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# RESEARCH ARTICLE

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# Decomposing fecundity and evaluating demographic influence of multiple broods in a migratory bird

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# Abstract

- Relevance of breeding season fecundity as a driver of population dynamics has been highlighted by many studies. Despite that, knowledge about how brood type specific (i.e. first, second or replacement) fecundity affects demography of multiple-brooded species is limited. In fact, estimation of brood type specific fecundity is often challenging due to imperfect detection of nesting attempts.
- 2. We examined the demographic contribution and the feedback on population density of different components of fecundity, along with other vital rates, in a facultative multiple-brooded migratory bird.
- 3. We used a novel formulation of a fecundity model that allows incorporating reproductive data for which information on the type of brood was unknown in some cases, and embedded it into an integrated population model (IPM) to obtain consensual estimates of all demographic rates, including brood type specific fecundities, reproductive success probabilities and proportion of breeding pairs that performed a second or replacement brood. We then conducted transient life table response experiments on IPM estimates to account for non-stationary environments. We applied the model to two 20-year datasets collected in a Swiss and a German local population of wrynecks *Jynx torquilla*.
- 4. Brood type specific fecundities and temporal patterns of brood type specific probabilities of success, number of successful and unsuccessful first broods, probability of starting a second or a replacement brood and proportion of pairs that performed a second or a replacement brood differed between the two populations. However, changes in immigration rate and apparent survival were the dominant contributors to temporal variation and large sequential changes in realized population growth rates in both populations. In the Swiss population we also found that second brood fecundity declined when population size increased.
- 5. Our study provides insight into the reproductive processes that affect population dynamics and mediate density-dependent fecundity in a migratory bird. In addition, the analytical approach proposed can be used in other studies of multiple-brooded species to maximize the use of available fecundity data through the estimation of unknown brood types, thus favouring a better understanding of the demographic contribution of brood type specific fecundity.

## KEYWORDS

density dependence, fecundity, integrated population model, *Jynx torquilla*, multiple broods, non-stationary, population regulation, reproductive success

# 1 | INTRODUCTION

Understanding factors and processes that regulate and limit animal populations is key for their management and conservation. Changes in population size are often driven by stochastic fluctuations in the environment and density dependence that affect variation in fecundity (Lack, 1966; Sæther et al., 2016). In addition, sensitivity of population growth to changes in vital rates is affected by species' life history (Sæther & Bakke, 2000). Short-lived species are expected to invest more in current reproduction, by maximizing the number of offspring even through multiple breeding attempts in the same season (Stearns, 1992). The proportion of females that produce multiple broods within a season can have a substantial effect on annual fecundity of a population (Nagy & Holmes, 2005). Fecundity plays an important role in the dynamics of local populations both directly, through recruitment, and indirectly if it affects breeding dispersal, survival and subsequent reproduction (Schaub et al., 2015). To improve our predictive ability of the dynamics of natural populations, a major aim in ecology, we need detailed knowledge of patterns of variation in key vital rates, like the number of reproductive attempts and related fecundity (Cornulier et al., 2009). Therefore, in a mechanistic modelling framework, decomposing fecundity into specific components related to the type of brood increases detail about the breeding process and enhances our ability to evaluate the demographic effects of the output of multiple broods.

Demographic studies have typically considered breeding season fecundity as a measure of reproductive output to test effects of factors (e.g. density dependence, individual quality, environment; Carrete et al., 2006; Nevoux et al., 2011; Woodworth et al., 2017) driving population changes of both single and multiple brooded species, especially in birds. Alternatively or in addition to breeding season fecundity, studies on multi-brooded species have used the rate of double brooding or the second clutch success as reproductive measures, linking these state variables to density dependence, individual quality, territory quality, timing of breeding, size of the first clutch, body condition and age of the parents (Grüebler & Naef-Daenzer, 2008; Hoffmann et al., 2015; Schaub et al., 2015; Verboven & Verhulst, 1996; Woodworth, Wheelwright, Newman, & Norris, 2017). Despite that, estimates of brood type specific (i.e. first, second or replacement) fecundity are limited and their demographic contribution in multiple brooded species is largely unknown.

Estimation of brood type specific fecundity requires that parent identity of all broods is known. This is hardly ever the case in empirical studies, because the identification of parents may be imperfect and because not all broods may be detected. In practice it often happens that parents remain unidentified in broods that fail early, since their capture is usually performed after hatching in order to reduce the risk of brood desertion. A further challenge is that dispersal between the first and second brood may result in immigration into or emigration out of the study area (e.g. Bötsch et al., 2012). All these problems can result in biased estimates of brood type specific fecundity and their frequencies (Cornulier et al., 2009; Hoffmann et al., 2015). Missing information on whether a brood was a first, a second or a replacement (i.e. a renest) forces researchers either to consider overall female fecundity in a breeding season (i.e. total number of offspring per female reaching some stage of advanced maturation and/or independence; Etterson et al., 2011), to discard reproductive records with missing data or assign missing brood type a priori based on specific assumptions.

Cornulier et al. (2009) proposed a method to estimate the number of breeding attempts conducted by individuals each year when only a sample of laying dates is observed, by modelling and separating the temporal distribution of first and subsequent reproductive attempts. In other words, breeding dates were used to estimate the annual number of breeding attempts. However, given the nature of the information treated, the Cornulier et al. (2009) approach does not provide estimates of fecundity. Clutch frequency estimation was also achieved by Rivalan et al. (2006) using methods for inference on stopover duration, and by Etterson et al. (2009) with a generalization of Markov chain models of avian nest success. Schaub et al. (2015) explicitly modelled the size of first and second clutches, the number of fledglings of first and second clutches, and the probability of producing two clutches in the same season in the barn swallow, but the model relied only on data without missing information on the type of brood. Other analytical approaches for fecundity estimation focus on breeding season fecundity and do not separate brood type specific fecundities. Examples are the scalar model of avian fecundity (Etterson et al., 2011) or a reproductive success model classically embedded into an integrated population model (IPM; Besbeas et al., 2002) that models the total number of offspring produced by a certain number of surveyed broods (Schaub & Abadi, 2011).

Here, we use a novel formulation of a fecundity model that allows incorporating reproductive data for which information on the type of brood was unknown in some cases, and embedded it into an IPM to obtain estimates of all demographic rates, including brood type specific fecundities and reproductive success probabilities. We apply the model to data from two local populations of the migratory wryneck *Jynx torquilla* and explore the relationship between demographic rates, including different components of fecundity and the proportion of breeding pairs that performed a second or replacement brood, and population growth while accounting for non-stationary environments, as well as the feedback of population density on vital rates.

# 2 | MATERIALS AND METHODS

## 2.1 | Study species and areas

The wryneck is a small (c. 35 g) migratory bird that breeds from April to August, produces a maximum of two broods per season, incubates eggs for 12-14 days and feeds altricial nestlings for about 20 days. The species is a secondary cavity breeder which feeds almost exclusively on ground-dwelling ants and overwinters in the Iberian Peninsula and north-western Africa (Cramp et al., 2000; van Wijk et al., 2013). Data were collected in two distinct populations, one located in south-western Switzerland, in the plain of the Rhône valley (canton of Valais, 46°14'N, 7°22'E, 450-520 m a.s.l., SW Switzerland) and the other one in north-eastern Germany (Saxony-Anhalt, 52°01'N, 13°04'E, 140-175 m a.s.l.). The Swiss study area (62 km<sup>2</sup>) is intensively cultivated with fruit tree plantations and vineyards, and is characterized by warm and dry summers. The German study area  $(4.5 \text{ km}^2)$  is a former military training area used for sheep and goat farming, and characterized by dry grassland and continental climate. We refer to figure 1 in Arlettaz et al. (2010) for a map of the Swiss study area, and to figure 1 in van Wijk et al. (2013) for a larger map with the position of the two study areas. In the Swiss study area, a total of 824 nest-boxes were installed on small agricultural shacks in the period 1998-2001, with a subset of 135 nest-boxes installed in 2008. In the German study area, a total of 110 nest-boxes were installed between 1999 and 2004. In both study areas wrynecks occupy not only nest-boxes but also smaller cavities both within and outside of the study area, like tree cavities or crevices under the roof of agricultural shacks, piles of wood and poles. However, nests outside of nest-boxes were not included in this study.

#### 2.2 | Data collection

Three types of demographic data were collected during 17 years (2002–2018) in the Swiss and during 20 years (1999–2018) in the German population: population count data, capture-mark-recapture data and fecundity data. All nest-boxes were checked every second week and occupied nest-boxes were checked every third to fifth day, from April to the end of July. As a measure of population size, i.e. number of breeding pairs using nest-boxes within each study area, we used the number of observed first broods each year (considering each first brood of an individual in a breeding season), that ranged from 18 to 56 (median 25) in the Swiss population, and from 6 to 48 (median 33) in the German population. A total of 3,381 (Swiss population) and 3,653 (German population) nestlings in the nest-boxes were ringed at an age of at least 10 days, along with 1,059 (Swiss population) and 702 (German population) adults captured with mist nets, clap traps in front of the nest-box entrance or directly taken

in the nest-box only 3 days after hatching. A subsample of nestlings (n = 159 and 292, in the Swiss and German population respectively) was genetically sexed based on blood samples, and sex ratio information was used to inform the model through a prior distribution (Appendix S1, 'Population model' section).

Nest-box inspection led to records of observed breeding attempts. A first brood is defined as the first brood of an individual in a given breeding season. A second brood is defined as a brood following a successful first brood, i.e. a first brood that produced at least one fledgling. A replacement brood is defined as a brood following failure of a first breeding attempt (replacement broods after failure of second breeding attempt were not recorded). In some cases, in the Swiss population only, there were doubts about the brood type, in particular, but not exclusively, when the adults could not be identified. Before modelling data, we allocated part of the missing values for brood type into first, second and replacement brood type based on available information and criteria explained in the section 'Preparation of fecundity data' in Appendix S1, in order to minimize the number of missing brood types that have to be estimated through the IPM. Thereafter, information on fecundity was summarized for the analysis, for each breeding attempt (n = 780 in the Swiss population and 796 in the German population), in (a) brood type (first, second or replacement brood), (b) laying date (day of year) and (c) number of fledglings. Data used in the analysis included 150 records (19%) with unknown brood type for the Swiss population, whereas all brood type records were ascertained in the German population; laying date and number of fledglings were known for all records. Breeding records for which laying date was unknown were discarded a priori, since unknown brood type records were estimated in the model by expressing the probability of being a first, second or replacement brood as a function of laying date (day of year; see below). The observed proportion of brood types differed between the two populations (65.8% and 69.2% of first broods, 12.6% and 21.6% of second broods, 2.4% and 9.1% of replacement broods, for the Swiss and German population respectively). The observed proportion of unsuccessful broods (i.e. no fledglings produced; 34% and 33.9%, for the Swiss and German population respectively) and the observed median number of fledglings (5, with a maximum of 12, in both populations, from a total number of fledglings of 3,516 and 3,705 for the Swiss and German population respectively) were very similar in both populations (Figures S3 and S4 in Appendix S1).

## 2.3 | Statistical analysis

The three population-specific datasets (time series of number of breeding pairs, fecundity data and individual encounter histories) were jointly analysed to obtain consensual estimates of demographic rates and population sizes, using an IPM (e.g. Besbeas et al., 2002; Schaub & Abadi, 2011; Schaub & Kéry, 2021). This analytical framework allows the estimation of latent demographic parameters, for which no or very few explicit data are available, such as immigration (Abadi et al., 2010; Schaub & Fletcher, 2015). Inference was based on

a joint likelihood derived by the multiplication of the single-dataset likelihoods described below.

# 2.4 | Population survey data

A state-space modelling approach was used, where the observation process is conditional on the state process (De Valpine & Hastings, 2002). The state process describes changes in population size over time as a function of demographic rates and proportion of breeding pairs that performed a second or a replacement brood by means of a population projection model. We used a female-based, prebreeding census model with two age classes, 1-year old (yearlings) and older than 1 year (adults), assuming that reproduction started at the age of 1 year. We used a two age-class model since true (chronological) age of individuals older than 1 year cannot be ascertained. Number of yearling females was split into number of yearlings from first (F), second (S) and replacement (R) broods. Changes in the age class-specific population sizes between year t and t + 1 were modelled with binomial and Poisson processes (Appendix S1 Equations S1-S7). The number of immigrants in year t was  $N_{imt} \sim Pois(\omega_t)$ , where  $\omega_t$  is the expected number of immigrants in year t (Schaub & Fletcher, 2015). Immigration  $(\omega_t)$  was modelled with random year effects and independently of other vital rates over time (Appendix S1 Equation S12). Age classspecific probabilities were defined for apparent survival of juveniles  $(\phi_{iut}, \text{survival from fledging until next breeding season})$  and adults  $(\phi_{adt}, \phi_{adt})$ ) from year t to t + 1. Brood type specific fecundity in year t (fec<sub>a,t</sub>, with  $g = \{F, S, R\}$ ; see below) was included in the state process along with the annual proportion of breeding pairs that performed a second or a replacement brood ( $\psi_{S,t}$  and  $\psi_{R,t}$  respectively). The observation model described the relationship between counts of breeding pairs and true population size using a log-normal model with observation (residual) variance  $\sigma_{obs}^2$  (Appendix S1 Equation S8).

### 2.5 | Capture-recapture data

Individual encounter histories were modelled using a two ageclass capture-recapture model (Kéry & Schaub, 2012; Lebreton et al., 1992), with recapture probability of marked birds modelled with associated temporal random effects (Appendix S1 Equation S13). Apparent survival probabilities ( $\phi_{ju,t}$  and  $\phi_{ad,t}$ ) were modelled with random year effects and assumed to vary independently of other vital rates over time (Appendix S1 Equations S9 and S10).

## 2.6 | Fecundity data and brood type

Brood type specific fecundity, defined as the number of fledglings per breeding female in year t from first (*F*), second (*S*) and replacement (*R*) broods, was estimated with a zero-inflated normal model while accounting for the fact that brood type was not available for

$$J_i \sim \text{Norm}\left(z_i \operatorname{fec}_{g_i, t}, \sigma_{fec, g_i}^2\right), \tag{1}$$

with  $z_i$  indicating a successful ( $z_i = 1$ ) or unsuccessful (i.e. failed) brood ( $z_i = 0$ ), and the brood type indicator variable  $g_i = \{F, S, R\}$ . The model for  $z_i$  implicitly accounts for zero inflation:

$$z_i \sim \text{Bern}(v_{g_i,t}),$$
 (2)

with  $v_{g_{i},t}$  representing the probability that brood *i* of type  $g_{i}$  in year *t* was successful. The brood type variable *g*, unknown in some cases, was categorically distributed:

$$g_i \sim \operatorname{Cat}(\pi_{i,g,t}),$$
 (3)

with probability  $\pi_{ig,t} = q_{ig,t} / \sum_{g} q_{ig,t}$ , that brood *i* in year *t* was of type *g*, expressed as a function of the laying date (day of year), assuming a quadratic relationship and additive temporal random variation:

$$\log(q_{ig,t}) = \alpha_{qg} + \beta_{qg} \operatorname{day}_i + \beta_{q2,g} \operatorname{day}_i^2 + \varepsilon_{qg,t} \quad \text{with } \varepsilon_{qg,t} \sim \operatorname{Norm}\left(0, \sigma_{qg}^2\right),$$
(4)

with the constraint that  $\log(q_{i,g=R,t}) = 0$  (i.e.  $q_{i,g=R,t} = 1$ ), and where  $\log(q_{i,g,t})$  represents the log odds ratio for category g relative to category g = R (Lunn et al., 2012). We adopted a quadratic relationship since we expected a peak in the log odds ratio for the probability of being a first or second brood, relative to replacement brood, sometime during the breeding season, or log odds ratio starting low and steadily increase, or vice versa. To avoid overparameterization, we used a time-invariant quadratic relationship, but allowed the log odds ratios to vary between years following random variation with brood type specific temporal random standard deviation  $\sigma_{q,q}$ . To facilitate interpretation of results, we derived the probabilities of being a first, second or replacement brood in relation to day of year as follows (Agresti, 2018; subscripts i and t omitted):  $\pi_{g=F} = q_{g=F} / (1 + q_{g=F} + q_{g=S}), \ \pi_{g=S} = q_{g=S} / (1 + q_{g=F} + q_{g=S}),$  $\pi_{g=R} = 1/(1 + q_{g=F} + q_{g=S})$ . The annual proportion of breeding pairs in the population that performed a second ( $\psi_{s,t}$ ) or a replacement brood ( $\psi_{R,t}$ ), included in the state process describing changes in population size over time (Appendix S1 Equations S2 and S3), were derived as the ratio between the annual average probability of being a second or a replacement brood ( $\overline{\pi}_{g,t}$ , with g = S or R respectively) and the annual average probability of being a first brood ( $\overline{\pi}_{g=F,t}$ ):

$$\psi_{g,t} = \overline{\pi}_{g,t} / \overline{\pi}_{g=F,t}.$$
(5)

Fecundity (fec<sub>g,t</sub>, with  $g = \{F, S, R\}$ ) was modelled with random year effects and assumed to vary independently of other vital rates over time (Appendix S1 Equation S11).

## 2.7 | Bayesian inference

The IPM was fit using a Bayesian formulation with Markov chain Monte Carlo simulations. Vague prior distributions were used for all parameters except for the proportion of female fledglings that was based on a subsample of genetically sexed nestlings (see Table S1 in Appendix S1 and the supplementary model code for details on prior specification). Summaries of the posterior distribution were calculated from 45,000 posterior samples (burnin = 500,000 iterations). We assessed convergence using the  $\hat{R}$ diagnostics (Brooks & Gelman, 1998) that was <1.02 for all parameters. Posterior predictive checks were performed to assess the goodness-of-fit of the different (sub)models (see Appendix S1). Models were implemented using the R (R Core Team, 2012) package NIMBLE (de Valpine et al., 2017).

# 2.8 | Probability of starting a brood and of brood success

Indicator variables of brood type *g* and brood success *z* were used to derive the following year-specific quantities in each study population: (a) total number of first, second and replacement broods, (b) number of successful and unsuccessful first broods, (c) probability of starting a second or replacement brood (*PrS* and *PrR*, respectively). Specifically, the probability of starting a second brood (*PrS*) was derived by the ratio of the total number of second broods and the number of successful first broods, and the probability of starting a replacement brood (*PrR*) was obtained by dividing the total number of replacement broods by the number of unsuccessful first broods.

## 2.9 | Annual fecundity

Annual fecundity per female (fec<sub>ave,t</sub>), was derived for each year *t* and population, along with its population-specific overall mean, from the probability that a brood of type *g* in year *t* was successful ( $v_{g,t}$  in Equation 2), the probability of starting a second or a replacement brood (*PrS*<sub>t</sub> and *PrR*<sub>t</sub> respectively), and fecundity of each brood type (fec<sub>*g*,*t*</sub>), by considering the six possible scenarios observed during the study period in the two populations: (a) successful first brood followed by a successful second brood, (b) successful first brood followed by an unsuccessful second brood, (c) successful replacement brood and a successful second brood, (e) unsuccessful first brood followed by a successful replacement brood and an unsuccessful second brood, (e) unsuccessful first brood followed by a successful replacement brood and an unsuccessful second brood, (e) unsuccessful first brood followed by a successful replacement brood and an unsuccessful second brood, (f) unsuccessful first brood followed by a successful first brood followed by a successful replacement brood and an unsuccessful second brood, and (f) unsuccessful first brood followed by a successful replacement brood and an unsuccessful replacement brood only. For  $g_i = \{F, S, R\}$  the equation for annual fecundity per female is as follows:

$$\begin{aligned} & \text{fec}_{\text{ave},t} = v_{F,t} \operatorname{Pr} S_t v_{S,t} (\text{fec}_{F,t} + \text{fec}_{S,t}) + v_{F,t} \operatorname{Pr} S_t (1 - v_{S,t}) \operatorname{fec}_{F,t} \\ & + v_{F,t} (1 - \operatorname{Pr} S_t) \operatorname{fec}_{F,t} + (1 - v_{F,t}) \operatorname{Pr} R_t v_{R,t} \operatorname{Pr} S_t v_{S,t} (\text{fec}_{R,t} + \text{fec}_{S,t}) \\ & + (1 - v_{F,t}) \operatorname{Pr} R_t v_{R,t} \operatorname{Pr} S_t (1 - v_{S,t}) \operatorname{fec}_{R,t} + (1 - v_{F,t}) \operatorname{Pr} R_t v_{R,t} (1 - \operatorname{Pr} S_t) \operatorname{fec}_{R,t}. \end{aligned}$$
(6)

The annual fecundity per female corresponds to the parameter that we would use in a population model if we had no information about its components.

# 2.10 | Demographic influence on population growth rate

We performed a retrospective analysis to understand population dynamics in relation to changes in demographic rates (brood type specific fecundity, juvenile and adult apparent survival, and immigration rate) and the structure of the breeding population based on brood type (i.e. proportion of pairs that performed a second or a replacement brood,  $\psi_s$  and  $\psi_R$  respectively) through population-specific transient life table response experiments (tLTRE; Koons et al., 2016; Koons et al., 2017) that account for the fact that populations are exposed to non-stationary environments. The first tLTRE measures the contribution of temporal variability in demographic rates and proportion of second and replacement broods to the temporal variance of realized population growth rate  $\lambda_t$ . The second tLTRE quantifies the contribution of differences in demographic rates and proportion of second and replacement broods to the change in  $\lambda_t$  between successive years. See Appendix S1 (Section S2) for further details.

# 2.11 | Density dependence

Correlations between (a) annual estimates of demographic rates in year *t* (apparent juvenile and adult survival and brood type specific fecundity) and total population size  $N_{tot}$  in year *t*, (b) annual proportion of breeding pairs that performed a second or a replacement brood and total population size  $N_{tot}$  in year *t* were computed along with correlation between (c) number of immigrants in year *t* and total population size in year *t*, to assess density dependence. Correlation coefficients were calculated under full consideration of the uncertainty in parameter estimates, using posterior samples and deriving the 95% credible interval (95% CRI) of each correlation coefficient and the probability that the latter was negative [p(r < 0)]. Correlations are expected to be free from possible bias related to the observation process, since sampling and process variance are separated in the IPM.

# 3 | RESULTS

The Swiss population decreased annually by 6.0% (geometric mean of population growth rate  $\lambda$  0.940, 0.913–0.961, 95% CRI) whereas the German population increased annually by 7.0% (geometric mean of  $\lambda$  1.070, 1.032–1.099; Figures 1 and 2h). Mean apparent survival probability was larger in the Swiss population than in the German one for both juveniles (0.075, 0.061–0.091 vs. 0.041, 0.027–0.059) and adults (0.403, 0.341–0.476 vs. 0.298, 0.230–0.369). Temporal





variability of juvenile and adult survival did not substantially differ between populations (i.e. 95% CRIs largely overlapped; Figure 2a,b; Appendix S2 Table S1). Annual estimates of the immigration rate ranged between 0.095 (0.000–0.255) and 0.316 (0.029–0.750) in the Swiss population, and between 0.397 (0.139–0.759) and 1.058 (0.412–2.000) in the German population (Figure 2g). In the absence of immigration, estimates of geometric mean of population growth rate would be considerably lower than growth rates obtained from the IPM (0.744, 0.655–0.844 for the Swiss population; 0.511, 0.411– 0.625 for the German population).

## 3.1 | Brood type specific fecundity

Missing brood type records were estimated based on the relationship between the probability of being a first, second or replacement brood and day of year (Figure 3; Appendix S2 Table S2). Brood type specific fecundity for first and second broods was similar in both populations (Figure 2c,d), whereas average fecundity of replacement broods was larger in the German population, despite the large uncertainty associated with the estimates for the Swiss population (Figure 2e). In the Swiss population fecundity was 7.396 (7.203-7.589) fledglings per breeding pair and year for first broods, 5.646 (5.160-6.135) for second broods and 5.954 (4.111-8.016) for replacement broods. In the German population fecundity for first broods was 7.800 (7.540-8.064) fledglings per breeding pair and year, for second broods 5.792 (5.355-6.241) and for replacement broods 6.838 (6.245-7.420). Annual fecundity per female was similar in both populations ( $fec_{ave} = 6.249$ , 3.581–8.405 in Switzerland, and 6.279, 3.173-9.951 in Germany; Figure 2f). Temporal variability of fecundity was similar in first and second broods (Appendix S2 Table S1) but lower in replacement broods of the German population ( $\sigma_{\text{fec } R} = 0.053, 0.003 - 0.156$ , against 0.339, 0.154 - 0.745, of the Swiss population).

Temporal patterns of brood type specific probabilities of success, number of successful and unsuccessful first broods, probability of starting a second or a replacement brood, and proportion of pairs that performed a second or a replacement brood differed among the two populations (Figure 4). In the Swiss population, mean probability of success across the whole study period was

the highest for first broods (0.736, 0.697-0.774), intermediate for second broods (0.540, 0.461-0.617) and the lowest for replacement broods (0.243, 0.163-0.328). In the German population, mean probability of success showed a similar pattern across brood types but with probability of success for replacement broods more than double the one in the Swiss population: 0.612 (0.572-0.651) for first broods, 0.551 (0.478-0.624) for second broods, and 0.520 (0.426-0.613) for replacement broods. Average probability of starting a second brood, across the whole study period, was smaller in the Swiss than in the German population (0.273, 0.255-0.292, vs. 0.526, 0.515-0.539), but the probability of starting a replacement brood did not differ between populations (0.270, 0.254-0.289, vs. 0.331, 0.320-0.341). Across the whole study period, the average proportions of breeding pairs that performed a second  $(\overline{\psi}_{s})$  or a replacement  $(\overline{\psi}_{R})$  brood were similar in the Swiss population ( $\overline{\psi}_{s} = 0.202, 0.170 - 0.235, \overline{\psi}_{R} = 0.210, 0.161 - 0.266$ ) but different in the German population ( $\overline{\psi}_{s} = 0.309, 0.283 - 0.334, \overline{\psi}_{R} =$ 0.136, 0.107-0.169; Figure 4).

#### 3.2 Demographic influence on population growth

Elasticities showed that the parameters that would have the greatest potential to affect realized population growth were similar in both populations. Ordered from the strongest to the weakest, parameters with the highest elasticity were adult apparent survival, juvenile apparent survival, first brood fecundity and immigration rate in the Swiss population, and immigration rate, adult apparent survival, juvenile apparent survival and first brood fecundity in the German population (Table 1). Decomposing the variance of realized population growth rates using tLTRE (Appendix S1 Equation S16) showed that temporal variation in immigration rate contributed most to temporal variability in realized population growth rates in both populations (58% and 87% of total variation in Switzerland and Germany respectively). Other parameters were more stable over time and their contribution was smaller: in the Swiss population, 30% by adult apparent survival, 6% juvenile apparent survival and 0.03% first brood fecundity; in the German population, 4% adult apparent survival, 9% juvenile apparent survival and 0.2% first brood fecundity. Fluctuations in brood type

**FIGURE 2** Estimates of year-specific demographic rates (a–g) and population growth  $\lambda_t$  (h) of the two wryneck populations. The vertical lines indicate the 95% credible intervals for the annual estimates. The horizontal black dotted line in (h) indicates population stability



specific fecundities altogether contributed 1.8% to temporal variation in realized population growth in the Swiss population and 0.3% in the German population. The sum of the contributions of fluctuations in proportions of breeding pairs that performed a second or a replacement brood was 4.3% in the Swiss population and 0.5% in the German population.

Changes in realized population growth rate between successive years ranged from -0.36 to 0.42 in the Swiss population, and

from -0.50 to 0.61 in the German population (Figure 5). Applying tLTRE to these sequential changes in realized population growth rate (Appendix S1 Equation S17) showed that when changes were substantial ( $\Delta > 0.1$  or  $\Delta < -0.1$ ) the dominant driver was adult apparent survival (69% of the cases) and immigration rate (31%) in the Swiss population, whereas in the German population immigration rate was the dominant factor in 83% of the cases followed by juvenile apparent survival (17%). Usually changes in brood type specific

**FIGURE 3** Relationship between probability that a brood is a first, second

or replacement brood as a function of

observed relative frequencies of each brood type for each laying date

the laying date (day of year). Grey shaded

areas represent the 95% credible interval for the estimates. Dots indicate the



fecundities and proportion of breeding pairs that performed a second or replacement brood contributed less than annual changes in immigration rate or apparent survival. In the Swiss population, however, changes in the proportion of replacement broods contributed equally or more than changes in immigration in 2007–2008, 2015– 2016, and 2016–2017 (Figure 5).

# 3.3 | Density dependence

In the Swiss population only, total population size at time t was negatively correlated with second brood fecundity at time t (r = -0.32, p(r < 0) = 0.95; Table 2). All other correlations were not statistically significant, i.e. 95% CRI of correlation coefficients included zero.

# 4 | DISCUSSION

Magnitude and temporal variability of demographic rates differed between the two study populations. In Germany, a lower juvenile and adult apparent survival probability suggests that a larger proportion of juveniles and adults may have emigrated from the study area compared to the Swiss population. This is likely to be related to the size of the German study area (Schaub & Royle, 2014) which is almost 14 times smaller than the Swiss study area. In general, the low juvenile apparent survival in both populations may reflect large natal dispersal. However, imperfect detection of recruits and the methodological problem of separating emigration and true survival (Schaub & Royle, 2014) limit the interpretation of these results. The immigration rate was about three times greater in the German than in the Swiss population, but estimates of growth rate assuming no



**FIGURE 4** Estimates of year-specific probabilities of success for first, second and replacement broods, numbers of successful and unsuccessful first broods and their total, probability of starting a second or replacement brood and proportion of breeding pairs that performed a second or a replacement brood. Vertical lines indicate the 95% credible intervals for the annual estimates

**TABLE 1** Estimated sensitivities and elasticities of realized population growth rate to changes in the underlying vital rates and proportion of breeding pairs that performed a second or replacement brood, and transient life stable response experiment (tLTRE) contributions to temporal variability in realized population growth rate, for the Swiss (2002–2018) and the German (1999–2018) wryneck populations

	Sensitivity		Elasticity			tLTRE contribution			
	Mean	2.5%	97.5%	Mean	2.5%	97.5%	Mean	2.5%	97.5%
Swiss population									
Juvenile survival, $\phi_{ju}$	4.614	3.838	5.422	0.363	0.281	0.459	0.0023	-0.0017	0.0130
Adult survival, $\phi_{ad}$	1.000	1.000	1.000	0.421	0.380	0.463	0.0104	-0.0002	0.0278
Fecundity first brood, fec <sub>F</sub>	0.036	0.028	0.045	0.273	0.211	0.344	0.0000	-0.0005	0.0006
Fecundity second brood, fec <sub>s</sub>	0.007	0.005	0.009	0.042	0.031	0.056	0.0002	-0.0002	0.0007
Fecundity replacement, fec <sub>R</sub>	0.007	0.005	0.010	0.048	0.031	0.072	0.0003	-0.0010	0.0023
Immigration rate, $\iota$	1.000	1.000	1.000	0.214	0.082	0.333	0.0230	0.0029	0.0728
Proportion second broods, $\psi_{S}$	0.202	0.156	0.255	0.042	0.031	0.056	0.0003	-0.0006	0.0017
Proportion replacement broods, $\psi_R$	0.220	0.154	0.312	0.046	0.031	0.067	0.0012	-0.0015	0.0060
German population									
Juvenile survival, $\phi_{ju}$	5.046	4.214	5.893	0.198	0.136	0.277	0.0090	-0.0030	0.0369
Adult survival, $\phi_{ad}$	1.000	1.000	1.000	0.271	0.220	0.327	0.0040	-0.0049	0.0230
Fecundity first brood, fec <sub>F</sub>	0.021	0.014	0.029	0.147	0.101	0.205	0.0002	-0.0009	0.0016
Fecundity second brood, fec <sub>s</sub>	0.006	0.004	0.009	0.034	0.023	0.048	0.0001	-0.0005	0.0008
Fecundity replacement, fec <sub>R</sub>	0.003	0.002	0.004	0.017	0.011	0.026	-0.0000	-0.0002	0.0002
Immigration rate, $\iota$	1.000	1.000	1.000	0.529	0.409	0.634	0.0959	0.0298	0.2469
Proportion second broods, $\psi_{S}$	0.122	0.083	0.171	0.034	0.023	0.048	0.0002	-0.0006	0.0013
Proportion replacement broods, $\psi_{P}$	0.143	0.098	0.202	0.040	0.027	0.057	-0.0003	-0.0020	0.0015

immigration suggest that both local populations are dependent on immigration for their persistence.

### 4.1 | Brood type specific fecundity

Decomposing fecundity in relation to brood type highlighted differences between the two study populations. The probability of starting a second brood was twice higher in the German than in the Swiss population, but second brood fecundities and their temporal random variabilities, as well as probabilities of success of second broods, were similar in both populations. The probability of starting a replacement brood was similar in both populations but the probability of success of replacement broods was more than twice higher in Germany and the related fecundity was almost one fledgling larger and less variable during the study period compared to the Swiss population. Despite these differences in brood specific fecundity, the annual fecundity per female did not differ between the two populations. A reduction in the annual fecundity per female in the German population, from an average of 6.804 fledglings (3.392 - 10.189) in the period 1999-2011 to 5.304 fledglings (3.021 - 7.753) in 2012-2018, may be due to a decline in the probability of success of first broods, from an average of 0.709 (0.391 - 0.946) in 1999-2011 to 0.431 (0.221 - 0.643) in 2012-2018. This matches the effect of predation on broods by

racoon *Procyon lotor* that were recorded starting from 2012 (Becker Tolkmitt & Nicolai, 2014). Evidence for racoon predation is also provided by the fact that the number of fledglings of successful first broods did not show a decline. The lower probability of success of first broods in Germany may result in larger breeding dispersal between consecutive seasons (Paradis et al., 1998), in line with the lower adult apparent survival and proportion of breeding pairs that performed a replacement brood.

### 4.2 | Demographic influence on population growth

We used IPM estimates of demographic rates and structure of the breeding population according to brood type, i.e. the proportion of breeding pairs that performed a second or replacement brood, in tLTRE to decompose the demographic drivers of change in realized population growth rates while accounting for non-stationary environments. Immigration rate was the dominant contributor to temporal variation in realized population growth rates in both populations. Despite the realized population growth rate was sensitive to proportional changes in first brood fecundity, but not to other brood specific fecundities or proportion of second or replacement broods, the contribution of first brood fecundity was low likely because of its little variability over time. In addition, higher sensitivity of population growth to immigration can be due FIGURE 5 Sequential changes in realized population growth rate for the Swiss and German wryneck populations, and contributions of the changes in demographic rates and proportion of breeding pairs that performed a second or replacement brood. The annual difference in realized population growth rate equals the sum across all contributions



	Mode	2.5%	97.5%	p(r < 0)
N <sub>tot,t-1</sub>	-0.21	-0.54	0.37	0.73
N <sub>tot,t</sub>	-0.11	-0.45	0.47	0.57
$N_{\text{tot},t}$	0.03	-0.44	0.52	0.42
N <sub>tot,t</sub>	-0.32	-0.61	0.07	0.95
$N_{\text{tot},t}$	0.04	-0.28	0.40	0.41
$N_{\text{tot},t}$	0.01	-0.43	0.52	0.44
$N_{\text{tot},t}$	-0.06	-0.35	0.31	0.62
$N_{\text{tot},t}$	-0.11	-0.47	0.38	0.62
$N_{\text{tot},t}$	0.15	-0.15	0.57	0.17
N <sub>tot,t-1</sub>	0.05	-0.34	0.44	0.41
$N_{\text{tot},t}$	0.10	-0.28	0.45	0.32
N <sub>tot,t</sub>	-0.04	-0.42	0.39	0.55
N <sub>tot,t</sub>	-0.06	-0.51	0.37	0.62
N <sub>tot,t</sub>	0.02	-0.44	0.48	0.46
$N_{\text{tot},t}$	-0.02	-0.45	0.39	0.55
N <sub>tot,t</sub>	-0.01	-0.45	0.45	0.50
$N_{\text{tot},t}$	-0.11	-0.49	0.38	0.63
N <sub>tot,t</sub>	0.17	-0.30	0.51	0.25
	N <sub>tot,t-1</sub> N <sub>tot,t</sub> N <sub>tot,t</sub>	Mode $N_{tot,t-1}$ -0.21 $N_{tot,t}$ -0.11 $N_{tot,t}$ 0.03 $N_{tot,t}$ -0.32 $N_{tot,t}$ 0.04 $N_{tot,t}$ 0.01 $N_{tot,t}$ -0.06 $N_{tot,t}$ 0.05 $N_{tot,t}$ -0.04 $N_{tot,t}$ -0.04 $N_{tot,t}$ -0.02 $N_{tot,t}$ -0.02 $N_{tot,t}$ -0.01 $N_{tot,t}$ -0.01 $N_{tot,t}$ -0.11 $N_{tot,t}$ -0.02 $N_{tot,t}$ -0.01 $N_{tot,t}$ -0.11 $N_{tot,t}$ -0.11 $N_{tot,t}$ -0.11	Mode         2.5% $N_{tot,t-1}$ -0.21         -0.54 $N_{tot,t}$ -0.11         -0.45 $N_{tot,t}$ 0.03         -0.44 $N_{tot,t}$ -0.32         -0.61 $N_{tot,t}$ 0.04         -0.28 $N_{tot,t}$ 0.01         -0.43 $N_{tot,t}$ -0.06         -0.35 $N_{tot,t}$ -0.11         -0.47 $N_{tot,t}$ -0.15         -0.15 $N_{tot,t}$ 0.05         -0.34 $N_{tot,t}$ 0.10         -0.28 $N_{tot,t}$ 0.01         -0.28 $N_{tot,t}$ 0.05         -0.34 $N_{tot,t}$ 0.10         -0.28 $N_{tot,t}$ -0.04         -0.42 $N_{tot,t}$ -0.04         -0.42 $N_{tot,t}$ -0.02         -0.44 $N_{tot,t}$ -0.02         -0.45 $N_{tot,t}$ -0.01         -0.45 $N_{tot,t}$ -0.11         -0.49 $N_{tot,t}$ 0.17         -0.30 <td>Mode         2.5%         97.5%           <math>N_{tot,t-1}</math> <math>-0.21</math> <math>-0.54</math> <math>0.37</math> <math>N_{tot,t}</math> <math>-0.11</math> <math>-0.45</math> <math>0.47</math> <math>N_{tot,t}</math> <math>0.03</math> <math>-0.44</math> <math>0.52</math> <math>N_{tot,t}</math> <math>-0.32</math> <math>-0.61</math> <math>0.07</math> <math>N_{tot,t}</math> <math>0.04</math> <math>-0.28</math> <math>0.40</math> <math>N_{tot,t}</math> <math>0.01</math> <math>-0.43</math> <math>0.52</math> <math>N_{tot,t}</math> <math>0.01</math> <math>-0.43</math> <math>0.52</math> <math>N_{tot,t}</math> <math>0.01</math> <math>-0.43</math> <math>0.52</math> <math>N_{tot,t}</math> <math>0.01</math> <math>-0.43</math> <math>0.52</math> <math>N_{tot,t}</math> <math>-0.06</math> <math>-0.35</math> <math>0.31</math> <math>N_{tot,t}</math> <math>0.05</math> <math>-0.34</math> <math>0.44</math> <math>N_{tot,t}</math> <math>0.10</math> <math>-0.28</math> <math>0.45</math> <math>N_{tot,t}</math> <math>-0.04</math> <math>-0.42</math> <math>0.39</math> <math>N_{tot,t}</math> <math>0.02</math> <math>-0.44</math> <math>0.48</math> <math>N_{tot,t}</math> <math>-0.01</math> <math>-0.45</math> <math>0.39</math> <math>N_{tot,t}</math> <math>-0.11</math> <math>-0.49</math> <math>0.38</math></td>	Mode         2.5%         97.5% $N_{tot,t-1}$ $-0.21$ $-0.54$ $0.37$ $N_{tot,t}$ $-0.11$ $-0.45$ $0.47$ $N_{tot,t}$ $0.03$ $-0.44$ $0.52$ $N_{tot,t}$ $-0.32$ $-0.61$ $0.07$ $N_{tot,t}$ $0.04$ $-0.28$ $0.40$ $N_{tot,t}$ $0.01$ $-0.43$ $0.52$ $N_{tot,t}$ $0.01$ $-0.43$ $0.52$ $N_{tot,t}$ $0.01$ $-0.43$ $0.52$ $N_{tot,t}$ $0.01$ $-0.43$ $0.52$ $N_{tot,t}$ $-0.06$ $-0.35$ $0.31$ $N_{tot,t}$ $0.05$ $-0.34$ $0.44$ $N_{tot,t}$ $0.10$ $-0.28$ $0.45$ $N_{tot,t}$ $-0.04$ $-0.42$ $0.39$ $N_{tot,t}$ $0.02$ $-0.44$ $0.48$ $N_{tot,t}$ $-0.01$ $-0.45$ $0.39$ $N_{tot,t}$ $-0.11$ $-0.49$ $0.38$

**TABLE 2** Assessing density dependence. Correlation coefficients (posterior modes, 95% credible intervals and probability that coefficients were negative [p(r < 0)]) between number of immigrants ( $N_{\text{Imm},t}$ ) and population sizes of the current ( $N_{\text{tot},t}$ ) and previous ( $N_{\text{tot},t-1}$ ) year, and between demographic rates (included the proportion of breeding pairs that performed a second or replacement brood) and population size of the current year

to the small spatial scale of the study population in relation to dispersal distances, with a large part of locally born individuals dispersing outside the study area (Matthysen et al., 2001; Schaub et al., 2006), a pattern that can be stronger in the small German population.

Large sequential changes in realized population growth rates were mostly due to sequential changes in apparent survival (adult survival in the Swiss and juvenile survival in the German population) and in immigration rate in both populations. The contribution of changes in brood specific fecundity and in the proportion of second or replacement broods was lower, although the proportion of breeding pairs that performed a replacement brood contributed to sequential changes in growth rates of the Swiss population in some years (Figure 5). A weak relationship between annual fecundity and population growth rate was also reported by Schaub et al. (2012) for the same Swiss population but for a shorter study period, using a classical fecundity model embedded in an IPM for estimating the total number of fledglings per female per season, and using correlation analysis instead of tLTRE.

### 4.3 | Density dependence

Second brood fecundity declined when the size of the Swiss population increased. No evidence of a feedback of density on vital rates was found in the German population. Negative density dependence on breeding season fecundity, rates of double brooding and success of second clutches has been described in birds (e.g. Hoffmann et al., 2015; Nagy & Holmes, 2005; Sillett et al., 2004; Woodworth, Wheelwright, Newman, & Norris, 2017; Woodworth, Wheelwright, Newman, Schaub, et al., 2017). Woodworth, Wheelwright, Newman, and Norris (2017) documented density dependence on second brood fecundity and on recruitment in the Savannah sparrow, with double-brooding and predation strongly influenced by local density. Our results show that a negative feedback of density can be present only on second brood fecundity but not on the other brood type specific fecundities nor on the breeding season fecundity. Second brood fecundity is still expected to have very low power to regulate the population, since the contribution of its fluctuations to the variability of population growth is very low.

# 4.4 | Decomposing fecundity

Our study provides insight into the reproductive processes in a migratory bird and its impact on population dynamics. We presented an analytical approach for explicitly modelling brood type specific fecundities within an IPM framework and for maximizing the use of available fecundity data through the estimation of unknown brood types on the basis of laying dates. By jointly using IPM estimates and tLTRE (Koons et al., 2016, 2017), we have also shown how decomposing fecundity into different components allows for more insights into the relative role of different brood types in multiple-brooded species while accounting for nonstationary environments. In addition, when specific fecundity data are available, estimating fecundity components opens the possibility of testing hypotheses about how individual trait distribution, environmental conditions and their interaction affect fecundity components and, ultimately, population dynamics (Plard et al., 2019). We distinguished brood types and characterized their reproductive outcome in terms of probability of success and number of fledglings, but the fecundity model can be extended to include additional components like clutch size, hatching and fledging success for each brood type. This can improve the mechanistic understanding, and possibly prediction, of reproduction and its demographic impact.

The model requires fecundity data typically collected in population dynamic studies where adults can be marked and re-detected and breeding attempts monitored with sufficient temporal resolution. The minimum set of data that should be available for each breeding attempt are: (a) parent identity, (b) laying date and (c) number of fledglings produced. Reproductive records with missing information on laying date were discarded and not modelled in our study. An exploratory analysis incorporating missing records of laying date, modelled as a random variable, showed problems in achieving convergence to the stationary distribution for laying date in both populations (results not shown). In addition, large overlap of brood type specific temporal distributions may challenge the estimation of brood type (Cornulier et al., 2009), especially in the case of replacement broods. Future work may use simulations to evaluate model performance in estimating brood type from (known) laying date, for different degrees of overlap in the temporal distributions. Although brood type specific fecundity contributed little to population dynamics in most years for the wryneck populations studied, this need not be the case for other species nor at larger spatial scales. The model could also include spatial information, i.e. spatial explicit breeding data, which might account for dispersal between broods and the estimation of habitat-specific productivity. Overall, given the large number of population studies on multiple-brooded species that routinely record fecundity data, for instance using nestboxes (Tinbergen & Boerlijst, 1990; Verhulst et al., 1997), the approach presented here can be applied to other ecological systems to understand better the demographic contribution of brood type specific fecundity.

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#### AUTHORS' CONTRIBUTIONS

S.T. and M.S. conceived the ideas and designed the methodology; M.S., D.B. and D.T. collected the data; S.T. and M.S. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

The data used in this paper are available on the vogelwarte.ch Open Repository and Archive http://doi.org/10.5281/zenodo.4438797 Tenan et al. (2021).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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