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Evolutionary demography: the dynamic and broad intersection of ecology and evolution

Estimating individual fitness in the wild using capture–recapture data

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Abstract The concept of Darwinian fitness is central in evolutionary ecology, and its estimation has motivated the development of several approaches. However, measuring individual fitness remains challenging in empirical case studies in the wild. Measuring fitness requires a continuous monitoring of individuals from birth to death, which is very difficult to get in part because individuals may or may not be controlled at each reproductive event and recovered at death. Imperfect detection hampers keeping track of mortality and reproductive events over the whole lifetime of individuals. We propose a new statistical approach to estimate individual fitness while accounting for imperfect detection. Based on hidden process modelling of longitudinal data on marked animals, we show that standard metrics to quantify fitness, namely lifetime reproductive success, individual growth rate and lifetime individual contribution to population growth, can be extended to cope with imperfect detection inherent to most monitoring programs in the wild. We illustrate our approach using data collected on individual roe deer in an intensively monitored population.

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Introduction

Darwinian fitness is the Holy Grail of evolutionary ecologists. While it is well established that the Malthusian parameter (r) provides a reliable measure of the average individual fitness in a population (Fisher 1930; Hamilton 1966; Lenski and Service 1982) in a deterministic environment, how to best estimate the fitness of a given individual in the wild remains an open question. Several estimates of individual fitness have been proposed, which differ mainly on whether they are single- or multiple generation estimates and they incorporate or not the timing of reproduction (e.g., Brommer et al. 2002, 2004). Rate-insensitive fitness measures only account for the number of offspring produced at some stage by a given individual during its lifetime. Two measures are commonly used in field studies: first, the lifetime reproductive success (LRS; Clutton-Brock 1988; Newton 1989) is the total number of offspring an individual has successfully raised at some age (e.g., birth, 1 year of age) or stage (e.g., newborn, weanling/fledging, first reproducers); second, the lifetime breeding success (LBS or R_0) is the total number of offspring an individual has produced soon after birth during its lifetime (e.g., Rose et al. 1998). On the other hand, rate-sensitive fitness measures account for both the number of offspring produced at some stage by a given individual during its lifetime and the ages at which these offspring have been produced. McGraw and Caswell (1996) proposed an estimate of individual fitness (λ_{ind} hereafter) that includes both magnitude and timing of survival and reproduction. As such, it has been argued to be a better estimate of fitness than LRS (Käär and Jokela 1998). However, the λ_{ind} metric has been criticized on the ground that the mean of the λ_{ind} does not match with the asymptotic population growth rate (λ) calculated from mean individual age-specific vital rates (Lenski and Service 1982) and that the timing of reproduction is unrealistically accounted for since all offspring produced by a given individual should reproduce at the very same age as their parent. Moreover, an empirical comparative analysis of detailed data including pedigrees showed that LRS worked well in both short-lived and long-lived birds (Brommer et al. 2004). However, both LRS and λ_{ind} are absolute measures, whereas Darwinian fitness is a relative concept. To address this issue, Coulson et al. (2006) developed the lifetime individual contribution (LIC) to population growth. This metric has the main advantages over LRS to account for survival and fecundity components on the same scale and to be a relative measure that is standardized for variation in population abundance.

Based on the empirical evidence, LRS, λ_{ind} and LIC are the most commonly used metrics in population studies of species in which individual reproductive success can be assessed directly from observations, such as in most species of mammals and birds (see Clutton-Brock 1988 and; Newton 1989 for case studies). This also includes human populations for which a continuous monitoring is sometimes available from birth to death (Käär and Jokela 1998; Korpelainen 2000; Lahdenpera et al. 2004; Moorad 2013). In the wild, individuals may or may not be detected (i.e., seen or captured) at various times in their lifetime, which raises the issue of a detection probability less than one (Lebreton et al. 1992; Nichols 1992). Ignoring imperfect detection can lead to flawed inference about evolutionary questions, fitness estimation making no exception (Gimenez et al. 2008). First, fitness components (survival and reproduction) are under-estimated if the date of death of an individual who was last encountered before the end of the study is wrongly assigned to the date it was last observed. Second, estimates of fitness metrics come without any quantification of sampling uncertainty related to the estimation of demographic rates. Third, dropping individuals for which some reproductive and/or mortality events could not be recorded due to non-detection can lead to biases in the estimation of fitness metrics. This is likely to be the case when the process leading to miss individuals depends on their reproductive status. And last but not least, discarding individuals with incomplete records results in smaller sample size and sub-optimal use of field data at the best, and more likely corresponds to an additional source of bias because a lower probability of detection is often associated with more cryptic behaviour typical of subordinates (e.g., Cubaynes et al. 2010). Within vertebrate populations in the wild for which individual fitness data are currently available, we thus expect mean individual fitness to be over-estimated and measures of variance in individual fitness to be under-estimated.

The purpose of this paper is to show how to obtain the three most commonly used fitness metrics while coping with imperfect detection. We use multistate mark-recapture (MR) models (Lebreton et al. 2009), which allow the estimation of survival and transition between reproductive states, and incorporate latent states alive with associated number of offspring to infer fitness metrics. We illustrate our approach by estimating individual fitness of roe deer (*Capreolus capreolus*) females in a population intensively monitored over > 30 years.

Model and individual fitness estimation

To analyse longitudinal data on marked animals, we use a state-space formulation of MR models (Gimenez et al. 2007; Royle 2008; Schofield and Barker 2008) that explicitly separates the demographic process of interest, here being alive in a particular breeding state, from the observations, i.e., the detection of animals (captures or sightings). Following Pradel's (2005) notation, we assume that individuals move between a set of states $\{e_1, \ldots, e_N\}$ where e_1 stands for being alive and non-breeding, e_N is the dead state and e_n is for being alive with $n-1$ offspring ($n > 1$). We denote $X_{i,t}$ the random state vector taking value 1 in the nth position if, at time t, individual i is in state e_n, and 0 in the other positions. These states are only partially observed through L possible events $\{v_1, \ldots, v_L\}$ where v_1 stands for non-detected, v_2 detected with no offspring and v_l is for detected (captured or seen) with $l-2$ offspring ($l > 2$). We denote $Y_{i,t}$ the random observation vector taking value 1 in the lth position if, at time t, event v_l happens to individual i.

Our model includes several parameters. Let $\phi_t^{k \to k'}$ be the probability that an individual alive at time t in state e_k is alive at time $t+1$ in state $e_{k'}$. It can be written as the product of survival ϕ_t^k in state e_k and transitions $\psi_t^{k \to k'}$ between states e_k and $e_{k'}$. The matrix Φ_t gathers the probabilities $\phi_t^{k \to k'}$ with states at time t (e_k) in rows and those at time $t+1$ in columns ($e_{k'}$). We also define b_t^{kl} the probability that event v_l happens to an individual in state e_k at time t. The matrix B_t gathers the probabilities b_t^{kl} with event (v_l) in columns and states (e_k) in rows at time t.

The state-space model relies on a combination of two processes. The state process specifies the state of individuals at time $t+1$ given their state at time t:

$$X_{i,t+1} | X_{i,t} \sim \text{multinomial}(1, X_{i,t}\Phi_t) \tag{1}$$

while the observation process specifies the observation of the individuals at time t given their state at time t:

$$Y_{i,t} | X_{i,t} \sim \text{multinomial}\left(1, X_{i,t}B_t\right) \tag{2}$$

To fit this model and obtain posterior distributions of survival and transitions between breeding states, we used Markov chain Monte Carlo (MCMC) simulations in a Bayesian context (e.g., King et al. 2010).

The estimates of individual fitness were obtained for each of the three metrics. The λ_{ind} were obtained as the dominant eigenvalue of a matrix built for each female (see Gaillard et al. 2000 for an application to the same roe deer population). This pre-breeding census matrix has, for each age x, the $f_x/2$ value on its first row—where f_x is the realized fecundity that is measured by the number of offspring produced at age x that were successfully weaned—and 1 in its subdiagonal (McGraw and Caswell 1996). The LIC of each individual was calculated as the sum of the individual's annual contributions (Coulson et al. 2006). The annual contribution of a female i to population growth between t and $t+1$, $P_{t(i)}$, is an individual's annual realized fitness, and was obtained as:

$$P_{t(i)} = \frac{S_{t(i)} - \overline{S_t}}{N_t - 1} + \frac{f_{t(i)} - \overline{f_t}}{N_t - 1} \qquad (3)$$

where $S_{t(i)}$ is the survival for a female i at time t (1 if it survives, 0 otherwise); $\overline{S_t}$ is the mean survival of all females in the population at time t, $f_{t(i)}$ is the realized fecundity for female i at time t, $\overline{f_t}$ is mean realized fecundity of all females in the population at time t, and N_t is the population size (females only) at time t. Lastly, the LRS was calculated as the number of offspring successfully weaned by a female over its lifetime. The code to calculate the fitness metrics is available from GitHub (https://github.com/oliviergimenez/estim_fitness).

The key here is to realize that, whenever a female is not detected, its number of offspring cannot be measured. However, the state-space formulation in conjunction with the MCMC machinery allows reconstructing the whole fate of any female i by considering the reproductive states $X_{i,t}$ as parameters to be estimated, just like the demographic parameters (e.g., Newman et al. 2006). At each MCMC step and for each female, age-specific numbers of weaned offspring are obtained, a pre-breeding census matrix is built and its dominant eigenvalue is calculated to get a value of λ_{ind} and LRS. The same procedure is used for LIC. We assumed offspring survival between weaning time and 1 year of age to be 1.

Application to roe deer

Data were collected on a population of roe deer in the enclosed forest of Trois Fontaines (1360 ha, 48°43′N, 2°61′E, North Eastern France). Animals were individually marked by ear-tags and numbered collars. Each year since 1975, between 8 and 12 days of capture were organized between December and March. Roe deer were captured by drive-netting, involving 150 ± 30 people and 2.5 km of nets and resulting in the capture of 120–300 roe deer a year. Marked adult females (> 2 years of age, the age at first parturition in roe deer; Gaillard et al. 1992) were monitored in autumn (October–December) to assess the number of fawns they successfully weaned in a given year (see McLoughlin et al. 2007 for further details). Because early summer survival is the most critical stage in roe deer (Gaillard et al. 2013), most fawns alive in late autumn are most likely to reach adulthood. The number of fawns observed at heel in autumn was therefore used as a reliable measure of annual reproductive success of a female. We measured reproductive success by the number of fawns a given female successfully weaned (i.e., observed at heel), which included three states (0, 1 and 2 fawns). We only recorded a few instances (about 1.6% of records) of females having three fawns at heel and pooled them with females observed with two fawns at heel. In total, we used roe deer reproductive histories of 271 females that were monitored between 1977 and 2011. We considered four states, e_1 = 'alive non-breeder', e_2 = 'alive and breeder with one fawn', e_3 = 'alive and breeder with two fawns', e_4 = 'dead'. Based on the roe deer life history (e.g., Gaillard et al. 1998), we considered several possible observations that were generated from these underlying states as v_1 = 'the animal is not seen', v_2 = 'the animal is seen without any fawn', v_3 = 'the animal is seen with one fawn', v_4 = 'the animal is seen with two fawns'. Age-dependence in ϕ_t^k was modelled using two classes: prime–aged (2–7 years) and old adults (8 years and older). Given that an individual is alive in a given state, it can survive and remain in the same state (terms in diagonal), survive and move to another state (off-diagonal terms), or die (last column). If an individual is dead, it remains dead (last row). Hence, we used:

$$\phi_t = \begin{bmatrix} \phi^{e_1}\psi^{e_1\rightarrow e_1} & \phi^{e_1}\psi^{e_1\rightarrow e_2} & \phi^{e_1}\psi^{e_1\rightarrow e_3} & 1-\phi^{e_1} \\ \phi^{e_2}\psi^{e_2\rightarrow e_1} & \phi^{e_2}\psi^{e_2\rightarrow e_2} & \phi^{e_2}\psi^{e_2\rightarrow e_3} & 1-\phi^{e_2} \\ \phi^{e_3}\psi^{e_3\rightarrow e_1} & \phi^{e_3}\psi^{e3\rightarrow e_2} & \phi^{e_3}\psi^{e_3\rightarrow e_3} & 1-\phi^{e_3} \\ 0 & 0 & 0 & 1 \end{bmatrix} \qquad (4)$$

Regarding the observation process, we specify that, given that an individual is alive in state non-breeder or breeder, it can be missed (first column) or controlled as a non-breeder or breeder respectively. Besides, given that an individual is dead, it is missed with certainty (last row). We therefore used:

$$B_t = \begin{bmatrix} 1-p_t^{e_1} & p_t^{e_1} & 0 & 0 \\ 1-p_t^{e_2} & 0 & p_t^{e_2} & 0 \\ 1-p_t^{e_3} & 0 & 0 & p_t^{e_3} \\ 1 & 0 & 0 & 0 \end{bmatrix} \qquad (5)$$

where we considered the probability $p_t^{e_k}$ that an individual i is detected at time t in state e_k (same probability for all breeder individuals). Uncertainty in assessing the breeding status was not due to the issue of detection only. If a female was detected in the field, its breeding status did not correspond necessarily to the observation made. For example, if a female was observed with no fawn, it actually might be in state e_2 or e_3 just because its fawns were not with it when it was detected. We incorporated uncertainty in state assignment in the calculation of individual fitness by adding probabilities of state assignment on top of the detection process (Pradel 2005; Gimenez et al. 2012). The observation matrix in Eq. 4 was modified consequently:

$$B_t = \begin{bmatrix} 1 - p_t^{e_1} & p_t^{e_1}\delta & 0 & 0 & p_t^{e_1}(1-\delta) \\ 1 - p_t^{e_2} & 0 & p_t^{e_2}\delta' & 0 & p_t^{e_2}(1-\delta') \\ 1 - p_t^{e_3} & 0 & 0 & p_t^{e_3}\delta' & p_t^{e_3}(1-\delta') \\ 1 & 0 & 0 & 0 & 0 \end{bmatrix} \tag{6}$$

in which we added the new event ‘breeding state not ascertained’ (last column) that could arise for non-breeders (first row) as well as breeders (second and third rows), though with potentially different probabilities: a non-breeder was assumed to be judged as a non-breeder with probability δ while a breeder was assumed to be judged as a breeder with probability δ'.

A preliminary analysis (see Table S1 in Electronic Supplementary Material) suggested that a model including (1) a survival probability varying over age and breeding status, (2) breeding status-specific detection probabilities and (3) constant-over-age transition probabilities between reproductive statuses was well supported by the data. We used the software JAGS (Plummer 2003) to fit this model to the MR female roe deer data in a Bayesian framework. Uniform prior distributions were used for all parameters. We ran two MCMC chains with a burn-in period of 5000 iterations followed by 20,000 iterations on which we based our inference. We checked convergence visually by inspecting the chains and by checking that the R-hat statistic was below 1.1. The code to fit the model is available from GitHub (https://github.com/oliviergimenez/estim_fitness).

Results

We found strong heterogeneity in detection due to the reproductive status (Table 1), with detection rate for breeders $p^{e_2=e_3}$ equal to 0.92 (SD 0.05) vs. that of non-breeders p^{e_1} equal to only 0.53 (SD 0.03). As expected, survival of old females [0.69 (SD 0.64) for non-breeders ϕ^{e_1}(o) and 0.83 (SD 0.05) for breeders $\phi^{e_2=e_3}$(o)] was lower than that of prime-aged females [0.84 (SD 0.02) for non-breeders ϕ^{e_1} (pa) and 0.97 (SD 0.02) for breeders $\phi^{e_2=e_3}$(pa)], regardless of their breeding status (Table 1). The probability of correct assignment for breeders δ' (0.93, SD 0.05) was much higher than that for non-breeders δ (0.26, SD 0.02).

Table 1 Parameter estimates (posterior mean) with standard deviation

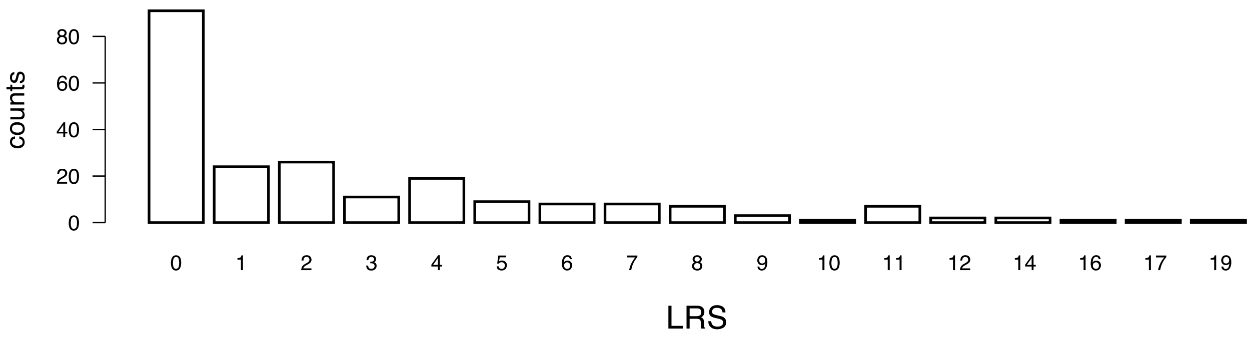
Parameter	Posterior mean estimate (standard deviation)
Detection of breeders $p^{e_2=e_3}$	0.92 (0.05)
Detection of non-breeders p^{e_1}	0.53 (0.03)
Survival of prime-age non-breeders ϕ^{e_1} (pa)	0.84 (0.02)
Survival of old non-breeders ϕ^{e_1} (o)	0.69 (0.04)
Survival of prime-age breeders $\phi^{e_2=e_3}$ (pa)	0.97 (0.02)
Survival of old breeders $\phi^{e_2=e_3}$ (o)	0.83 (0.05)
Transition non-breeder to 1 fawn $\psi^{e_1\to e_2}$	0.13 (0.02)
Transition non-breeder to 2 fawns $\psi^{e_1\to e_3}$	0.12 (0.02)
Transition 1 fawn to non-breeder $\psi^{e_2\to e_1}$	0.54 (0.06)
Transition 1 to 2 fawns $\psi^{e_2\to e_3}$	0.25 (0.04)
Transition 2 fawns to non-breeder $\psi^{e_3\to e_1}$	0.49 (0.05)
Transition 2 to 1 fawn $\psi^{e_3\to e_2}$	0.34 (0.04)
Proportion of non-breeders π^{e_1}	0.64 (0.04)
Proportion of females with 1 fawn π^{e_2}	0.15 (0.03)
Assignment non-breeder δ	0.26 (0.02)
Assignment breeder δ'	0.93 (0.05)

The distribution of individual fitness was far from normal for LRS (Fig. 1a), bimodal for λ_{ind} with two groups of individuals (Fig. 1b), one with main value of fitness centred on around 0.1 and the other on 1.4 and symmetric for LIC (Fig. 1c).

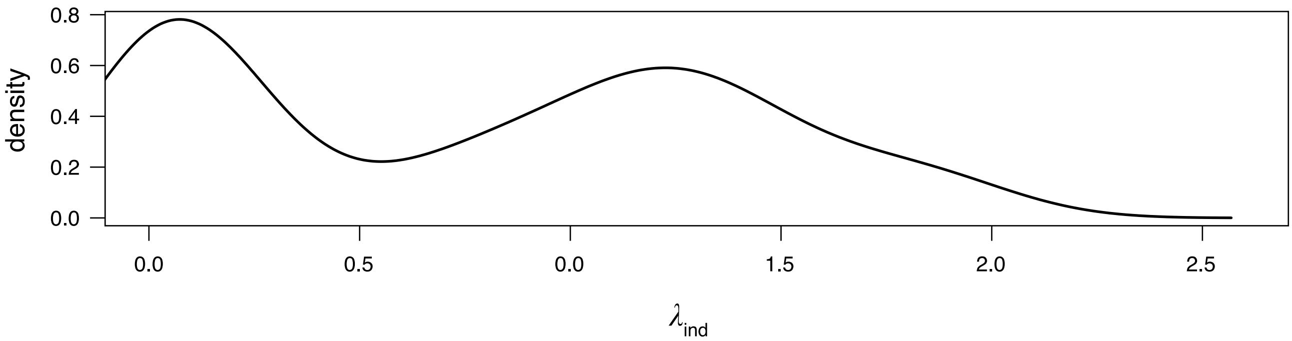
Discussion

In this work, we have extended the estimation of standard individual fitness metrics to account for imperfect detection. By reconstructing the whole life history, our approach allows the use of every individual even though some reproductive events were not recorded. Besides, by allowing the simultaneous estimation of demographic parameters and individual fitness, our approach can be combined with the tools developed in the MR literature to explore individual (Royle 2008; Gimenez and Choquet 2010) and environmental (Grosbois et al. 2008) variability in demographic parameters, and how this translates to variation in individual fitness. Last, an alternative approach—the Viterbi algorithm—exists in the Frequentist framework (Rouan et al. 2009) to find the most probable path of breeding states for each individual. However, in contrast with the Bayesian approach, the Viterbi algorithm does not easily allow propagating sampling uncertainty in the demographic parameter estimates to the fitness metrics estimates. A limitation of our approach is

(a) Lifetime reproductive success (LRS)



(b) Individual fitness (λ_{ind})



(c) Lifetime individual contribution (LIC)

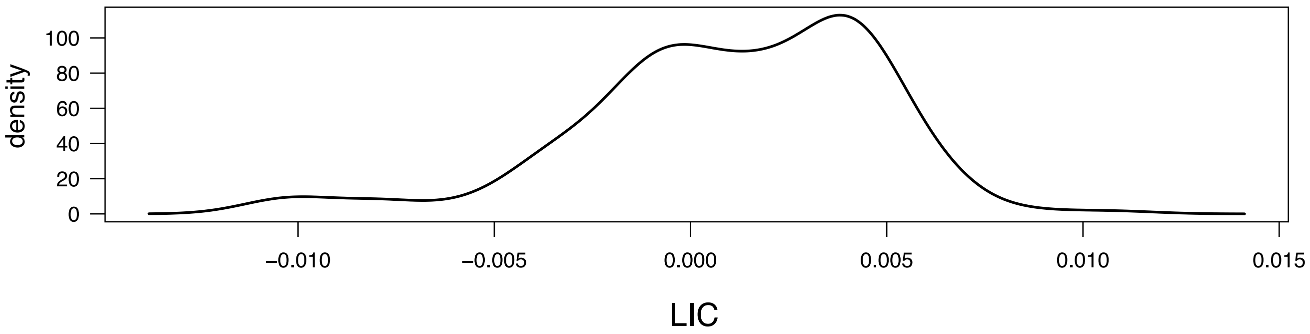


Fig. 1 Capture-recapture estimates of fitness metrics for roe deer: **a** lifetime reproductive fitness (bar plot), **b** individual fitness (kernel density estimate) and **c** lifetime individual contribution (kernel density estimate)

when individuals have many offspring (e.g., fishes), which requires extending the number of breeding states. This, in turn, comes with an exponential increase in the number of transition probabilities, which might hamper parameter estimation. If the focus of the analysis is in estimating fitness and not necessarily in making inference about the transition probabilities, then a solution to the issue of many states is to allocate states to bins of some length and use the midpoint of these intervals as new states to reduce the state space (Zucchini et al. 2016; Cowen et al. 2017 for an application).

From a more biological viewpoint, this new statistical approach applied to the long-term monitoring of female reproductive success in an intensively studied population of roe deer gave support for some previous findings but also provided new information.

The marked differences in detection probability between successful and unsuccessful females highlighted by the analyses correspond to a key finding that has not been yet reported in roe deer. However, the higher detection probability for successful females compared to unsuccessful females could be expected to occur in ungulates in relation to the much higher activity of lactating females, especially foraging activity (Neuhaus and Ruckstuhl 2002 in Alpine Ibex *Capra ibex*; Hamel and Côté 2008 in Mountain Goat *Oreamnos* *americana*; Ruckstuhl and Neuhaus 2002 for a review). Roe deer females allocate a lot to reproduction at each breeding attempt by producing two fawns that are large at birth and grow fast during the weaning period (Gaillard et al. 1993). Moreover, roe deer females are income breeders (Andersen et al. 2000), which do rely on available resources rather than on body reserves to meet the high energy expenditure they allocate to reproduction. Thus, successful females have to forage most of their time to find abundant and rich food, whereas barren females or females that lost their fawns right after birth have much lower energy requirements and are expected to be much less active. A marked increased activity of roe deer females with fawns at heel, which matches with an increase in metabolic rate (by 27%, Mauget et al. 1997), is thus likely to cause the almost twofold increase in detection probability of breeding females compared to non-breeding females we report here.

In addition of being easier to detect, females with fawns at heel survived better than females that failed weaning any fawn in a given year. Such a positive association between reproductive success and subsequent survival supports previous analyses of reproductive trajectories performed in the same population (Plard et al. 2012) and demonstrates the existence of a strong among-female variation in demographic performance and the absence of a detectable trade-off between current reproduction and future performance, as it has often been reported in vertebrate populations (see e.g., Cam et al. 2002 on Kittiwakes *Rissa tridactyla*; Barbraud and Weimerskirch 2005 on Blue petrel *Halobaena caerulea*; Beauplet et al. 2006 on Subantarctic fur seal *Arctocephalus tropicalis*; Le Bohec et al. 2007 on King penguin *Aptenodytes patagonicus*; Weladji et al. 2008 on Reindeer *Rangifer tarandus*; Maniscalco et al. 2010 on Steller sea lion *Eumatopias jubatus*). This positive association between current reproduction and subsequent survival indicates that individual variation in resource acquisition is larger than individual variation in resource allocation (van Noordwijk and de Jong 1986). Variation in resource acquisition among individuals is often interpreted in terms of individual quality (sensu Wilson and Nussey 2010). Under this concept, individuals can be ranked along a high-low demographic performance continuum. However, what causes the position of individuals on this continuum is subjected to debate (Tuljapurkar et al. 2009; Cam et al. 2016). Several factors are likely interplaying to shape the distribution of individuals among successful vs. unsuccessful trajectories. In roe deer females, the home range quality in terms of food resources seems to play a key role. Thus, females having access to meadows during the critical fawn rearing period raised twice more offspring than other females (McLoughlin et al. 2007) and fawns whose mother home range included hornbeam (*Carpinus betula*) survived much better than fawns born in areas without hornbeam (Pettorelli et al. 2005). Interestingly, we did not detect any association between previous and future reproduction. Previous studies of vertebrate populations have often reported some association, although varying in direction. For instance, Morano et al. (2013) reported a negative influence of recruiting an offspring on the pregnancy rate in the subsequent breeding season in elk (*Cervus elaphus canadensis*) and Stoelting et al. (2014) found that breeding in a given year reduced the probability of reproducing the year after in California spotted owl (*Strix occidentalis occidentalis*), whereas Blomberg et al. (2013) and Hernández-Matías et al. (2011) reported a positive association between reproductive success over two consecutive years in Greater sage grouse (*Centrocercus urophasianus*) and Bonelli's eagle (*Aquila fasciata*), respectively. For income breeders such as roe deer females, a positive rather than negative association is expected because of the absence of accumulated body reserves, which provide a functional link between consecutive reproductive attempts in capital breeders. However, the reproductive success of roe deer is highly dependent on the immediate availability of food resources in spring (Gaillard et al. 2013). Strong yearly variation in food resources caused by variable weather conditions, which has not been accounted for in the present analysis, is likely to explain this lack of association between consecutive reproductive attempts. Such findings differ from previous analyses of reproductive roe deer trajectories in that population. Indeed, Plard et al. (2012) found that a female that weaned two fawns in a given year had a probability to wean again two fawns the year after more than twice that of failing to wean any fawn. On the other hand, females that failed to wean any fawn in a given year had equal probability to fail again, wean only one fawn, or wean two fawns. The discrepancy might be explained by the much lower detection probability of females without fawns at heel, which is controlled for in the present study but was not in Plard et al.'s (2012) analysis.

The three metrics of individual fitness we estimated in roe deer females all displayed a marked deviation from a normal distribution. Compared to the normal distribution, the observed distribution of LRS, individual growth rates and individual contributions all indicated a much larger variation in fitness among females, a finding supporting a previous result reported from a much lower sample size of females intensively monitored for 5 years (Gaillard et al. 1998). On the other hand, the ratio between successful and unsuccessful females markedly differed between the present analysis and our previous study. While only five out of 37 females were highly unsuccessful in Gaillard et al. (1998) of 5-year reproductive success between 1978 and 1995 (see Fig. 4, p. 2884), more than half of females were highly unsuccessful in terms of LRS between 1977 and 2011 in the present study (see Fig. 1a). Although environmental conditions have worsened a lot over time in the study site (Gaillard et al. 2013), a high proportion of unsuccessful females were also observed before 1995 in this analysis. Not accounting for the lower detection rate of unsuccessful females likely led to overestimate the overall population recruitment. However, the discrepancy is also likely overestimated by markedly different assessment of LRS. In the first study, LRS was inferred from annual reproductive success during the first 5 years with available data for a given female. On the other hand, in the present study, LRS was inferred from a markedly different number of reproductive attempts across females.

The distributions of individual fitness suggest that the population studied should be better viewed as a mixture of good (or robust) and poor (or frail) females with some individuals displaying intermediate performance than as a continuous distribution. This has important consequences for modelling individual heterogeneity in wild populations. While the use of random effect models assuming a normal distribution of individual differences in the focal trait has become the rule (van de Pol and Verhulst 2006; van de Pol and Wright 2009), our detailed analysis or life history trajectories clearly indicates that the distribution of individual performance markedly deviates from a normal distribution, and rather exhibits a bimodal distribution that should be better captured by mixture models (Hamel et al. 2017). In support, a recent comparative analysis of individual heterogeneity in adult survival across a selected set of mammal and bird species has shown that a mixture model including two classes of individuals (i.e., frail vs. robust) consistently provided a better fit to observed data than random effect models based on a normal distribution of individual performance (Péron et al. 2016).

The new statistical approach we propose to estimate the distribution of fitness among individuals within a given population where individual reproductive success can be assessed by observations of mother-offspring associations allows accounting for both imperfect detection and differences in detection probability among individuals with different reproductive status. The application to roe deer females in an intensively monitored population demonstrates the potential of this approach. In particular, this analysis suggests that previous analyses of fitness distribution assessed from observed life histories trajectories are likely to have over-estimated the average individual fitness, and thereby the population growth rate (Fisher 1930) because of the expected lower detection probability of unsuccessful individuals. Such biases have obvious negative consequences in a management or conservation context. We thus urge future studies to account for both imperfect detection and differences in detection probability among individuals with different reproductive status in order to provide reliable estimates of individual fitness and of its distribution at the level of the population.

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