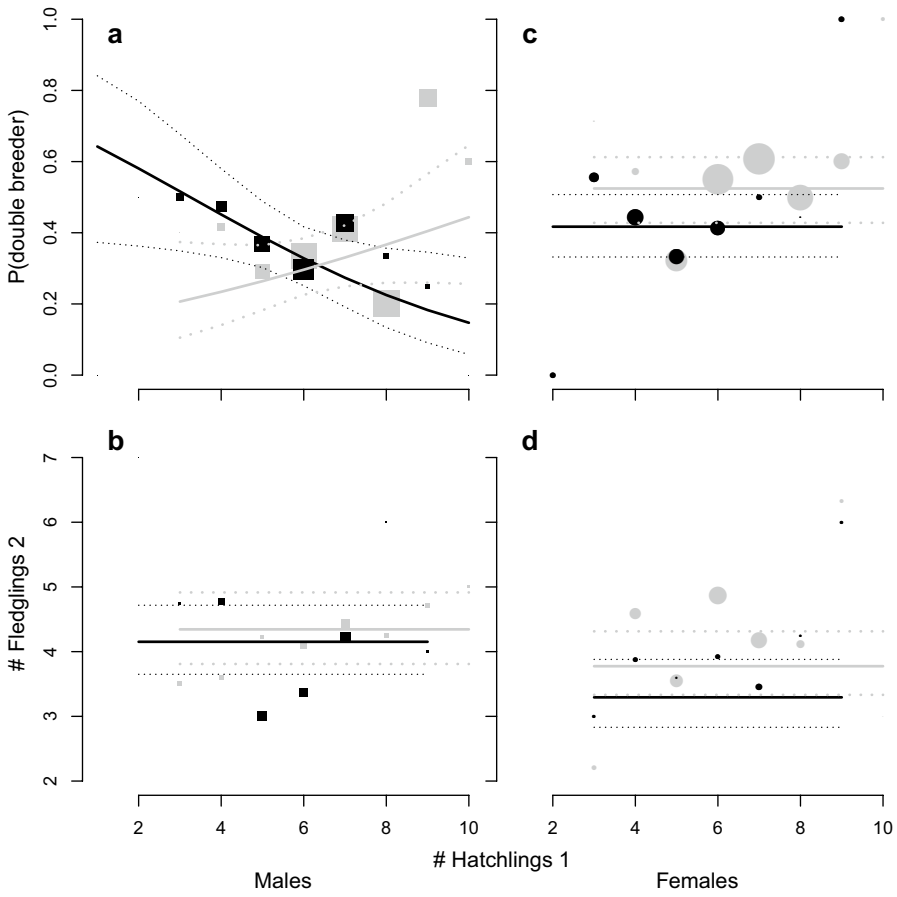

Fig. 1 Intra-seasonal reproductive costs on the success of a potential second brood in hoopoes. Influence of the number of hatchlings in the first brood on the probability of being a successful double breeder (**a**, **c**) and on the number of fledglings raised in a successful second brood (**b**, **d**). Years of relatively low and high (comparing to the mean annual individual productivity over the study period) annual productivity are shown in black and grey, respectively. Males and females are shown with squares and circles whose size is proportional to the number of individuals they represent, respectively. 95% confident intervals of predicted relationships are presented.

Inter-seasonal reproductive costs on the success of first and second broods

Inter-seasonal reproductive costs were detected in females, but not in males. The probability of having a first successful brood was high in all individuals and was not influenced by any of the variable tested (Table S1, Fig. 2a). However, the number of fledglings of a first brood was negatively influenced by the number of broods produced in the previous year in females but not in males (Fig. 2b). The number of fledglings of the first brood was positively correlated with the mean number of hatchlings per brood produced in the previous year in low but not in high-quality males (Fig. S2, Table S1) probably because most high-quality but not low-quality males were double-breeders. The number of fledglings of a first brood was higher in broods that were laid early in both sexes (Table S1).

The probability of being a successful double-breeder was positively correlated with the number of broods laid in the previous year in both sexes and particularly in high-quality individuals (Fig. 2c, Table S2). This suggests that high-quality individuals that were double-breeders in a given year remained double-breeder in the following year. This positive correlation tended to disappear in females in years of high productivity (Table S2) probably because more individuals were double-breeders. None of the variables tested influenced significantly the number of fledglings produced by males in a successful second brood (Fig. 2d, Table S2). The number of fledglings of the second brood decreased with hatching date of the first brood in females (Table S2). It also tended to decline with the previous mean number of hatchlings produced per brood in low productivity years but did not change with the number of broods laid in the previous year (Fig. 2d, Table S2).

Reproductive costs on survival

No reproductive cost on annual male survival was detected (Fig. 3a, Table S3). Male annual survival increased with individual quality and tended to be positively correlated with the number of broods produced in the previous year (Table S3).

Female annual survival tended to be influenced by an interaction between the number of broods produced in the previous year and the mean annual individual productivity (Fig. 3b, Table S3). It generally increased with the number of broods produced in the previous year. However, in recent years with very low mean annual productivity, a reproductive

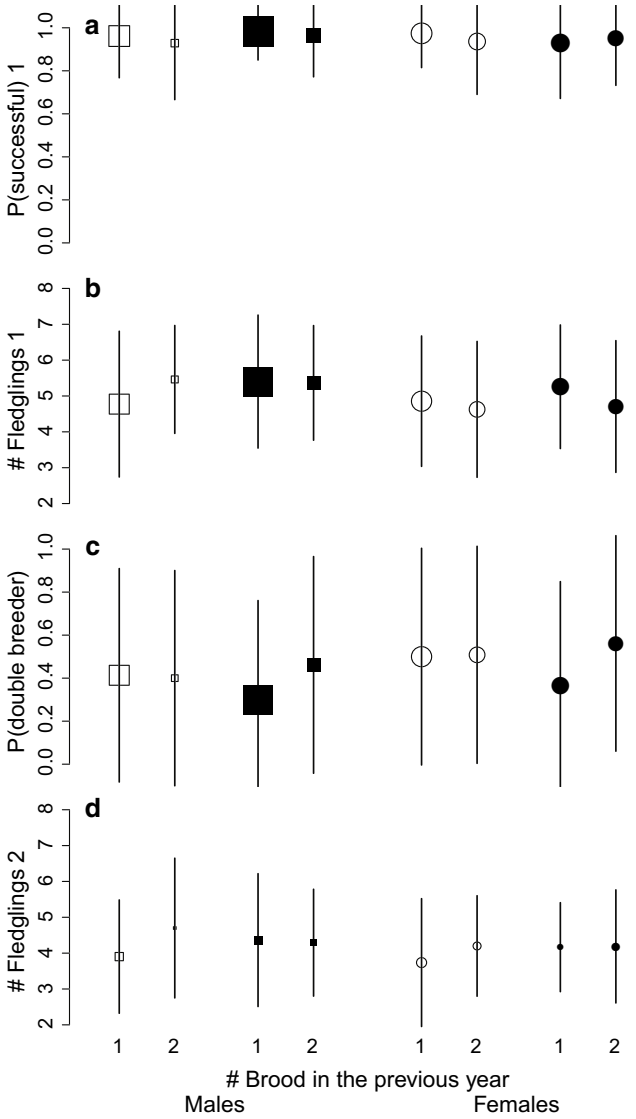

Fig. 2 Inter-seasonal reproductive costs on reproductive success in hoopoe. Influence of individual PC1 and the number of broods produced in the preceding year on the probability of having a successful first brood (**a**), on the number of fledglings of a first successful brood (**b**), on the probability of being a successful double-breeder (**c**), on the number of fledglings of a successful second brood (**d**). Individuals with low and high PC1 are shown with opened and filled symbols, respectively. Males and females are shown with squares and circles whose size is proportional to sample size, respectively. Average values are shown +/− one standard deviation.

cost appeared on subsequent survival. The year 2015, for instance, was a year of very low mean annual productivity (4.4 fledglings per parent). The subsequent female survival probability was 0.28 (95% credible interval: 0.22–0.34) vs. 0.25 (0.17–0.32) when females produced one vs. two broods, respectively.

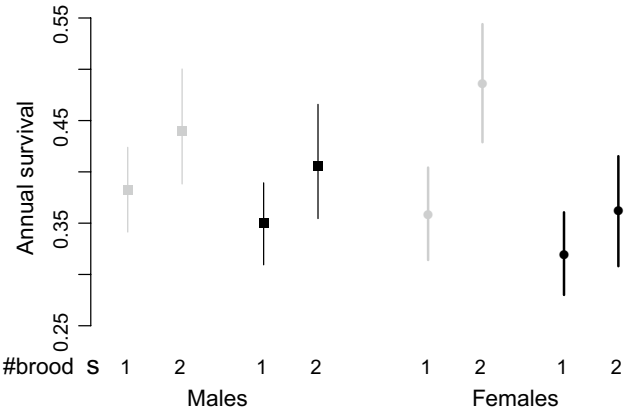

Fig. 3 Inter-seasonal reproductive costs on annual survival in hoopoe. Influence of the number of broods produced on the subsequent annual survival. Males and females are shown with squares and circles, respectively. Predicted annual survivals in years of low and high productivity (first and third quartile of the mean annual individual productivity distribution) are shown with their 95% credible interval in black and grey, respectively.

Discussion

Reproductive costs are expressed differently in males and females in our hoopoe population, and with respect to annual quality. By including influences of intra- and inter-seasonal reproductive effort in the same model, we could show that males expressed only intra-seasonal costs on reproductive success, while females experienced inter-seasonal costs mainly on reproductive success and on survival.

Reproductive costs showed up in years of low productivity

Intra-seasonal reproductive costs in males and inter-seasonal reproductive costs on survival and on the success of the second brood in females were detected only in years of low productivity, but in all individuals regardless of their quality. Positive correlation between the successive (over years) probabilities of being a successful double-breeder was detected in high-quality individuals in years of low and high quality, suggesting that high-quality individuals do not limit their reproductive effort in harsh years. Patterns of reproductive costs were thus similar between low- and high-quality individuals. However, we did not test the influence of age on these patterns. Different patterns between low- and high-quality individuals can also arise along their trajectories (van de Pol and Verhulst 2006) with low-quality individuals suffering higher costs of reproduction in early or late life.

Mean annual individual productivity has declined in the population in the last 15 years (Fig. S1). Reproductive costs were thus mainly present in recent years when mean productivity was particularly low. There are several hypotheses that

can explain the appearance of reproductive costs in recent years. First, the decline of the population in recent years may have favoured the use of nestboxes by more low-quality individuals (Møller 1992) that would have immigrate into the population, decreasing the average productivity. However, PC1 showed no detectable trend over the study period. Thus we do not expect that the percentage of low-quality individuals has increased in our population. Moreover, because the mean annual productivity has started to decline while the population size was still increasing and have kept declining with the same rate independently of population size (Fig. S1), we do not expect any density-dependent effect to be the cause of the decline in mean annual productivity. Second, we do not expect an Allee effect to have influenced our population (Courchamp et al. 1999). The recapture probability has not declined [trend: 0.101 (− 0.005; 0.205)] suggesting that the breeding probability remained fairly stable over time. Third, general environmental conditions (changes in the habitat, prey abundance and quality, and/or human disturbance) may have gradually deteriorated over the course of the study and may have caused the decline in mean annual individual productivity. Favourable conditions allowed hoopoes to have both high reproductive success in successive attempts and high survival probability. When conditions became unfavourable, trade-offs between demanding activities emerge, as found in other species (Barbraud and Weimerskirch 2005; Descamps et al. 2009). Generally in birds, when parents are not able to supply sufficient food for the whole brood, they preferentially feed chicks having a higher survival probability (Caro et al. 2016), typically causing a brood reduction. Hoopoes display asynchronous hatching which is generally seen as a strategy to maximize success under environmental variability (Hahn 1981). In unfavorable conditions and when hoopoe parents have a limited amount of food to allocate to current reproduction, they might feed only large chicks (Martín-Vivaldi et al. 1999; Ryser et al. 2016).

Reproductive costs are often detected in wild populations when the environmental conditions become suddenly poor (Tavecchia et al. 2005; Hamel et al. 2010). In our study, the environmental conditions seem to have declined gradually. In this situation, one may expect a selection for high-quality individuals over the course of the study that would have also masked reproductive costs. However, individual PC1 has not increased over the course of the study. In accordance with this absence of selection, many species do not show the expected change in traits in response of a gradual environmental change (Merilä et al. 2001). For instance, the mismatch between the phenology of many species of birds and mammals and the availability of their resources has increased these last years (Visser and Both 2005; Plard et al. 2014). This mismatch has gradually affected the environmental conditions for these populations and negatively influenced their reproductive success and population growth rate. Gradual environmental change can thus impact negatively some species if their response is too slow or maladaptive. That is probably what we observe in our hoopoe population with a gradual degradation of their general environmental conditions, irrespective of their cause.

Intra-seasonal costs, a common rule?

Because the successes of first and second broods of double brooding hoopoes have been found to be positively correlated (Martín-Vivaldi et al. 1999; Hoffmann et al. 2015), we expected no intra-seasonal costs. Indeed, until 2012, no intra-seasonal reproductive costs were detected (Hoffmann et al. 2015). However, in recent years when the mean annual productivity became particularly low, we found that males experienced intra-seasonal costs. Intra-seasonal costs could have evolved to avoid jeopardizing next year survival and be widespread among species that lay multiple broods within a breeding season. Intra-seasonal costs have been shown in many other birds but studies from other taxa are rarer. In house wrens (*Troglodytes aedon*) for instance, nestlings of a second brood were lighter if the female reared an experimentally enlarged first brood (Robinson and Rotenberry 1991). In the Eastern phoebe (*Sayornis phoebe*), the number of fledglings of a second brood decreased when the first brood had been enlarged (Conrad and Robertson 1992). In other taxa such as in the earwig (*Forficula auricularia*) for instance, females that have tended their first clutch delayed the laying of their following clutch by a week, but there was no evidence of reproductive cost on the size or the survival of the second clutch (Kölliker 2007).

Why intra-seasonal costs in males, but not in females?

This finding might be related with the sex-specific feeding patterns of hoopoes. Hoopoe males feed the females during incubation and in the first days after hatching, whereas afterwards both parents feed the chicks (Martín-Vivaldi et al. 1999; Arlettaz et al. 2010a). Double breeding females typically leave the brood before the young become independent such that males have to continue feeding the nestlings until independence. Males collect also more and larger prey items for the nestlings (Ryser et al. 2016). Apparently, this is not costly under favourable conditions, but our results suggest that it entails costs under unfavorable circumstances. This sex-specific parental investment at the end of the first brood may explain the presence of intra-seasonal costs in males but not in females. Although males and females are not expected to share equally parental care (Kokko and Jennions 2008), sex-specific patterns of intra-seasonal costs have rarely been investigated. Such differences between sexes might well be more common than we think. The few empirical studies

available show relatively higher reproductive cost on female rather than on male survival, for instance (Liker and Székely 2005; Verhulst 1998; Siefferman and Hill 2008). Different life-history strategies between males and females may induce different investment in parental care when nestlings are close to fledging. These sex-specific strategies could thus also lead to sexual conflict in parental care (Chapman et al. 2003; Lessells and McNamara 2012).

Males and females show different life-history strategies

Our results suggest that males are more careful when investing energy within one reproductive season, whereas females try to maximize the success of each reproductive season at the expense of the next one. In many species, females provide larger care to offspring than males which tend to multiply their reproductive attempts (Queller 1997). Even if males provide a large part of parental care in hoopoes, successive annual reproductive successes of male positively correlate. High-quality males that are double breeders tend to remain double-breeders, and in low-quality males for which most are single breeder, the number of fledglings of the first brood is positively correlated with the mean number of hatchlings per brood raised in the previous year. These results support the hypothesis that intra-seasonal costs should be outweighed by higher success in future reproductive seasons (Grüebler and Naer-Daenzer 2008). Our results show that double-brooding is costly in females. Males would thus minimize inter-seasonal costs by reducing the number of broods raised within a breeding season and thus limiting the reproductive effort. Experienced hoopoe males often defend better territories and thus should benefit from higher reproductive success as they get older (Tschumi et al. 2014). Moreover, survival of high-quality males is higher than overall female survival (Plard et al. 2017). Thus, males display a slightly slower life-history strategy than females. Our study suggests that the sex-specific difference in life-histories is related to different strategies between investing either in the first brood, in the second brood and/or in survival each year.

Conclusions

Reproductive costs can differ between males and females. This correlative study provides evidence that males have short-term reproductive costs while females experience delayed reproductive costs. However, experimental approaches would be necessary to understand which activities incur what kind of physiological costs in the two genders. More investigations of intra- and inter-seasonal reproductive costs in other species are necessary until we can generalise about how such gender-specific patterns relate to life-history strategies. Our study suggests that life-histories strategies can vary within a species exhibiting bi-parental care when individuals invest differently in reproduction according to circumstances and/or own intrinsic quality. This suggests that heterogeneous and sex-specific reproductive tactics may influence the dynamic of populations. This calls for further studies of the effects of sex-specific life-histories on population evolution.

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Author contribution statement FP and MS designed the study. FP carried out the analysis and wrote the manuscript. RA and MS provided the data and helped commenting the manuscript. All authors gave final approval for publication.

Compliance with ethical standards

Data accessibility Data would be made available conditional of the acceptance of the paper.

Conflict of Interest The authors declare that they have no conflict of interest.

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