

Sex-Specific Heterogeneity in Fixed Morphological Traits Influences Individual Fitness in a Monogamous Bird Population

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ABSTRACT: Theoretical work has emphasized the important role of individual traits on population dynamics, but empirical models are often based on average or stage-dependent demographic rates. In this study on a monogamous bird, the Eurasian hoopoe (*Upupa epops*), we show how the interactions between male and female fixed and dynamic heterogeneity influence demographic rates and population dynamics. We built an integral projection model including individual sex, age, condition (reflecting dynamic heterogeneity), and fixed morphology (reflecting fixed heterogeneity). Fixed morphology was derived from a principal component analysis of six morphological traits. Our results revealed that reproductive success and survival were linked to fixed heterogeneity, whereas dynamic heterogeneity influenced mainly the timing of reproduction. Fixed heterogeneity had major consequences for the population growth rate, but interestingly, its effect on population dynamics differed between the sexes. Female fixed morphology was directly linked to annual reproductive success, whereas male fixed morphology also influenced annual survival, being twice higher in large than in small males. Even in a monogamous bird with shared parental care, large males can reach 10% higher fitness than females. Including the dynamics of male and female individual traits in population models refines our understanding of the individual mechanisms that influence demographic rates and population dynamics and can help in identifying differences in sex-specific strategies.

Keywords: body condition, dynamic heterogeneity, fixed heterogeneity, individual quality, integral projection model.

Introduction

Models of population dynamics often describe successive population sizes based on average or stage-dependent rates of reproduction and survival without taking into account differences at the individual level (Caswell 2001). However,

population dynamics are directly linked to individual trajectories and interactions among them (Coulson et al. 2011). Including the mechanisms by which individual traits and their interactions influence demographic rates can help us to get a better understanding of population dynamics (Vindenes and Langangen 2015; Griffith et al. 2016). Despite a lot of theoretical work showing that individual heterogeneity in phenotype, genotype, or cohort environment can affect reproductive and survival rates and, thus, population dynamics (Łomnicki 1978; Kendall and Fox 2003; Kendall et al. 2011; Vindenes and Langangen 2015; Plard et al. 2016), empirical studies remain scarce, mainly due to a lack of long-term individual data and of population models including patterns at the individual level (but see, e.g., Coulson et al. 2001). Here, we present a two-sex model on a bird population where we show how the interactions between males' and females' fixed and dynamic individual heterogeneity influence demographic rates and population dynamics.

One of the main differences between individuals within a population is sex. However, because data on the reproductive success of males are typically difficult to collect, sex is often ignored in population models (but see Le Galliard et al. 2005; Jenouvrier et al. 2010; Miller and Inouye 2011; Schindler et al. 2013). Males and females may show different dynamics according to variable selective pressures depending on sexual selection, reproductive tactic, or mating system (Doebeli and Koella 1994; Lindström and Kokko 1998; Rankin and Kokko 2007). Males and females display different demographic rates, and in particular, females live longer in polygynous mammal species but die earlier than males in many monogamous bird species (Liker and Székely 2005; Clutton-Brock and Isvaran 2007). Different strategies to increase individual reproductive success have also been reported between males and females of a same species. For instance, in polygynous species, males invest in secondary sexual traits, whereas females in-

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vest in parental care to maximize their reproductive success (Clutton-Brock et al. 1982). In monogamous species, mutual mate choice has been observed (Jones and Hunter 1993), but parental investment as well as mate choice is expected to be biased toward a sex according to mate encounter rate or variability in mate quality, for instance (Owens and Thomson 1994; Kokko and Johnstone 2002; Kokko and Jennions 2008). Annual reproductive success depends on individual characteristics of both parents through transmission of genes and parental investment. In bird species with biparental care, the characteristics of both parents can be of major importance for offspring survival (Burley 1988; Sheldon 2000; Badyaev and Hill 2002; Moreno et al. 2002). As a consequence, including dynamics of both sexes in population models is likely to improve our understanding of the evolution of sex-specific strategies and their influence on population dynamics.

In addition to sex, yearly and total individual contributions to population growth vary according to individual heterogeneity that can be split between dynamic and fixed heterogeneity (Tuljapurkar et al. 2009). Dynamic heterogeneity varies over time according to stochastic environmental variation, which influences resource availability. Variation in resource acquisition should be reflected by individual condition, and we refer here to “condition” as the year-dependent state of an individual (McNamara and Houston 1996). Condition was often found to influence timing of reproduction (Drent and Daan 1980) but also the probability of reproduction or the number of offspring produced (Lack 1947; Monaghan and Nager 1997). Fixed heterogeneity is determined at birth or at independence and can be related to all traits that are fixed at this time. Fixed heterogeneity is often linked to individual quality. Here, we used the definition of “quality” proposed by recent reviews: a fixed covariation among individual traits, that is, positively related to individual fitness (Wilson and Nussey 2010; Bergeron et al. 2011). Differences in individual quality have been demonstrated in many species (Cam et al. 2002; Hamel et al. 2009; Aubry et al. 2011; Chambert et al. 2014; Plard et al. 2015), with high-quality individuals achieving higher survival and/or reproductive rates resulting in higher fitness compared to low-quality individuals. The covariation among fixed individual traits can thus be an appropriate predictor of individual quality if it is positively linked with fitness. Here, we investigate if heterogeneity in fixed individual morphological traits is positively related to fitness.

Integral projection models (IPMs) allow for inclusion of information at the individual level (e.g., phenotype, genotype) to parametrize demographic rates and to build population dynamics models (Easterling et al. 2000; Ellner and Rees 2006). Here, we built a two-sex IPM (Schindler et al. 2013) including individual age and dynamic (condition) and fixed (morphology) heterogeneity to understand how these individual structures and their interactions influenced the

demographic rates and the population dynamics of the Eurasian hoopoe (*Upupa epops*). This bird species represents a particularly interesting case because this is a monogamous species with biparental care. Pairs remain together to raise one brood, but partners often change between successive broods. They can have several successful broods each year such that annual reproductive success is variable among individuals (Hoffmann et al. 2015). Moreover, older and heavier males frequently occupy territories that offer more food (Guillod et al. 2016) resulting in higher reproductive success (Tschumi et al. 2014), which suggests that some individuals contribute more to population growth than others. In this study, we first analyzed the associations between individual characteristics and survival and reproductive rates to disentangle the influence of individual age, condition, and fixed heterogeneity on demographic rates in each sex. We formulated specific predictions: (i) We expected individual age and fixed heterogeneity to influence annual survival. As individuals in good condition should be able to allocate more energy to annual reproduction, (ii) we expected individual condition to influence annual reproductive success. Second, we built an IPM to study how the trait distributions of the two sexes interacted to influence demographic rates and individual fitness, which we defined as the individual reproductive value at fledging (Moorad 2014). Third, we conducted perturbation analysis to understand how sex-specific condition and fixed morphology influenced the population growth rate.

Methods

Studied Population

The hoopoe is a nonpasserine bird of about 75 g with a generation time of less than 2 years that breeds in Europe from April to August. This long-distance migrant spends the nonbreeding season in Africa (Bächler et al. 2010; van Wijk et al. 2016) and feeds mostly on large ground-dwelling insects. Our study was carried out from 2002 to 2015 on the plain of the Upper Rhône Valley (Central Valais, southwestern Swiss Alps; lat. 46°14'N, long. 7°22'E, alt. 460–520 m, 64 km²). The study site is devoted to intensive farming consisting of dwarf fruit tree plantations, vegetables, and vineyards. High-intensity farming has resulted in an almost complete eradication of cavity trees, depriving these cavity-nesting birds from breeding sites. Since 1998, about 700 nest boxes have been placed, mostly in pairs, at 350 locations throughout the study area (Arlettaz et al. 2010). As the study population uses almost exclusively nest boxes as nesting sites, the population grew quickly to about 80 breeding pairs (Arlettaz et al. 2010; Schaub et al. 2012). However, during the past 8 years, the population has been slightly but steadily declining.

Nest boxes were checked every second week during the breeding season, from the end of April to the beginning of

August. The reproductive data were collected from the nest boxes containing broods. Active broods were additionally checked every third to fourth day to record clutch size, hatching date, and number of fledglings. Because extra-pair paternities are rare in this population, a male captured at a nest box entrance is the biological father, in most cases (Berthier et al. 2012).

We distinguished between three age classes in our population: nestlings (age 0), yearlings (age 1), and adults (age >1). All nestlings were ringed, and tarsus length and body mass were measured, but nestlings could not be sexed. Yearlings and adults were captured after hatching of their nestlings using mist nets or clap traps, or they were taken directly from the nest box by hand. They were aged as yearling or adult based on molt, sexed by inspecting the size of the uropygial gland (Martín-Vivaldi et al. 2009), and ringed if captured for the first time. Several measures were recorded at each capture: tarsus length, body mass, bill length, and length of different feathers. Using repetitive measures of the same individual within the same year, measurement error was estimated to be less than 2 and 5 mm for bones (also bill) and feathers, respectively.

Dynamic and Fixed Heterogeneity

Body condition was used as a measure of dynamic heterogeneity. Annual adult and yearling condition was expressed by the residuals of a linear model that linked annual body mass to tarsus length and included an interaction between sex and the number of days between hatching date of their brood and capture date. The interaction was used to correct for sex-specific variation in body condition due to subsequent parental effort when feeding offspring. Individual condition was estimated at each clutch. When an individual had several clutches in a given year, the annual body condition was defined as the mean of individual conditions within a year.

Body mass and tarsus length of nestlings vary greatly in the first days of life but reach an asymptotic phase after 15 days (Hildebrandt and Schaub, forthcoming). Hence, we included only nestlings that were at least 15 days old when measured. The age of nestlings was not exactly known for all individuals but estimated as the number of days since hatching of the first egg in the brood. Because the female often starts incubating as soon as the first egg is laid, hatching is asynchronous. The age of some nestlings was probably overestimated and, consequently, their condition underestimated. We checked that the models including nestling condition as an explanatory variable were not driven by nestlings with relatively weak condition. This visual inspection revealed that the relationships between yearling condition and nestling condition and nestling condition and parental condition were not driven by nestlings with weak condition (figs. D1, D3; figs. A1, A2, C1–C3, D1–D6, E1, E2 are available online).

We measured fixed heterogeneity by variation in morphology among individuals. Six adult morphological traits were used to perform a principal component analysis: bill length, tarsus length, wing length, feathered crest length, and lengths of the central tail feather and of the fifth primary feather (P5; for morphological descriptive statistics of male and female hoopes, see table A1; tables A1, B1, B2, C1–C4, D1–D6 are available online). These traits can increase slightly between 1 and 2 years old but then remain constant until death. We thus used the mean of all individual measures as adult bird. When we had only individual measures as yearling, we estimated adult trait size using the positive relationships between adult and yearling traits (bill: $R^2 = 0.80$, tarsus: $R^2 = 0.75$, wing: $R^2 = 0.75$, crest: $R^2 = 0.60$, P5: $R^2 = 0.72$, tail: $R^2 = 0.40$). We did not have access to morphological traits for birds that died before 1 year old. As these six traits were strongly correlated, the first axis (the first principal component [PC1]) explained 61% of the variation (fig. A1) and was used as a measure of fixed heterogeneity. PC1 was a good indicator of the overall size of an individual. High values of PC1 indicated long feathers, wings, bill, and tarsus.

PC1 and body condition were scaled (standardized) to favor convergence of the different models and comparison of results for the different demographic rates. When reporting effect sizes in the results, we refer to individuals at the first and third quartiles of the sex- and age-specific body condition and fixed heterogeneity (PC1) as individuals in poor and good condition and as small and large individuals, respectively.

Influence of Dynamic and Fixed Heterogeneity on Survival and Reproductive Rates

Survival Rates. We used the Cormack-Jolly-Seber (CJS) model to analyze survival as not all individuals were recaptured every year (Lebreton et al. 1992) and evaluated its goodness of fit using U-CARE (Choquet et al. 2009). CJS models allow estimating probabilities of recapture and of apparent survival (i.e., the probability of surviving and remaining in the study area), which includes emigration. Because biased estimates of recapture probabilities can influence estimates of annual survival probabilities, we performed a preliminary analysis to select the variables influencing recapture probability. Then, we used the selected model for recapture probabilities to assess the variables influencing survival probability. To reduce computation time, we split the analysis of first-year and after-first-year survival, the latter taking information only from the individuals that were captured at least once as yearling or adult.

The overall goodness of fit of a CJS model that included two age classes (first-year vs. older-year survival) was not significant ($\chi^2 = 37.68$, $df = 31$, $P = .19$), but subtest 3.SR was significant ($\chi^2 = 34.81$, $df = 12$, $P < .01$), indicating a

more complex age pattern in our data (Choquet et al. 2009). We have therefore included an age effect with three classes (first-year survival [survival from nestling to yearling], yearling survival [survival from yearling to adult], and adult survival [survival as adult]) in the starting model.

First, in the preliminary analysis, we used the whole data set ($N = 6,464$ individuals) to select the variables influencing recapture probabilities. Because males were more difficult to catch than females, we tested for a sex effect in addition to an age effect on the recapture probability (only yearling vs. adult because recapture of nestlings is impossible). Survival probability was modeled by including an interactive effect between age and sex and an additive random effect of year.

Second, the influence of nestling condition on first-year survival was tested using all individuals that were marked and measured as nestling ($N = 5,229$). We could not investigate the influence of sex and PC1 because they were not known in nestlings. Therefore, we assumed that male and female survival up to 1 year old was the same.

Third, all the capture histories of individuals of at least 1 year old that were sexed and for which all morphological traits were measured at least once ($N = 1,040$) were selected to test for an effect of individual annual body condition and PC1 on yearling and adult survival. Because the model did not allow continuous and time-varying variables to be missing when individuals are not recaptured, we have simulated data on body condition that were lacking within the survival model (King et al. 2009) using a linear function linking condition at time t to condition at time $t + 1$. Individual condition was missing when individuals were not recaptured. We have tested the effect of individual age (yearling and adult survival), sex, PC1, and condition on survival. Three-way interactions between age, sex, and PC1 and age, sex, and condition were investigated (table B1).

We performed these three Bayesian analyses using JAGS (Plummer 2003) run from R (R Core Team 2014) using package jagsUI (Kellner 2015). We defined normal distributions with mean 0 and variance 10^3 for regression slopes and uniform distributions over the interval [0,100] for the standard deviations of body condition as vague priors (Kéry and Schaub 2012). We generated three chains of length 40,000 and used the first 5,000 as burn-in for the analysis of yearling and adult survival. For the analyses of recapture probabilities and first-year survival, we generated three chains of length 10,000 and used the first 3,000 as burn-in. Convergence of chains was assessed using the Gelman and Rubin convergence diagnostic ($R < 1.01$; Gelman and Rubin 1992). From the starting models, we removed the variables for which 95% credible intervals included 0.

Reproductive Rates. To investigate the relationships between individual traits and reproductive success ($N = 900$), we

analyzed separately clutch size and fledgling success. We analyzed clutch size using linear models with normal distributions. Fledgling success was defined as the proportion of eggs that yielded a fledgling. It was analyzed using generalized linear models with logit links and binomial distributions.

The influence of the following variables was investigated on clutch size: condition, PC1, and age (yearling vs. adult) of male and female parents plus hatching period. Hatching period (variable with two levels) was included instead of the continuous variable hatching date because the latter would have resulted in an IPM with three continuous variables (hatching date in addition to condition and PC1 of parents) that is impossible to run due to current memory capacity. Hoopoes can have two successful clutches each year. Because clutch size and fledgling success depended more on hatching date rather than whether a clutch is a first or a second brood (Hoffmann et al. 2015), we have divided the hatching dates into two periods (fig. C1). The first period included only first clutches and lasted until the end of May. The second period contained all clutches in the rest of the year.

The most complex model considered for clutch size included four (two for each parents) triple interactions between the hatching period, age (yearling vs. adult), and PC1 of each parent and between hatching period, age, and condition of each parent (table C1). The most complex model for fledgling success included clutch size as an explanatory variable in addition to the same explanatory variables used to analyze clutch size (table C3). Year was included as a continuous fixed effect in models of fledgling success because fledgling success (but not clutch size) has been observed to decrease during the study period. All models were run in R, using the functions `lm` and `glm` and the `lme4` package, and the function `lmer` when random effects were included (see below). Selection of interactions between variables and of simple effects of variables was performed using Akaike information criterion (AIC) by successive simplifications of the models. We sequentially removed the variables with the weakest effect on the model based on differences of AIC between successive and nested models. Because any small effect included in the IPM can have large effects on the predicted population dynamics, we chose the model with the smaller number of parameters when two competing models had $\Delta\text{AIC} < 2$, following the principle of parsimony. We visually inspected the residuals of each selected model and checked the influence of possible outliers by repeating model selections when all data points whose Cook distances were larger than 0.01 (Cook 1977) were excluded. Outliers had no effect on model selection (results not shown).

Population Model

To predict the relationships between individual yearly reproductive success and individual condition and PC1, we needed

to take account of the actual mate at each reproductive attempt. We thus built an integral projection model including individual sex, age, PC1, and condition. At equilibrium, when the population has reached its stable distribution, this IPM gave us the relative proportion of males and females with a given condition and PC1. The probability for each possible mating pair was predicted in relation to mate preference and availability at equilibrium, and the relationships between fitness and individual condition and PC1 were estimated. We used a postbreeding model with an annual census time at fledgling. We included three age classes: nestling, yearling, and adult (see the life cycle; fig. A2). We first present the overall IPM, and then we explain how we modeled the different functions that made up the IPM. Finally, we describe the model outputs and the perturbation analyses.

Building the Integral Projection Model. The density of males and females in the population is described by the vectors $\mathbf{n}_m(t, a, c, b)$ and $\mathbf{n}_f(t, a, c, b)$. The subscripts m and f refer to males and females, respectively. The indices $t, a, c,$ and b represent time, age, condition, and PC1. The density of individuals at least 1 year old at $t + 1$ ($a \geq 1$, yearlings and adults) depends on the density of all individuals at time t , the transition (\mathbf{T}) of condition between t (c) and $t + 1$ (c'), and the survival (\mathbf{S}) functions. PC1 is fixed for a given individual. For $a \geq 0$, we have

$$\begin{aligned} \mathbf{n}_m(t + 1, a + 1, c', b) &= \iint \mathbf{T}_m(t, a, c' | c, b) \mathbf{S}_m(t, a, c, b) \mathbf{n}_m(t, a, c, b) dc db, \\ \mathbf{n}_f(t + 1, a + 1, c', b) &= \iint \mathbf{T}_f(t, a, c' | c, b) \mathbf{S}_f(t, a, c, b) \mathbf{n}_f(t, a, c, b) dc db. \end{aligned} \tag{1}$$

The density of nestlings ($a = 0$) at $t + 1$ depends on the density of all individuals at time t . Between census at t and $t + 1$, all males and females may survive, acquire a new condition, and then reproduce. We split the reproductive function into several functions; first, each individual had a probability of breeding in a given year \mathbf{B}_f and \mathbf{B}_m . Second, each breeding individual had a probability of reproducing at each breeding attempt. We modeled two breeding attempts: the first and second hatching periods as defined above. Thus, breeding males and females had the probabilities $\mathbf{P}_{m,h}(a, c, b)$ and $\mathbf{P}_{f,h}(a, c, b)$ of having a brood at each hatching period ($h = 1$ and $h = 2$). Individuals can have two broods per year if $\mathbf{P}_1(a, c, b) \times \mathbf{P}_2(a, c, b) > 0$. Third, for each hatching period, pairs were formed among available males (σ for father) and females (φ for mother) using the mating function $\mathbf{M}_h(c^\sigma, b^\sigma, c^\varphi, b^\varphi)$. Fourth, each pair produced a number of fledglings $\mathbf{R}_h(a^\sigma, a^\varphi, c^\sigma, b^\sigma, c^\varphi, b^\varphi)$ at each reproductive attempt. We summed reproductive successes of both reproductive attempts to obtain individual annual reproductive success.

All offspring then inherit a given nestling condition c' and a fixed PC1 b' using the inheritance function $\mathbf{I}(c', b' | a^\sigma, a^\varphi, c^\sigma, b^\sigma, c^\varphi, b^\varphi)$. For male offspring (equation for female offspring is similar, but replacing s with $1 - s$; s is the sex ratio at fledging), we get

$$\begin{aligned} \mathbf{n}_m(t + 1) &= s \sum_a \iiint \iiint \mathbf{I}_m [C_1 \mathbf{R}_1 \mathbf{M}_1 \mathbf{P}_{f,1} \mathbf{P}_{m,1} \\ &\quad + C_2 \mathbf{R}_2 \mathbf{M}_2 \mathbf{P}_{f,2} \mathbf{P}_{m,2}] \mathbf{B}_f \mathbf{T}_f \mathbf{S}_f \mathbf{n}_f \mathbf{B}_m \mathbf{T}_m \mathbf{S}_m \mathbf{n}_m \tag{2} \\ &\quad dc^\sigma db^\sigma dc^\varphi db^\varphi. \end{aligned}$$

For the sake of readability, we removed the explanatory variables of each function. Here, C_h is the normalization constant for each hatching period such that all males and females reproduce no more than once per hatching period; C_h thus acts as an upper constant for reproduction in hatching period h :

$$C_h = \frac{\iint \mathbf{P}_{f,h} \mathbf{B}_f \mathbf{T}_f \mathbf{S}_f \mathbf{n}_f dc^\sigma db^\sigma}{\iiint \iiint \mathbf{M}_h \mathbf{P}_{f,h} \mathbf{P}_{m,h} \mathbf{B}_f \mathbf{T}_f \mathbf{S}_f \mathbf{n}_f \mathbf{B}_m \mathbf{T}_m \mathbf{S}_m \mathbf{n}_m dc^\sigma db^\sigma dc^\varphi db^\varphi}, \tag{3}$$

if the number of breeding females during a hatching period was less than the number of breeding males. Otherwise,

$$C_h = \frac{\iint \mathbf{P}_{m,h} \mathbf{B}_m \mathbf{T}_m \mathbf{S}_m \mathbf{n}_m dc^\sigma db^\sigma}{\iiint \iiint \mathbf{M}_h \mathbf{P}_{f,h} \mathbf{P}_{m,h} \mathbf{B}_f \mathbf{T}_f \mathbf{S}_f \mathbf{n}_f \mathbf{B}_m \mathbf{T}_m \mathbf{S}_m \mathbf{n}_m dc^\sigma db^\sigma dc^\varphi db^\varphi}. \tag{4}$$

The continuous IPM can be approximated as a high-dimensional discrete matrix (Easterling et al. 2000), and we used 50 midpoints for each continuous trait. Program R (R Core Team 2014) was used to build the IPM and to perform the associated analyses.

Functions of the IPM. In this part, we describe how the different functions constituting the IPM were defined.

Breeding function. The breeding probabilities (\mathbf{B}) were estimated using the estimates of recapture probabilities. We are confident that most broods occurred in artificial nest boxes because there are hardly any large enough natural breeding cavities in the study area (Arlettaz et al. 2010). The capture intensity was high: 76% of the target individuals were captured each year. We therefore assumed that if an individual was not captured and known to be alive, either it did not breed or it failed to breed.

Timing function. A breeding individual can have a brood during the first and the second hatching periods. To estimate the probability for a breeding individual of having a clutch during the first and the second hatching periods (functions \mathbf{P} of the IPM), we created two variables. For each hatching period, this variable equaled 1 if the individual bred during this hatching period and 0 otherwise. Using a generalized

linear model with a logit link and a binomial distribution, we investigated the effects of individual sex, age, PC1, and condition on these probabilities. The sex was included forming interactions with each variable in the most complex models ($N = 1,631$; table D5).

Males with good condition defend good territories (Tschumi et al. 2014), and females with good condition are expected to return from migration before females with low condition and to choose the best mate available according to morphological and behavioral traits. We thus expected males and females in good condition to mate assortatively. The mating function (\mathbf{M}) was defined using an assortative mating function (Schindler et al. 2013) such that pairs will be formed by females and males of similar PC1 or condition if the correlation coefficients between mates for PC1 ($\rho_b(h)$) or condition ($\rho_c(h)$) at each hatching period were significantly positive. As the mean female PC1 is smaller than the male PC1, we included the difference between males' and females' mean PC1 ($\bar{b}^\delta, \bar{b}^\varphi$) in the function

$$\mathbf{M}(t, c^\delta, b^\delta, c^\varphi, b^\varphi, h) = \frac{0.5 e^{(c^\delta - c^\varphi)^2 \rho_c(h) + ((b^\delta - \bar{b}^\delta) - (b^\varphi - \bar{b}^\varphi))^2 \rho_b(h)}}{10}. \quad (5)$$

For each reproductive attempt, $\rho_b(h)$ and $\rho_c(h)$ were estimated using the correlation between mate PC1 and conditions, and we tested whether correlation coefficients were significantly different from 0. The factor 10 (denominator) was chosen such that the range of mating probabilities was included between 0 and 1. Changing this parameter did not influence our conclusions because the mating function gave the relative probabilities of mating among breeding individuals (when correcting by C_h) but did not influence the number of pairs.

Reproductive success and survival functions. The reproductive success (\mathbf{R}) was the product of clutch size and fledging success. These two functions as well as the survival function (\mathbf{S}) were parametrized using the parameters obtained from the previous section. The sex ratio of nestlings was assumed to be even, as suggested by preliminary genetic analysis in this population (Schaub et al. 2012).

Inheritance function (I). Because nestling PC1 was not available, we assumed that the inheritance functions for PC1 and condition were independent. These functions were modeled with normal distributions, with mean and variance estimated from the data. We tested the influence of the age of each parent and of the mean parental condition and PC1 on offspring condition as a nestling ($N = 3,980$) and on offspring PC1 at adult age ($N = 385$; table D1). For PC1, we also included the sex of the offspring. Sex was not included in the inheritance function for condition because it was unknown for most nestlings. The best models of offspring condition and PC1 were selected and used to parametrize the

mean of each inheritance function. To parametrize the variance of each inheritance function, we took the square of the residuals from the model describing the mean of the function and investigated the influence of the same explanatory variables on these square residuals (table D1).

Transition function between annual condition (T). The transition function for condition was modeled (as the inheritance functions) using a normal distribution. Individual condition can increase or decrease each year and is described by two transition functions: the transitions for yearling (from nestling in t to yearling in $t + 1$, $N = 409$) and for adult condition (from yearling condition in t to adult condition in $t + 1$ or from adult condition in t to adult condition in $t + 1$, $N = 476$). We investigated the influence of the interactions between individual condition at time t , PC1, and sex on individual condition at time $t + 1$ (table D3). For the adult model, a possible effect of individual age (yearlings vs. adults) was also tested, and individual identity was included as a random effect as we had repeated measurements for some individuals.

For all functions, model selection was performed using AIC by successive simplifications of the models as described in the part on reproductive rates. All data used in this analysis are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.61cf7> (Plard et al. 2018).

Output from the IPM and Perturbation Analyses. Fitness. We quantified the influence of individual PC1 and condition at birth on fitness, which was measured by the individual reproductive values at fledging age (Moorad 2014). Reproductive values measure the extent to which individuals contribute to future population growth (Fisher 1930). The life cycle of the study species with two reproductive age classes (fig. A2) and a constant adult survival (Schaub et al. 2012) corresponds to the model where maximizing reproductive value results in maximizing fitness (Caswell 2001). Moreover, IPMs allow estimating reproductive values directly according to individual traits. We applied the method explained in Schindler et al. (2015) to our specific case. To summarize, we estimated the generation matrix for our IPM and used the main left eigenvector of this matrix to estimate sex-, PC1-, and condition-dependent reproductive values at first age. We conducted a bootstrap to estimate the 95% confidence interval of reproductive values.

Perturbation analyses. We performed short-term and long-term perturbation analyses. The short-term perturbation analysis measures the impact of a change of the population distribution on population growth rate after 1 year. We increased and decreased the mean of each sex- and age-class dependent distribution of PC1 and condition by 1 standard deviation. This transient perturbation measures the effect on the population after a change in the mean individual trait that can be produced by a mutation, directional selection, or drift.

In the long-term perturbation analysis, we estimated the relative change in the asymptotic population growth rate after a successive increase of each parameter by 0.001. The perturbations of the slopes of the survival and the reproductive rates show how the population growth rate would change if the strength of the selection acting on individual condition or PC1 gets stronger.

Results

Influence of Dynamic and Fixed Heterogeneity on Survival and Reproductive Rates

Among the models tested, the one that described best the recapture probabilities depended on age only ([0.58;1.45]; table B1; here and below, ranges given in square brackets are 95% credible intervals). The recapture probabilities were 0.69 [0.62;0.74] and 0.85 [0.78;0.91] for yearlings and adults, respectively. First-year survival (from nestling to yearling) was positively influenced by nestling condition (slope: 0.23 [0.12;0.33]; fig. 1A; table B2), with nestlings in poor and good condition (at the first and the third quartiles of the nestling condition distribution) having survival probability of 0.11 and 0.14, on average, respectively. After the first year, contrary to our hypothesis i, individual fixed heterogeneity did not influence similarly female and male yearling and adult survival (tables B1, B2). Fixed heterogeneity (PC1) influenced positively male survival (slope: 0.41 [0.17;0.65]; table B2; being 0.34 and 0.41 for small and large adult males and 0.32 and 0.40 for small and large yearling males, on average, respectively; fig. 1B) but tended to influence negatively female survival (95% credible interval of the slope included 0 [-0.40;0.05]).

Contrary to our hypothesis ii, fledgling success was influenced by both fixed and dynamic heterogeneity. The model selected for clutch size included an effect of hatching period ($\Delta\text{AIC} = 150.60$; ΔAIC are reported between two nested models: the first being the selected model, the second differs from the first by the exclusion of the focal variable, here, hatching period; table C1). Clutch size was 7.88 and 6.65, on average, for clutches hatching in the first and second periods, respectively (table C2). Following the principle of parsimony, the effect of maternal condition on clutch size was not retained even if maternal condition had a weak positive effect on clutch size ($\Delta\text{AIC} = -0.79$, when including maternal condition; table C1). The characteristics of the male parent had no effect on clutch size but influenced fledgling success. According to the best selected model (tables C3, C4), fledgling success was slightly positively affected by paternal condition ($\Delta\text{AIC} = 2.07$, when excluding paternal condition from the selected model; fig. 2E) and influenced by four interactions: the interactions between maternal PC1 and clutch size ($\Delta\text{AIC} = 6.03$, when excluding this interaction from

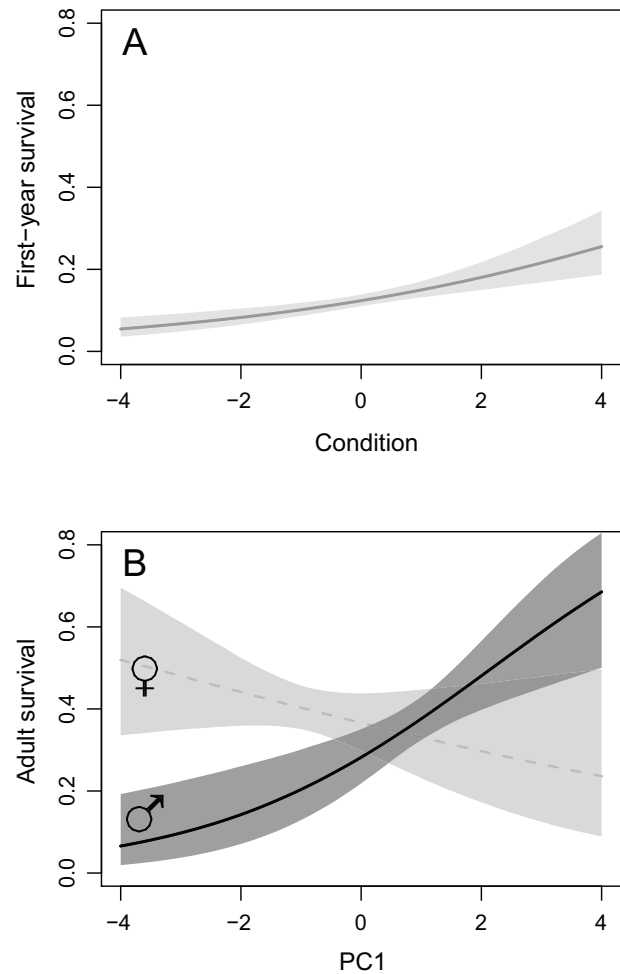


Figure 1: Relationships between nestling condition and first-year survival (A) and between individual fixed morphological traits (PC1) and individual yearling and adult survival (B) of hoopoes. Relationships with 95% credible intervals predicted from the survival model are shown.

the selected model; table C3); between maternal age and hatching period ($\Delta\text{AIC} = 9.98$, when excluding this interaction from the selected model); between maternal PC1 and maternal age ($\Delta\text{AIC} = 9.08$, when excluding this interaction from the selected model); and between clutch size, paternal PC1, and paternal age ($\Delta\text{AIC} = 8.01$, when excluding this triple interaction but keeping the double interactions from the selected model). Maternal PC1 influenced positively fledgling success for adult mothers that laid large clutches (success of 0.54 and 0.59 for small and large mothers that had large clutches, respectively) but was not significant for first-year mothers or for mothers having small clutches (fig. 2A, 2B). Paternal PC1 had a positive effect on fledgling success for adult fathers or for first-year fathers that had a small clutch (success of 0.63 and 0.67 for small and large fathers that had

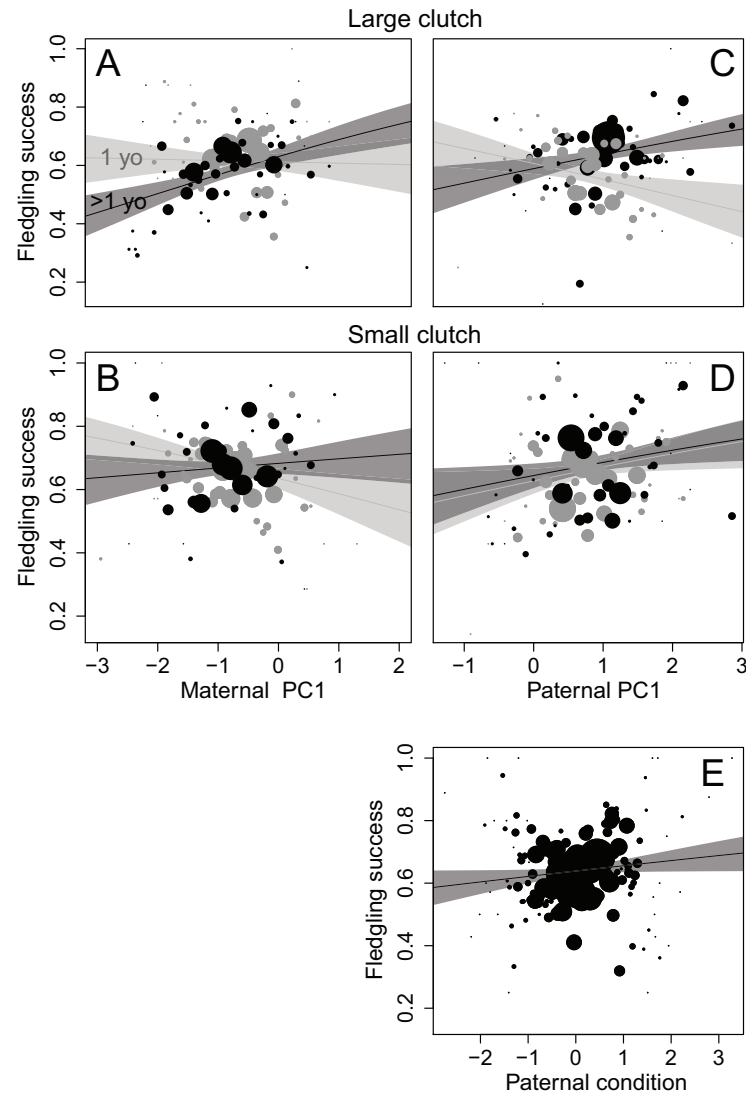


Figure 2: Relationships between parental traits and fledgling success. A–D, Influence of maternal and paternal fixed morphological traits (PC1) and age and clutch size (small vs. large) on fledgling success. E, Influence of paternal condition on fledgling success. Fledgling success of yearling and adult parents are represented in gray and black, respectively. The size of the points is proportional to the number of clutches they represent. For the sake of clarity, clutch size (a continuous variable in models) was represented with two groups: small (≤ 7 eggs) and large (≥ 8 eggs) clutches.

a small clutch, respectively; fig. 2C, 2D). However, the fledgling success of fathers that bred for the first time and had a large clutch was negatively correlated with paternal PC1 (success of 0.60 and 0.58 for small and large yearling fathers that had a large clutch, respectively; fig. 2C).

Other Functions of the IPM, Interaction between Sexes, and Annual Reproductive Success

We first present the selected models used to build the functions constituting the IPM, except the survival and the recruitment functions, for which we used the relationships

described above. Then, we show the resulting influence of individual traits on individual reproductive success, accounting for mate availability and traits.

Inheritance. Offspring inherited condition and PC1. Nestling condition was positively influenced by mean parental condition (slope: 0.13 ± 0.02 ; this slope is not an estimate of heritability as offspring and parental conditions were measured at different ages; Chevin 2015; fig. D1A) and mean parental PC1 (slope: 0.11 ± 0.03 ; fig. D1B) and by paternal age (0.10 ± 0.03) and maternal age (0.07 ± 0.03 ; tables D1, D2). Offspring PC1 was positively influenced by mean pa-

rental PC1 (slope of the parent-offspring regression equivalent to heritability: $h^2 = 0.58 \pm 0.05$) and maternal age (0.18 ± 0.06) and was larger in male offspring (1.41 ± 0.06) than in female offspring (tables D1, D2; fig. D2A; see table A1 for unscaled values).

Growth. Individual condition changed each year. Yearling individual condition was positively correlated with nestling condition (slope: 0.24 ± 0.06 ; fig. D3A) and PC1 (slope: 0.26 ± 0.08 ; fig. D3B). The sex was also selected in this model and counterbalanced the sex difference in PC1 (tables D3, D4). Adult condition at $t + 1$ was linked to condition at t (slope: 0.43 ± 0.04 ; fig. D4A) and PC1 (slope: 0.09 ± 0.03 ; fig. D4B; tables D3, D4).

Forming Pairs. Among the individuals that reproduced, the probability of reproducing at each hatching period depended on individual condition, age, and sex (tables D5, D6; fig. D5). Most adult breeders reproduced during the first period (probability of 0.83 on average), and some of them (56% of males and 65% of females) also reproduced during the second period for a first or a second clutch (figs. D5, D6). First-year breeders had similar probabilities of having a clutch during the first and second hatching periods (0.63 and 0.62, respectively). Birds in good condition reproduced earlier in the season than birds in poor condition (fig. D5). Mate condition but not PC1 was positively correlated during the first ($\rho_{\text{cond}} = 0.17$, $P < .01$, $\rho_{\text{pc1}} = -0.07$, $P = .12$, $df = 487$) but not during the second hatching period ($\rho_{\text{cond}} = 0.056$, $P = .33$ and $\rho_{\text{pc1}} = 0.01$, $P = .76$, $df = 409$).

These functions allowed us to estimate the individual reproductive success taking account of individual traits, individual preferences, mate availability, and mate traits. Female PC1 was the main driver of annual reproductive success, but the relatively large influence of male and female condition shows that timing of reproduction also had a large impact on reproductive success (fig. 3A–3D).

Influence of Condition and PC1 on Fitness

Individual PC1 was positively linked to individual fitness in males but not in females. Large males had 38% higher fitness than small males (fig. 3E). Individual fitness increased with individual condition at birth, similarly in males and females (fig. 3F).

Influence of Sex-Specific Trait Distributions on Population Dynamics

We found a population growth rate of 0.66 [0.61;0.69]. This value is substantially underestimated because the IPM included emigration via apparent survival but not immigration. If we include immigration, which is about 0.3 in this

population (Schaub et al. 2012), annual population growth rate would be around 0.96, which would correspond to the observed slight decline. However, this underestimation did not impact our inference, which was based on relative comparisons but not on absolute values of the population growth rate.

The short-term perturbation analysis showed that increasing the mean of male and female adult PC1 by 1 standard deviation increased population growth rate by 6% and 1%, respectively (fig. E1). The influence of PC1 on population growth rate was larger in males than in females, because PC1 affected survival in males in addition to reproduction. Increasing the mean of male nestling condition by 1 standard deviation increased the population growth rate by 6% after 1 year (vs. 2% for females), probably because this allowed more males to breed during the second hatching period. Changing the distribution of adult or yearling male and female condition did not influence population growth rate much (fig. E1).

While the short-term perturbation analysis showed that the realized annual population growth rate was similarly sensitive to changes in male adult PC1 and male nestling body condition, the long-term perturbation analysis revealed that population growth rate at equilibrium was more sensitive to changes in PC1 than to changes in body condition (figs. 4, E2). The slope linking PC1 to adult survival had a higher impact on the population growth rate at equilibrium (increase by 0.34) than the slope linking nestling condition to first-year survival (increase of 0.08). Male and female PC1 also directly influenced fledgling success (fig. 4).

Discussion

Sex-specific distributions of fixed heterogeneity (PC1) influenced population dynamics differentially as female fixed heterogeneity was directly linked to annual reproductive success, whereas male fixed heterogeneity influenced yearling and adult survival. Consequently, large males reached the highest fitness. We found that nestling condition had long-lasting effects on adult condition, similarly to findings from other bird and mammal species (Lindström 1999; Cam and Aubry 2011). Our results also showed that nestling condition positively influenced individual fitness mainly through first-year survival. Unfortunately, we had no access to nestling sex or fixed heterogeneity to assess their effects on first-year survival.

Dynamic Heterogeneity Influenced the Timing of Reproduction, Whereas Fixed Heterogeneity Influenced Survival and Fledgling Success

We showed that survival and fledgling success were linked to fixed heterogeneity, whereas dynamic heterogeneity had

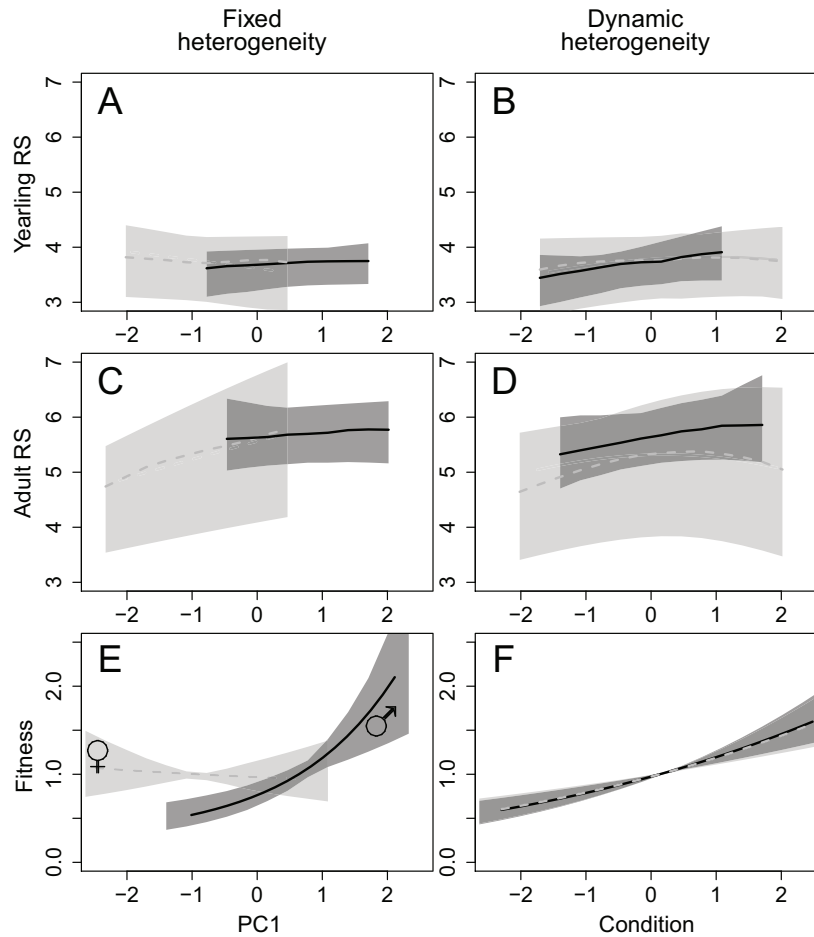


Figure 3: Influence of fixed and dynamic heterogeneity on reproductive rates and fitness predicted from the integral projection model. *A–D*, Influence of individual fixed (PC1) and dynamic (condition) heterogeneity on yearling and adult annual reproductive success (RS), including the individual probability of breeding, the mate preference and availability, and the success of a given pair. *E–F*, Relationships between individual fixed (PC1) and dynamic (nestling condition) heterogeneity and individual fitness measured by the individual reproductive value at fledging age. Males and females are represented by black continuous and gray dashed lines, respectively. The prediction ranges were determined based on age- and sex-dependent distributions of condition and PC1. Gray areas indicate 95% credible intervals estimated from the bootstrap.

greater influence on risk proneness, notably on when to reproduce and how large a clutch should be. Body condition influenced the timing of reproduction, as individuals in good condition started reproduction earlier than individuals in poor condition (fig. D5). Females took the risk of laying large clutches of double, if not triple, brooding if they were in good condition and if they started breeding early in the season (Hoffmann et al. 2015). Hatching date is a main determinant of reproductive success in many bird species (Spear and Nur 1994). Fledgling success was primarily influenced by maternal and paternal fixed heterogeneity but also depended on paternal condition (fig. 2). Males in good condition occupied territories of higher qualities than males in poor condition (Tschumi et al. 2014). The role of male parents for fledgling

success was obvious as they fed the mothers during incubation. However, whether mothers played a determinant role in fledgling success was less obvious. The positive influence of maternal traits on annual reproductive success (fig. 3C, 3D) was in accordance with the crucial role of mothers suggested by Martín-Vivaldi et al. (1999) because mothers are able to differentially allocate the food among nestlings (Martín-Vivaldi et al. 1999). Indeed, hoopoe mothers enter in the nesting cavity to feed all nestlings similarly, whereas fathers give the food to competitively stronger nestlings (Ryser et al. 2016).

Annual survival was linked to fixed morphology in males (fig. 1B). The long-term perturbation analysis showed that the distribution of male fixed heterogeneity and the strength

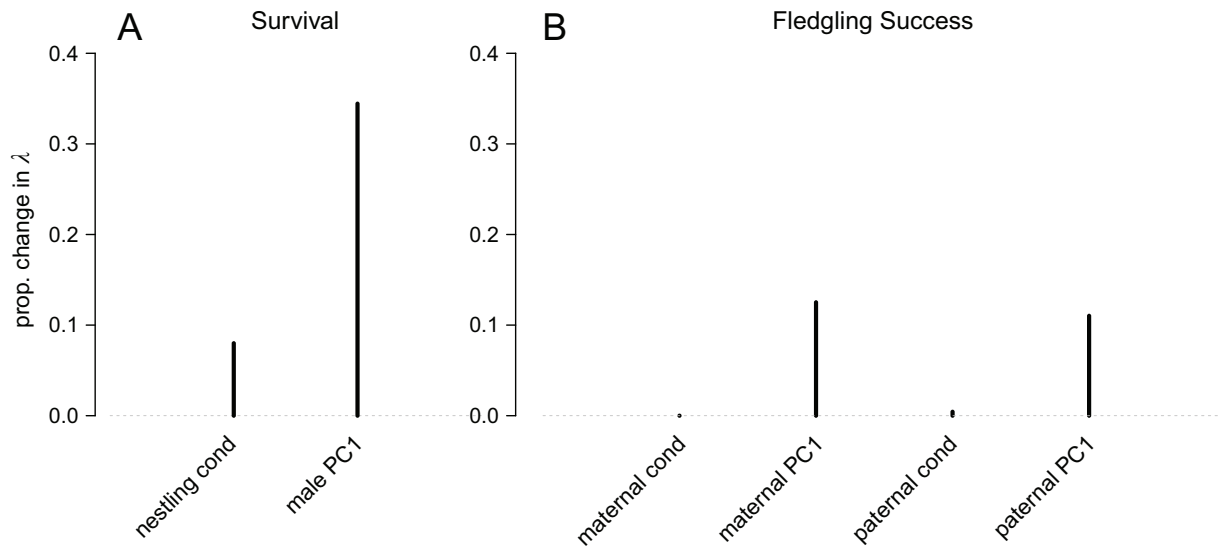


Figure 4: Proportional changes in the population growth rate after an increase of 0.001 of the slopes with respect to the influence of condition and fixed morphological traits (PC1) on the survival and the fledgling success (long-term perturbation). Perturbations of parameters of other functions are displayed in figure E2.

of selection through survival on fixed heterogeneity influenced much more the population dynamics than individual condition. Annual reproductive success appeared to be more variable (fig. 3A–3D) than adult survival and more dependent on variation in annual environmental condition. Consequently, our study showed that population dynamics was more influenced by male fixed heterogeneity than by female fixed heterogeneity or by their condition. Nevertheless, the short-term perturbation analysis showed that individual condition has a large effect on the productivity of the population in a given year.

Possible Differences in Sex-Specific Life-History Strategies

Because maternal and paternal fixed heterogeneity both influenced annual fledgling success, we would have expected large females and males to contribute equally to population growth. However, accounting for reproductive timing, mate availability and preference, and individual age, our population model revealed that, at the individual level, large males reached higher fitness than large females (fig. 3E). Large males managed to contribute more to the population by multiplying the possible number of broods they had during their life and by increasing their reproductive success as they got older. In this relatively short-lived and slightly declining species, it was more rewarding to accumulate broods over several years than to try to have high annual reproductive success early in life.

These differences in demographic rates suggest that males and females followed different life-history strategies. A possible hypothesis would be that females invest more in

reproduction than males, particularly as yearlings, and would thus pay a higher cost of reproduction in terms of survival than males (Williams 1966; Reznick 1985). Because female adult survival tended to decrease with female fixed heterogeneity (fig. 1B), our results were in accordance with a large investment of females in reproduction. Nevertheless, future research is needed to directly test it. Our results also showed a negative relationship between fledgling success and paternal quality among first-year breeding fathers that had to feed large clutches (fig. 2C). This suggests that males with high PC1 invested less in reproduction in their first year when facing the high energetic expenditure required to feed a large clutch. Large fathers may invest less in first reproduction because they may expect higher reproductive success due to higher genetic quality of their offspring (Møller and Thornhill 1998; Kokko and Jennions 2008). Alternatively, they may alter their allocation according to the variability in mate quality (Owens and Thomson 1994; Kokko and Johnstone 2002) and favor their own survival at the expense of reproductive success. For large males, it was more important to invest in body condition in the first year in order to defend a better territory (Tschumi et al. 2014) in later years and thus have access to better females.

Fixed Heterogeneity and Individual Quality

The dynamics of traits in this population seemed to be mainly driven by the difference of survival among individuals and thus by fixed heterogeneity among males. If quality is the covariation among traits that is positively correlated to fitness (Wilson and Nussey 2010), our measure of

fixed individual heterogeneity appeared to be a better measure of quality in males than in females. Indeed, fixed male morphology directly influenced male fitness, whereas female fitness seemed to be unaffected by female morphology. A first possible explanation of this finding is that heterogeneity in quality is much higher among males than among females. A second possibility is that female quality is not well approximated by our PC1. A third possibility is that while female fixed heterogeneity was positively linked to annual reproductive success, an opposite pressure selecting for sexual dimorphism between parents negatively influenced mother size.

Sexual dimorphism of bill lengths may favor a larger diversity of prey brought back to the nest (Ryser et al. 2016). In hoopoes, fathers focus more on mole crickets, which constitute a large prey and provide the main energetic basis to the whole brood, whereas mothers have a more diverse diet with smaller prey (Guillod et al. 2016). Nestlings can benefit from smaller prey, provisioned in the first days of life, whereas large prey can be more profitable when nestlings get bigger (Fournier and Arlettaz 2001; Guillod et al. 2016). As hoopoe nestlings hatch asynchronously, small nestlings that need small food items are present over a long period of time. Fathers with long bills may have enhanced access to underground prey, notably to mole crickets. For mothers, the width rather than the length of the bill could influence foraging success, as a large bill could help to successfully catch smaller prey such as caterpillars or other insect larvae (Guillod et al. 2016).

Dynamic heterogeneity was partly influenced by fixed heterogeneity because the latter influences the transition between stages and has long-lasting effects on individual trajectories. Annual transitions between successive condition partly depended on previous condition and fixed morphological heterogeneity (fig. D4A, D4B). Similarly, nestling condition was affected both by parental dynamic and fixed heterogeneity (fig. D1A, D1B). The successive transitions between stages are thus influenced by the previous individual stage (McNamara and Houston 1996), by fixed heterogeneity, and by environmental variation. The definition of dynamic heterogeneity was first introduced as the life-history differences among individuals that are generated by a mathematical stochastic process, typically a Markov chain (depending on the previous stage and current environment variation) to describe changes in stages (Tuljapurkar et al. 2009). This definition must thus include all three processes (previous individual stage, fixed heterogeneity, and environmental variation) and not only stochastic environmental variation.

Conclusions

We showed that population dynamics of a monogamous bird species was influenced by fixed individual heterogeneity

of males, mainly, and of females, partly. Our models enabled us to draw a detailed picture of the interactive effect of individual traits on population dynamics. Moreover, it has emphasized that different sex-specific strategies can also occur in a monogamous bird and suggests that it could be widespread in many different species. Interactions between sex-specific distributions of traits influence individual annual reproductive success and fitness. As a consequence, the role of the interaction between sex-specific heterogeneity in the evolution of traits needs to be better quantified because this evolution is not linearly depending on sex-specific viability and fertility selection.

Population dynamics are driven by interactions between individual trajectories. Our results showed that individual fixed traits can partly determine individual trajectory and, thus, the individual contribution to the population. Targeting the individuals that contribute the most to population growth will then help us to make better forecasting and management plans of wild populations (Clark et al. 2011).

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Left, hoopoes breed in nest boxes installed in vineyards and fruit-tree plantations in the Swiss Alps. *Center*, a young brood of hoopoes. Photo credits: Michael Schaub. *Right*, an adult hoopoe with its particular long bill and feathered crest. Photo credit: Raphaël Arlettaz.