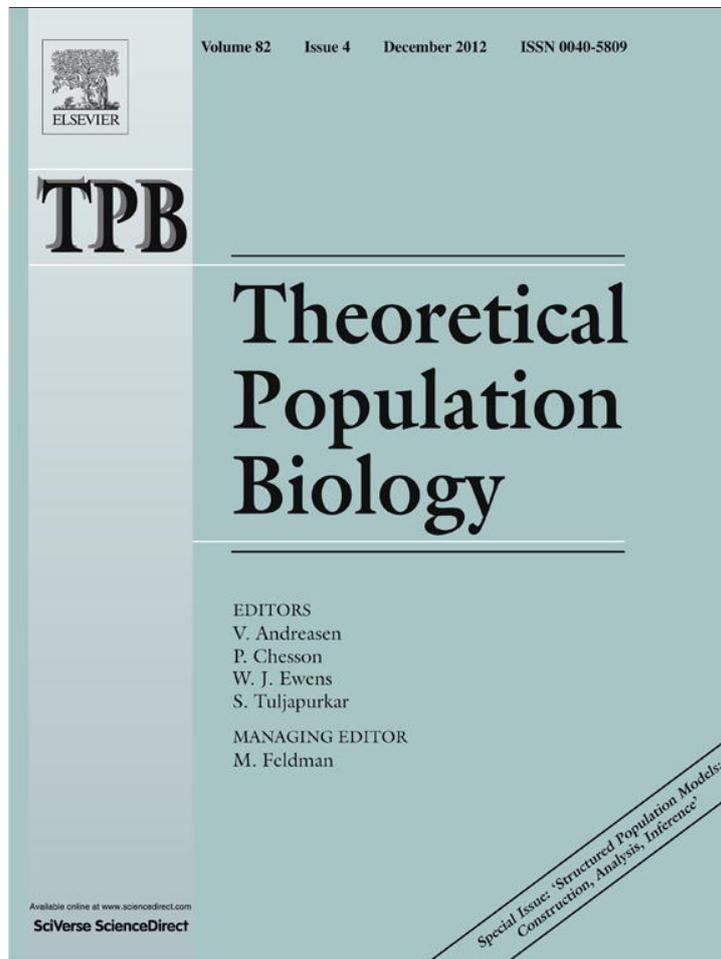


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Modeling reproductive trajectories of roe deer females: Fixed or dynamic heterogeneity?

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ABSTRACT

The relative role of dynamic and fixed heterogeneity in shaping the individual heterogeneity observed in most life-history traits remains difficult to quantify. In a recent work, Tuljapurkar et al. (2009) suggested modeling individual heterogeneity in lifetime reproductive success by a null model building reproductive trajectories from a first-order Markov chain. According to this model, among-individual differences in reproductive trajectories would be generated by the stochastic transitions among reproductive states (such as breeder and non-breeder) due to dynamic heterogeneity. In this work, we analyze the individual variation in three reproductive metrics (reproductive status, fecundity, and reproductive success) in two populations of roe deer intensively monitored using Tuljapurkar et al. (2009)'s dynamic model. Moreover, we challenge the Tuljapurkar model previously used as a biological null model to test whether the observed distribution of reproductive success over the lifetime was generated by a stochastic process by modifying two steps of the previous model to build a full stochastic model. We show that a distribution generated by the full dynamic model proposed by Tuljapurkar et al. (2009) can be consistently interpreted as only generated from a stochastic biological process provided that the probabilities of transition among reproductive states used are independent of the current reproductive state and that the positive co-variation that usually occurs between survival and reproduction among individuals is removed. Only the reproductive status of roe deer females could be restricted to a stochastic process described by the full stochastic model, probably because most females (>90%) were breeders in a given year. The fecundity of roe deer females could not be adequately described by the full dynamic and full stochastic model, and the observed distribution of female reproductive success differed from the one generated by a full dynamic model in which each individual reproductive trajectory was independent of the individual lifespan (second step of the full dynamic model changed). While there was clear evidence that dynamic heterogeneity occurred and accounted for a large part of the observed among-individual variation in reproductive trajectories of roe deer females, a stochastic process did not provide a suitable model for all reproductive metrics. Consequently, models including additional fixed and dynamic traits need to be built in order to separate the relative role of fixed and dynamic heterogeneities in generating reproductive trajectories.

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1. Introduction

Individual heterogeneity is pervasive in most organisms, and it corresponds to the variation observed in a trait among individuals within a given population. These differences need to be accounted for to assess within-individual changes in age-dependent life-history traits reliably (Vaupel and Yashin, 1985). Diversity in maternal and environmental factors generates differences in individual reproductive abilities (Cam and Monnat, 2000; Beauplet

et al., 2006; Knape et al., 2011) and modifies the shape of age dependence in survival. The positive co-variation between survival and reproduction induced by phenotypic and environmental variations can often mask actuarial senescence (Service, 2000; Nussey et al., 2008). Individual heterogeneity, thus, plays a main role in shaping population dynamics (Bjørnstad and Hansen, 1994; Cam et al., 2002; Vindenes et al., 2008; Kendall et al., 2011).

The different sources of heterogeneity are often poorly investigated, and their relative roles in structuring the observed variation in life-history traits remain unknown. A recent study by Tuljapurkar et al. (2009) provided a way to disentangle the dynamic and fixed heterogeneity. Dynamic heterogeneity involves within-individual differences in life-history traits that are generated by a random process that produces transitions between

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states depending on the current state along the trajectory of a given trait. Dynamic heterogeneity is generated by environmental changes involving fluctuations of climate, of resource availability, or of the prevalence of parasites that occur through time in a given population. At a given time, all individuals in the population should face similar environmental conditions. The way each individual responds to changes of environmental conditions leads to another kind of heterogeneity, which corresponds to the state-dependent condition model proposed by McNamara and Houston (1996). Even if the original definition of dynamic heterogeneity by Tuljapurkar et al. (2009) was not explicit about that, how an animal is affected by its environment in a given year is likely to be driven by fixed traits (see, e.g., Descamps et al. 2011) rather than by a stochastic process. On the other hand, fixed heterogeneity is fixed at birth by processes such as genetic, maternal, and cohort effects (Tuljapurkar et al., 2009).

The relative influence of fixed and dynamic heterogeneity in producing observed individual heterogeneity remains poorly known because separating their different roles is difficult. Until recently, individual heterogeneity has mainly been interpreted in terms of fixed heterogeneity, leading to a continuum of individual quality (Bérubé et al., 1999; Hamel et al., 2009b; Moyes et al., 2011). Individual quality can be viewed as a co-variation among different fixed life-history traits, which is positively associated with Darwinian fitness of individuals (Wilson and Nussey, 2010; Lailvaux and Kasumovic, 2010; Bergeron et al., 2011). The concept of quality is rooted in the measure of frailty defined by Vaupel et al. (1979) as the relative propensity for a given individual to survive better or worse than the average individual in the population, which, in its original definition, remains constant from birth onwards. Such a fixed heterogeneity may be stochastic or linked to variation in traits that markedly influence yearly reproductive performance of individuals such as birth mass, age at first reproduction, or longevity (Beauplet et al., 2006; Hamel et al., 2009b; Aubry et al., 2011).

While the influence of fixed heterogeneity in shaping individual trajectories has been reported from empirical analyses for several populations of vertebrates (see the previous paragraph), recent studies of dynamic heterogeneity have shown that random processes strongly contribute to generate individual heterogeneity (Steiner et al., 2010; Orzack et al., 2011) in populations. For instance, the observed individual heterogeneity in lifetime reproductive success resulted mostly from a random process in the swan (Tuljapurkar et al., 2009) and the kittiwake (Steiner et al., 2010; Steiner and Tuljapurkar, 2012). In these studies, dynamic heterogeneity has been modeled using a Markov chain, i.e. a random model describing the transitions among states (Tuljapurkar et al., 2009). In a first-order Markov chain process, the distribution probability of the next state depends on the current state only. To model the distribution of reproductive success generated by dynamic heterogeneity only, Tuljapurkar et al. (2009) built reproductive trajectories of length n using a first-order Markov chain. We will refer to this model as the *full dynamic model*. This full dynamic model has been interpreted as a null model to be compared with empirical data and to test whether an observed distribution of lifetime reproductive success is fully generated by dynamic heterogeneity, i.e., by stochastic transitions among states (Steiner et al. 2010; Orzack et al. 2011; see Box 1 for definitions of the terms used).

An important specificity of the full dynamic model is that the transition matrix used to generate the theoretical distribution of lifetime reproductive success is estimated from empirical data obtained from long-term monitoring of individuals. This crucial step makes the assumption that the transition between two consecutive states in the real world is also stochastic. Previous empirical works, however, showed that annual reproductive success correlates positively with phenotypic attributes of females such as body

mass (Hamel et al., 2009b). If a stochastic process was at work in the transition between successive states, one could not predict the reproductive success of individuals. In fact, each transition in the time series of states observed in an individual reproductive trajectory is governed by the interplay between the strength of reproductive costs and the value of phenotypic attributes of the individual, all of which include some stochastic variation but cannot be reduced to events only influenced by environmental stochasticity. Because the data on which the estimation of transition probabilities for the full dynamic model may include a non-stochastic part, the interpretation of the first-order correlation between successive states as representing a stochastic process only in the full dynamic model can be questioned on biological grounds.

We aimed here to assess whether the model proposed by Tuljapurkar et al. (2009) could be considered as an appropriate biological null model to test the null hypothesis that an observed distribution of lifetime reproductive success is generated solely by a stochastic process. First, taking advantage of a detailed long-term monitoring of roe deer (*Capreolus capreolus*) in two French populations, we used three reproductive metrics – *reproductive status* (breeder versus non-breeder); *fecundity* (the number of newborns produced); *reproductive success* (the number of weaned offspring) – to determine whether the observed individual heterogeneity occurring in reproductive performance is generated by dynamic heterogeneity only. Our case study on roe deer reproduction demonstrates that, while some metrics of reproduction can be satisfactorily described by the full dynamic model, other metrics cannot. Consequently, reproductive metrics including different life-history traits are governed by different processes. Second, to test if the full dynamic model is an appropriate null model representing a truly stochastic model, we changed two steps of Tuljapurkar et al. (2009)'s model sequentially: (1) we estimated transition probabilities among states independently of the current state and compared the results with the full dynamic model; and (2) we removed the correlation between survival and reproductive transitions and investigated its role in shaping the individual heterogeneity. Third, we quantified the influence of age and time in shaping the dynamic heterogeneity. We show that the distribution generated from the full dynamic model of Tuljapurkar et al. (2009) cannot be interpreted as a distribution generated only by dynamic heterogeneity.

2. Background

2.1. Reproductive trajectories and dynamic heterogeneity

The life of a given individual can be described as a succession of states from birth to death. This succession of transitions between states is called a trajectory. When reproductive states are considered, the trajectory becomes a reproductive trajectory. Each individual can be characterized by its own reproductive trajectory. For instance, when the reproductive performance is measured by reproductive success, a reproductive trajectory corresponds to a succession of numbers representing the numbers of young weaned by a given individual at each reproductive event. Whether a trajectory is pre-programmed at birth or occurs randomly is a question that studies analyzing fixed and dynamic heterogeneity try to answer. To understand whether reproductive events over an individual lifetime can be modeled as random trajectories generated by a stochastic process, we built the full dynamic model on reproductive trajectories of length n using a first-order Markov chain (Tuljapurkar et al., 2009). In this model, each simulated trajectory w has a weight W_w which corresponds to the probability of this trajectory occurring; it is a product of the transition probabilities (ψ) between successive states s_t and s_{t+1} : $W_w = \prod_{t=1}^{n-1} \psi(s_t, s_{t+1})$.

Box.1 Definitions

Stochastic process (used as a biological term): A given state of the reproductive trajectory of an individual following a stochastic process is independent of the previous states, of the future states, of individual lifespan and of individual birth environment.

Random process (used as a mathematical term): A mathematical process as opposed to a deterministic process. Even when the initial conditions are known, the result of the process can take many different possibilities.

Dynamic heterogeneity: Individual heterogeneity due to stochastic change in environmental conditions.

Fixed heterogeneity: Individual heterogeneity shaped by fixed trait(s) at birth.

Full dynamic model: The model described by Tuljapurkar et al. (2009).

Full stochastic model (model described in this study): The model based on the full dynamic model with two modifications:

(1) transition probabilities are estimated from a stochastic dataset and so are independent of the current state;

(2) trajectory weights are estimated as follows: $W_w = \prod_{t=1}^{n-1} T(s_t, s_{t+1})$, where n is the maximum age in the population and T is the transition probability between two successive reproductive states knowing that the individual has survived.

2.2. Multistate capture–recapture models

Estimates of transition probabilities among states, $\psi(s_t, s_{t+1})$, can be obtained from the transition matrix of multistate capture–recapture models. These models require long-term and intensive monitoring of a large number of individuals (Lebreton et al., 2009). Basically, the probability of controlling a given animal in the state s_{t+1} at occasion $t + 1$ knowing that it was in the state s_t at the previous time step t is the product of the transition probability $\psi(s_t, s_{t+1})$ (used in the full dynamic model) and the probability of recapturing this individual. A transition probability can be further decomposed into the probability of transition from state s_t to state s_{t+1} knowing that this animal has survived $T(s_t, s_{t+1})$ (used in the full stochastic model), and the probability of survival between occasion t and $t + 1$, $\varphi(t)$. The matrices of transition between states, of survival, and of recapture are estimated from a first-order Markov chain, but they can vary with other factors such as environmental conditions or age. In this case, several matrices of transition are estimated according to the number of levels of this structuring factor. As a consequence, to find the optimal model describing the observed data, a model is required to retain the model that obtains the best compromise between accuracy (i.e., a low deviance) and precision (i.e., a low number of parameters) (Lebreton et al., 1992).

3. Populations and variables

3.1. Two roe deer populations

Data were collected on two different populations of roe deer from France. The two populations lived in the enclosed forests of Chizé (2614 ha, 46°05'N, 0°25'W, Western France) and Trois-Fontaines (1360 ha, 48°43'N, 2°61'E, North Eastern France). These two populations faced contrasting environmental conditions and had markedly different demographic characteristics (see Gaillard et al., 1993; Nilsen et al., 2009, for detailed information). Trois-Fontaines has a continental climate with rather cold winters and Chizé has an oceanic climate with Mediterranean influence, with mild winters and frequent summer droughts. These two populations have been intensively monitored by the Office National de la Chasse et de la Faune Sauvage for more than 30 years. Animals are individually marked by ear-tags and numbered collars, and some females have been equipped with VHF (very high frequency) or GPS (global positioning system) collars. Each year, between 8 and 12 days of capture are organized between December and March in both study sites. Roe deer are captured by drive-netting. Each drive involves 150 ± 30 people and

2.5 km of nets, resulting in the capture of 120–300 roe deer a year in each site. Captured animals are sexed and weighed. The female reproductive status (pregnant or not) and the number of embryos carried are determined by ultrasonography at Chizé. At Trois-Fontaines, marked adult females (i.e., >2 years of age) are monitored in fall (autumn) to assess the number of fawns they weaned in a given year. Because early summer survival is the most critical stage in roe deer (Gaillard et al., 2000), most fawns alive in late fall will reach adulthood. The number of fawns alive in fall was therefore used as a measure of annual reproductive success of a female at Trois-Fontaines.

3.2. Three reproductive metrics

Roe deer females give birth to one to three (most often two) fawns each year in May, generally from 2 years of age onwards, and can live up to 18 years. Most roe deer females in the study sites died between 8 and 12 years old. Three reproductive metrics were analyzed in this study: *reproductive status* (on 268 females at Chizé between 1988 and 2010), *fecundity* (on 260 females at Chizé between 1988 and 2010), and *reproductive success* (on 253 females at Trois-Fontaines between 1976 and 2005). *Reproductive status* included two states (breeder and non-breeder) and was assessed by ultrasonography during winter captures in January–February. *Fecundity* corresponded to the number of fetuses recorded using ultrasonography and included three states (0, 1, and 2 embryos). *Reproductive success* was measured by the number of fawns a given female successfully weaned (i.e., observed at heel) and included three states (0, 1, and 2 fawns). We estimated the survival and transition matrices between states for the three reproductive metrics. Preliminary analyses were conducted to select the best capture recapture model (Table S1 in supplementary material) for each of the three reproductive metrics. We used the R (R Development Core Team, 2011) package Rmark (Laake and Rexstad, 2008) to construct models for program Mark (White and Burnham, 1999). The best models describing transition probabilities for roe deer females were similar for *reproductive status* and *fecundity*, and they included the effects of age (i.e., prime-aged versus senescent females) and time (i.e., years with high versus low population density) on survival probability, an effect of age (i.e., prime-aged versus senescent females) on transition probability, and a constant recapture probability. *Reproductive success* was best modeled by including the effect of age (i.e., prime-aged versus senescent females) on survival probability, a constant transition probability, and a full time dependence in recapture probabilities.

4. Modeling dynamic heterogeneity and stochastic process

We first replicated Tuljapurkar et al. (2009)'s approach and modeled our three reproductive metrics using the full dynamic model (4.1). We then modified this model with a two-step process (4.2 and 4.3). Finally, we looked at the influence of age and time in shaping the dynamic heterogeneity (4.4).

4.1. The full dynamic model

To assess the amount of heterogeneity from the observed transition matrix, Tuljapurkar et al. (2009) used the entropy (Tuljapurkar, 1982). We also used this metric to measure how fast individual heterogeneity increases along trajectories. However, the formula provided by Tuljapurkar et al. (2009) cannot be applied to the age-dependent matrices obtained for *reproductive status* and *fecundity*. Consequently, in addition, to estimate the entropy H (Tuljapurkar et al., 2009) of each matrix (2 for prime-aged and senescent females for *reproductive status* and *fecundity* and 1 for all ages for *reproductive success*), we computed a scaled sequence entropy, H_s (one for each age) for each reproductive metric as follows (Tuljapurkar, personal communication). At each age $A > 1$ (female roe deer produce offspring from 2 years of age onwards), there are $\text{number of states}^{\text{number of occasions}}$ possible trajectories to follow for a female ($N = 2^{A-1}$ for *reproductive status* and $N = 3^{A-1}$ for *fecundity* and *reproductive success*). Each trajectory w is weighted by its probability of occurring, $W_w = \prod_{t=1}^{A-1} T(s_t, s_{t+1})$. We simulated 10^7 individuals and attributed a trajectory to each individual. Let $p(i)$ be the fraction of individuals with trajectory i . Then, the sequence entropy is defined as $h = -\sum_i p(i) * \log(p(i))$, and the scaled sequence entropy is $H_s = h/(\log N)$.

Another relevant metric defined by Tuljapurkar et al. (2009) is the persistence, which provides information on how long an individual stays in the state successful or unsuccessful. As for entropy, the formula of persistence given by Tuljapurkar et al. (2009) cannot be estimated for age-dependent matrices. So, we estimated a sequence persistence as the conditional probability for a given individual to be in the final state s at age A , knowing that it was in the same state s at 2 years old, the starting age of the female reproductive trajectories (calculated for A between 3 years old and 20 years old) (Tuljapurkar, personal communication).

We then compared, at the population level, the observed distribution of cumulated number of successes (i.e., cumulated number of breeding events for *reproductive status*, cumulated number of embryos for *fecundity*, and cumulated number of fawns weaned for *reproductive success*) to the distribution generated from a first-order Markov model using the observed transition and survival matrices (full dynamic model). The observed matrices refer to the matrices estimated by the multistate capture–mark–recapture models using the dataset of the studied population (observed dataset). To generate the expected distribution of successes from the full dynamic model, we simulated 3000 different trajectories and attributed a trajectory to each individual according to the trajectory weight. Trajectory weights were calculated for an individual i according to the observed age of last recapture of this individual ($A_{i,\max}$) and to the survivorship of the trajectory (Tuljapurkar et al., 2009). For each individual i , a trajectory w would have a corresponding weight $W_{w,i} = \prod_{t=1}^{A_{i,\max}-1} (T(s_t, s_{t+1})\varphi(t))$, where T and S are the observed transition and survival probabilities, respectively. 10^5 individuals were simulated (the number of individuals must be large enough, so that each trajectory can be attributed, once weighted by its probability of occurring, to the right portion of individuals). Once a trajectory among the 3000 was attributed to individual i , we simulated the observed recapture probability along the trajectory and cumulated the number of successful reproductive states only over the occasions where the animal was recaptured. The generated distribution was averaged

among 50 simulated populations of 10^5 individuals. Two statistical tests were performed to test the difference between the observed and generated distributions: the Kolmogorov–Smirnov test, which is very conservative and was used by Tuljapurkar et al. (2009), and an adjusted χ^2 test, which is less conservative.

4.2. Stochastic transition matrix

To relax the potential relationship between successive states, we used transition and survival matrices estimated from simulated datasets instead of the observed transition and survival matrices, estimated from observations of individuals. The observed dataset consists of individual capture histories in which each line represents an individual and each column a year. Each element of the dataset was either a 0 when the individual was not captured or a positive number between 1 and 3 corresponding to the individual state when captured. We first ordered the observed dataset of capture histories by age to have lines representing individuals and columns representing ages to keep the age structure of the population while breaking the time structure. Then each column was randomized to separate the successive transitions of observed individual trajectories. By doing this, we allowed successful trajectories to mix with unsuccessful trajectories to generate random trajectories from observed states. We repeated this procedure to obtain 1000 randomized datasets. Finally, we obtained the average simulated transition and survival matrices with their confidence intervals.

The simulated transition matrix intuitively provides information about the proportion of individuals in each state in the population according to the different age classes. The simulated probabilities of transition depend on the next state but no longer on the current state, as two consecutive states were rearranged randomly. Conversely, in the observed matrix transition, as defined by a first-order Markov process, the transition probability from one state to the next state depends on the current state. We compared the estimations of transition probabilities obtained from this simulated transition matrix with those obtained from the observed transition matrix using their confidence intervals. The comparison tests the propensity for an individual to stay in the same state (remains successful or remains unsuccessful) between time t and $t+1$ between the studied and the average simulated population. If the observed and simulated transitions are different, then using the observed transition probabilities as in 4.1 to simulate trajectories would make these trajectories not fully stochastic. We also calculated and compared the observed and simulated persistence. Then, a distribution of the cumulated number of successes was generated from the simulated transition and survival matrices and compared to the distribution generated from the observed transition and survival matrices (full dynamic model), and to the observed distribution of the cumulated number of successes. This procedure was repeated for each reproductive metric.

4.3. Separating survival from reproductive transitions

The second step consisted in separating survival from reproduction when calculating the probability weight of each trajectory. In Tuljapurkar et al. (2009)'s model, reproductive transition and survival were coupled in the way trajectories were weighted. A trajectory w is attributed to a given individual i according to the probability weight $W_{w,i}$ of the trajectory that was the survivorship of this trajectory calculated at the age of last observation $A_{i,\max}$ of the individual i : $W_{w,i} = \prod_{t=1}^{A_{i,\max}-1} (T(s_t, s_{t+1})\varphi(t))$ (see above). In other words, an individual with a short lifespan will have a

different probability of following a given trajectory than an individual with a long life. In a null model in which reproductive trajectories are generated only by stochasticity, successful trajectories should be attributed randomly among long-lived and short-lived individuals. Consequently, we generated a distribution of cumulated number of successes by attributing a trajectory to each individual with a probability weight calculated independently of the individual: $W_w = \prod_{t=1}^{n-1} T(s_t, s_{t+1})$, where n is the maximum age in the population. Survival probability was removed in calculating the trajectory probability weights as well as the selection of a particular trajectory according to the age of last recapture of the individual.

Finally, the distribution generated by separating survival from reproduction was compared to the distribution generated from the full dynamic model, and to the observed distribution. When the first two distributions differed, we looked at the co-variation between mean annual success and lifespan. We used the number of capture events as a proxy of lifespan, the animals being captured every second year on average.

4.4. Influence of age and time

Finally, we look at the influence of age and time in shaping the dynamic heterogeneity. Our model selection (Table S1) drove us to estimate age-dependent transition and age-dependent and time-dependent survival matrices for both *reproductive status* and *fecundity* to describe the transitions among states. *Reproductive success* was best modeled by an age-dependent survival matrix and an age-independent and time-independent transition matrix (see Table S1 for detailed information about model selection). We tested the importance of age and time structure by modeling reproductive trajectories from two models: an age-independent model and a time-independent model. Heterogeneity generated by age and time being part of dynamic heterogeneity, the analysis of the influence of age and time should lead to a better understanding of the different sources of dynamic heterogeneity.

5. Results

5.1. The full dynamic model

Following Tuljapurkar et al. (2009), we estimated the entropy, scaled sequence entropy, and sequence persistence for each reproductive metric. We then showed that *reproductive status* and *reproductive success* can be modeled with a full dynamic model, whereas the distribution of the number of embryos (*fecundity*) generated from the full dynamic model was different from the corresponding observed distribution.

5.1.1. Reproductive status

The transition matrix of reproductive status included two states: breeder (B) and non-breeder (NB). The age-dependent (i.e., prime-aged versus senescent females) transition matrices were estimated using a multistate capture–recapture model with a first-order Markov chain (Table 1). The probability of remaining a breeder two consecutive years was very high among prime-aged females ($B \rightarrow B = 0.95$) but decreased to 0.5 for senescent females. The probability to remain non-breeder (NB) two consecutive years was 0.30 and 0.74 among prime-aged and senescent females, respectively. The entropy H was estimated at 0.34 and 0.89 for the two corresponding matrices. The entropy among prime-aged females was especially low in comparison to the values previously reported in vertebrate species (>0.5 for all species, Tuljapurkar et al. 2009). Low entropy means that the transitions between reproductive statuses produced little heterogeneity in the population among prime-aged females. Here,

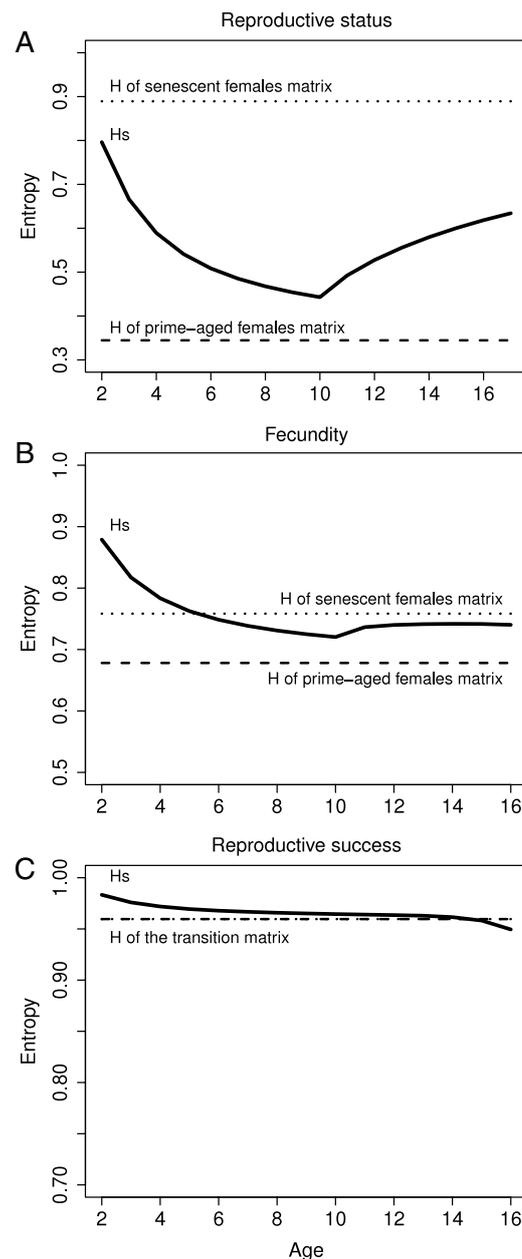


Fig. 1. Scaled sequence entropy (H_s) of three reproductive metrics of roe deer females from two populations intensively monitored in France. Sequence scaled entropies were calculated by age from the transition matrix of (A) *reproductive status*, (B) *fecundity*, and (C) *reproductive success*, and are presented by a black line. The entropy (H) of each transition matrix was also calculated following Tuljapurkar et al. (2009) and is reported by a dotted line for the senescent female matrix and by a dashed line for the prime-aged female matrix of *reproductive status* and *fecundity*. The entropy of the *reproductive success* transition matrix is reported by a dashed line.

we also calculated a scaled sequence entropy (Fig. 1(A)), which decreased from 2 to 11 years of age and increased among senescent females, meaning that there was very low heterogeneity in the population at the end of the prime-aged stage. The distribution of cumulated number of breeding events during the study period generated from the full dynamic process using 50 simulated populations was not statistically different from the observed distribution (Fig. 2(A), Kolmogorov–Smirnov test: $K = 0.0374$, $P > 0.9$, adjusted χ^2 test: $\chi^2 = 6.204$, $P = 0.714$).

5.1.2. Fecundity

The transition matrix of fecundity included three states: no embryo (0E), one embryo (1E), and two embryos (2E), and was

Table 1

Comparison of the transition probabilities estimated from observed and simulated datasets. The observed transition matrix was obtained from the capture–recapture analysis of individual trajectories using a first-order Markov chain. The simulated transition matrix was estimated from 1000 simulated datasets generated by a randomization of the age columns of the observed dataset. Transition matrices of the three following reproductive metrics are presented: *reproductive status* with two states (breeder (B) and non-breeder (NB)), *fecundity* with three states (0 embryo (OE), 1 embryo (1E), and 2 embryos (2E)) and *reproductive success* with three states (no fawn weaned (OF), 1 fawn weaned (1F), and 2 fawns weaned (2F)). The transition matrices of *fecundity* and *reproductive status* were age-dependent (prime-aged versus senescent females). One transition probability is reported per line to facilitate the comparison between observed and simulated transition probabilities. Redundant values are reporting between brackets. The confidence intervals (CIs) of simulated values are presented, and statistically significant differences between transition probabilities are reported in bold.

Transition probability	Estimate from observed dataset, full dynamic model	From simulated datasets		
		Estimate	CI 5%	CI 95%
<i>Reproductive status</i>				
Prime-aged				
(NB → NB)	0.30	0.07		
NB → B	0.70	0.93	0.77	1
(B → B)	0.95	0.93		
B → NB	0.05	0.07	0.06	0.08
Senescent				
(NB → NB)	0.74	0.85		
NB → B	0.26	0.15	0.07	0.24
(B → B)	0.50	0.55		
B → NB	0.50	0.45	0.39	0.52
<i>Fecundity</i>				
Prime-aged				
(OE → OE)	0.31	0.07		
OE → 1E	0.13	0.21	0.05	0.40
OE → 2E	0.56	0.72	0.50	0.91
(1E → 1E)	0.33	0.23		
1E → OE	0.07	0.08	0.02	0.12
1E → 2E	0.60	0.70	0.60	0.79
(2E → 2E)	0.75	0.71		
2E → OE	0.05	0.07	0.05	0.097
2E → 1E	0.20	0.22	0.187	0.248
Senescent				
(OE → OE)	0.73	0.82		
OE → 1E	0.11	0.08	0	0.16
OE → 2E	0.16	0.10	0	0.17
(1E → 1E)	0.2	0.18		
1E → OE	0.63	0.72	0.40	1
1E → 2E	0.17	0.09	0	0.36
(2E → 2E)	0.17	0.30		
2E → OE	0.45	0.31	0.19	0.47
2E → 1E	0.38	0.39	0.24	0.51
<i>Reproductive success</i>				
(OF → OF)	0.37	0.26		
OF → 1F	0.33	0.31	0.21	0.41
OF → 2F	0.30	0.43	0.33	0.54
(1F → 1F)	0.35	0.29		
1F → OF	0.25	0.25	0.18	0.33
1F → 2F	0.40	0.45	0.37	0.54
(2F → 2F)	0.53	0.45		
2F → OF	0.21	0.26	0.21	0.32
2F → 1F	0.26	0.29	0.23	0.35

age dependent (Table 1). The state OE was similar to the state NB in the reproductive status matrix, and so the transition probabilities were similar. All the transitions going towards the state 2E were high in prime-aged females (from 0.56 to 0.75) and low in senescent females (from 0.16 to 0.17), indicating that senescent females tended to have zero or one embryo most of the time. Among prime-aged females, the probability of remaining in state 2E was higher (0.75) than the transitions from 2E to either 1E (0.20) or OE (0.05). Consequently some females tended to remain in the most successful state (2E) throughout their prime-aged stage. The entropy was estimated at 0.68 and 0.76 for the prime-aged and senescent transition matrices, respectively. The scaled sequence entropy varied weakly among ages (between 0.9 and 0.7, Fig. 1(B)). Consequently, a rapid heterogeneity would occur along different trajectories. For fecundity, the population distribution of the cumulated number of embryos generated by the full dynamic model was different from the observed distribution (Fig. 2(B)). Indeed, while the conservative Kolmogorov–Smirnov

test did not lead to rejection of the null hypothesis ($K = 0.07$, $P = 0.559$), the adjusted χ^2 test did ($\chi^2 = 58.24$, $P < 0.001$). The distribution generated from the full dynamic model included too many females with even number of embryos during the study period compared to odd number of embryos implying that, randomly, too many females were in state 2E compared to state 1E. Dynamic heterogeneity alone was therefore not appropriate to model the individual variation observed in *fecundity* of roe deer females at Chizé.

5.1.3. Reproductive success

The transition matrix of reproductive success included three states: 0 fawn (OF), 1 fawn (1F), and 2 fawns (2F) weaned (Table 1). Whatever its age, a female that failed to wean a fawn a given year had about the same probability to raise 0, 1, or 2 fawns the following year. However, a female that weaned at least one fawn in a given year weaned at least one fawn the year after with a probability of 0.75, and more than half of the females

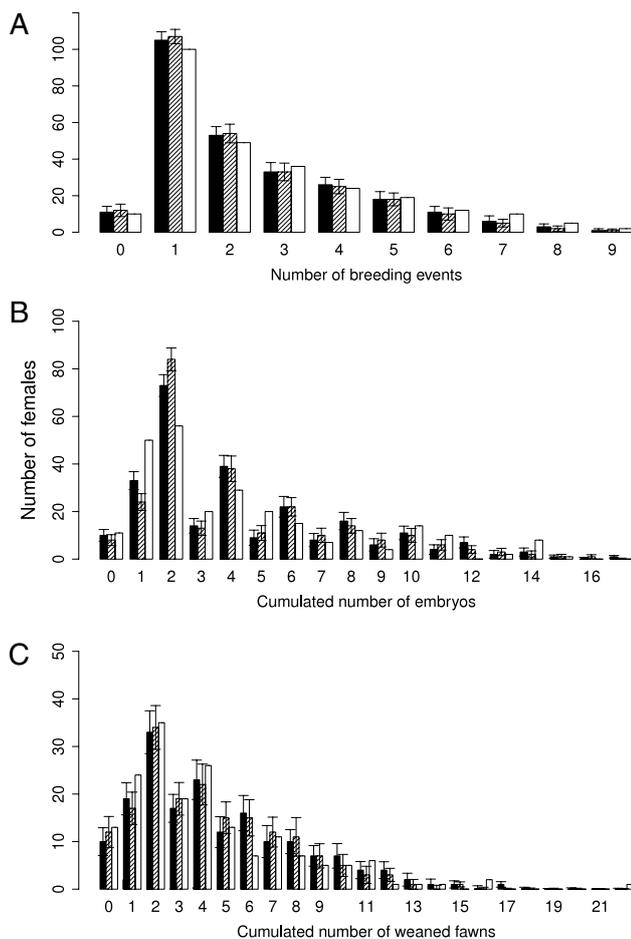


Fig. 2. Distributions of cumulated number of successes of three reproductive metrics of roe deer females from two populations monitored in France. Two of the three distributions presented were generated by a first-order Markov model using a transition matrix calculated from the observed dataset (full dynamic model, black bars) and from random datasets (hatched bars). The last distribution corresponds to the observed distribution (white bars). The three panels present the three reproductive metrics: (A) *reproductive status* of female roe deer at Chizé, (B) *fecundity* of female roe deer at Chizé, and (C) *reproductive success* of female roe deer at Trois-Fontaines. Standard errors are reported for each generated distribution. Only the generated distributions of cumulated number of embryos (*fecundity*) differ from the observed distribution (for both χ^2 tests, $P < 0.001$). The three distributions of cumulated breeding events (*reproductive status*) are similar as well as the three distributions of cumulated number of fawns weaned (*Reproductive success*) (for all χ^2 tests, $P > 0.48$).

that weaned two fawns a given year also weaned two fawns the following year, indicating that the females that were successful in a given year tended to stay successful. The entropy and scaled sequence entropy of this matrix were very high (0.96), suggesting a strongly increasing heterogeneity along trajectories (Fig. 1(C)). The distribution of *reproductive success* generated from a full dynamic model was not different from the observed distribution (Fig. 2(C), $K = 0.090$, $P = 0.465$; $\chi^2 = 21.51$, $P = 0.486$).

5.2. Stochastic transition matrix

The transition matrices obtained from simulated datasets were statistically different from the transition matrix obtained from the observed dataset (Table 1). Consequently, the trajectories generated from the observed transition included information on the propensity for a female to remain in the same state. For instance, in the transition matrix of *reproductive status* of prime-aged females, the probability of remaining in state NB was

higher when estimated from the observed dataset than when estimated from the simulated datasets (Table 1, permutation test: $P = 0.022$). From a stochastic process (i.e., from the simulated datasets), 93% of the non-breeders in a given year will become breeders in the following year. However, from the observed data, as much as one third of the non-breeders stayed non-breeders in the following year, revealing that some individuals remain unsuccessful more often than expected under a purely random process. The same situation was reported for *fecundity* (Table 1). The probability to stay in state 1E among prime-aged females estimated from the observed trajectories was higher than the same transition estimated from simulated datasets (permutation test: $P = 0.042$), showing that females have a higher probability to stay in the same state than expected from a stochastic process. The transition matrices of senescent females were not statistically different when estimated from the observed and simulated datasets, probably due to the low number of senescent females. Concerning the *reproductive success* of females at Trois-Fontaines, the probability of staying in state 0F from one year to the next (0.37) was also higher than expected from a stochastic process (0.26, permutation test: $P = 0.019$). However, the transitions between successful states (1F and 2F) were similar when estimated from the observed and the simulated datasets (Table 1), showing that transitions between states 1F and 2F corresponded to a stochastic process.

The measure of persistence indicated the propensity for roe deer females to remain successful or unsuccessful. We estimated a sequence persistence as the conditional probability of a given individual to be in a state a given year knowing that this individual was in the same state at 2 years of age. Among the three reproductive metrics, the main difference between sequence persistence from the observed transition matrix and the one estimated from simulated datasets was the longer time it took for the observed persistence to converge (Fig. 3). This means that, within a short period, the conditional probability for a female to stay in the same state was higher when estimated from the observed dataset than when estimated from the simulated datasets. Moreover, the probability of ending as a breeder (according to persistence of *reproductive status* and *fecundity*) among senescent females was a bit higher when estimated from the observed dataset than when estimated from the simulated datasets (Fig. 3). The distributions of cumulated number of successes of the reproductive metrics did not differ whether they were generated from the simulated or the observed (full dynamic model) transition matrices (Fig. 2; for all χ^2 tests, $P > 0.90$).

5.3. Separating survival from reproductive transitions

The distributions of cumulated number of weaned fawns generated by reproductive trajectories (i.e., a measure of lifetime reproductive success) weighted by reproductive transitions only (i.e., independent of survival) were statistically different from the observed distribution (Fig. 4(C); $\chi^2 = 41.32$, $P = 0.017$). Survival was positively correlated to mean annual reproductive success when generated by the full dynamic model (Pearson correlation: $\rho = 0.084$, $t = 7.95$, $P < 0.001$). This correlation became negative when removing survival from the estimation of probability weights (Pearson correlation: $\rho = -0.045$, $t = -4.20$, $P < 0.001$), probably because when using a random distribution of yearly reproductive success among females (with a probability of 0.25 to wean no fawn in a given year), long-lived females were more likely to wean no fawn at least once in their lifetime because of their high number of reproductive events compared to short-lived females. Too many females that were captured once or twice weaned two fawns when survival and reproductive transitions were separated, whereas, when

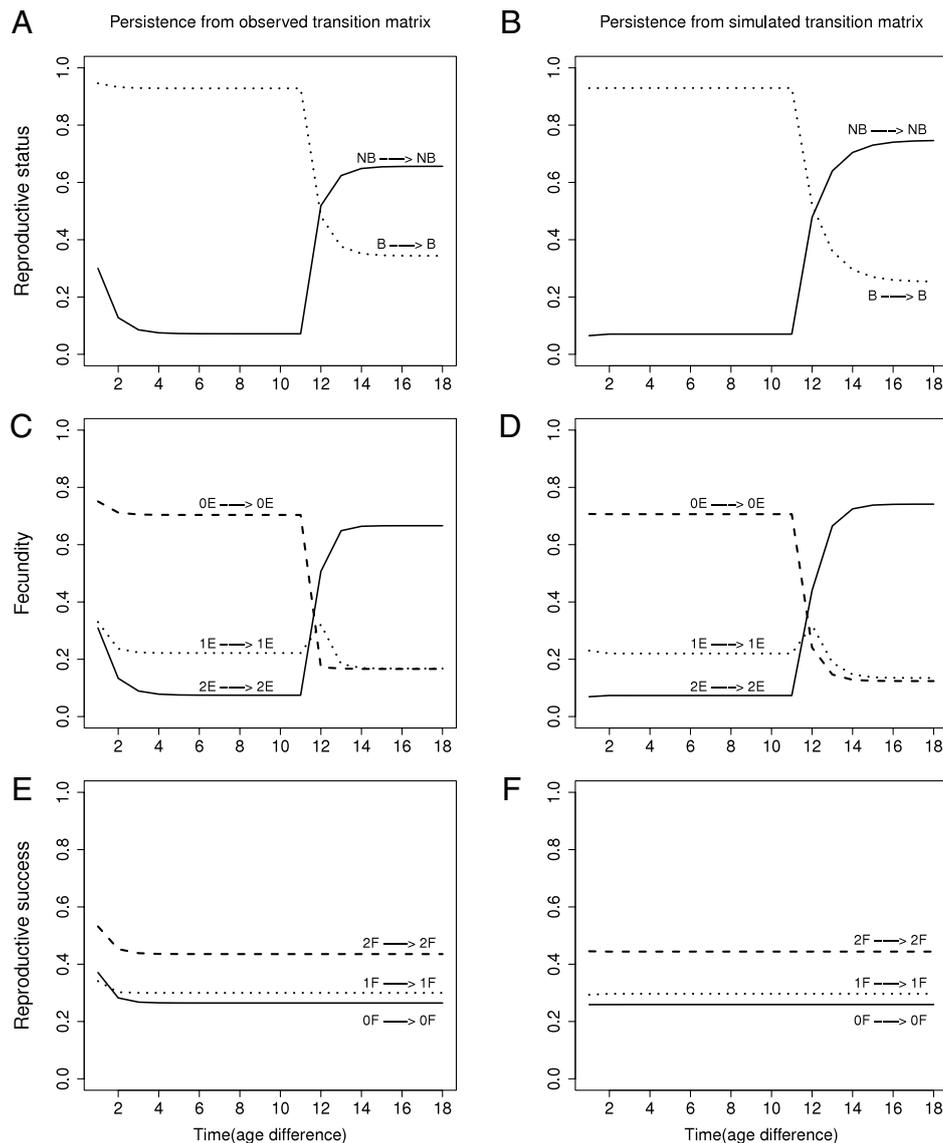


Fig. 3. Assimilated persistence of three reproductive metrics for roe deer females monitored in two populations in France. Age-dependent persistence was calculated for a given age A as the probability for a given individual to be in a given state at age A knowing that it was in this same state at 2 years old (i.e., first breeding). Estimated persistence from the transition matrix calculated from the observed dataset and from simulated ones are reported on the left and on the right, respectively, for *reproductive status* (A, B), *fecundity* (C, D) and *reproductive success* (E, F). Persistence was estimated for each state, presented as two (for *reproductive status*) or three (for *fecundity* and *reproductive success*) different lines.

survival and reproductive transitions were coupled, these females raised 0 or 1 fawn. Consequently short-lived females tended to wean fewer fawns at a given time than expected from the simulated dataset. The distribution of cumulated number of embryos (*fecundity*) when separating survival and reproduction was different from the observed distribution (Fig. 4(B); $\chi^2 = 77.39, P < 0.001$), as was the distribution generated from the full dynamic model (see above). In contrast, the distribution of the cumulated number of breeding events (*reproductive status*) generated by separating survival and reproductive transitions was similar to the observed distribution (Fig. 4(A); $\chi^2 = 7.23, P = 0.580$).

5.4. Influence of age and time

We estimated age-independent transition and survival matrices (with no time dependence) for the *reproductive success*. We estimated both a time-independent matrix and an age-dependent survival and transition matrix, and an age-independent survival

(with a time effect) matrix and a transition (no time effect) matrix for the *reproductive status* and the *fecundity*. For each of these two metrics, the distributions of the cumulated number of successes generated from age-independent and time-independent models of survival and transition were not different from the distribution generated from our age-dependent and time-dependent model (Table 2). For *reproductive success*, the distribution generated from the age-independent model was not different from the distribution generated from our age-dependent model (Table 2). The distribution of *fecundity* generated from age-independent and time-independent models was statistically different from the observed distribution (Table 2; for both adjusted χ^2 tests, $P < 0.001$).

6. Discussion

Although all reproductive and survival trajectories of life-history traits analyzed to date were successfully modeled by using the full dynamic model (Tuljapurkar et al., 2009; Steiner et al.,

Table 2

Comparison of distribution of cumulated number of successes generated from the age-independent model (Age-IND) and the time-independent model (Time-IND) for three reproductive metrics (*reproductive status*, *fecundity*, and *reproductive success*) to the distribution generated from the best selected model (full dynamic model) and to the observed distribution. Transition matrices were estimated from three different models (best model, Age-IND, and Time-IND). Then the distributions were generated using a full dynamic process (using a first-order Markov chain) following Tuljapurkar et al. (2009). Two statistical tests were performed: a very conservative one, the Kolmogorov–Smirnov test (K–S values (KS) and P-values are shown) and a less conservative one: an adjusted χ^2 -test (χ^2 values and P-values are presented).

	Distribution generated from the full dynamic model				Observed distribution			
	KS	P-value	χ^2	P-value	KS	P-value	χ^2	P-value
<i>Reproductive status</i>								
Age-IND	0.022	>0.99	2.08	>0.99	0.019	>0.99	4.15	0.941
Time-IND	0.007	>0.99	0.70	>0.99	0.041	0.977	9.71	0.383
<i>Fecundity</i>								
Age-IND	0.046	0.944	7.01	>0.99	0.116	0.062	80.99	<0.001
Time-IND	0.039	>0.99	10.65	0.867	0.069	0.559	101.59	<0.001
<i>Reproductive success</i>								
Age-IND	0.051	0.976	1.16	>0.99	0.096	0.388	17.16	0.504

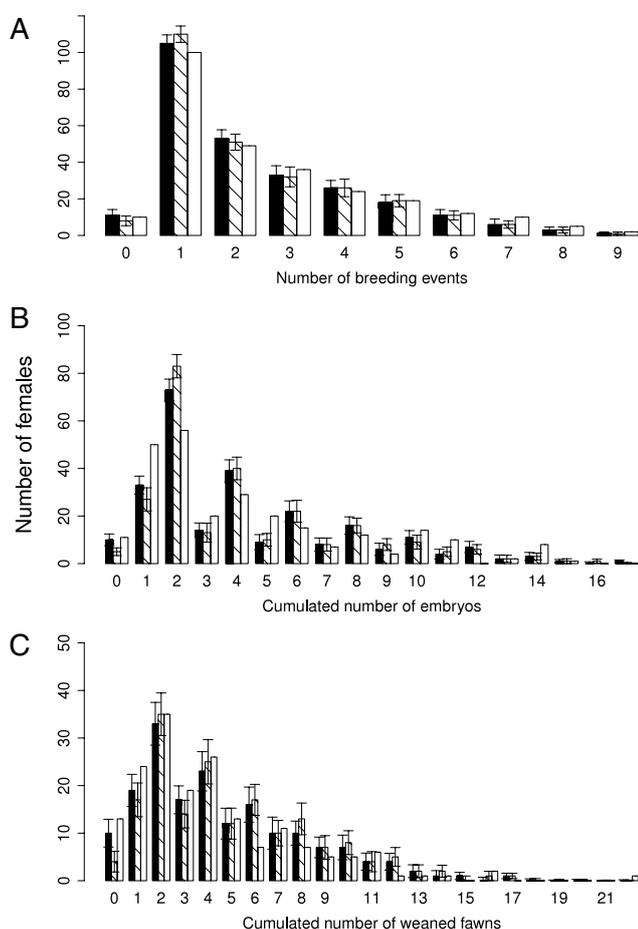


Fig. 4. Comparison of distributions of cumulated number of successes for roe deer females monitored in two populations in France. Distributions were generated by separating or coupling survival and reproductive transitions. In each panel, three distributions are presented: the observed distribution (white bars) and the two distributions generated by coupling (full dynamic model, black bars) or separating (hatched bars) survival and reproductive transitions when estimating trajectory probability weights. The three panels represent the three reproductive metrics: (A) *reproductive status* of roe deer females at Chizé, (B) *fecundity* of roe deer females at Chizé, and (C) *reproductive success* of roe deer females at Trois-Fontaines.

2010), we show here that the full dynamic model did not provide an appropriate description of reproductive trajectories based on *fecundity* measures for roe deer at Chizé. Moreover, our results suggest that the full dynamic model requires two modifications to test the following biological null hypothesis appropriately: “a

given lifetime reproductive metric distribution is generated only by dynamic heterogeneity”.

The full dynamic model uses a first-order Markov chain to simulate trajectories of length n . The first-order Markov chain is a random process, by definition. However, the transition probabilities chosen to parameterize this Markov chain are not random in this particular model. Our first modification showed that the simulated transition matrix differed from the observed transition matrix used in the full dynamic model. Indeed, a female that was successful in a given year will have a lower probability to be successful again in the following year when estimated from a stochastic model than when estimated from observed data. Likewise, an unsuccessful female will have a lower probability to be unsuccessful again in the following year when estimated from a simulated transition matrix than when estimated from the observed transition matrix. Moreover, the persistence in a given state is higher when calculated from the observed data than from the simulated datasets. A possible way to interpret that a female tends to stay in the same reproductive state more than expected from a stochastic process would be to link the annual reproductive state to a fixed trait and so to a fixed heterogeneity (a given individual would have a high probability of reproducing all through its life). However, we cannot exclude that this result could be linked to dynamic heterogeneity (it would be easier for a female living in a high-quality habitat to be successful at each reproductive attempt than for a female living in a low-quality habitat). Consequently, the first step to change in the full dynamic model to obtain a null model generated only from stochasticity involves estimating transition probabilities from simulated datasets instead of the observed dataset.

The second step that should be changed in the full dynamic model of Tuljapurkar et al. (2009) is how the trajectory weights are calculated and then attributed to a given individual. We did not generate a model in which each trajectory has the same weight simply because it is not biologically meaningful. Indeed, in a population of roe deer where 95% of the females are breeders, we cannot simulate individuals with a trajectory constituted by only non-breeder states. However, attributing a trajectory to a given individual, based on survival, reproductive transitions, and age of last observation, as in the full dynamic model, generates a coupling between survival and reproduction. When we separated survival from reproductive transitions, the simulated distribution of reproductive success differed from the observed one. The study by Steiner et al. (2010) showed that a correlation between survival and reproduction can occur from a null model when using the full dynamic model of Tuljapurkar et al. (2009). Here, we went one step beyond to show that this correlation can be removed by estimating the weights from reproductive transitions only, using the full stochastic model. Even if a positive

correlation could be generated by a random process in many cases (Steiner et al., 2010; Orzack et al., 2011), the link between age at last reproduction and reproductive trajectory probability weight is the principal cause of the positive correlation we observed in this study.

The full dynamic model tests the null hypothesis that the “distribution of lifetime reproductive success is generated by a stochastic process”. To test this null hypothesis, the observed and simulated distributions are compared. Despite marked differences between the simulated and observed transition matrices, the generated distributions of reproductive metrics using a first-order Markov chain (full dynamic model) from the simulated and observed transition matrices did not differ. In other words, we obtained the same distribution from two different Markov chains. From this, we can make at least two conclusions. First, the similarity of these distributions indicates that the population at a given time was homogeneous, but does not inform on the processes that contributed to reaching this stationary population “state”. Different processes can lead to the same distribution. Consequently, the comparison of distributions only indicates that a dynamic heterogeneity process can reliably represent observed reproductive trajectories, but information on the individual level is lacking. Moreover, considering the *reproductive status* metric, 95% of the adult female roe deer were breeders each year at Chizé. Then the distribution of non-breeders will generate only limited variability, hardly detectable in a distribution. The low heterogeneity estimated from entropy (Tuljapurkar et al., 2009) that is generated by the successive transitions between *reproductive statuses* also supports the hypothesis that statistical comparisons of distributions do not allow detecting a weak deviation between the observed and generated distributions of reproductive successes.

Second, a first-order Markov chain creates a stochastic structured variance among individuals. This means that an observed structured variance among individuals in trait trajectories can be accounted for by a stochastic process only, as suggested by Steiner et al. (2010) and Tuljapurkar et al. (2009). Some individuals can follow a trajectory through stochastic events but the structure variance could also be created by some unknown fixed variable. The individual variance produced by a first-order Markov chain could be analyzed with a random effect of the individual on the intercept in another study, as is commonly done when studying individual heterogeneity. This random individual effect would be strong, but it must then be interpreted only by what it is: a random variable reflecting a structured variance among individuals. However, random effects have commonly been interpreted as a signature of individual quality (Cam et al., 2002) or fixed heterogeneity, in other words, while a measurable trait (such as lifetime reproductive success or longevity) is needed to quantify this heterogeneity among individuals before attributing this individual heterogeneity to an individual quality. The definition of quality in the literature is subject to confusion, and authors often do not make the difference between the qualitative and the quantitative meaning of quality (Cam et al., 2004). The qualitative meaning of quality refers to the differences in individual performances and implies that some individual have better performance than others, while the quantitative meaning of quality refers to individual differences that were quantified but were not correlated to any performance trait. Basically, in this last meaning, quality refers to some individual variation caused by an unknown process. To avoid this confusion, we recommend using the word quality only when referring to the qualitative definition.

Our results showed that a positive correlation occurs between reproductive success and lifespan in roe deer when using the full dynamic model. Such correlation was caused directly by a link between age at last reproduction and reproductive trajectory. Moreover, we demonstrated that this positive correlation was not generated by a stochastic process, even if this positive correlation was weak ($\rho = 0.084$), and remained statistically

significant because of the large numbers of simulated individuals. Nonetheless, this model suggests that long-lived females usually considered as good-quality individuals (Hamel et al., 2009a; Wilson and Nussey, 2010; Bergeron et al., 2011) weaned more fawns in a given year than short-lived females.

The observed distribution of the cumulated number of embryos produced per female during the study period statistically differed from the distribution generated from a full dynamic model using a first-order Markov chain. The distribution generated by the full dynamic model overestimated the number of females that have two embryos. We were led to reject our null hypothesis, and these results suggest that dynamic heterogeneity is not sufficient to account for the individual heterogeneity observed in the fecundity trajectories of roe deer females. Two reasons may explain the rejection of the null hypothesis. Either the process is not Markovian, or different individual trajectories should come from different Markov chains. In this second hypothesis, two different Markov chains could be generated from two different groups of individuals, for example. A way to test this hypothesis would be to add fixed individual traits such as body mass or a dynamic traits such as resource quality or abundance to the model and test whether such a model would provide a better fit. If this were the case, one could show the relative part of the dynamic and fixed heterogeneity in shaping the structured variance among individuals. Even if our results did not allow us to reach such a final conclusion, the literature previously published on individual variation in life-history traits of large mammals suggest that fixed heterogeneity has a main role in shaping this structured variance among individual.

Trajectories of the *reproductive status* of females (breeder versus non-breeder) perfectly matched expectations from a full dynamic model. As the non-breeder state of the *reproductive status* corresponds to the 0 embryo state of the *fecundity*, the contribution of fixed heterogeneity should influence litter size. Two hypotheses could account for a fixed heterogeneity in litter size. First, females could have two embryos for two or three consecutive years and then reduce to one embryo the following year. This pattern of reproductive states would involve reproductive costs occurring on a two or three year period. Such a pattern would be very difficult to identify (e.g., cannot be modeled using a first-order Markov chain), but could occur in food-limited populations like Chizé (Nilsen et al., 2009). However, this hypothesis is not expected based on the tactic of resource allocation to reproduction displayed by female roe deer. Roe deer females are income breeders (Andersen et al., 2000) that do not rely on body reserves for raising offspring, and use currently available resources (Jönsson, 1997). The absence of any reproductive cost in terms of reproduction in female roe deer recently reported (Hamel et al., 2009a) also causes the hypothesis of reproductive costs to be unlikely. Alternatively, fixed heterogeneity in fecundity could be induced by the between-individual differences in phenotypic quality. Litter size in polytocous large mammals (Gaillard et al., 2000) and in roe deer in particular (Andersen et al., 2000) is tightly associated with body mass. Heavy females are more likely to produce twins than light females, which usually produce singletons. As the adult body mass varies little from year to year in adult roe deer (Andersen et al., 2000), heavy females should have two embryos most years, whereas light females should have most of the time only one embryo.

If both fixed heterogeneity and dynamic heterogeneity are necessary to model reproduction, their relative roles are difficult to quantify (Orzack et al., 2011; Caruso et al., 2012). Adding the effect of age and time to estimate the transition matrix with a dynamical process does not appear to change the generated distribution markedly. As a result, differences existing between age- (respectively, time-) dependent and independent transition

matrices cannot be distinguished at the population level, and so time and age seem to be negligible factors when considering the population distribution of reproductive success over lifetime events, whereas they appear to be the structuring factors shaping variation among individual transitions between reproductive states. Then dynamic heterogeneity would be mainly generated by a stochastic process between reproductive states rather than by environmental changes or a change in age structure in roe deer. However, these results could be different in populations with more complex age structures (Nussey et al., 2008; McCleery et al., 2008; Aubry et al., 2011) or those affected by environmental changes more strongly (Grøtan et al., 2008).

7. Conclusion

The dynamic model of heterogeneity proposed by Tuljapurkar et al. (2009) can be viewed as a null model generated only by stochasticity when using simulated datasets and removing the correlation between survival and reproduction. Moreover, it is very difficult to disentangle fixed and dynamic heterogeneity when low variability occurs in a life-history trait. We demonstrated that the fecundity of female roe deer is not only shaped by dynamic heterogeneity and that the yearly reproductive success could be correlated with survival. We can thus conclude that dynamic heterogeneity alone cannot model all the reproductive trajectories of vertebrates as reported until now (Tuljapurkar et al., 2009; Steiner et al., 2010; Orzack et al., 2011).

However, as shown by Orzack et al. (2011), Steiner et al. (2010), and Tuljapurkar et al. (2009), we suggest that among-individual structured variance in a given trait can be modeled as a stochastic process. Individual differences could not be interpreted as an individual quality before the process that generates these differences has been identified. Further analyses remain to be done to quantify the relative role of fixed and dynamic heterogeneity. A step forward would be to add fixed and dynamic covariates (Caruso et al., 2012; Orzack et al., 2011) to assess whether they improve the models and explain the remaining variance. Another possibility would be to employ an integral projection model to estimate the Markov chains for individuals born to different body sizes (Coulson et al., 2010). We have to be careful how to interpret the comparison of generated and observed distributions, because a similar distribution may be generated by different processes. This distribution comparison is a test with a high type II error rate according to the null hypothesis tested. Moreover, it is not sufficient to compare the different trajectories present in a population. At the individual level, the trajectories observed have to be compared to simulated trajectories.

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Appendix. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2012.03.006>.

References

- Andersen, R., Gaillard, J.M., Linnell, J.D., Duncan, P., 2000. Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.* 69, 672–682.
- Aubry, L., Cam, E., Koons, D., Monnat, J., Pavard, S., 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *J. Anim. Ecol.* 80, 375–383.
- Beauplet, G., Barbraud, C., Dabin, W., Küssener, C., Guinet, C., 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112, 430–441.
- Bergeron, P., Baeta, R., Pelletier, F., Réale, D., Garant, D., 2011. Individual quality: tautology or biological reality? *J. Anim. Ecol.* 80, 361–364.
- Bérubé, C.A.H., Festa-Bianchet, M., Jorgenson, J.T., 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80, 2555–2565.
- Bjørnstad, O., Hansen, T., 1994. Individual variation and population dynamics. *Oikos* 69, 167–171.
- Cam, E., Link, W.A., Cooch, E.G., Monnat, J.Y., Danchin, E., 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *Am. Nat.* 159, 96–105.
- Cam, E., Monnat, J.Y., 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *J. Anim. Ecol.* 69, 380–394.
- Cam, E., Monnat, J., Royle, J., 2004. Dispersal and individual quality in a long lived species. *Oikos* 106, 386–398.
- Caruso, T., Taormina, M., Migliorini, M., 2012. Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. *J. Anim. Ecol.* 81, 214–221.
- Coulson, T., Tuljapurkar, S., Childs, D.Z., 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *J. Anim. Ecol.* 79, 1226.
- Descamps, S., Bêty, J., Love, O.P., Gilchrist, H.G., 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. *Funct. Ecol.* 25, 671–681.
- Gaillard, J.M., Delorme, D., Jullien, J.M., 1993. Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* 94, 57–61.
- Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toigo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393.
- Grøtan, V., Sæther, B., Filli, F., Engen, S., 2008. Effects of climate on population fluctuations of ibex. *Glob. Change Biol.* 14, 218–228.
- Hamel, S., Côté, S.D., Gaillard, J.M., Festa-Bianchet, M., 2009a. Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* 78, 143–151.
- Hamel, S., Gaillard, J.M., Festa-Bianchet, M., Côté, S.D., 2009b. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90, 1981–1995.
- Jönsson, K.I., 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78, 57–66.
- Kendall, B., Fox, G., Fujiwara, M., Nogeire, T., 2011. Demography heterogeneity, cohort selection and population growth. *Ecology* 92, 1985–1993.
- Knape, J., Jonzén, N., Sköld, M., Kikkawa, J., McCallum, H., 2011. Individual heterogeneity and senescence in Silvereyes on Heron Island. *Ecology* 92, 813–820.
- Laake, J., Rexstad, E., 2008. RMark - An Alternative Approach to Building Linear Models in MARK. Mark-Book. E. Cooch and White G. Appendix C.
- Lailvaux, S.P., Kasumovic, M.M., 2010. Defining individual quality over lifetimes and selective contexts. *Proc. R. Soc. B* 278, 321–328.
- Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62, 67–118.
- Lebreton, J., Nichols, J., Barker, R., Pradel, R., Spindelov, J., 2009. Modeling individual animal histories with multistate capture–recapture models. *Adv. Ecol. Res.* 41, 87–173.
- McCleery, R., Perrins, C., Sheldon, B., Charmantier, A., 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proc. R. Soc. B* 275, 963–970.
- McNamara, J.M., Houston, A.I., 1996. State-dependent life histories. *Nature* 380, 215–221.
- Moyes, K., Morgan, B., Morris, A., Morris, S., Clutton-Brock, T., Coulson, T., 2011. Individual differences in reproductive costs examined using multi-state methods. *J. Anim. Ecol.* 80, 456–465.
- Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., van Laere, G., Linnell, J.D., 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *J. Anim. Ecol.* 78, 585–594.
- Nussey, D.H., Coulson, T.N., Festa-Bianchet, M., Gaillard, J.M., 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. *Funct. Ecol.* 22, 393–406.
- Orzack, S.H., Steiner, U.K., Tuljapurkar, S., Thompson, P., 2011. Static and dynamic expression of life history traits in the northern fulmar *Fulmarus glacialis*. *Oikos* 120, 369–380.
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Service, P.M., 2000. Heterogeneity in individual mortality risk and its importance for evolutionary studies of senescence. *Am. Nat.* 156, 1–13.
- Steiner, U.K., Tuljapurkar, S., 2012. Neutral theory for life histories and individual variability in fitness components. *Proc. Natl. Acad. Sci. USA* 109, 4684–4689.

- Steiner, U.K., Tuljapurkar, S., Orzack, S.H., 2010. Dynamic heterogeneity and life history variability in the kittiwake. *J. Anim. Ecol.* 79, 436–444.
- Tuljapurkar, S.D., 1982. Why use population entropy? It determines the rate of convergence. *J. Math. Biol.* 13, 325–337.
- Tuljapurkar, S., Steiner, U.K., Orzack, S.H., 2009. Dynamics heterogeneity in life histories. *Ecol. Lett.* 12, 93–106.
- Vaupel, J., Manton, K., Stallard, E., 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16, 439–454.
- Vaupel, J.W., Yashin, A.I., 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. *Am. Stat.* 39, 176–185.
- Vindenes, Y., Engen, S., Sæther, B., 2008. Individual heterogeneity in vital parameters and demographic stochasticity. *Am. Nat.* 171, 455–467.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, 120–138.
- Wilson, A.J., Nussey, D.H., 2010. What is individual quality? an evolutionary perspective. *Trends Ecol. Evol.* 25, 207–214.