What shapes fitness costs of reproduction in long-lived iteroparous species? A case study on the Alpine ibex

Alexandre Garnier,[1] Jean-Michel Gaillard,[2] Dominique Gauthier,[3] and Aurélien Besnard[4,5]

[1]*Parc National de la Vanoise, 135 rue du Docteur Julliand, Chambéry 73000, France*
[2]*Laboratoire de Biométrie et de Biologie Evolutive, UMR 5558, Université Claude Bernard Lyon 1, 43 bd du 11 novembre 1918, Villeurbanne Cedex 69622, France*
[3]*Laboratoire Vétérinaire et d'Hygiène Alimentaire des Hautes Alpes, 5 rue des Silos, BP 63, Gap Cedex 05002, France*
[4]*CEFE UMR 5175, CNRS–Université de Montpellier–Université Paul-Valéry Montpellier– EPHE, Laboratoire Biogéographie et écologie des vertébrés, 1919 Route de Mende, Montpellier Cedex 5, 34293, France*

Abstract. The fitness costs of reproduction can be masked by individual differences, and may only become apparent during adverse environmental conditions. Individual differences, however, are usually assessed by reproductive success, so how fitness costs are influenced by the interplay between the environmental context and overall individual differences requires further investigation. Here, we evaluated fitness costs of reproduction based on 15 yr of monitoring of individual Alpine ibex (*Capra ibex*) during a period when the population was affected by a severe disease outbreak (pneumonia). We quantified fitness costs using a novel multi-event capture–mark–recapture (CMR) modeling approach that accounted for uncertainty in reproductive status to estimate the survival and reproductive success of female ibex while also accounting for overall individual heterogeneity using mixture models. Our results show that the ability of females to reproduce was highly heterogeneous. In particular, one group including 76% of females had a much higher probability of giving birth annually (between 0.66 and 0.77, depending on the previous reproductive status) than females of the second group (24% of females, between 0 and 0.05 probability of giving birth annually). Low reproductive costs in terms of future reproduction occurred and were independent of the pneumonia outbreak. There was no survival cost of reproduction either before or after the epizootic, but the cost was high during the epizootic. Our findings indicate that adverse environmental conditions, such as disease outbreaks, may lead to survival costs of reproduction in long-lived species and select against females that have a high reproductive effort. Thereby, the occurrence of adverse conditions increases the diversity of reproductive tactics within a population.

Key words: Alpine ibex; Capra ibex; French Alps; individual quality; large herbivores; mixture models; multi-event capture–recapture models; reproductive tactics; trade-offs; Vanoise National Park, Savoie, France.

Introduction

Trade-offs among fitness components is the central tenet of life-history theories (Stearns 1992). To maximize fitness, individuals must optimize allocation of resources among growth, survival, and reproduction (Cody 1966). This principle of allocation states that increasing reproductive effort should negatively impact future survival and/or reproduction, resulting in costs of reproduction.

In long-lived iteroparous vertebrates, trade-offs between current and future reproduction have been repeatedly described in populations of birds (Gustafsson and Sutherland 1988, Le Bohec et al. 2007) and mammals (Boyd et al. 1995, Moyes et al. 2011). Current reproduction negatively influences body condition, and

thereby the reproductive effort at the following reproductive event (Festa-Bianchet et al. 1998, Testa and Adams 1998).

By contrast, trade-offs between current reproduction and future survival have been less frequently reported in long-lived iteroparous species, for which reproductive costs should affect reproduction rather than survival (Hamel et al. 2010). Furthermore, the ability to detect these trade-offs may be limited to cases in which resource allocation is more variable than resource acquisition (van Noordwijk and de Jong 1986). Individuals occupying resource-rich home ranges might be able to allocate more to reproduction, allowing them to survive and to reproduce again the following year. In contrast, individuals in resource-poor home ranges might suffer from increased mortality risk and reproductive failure. In large mammalian herbivores, such heterogeneity in resource availability generally overrides reproductive costs, leading to positive

[5]E-mail: aurelien.besnard@cefe.cnrs.fr

correlations between current reproduction and future performance (Weladji et al. 2008, Hamel et al. 2009a).

Environmental conditions also influence the magnitude of reproductive costs. Reproductive costs may be restricted to contexts where resources are very limited (Clutton-Brock et al. 1996, Tavecchia et al. 2005). However, previous studies of variation in reproductive fitness costs in response to highly different environmental conditions either ignored individual differences (Toïgo et al. 2002, Descamps et al. 2009) or measured these differences based on reproductive success (Lescroel et al. 2009, Robert et al. 2012). Only accounting for a priori measured individual heterogeneity is likely to underestimate overall individual differences that may mask the reproductive costs. We took advantage of data from a long-term monitoring program of a population of Alpine ibex (*Capra ibex*) in the Vanoise National Park in France affected by a contagious pneumonia epizootic to test whether fitness costs of reproduction appear only in years when the pneumonia outbreak negatively influenced ibex population dynamics once overall individual differences have been accounted for, i.e., without any a priori on traits involved in heterogeneity between individuals.

Methods

Population studied

We monitored ibex in the Vanoise National Park (45° N, 7° E) in the Maurienne province of Savoie in France. The elevation of our study site ranged from 1000 to 3697 m and consisted mainly of rocky ridges and large mountain slopes, with a predominance of herbaceous vegetation. The weather conditions were typical of the internal zone of the Alps, with snowy winters and mild summers (average temperature of $16° \pm 2°C$). From 1991 to 2005, the ibex population slowly increased in size; then, between the spring of 2007 and the summer of 2008, a massive mortality occurred. We recovered 63 and 132 dead ibex in 2007 and 2008, respectively, whereas an average of only 28 dead ibex (from 0 to 48) was recovered each year during the previous 10 yr. Some ibex were observed coughing and in poor condition before dying (14 out of 18 autopsied ibex were cachectic). The necropsies that we performed indicated an unusual epizootic interstitial pneumonia (in 13 out of 18 autopsied ibex). Other analyses revealed the presence of contagious agalactia (Tardy et al. 2012). Subsequent population censuses confirmed the decrease of the population from 1018 individuals in 2005 to 722 in 2008. The population size continued to decrease to 410 ibex in 2011, when the decline halted. During the disease outbreak, other environmental conditions, such as temperature, precipitation, or vegetation productivity, did not markedly change.

Measure of reproductive status

Our study is based on longitudinal data collected on female ibex that were captured each spring and individually marked with visual collars and color-coded ear tags. Age at capture was determined by counting horn annuli (Geist 1966). Between 1 June 1997 and 31 May 2012, a total of 71 adult females were captured and marked, resulting in an average of 5.6 newly marked individuals/yr (range 2–18/yr). Although ibex can give birth at 2 yr of age in populations with a colonizing demographic regime (Toïgo et al. 2002), 94% of females did not mature at this age in the slow-growing population of Maurienne (Girard et al. 1998). Moreover, 3-yr-old females were only half as successful at raising a kid as older females (Toïgo et al. 2002). Based on the low reproductive success of 3-yr-old females throughout our study period (81% of the 26 females we monitored at 3 yr of age were never seen with a kid), we discarded them from subsequent analyses. Adult females in our study thus correspond to females aged 4 yr and older in the following analyses. Because none of the 3-yr-old females that we monitored died and were thus monitored as older individuals, such a left-censure cannot have biased our assessment of the magnitude and role of female heterogeneity on reproductive patterns. Due to generally high yearly survival, marked females were monitored over many years (4.91 ± 2.91 yr, mean ± SD; range 0.34–11.90 yr).

We regularly surveyed the study area throughout the year (~130 person-days/yr) to record marked females. On average, 22.06 ± 4.96 females (mean ± SD) were monitored annually (22.80 ± 5.46 females before the epizootic; 20.00 ± 4.00 during the epizootic; 19.00 ± 5.22 after the epizootic); the exact number of females monitored each year is given in the Appendix S5: Fig. S5). Each female was observed on average 10.65 times/yr (range 1–36 times/yr). For each female monitored, we used field observations to determine whether or not she had a kid. Monitoring reproductive status throughout the year leads to additional methodological issues. In particular, because ibex raise their kids in groups, the reproductive status of females may be uncertain to observers. Although assigning a kid to a marked female in summer is quite easy to do, correctly identifying reproductive status becomes increasingly difficult after weaning (from fall to the end of the following spring). At this time, bonds between mothers and kids are less tight and vary over time. We thus assessed the level of uncertainty in reproductive status in the field based on observed behaviors of females and kids using a scale of increasing confidence (Table 1).

Individual quality is usually measured as an index including survival and/or reproductive performance of a female throughout its life (Hamel et al. 2009a, Lescroel et al. 2009). However, such quality indices

TABLE 1. The five possible degrees of confidence recorded in the field for each observation of a given ibex female in Vanoise National Park, Savoie, France.

Reproductive status	Nursing behavior
Not breeding	Focal female observed alone
Certainly breeding	Kid suckling or contact between the focal female and a kid
Probably breeding	Kid close to the focal female (<1 m when moving)
Possibly breeding	Same number of kids and females in a group
Undefined	No information about reproductive status from the observation

only account for variation in measured traits, which are unlikely to capture the total individual differences. In this study, we considered the total individual differences by modeling individual heterogeneity as a two-state metric ("good" vs. "poor") following Vaupel and Yashin (1985) for each demographic component that we studied. Then we compared female survival and reproductive status among (1) females that reproduced but failed to raise a kid (2) females that reproduced successfully (i.e., raised a kid that survived until the next spring), and (3) females that did not reproduce (for a similar approach, see Lescroel et al. 2009). Like most large mammals, the Alpine ibex is closer to the "capital" end of the "capital–income" continuum of reproductive tactics (sensu Jönsson 1997). Ibex females must store large energy reserves to sustain the marked increase of energy requirements needed for late gestation/early lactation (Sadleir 1969). Therefore, we expected the reproductive success in a given year to negatively influence the subsequent reproductive success, as reported for other mountain ungulates such as bighorn sheep (*Ovis canadensis*) (Festa-Bianchet et al. 1998). Yet under favorable environmental conditions, we expected individual differences in quality to override any fitness costs of reproduction, so that successful breeders would be more likely to survive and successfully reproduce in the next breeding season than females that did not reproduce or that failed to raise a kid (Weladji et al. 2008, Hamel et al. 2009a). Under harsh environmental conditions caused by the pneumonia outbreak, the costs of reproduction should be more apparent, so we expected that females that successfully raised a kid would have a lower probability of survival and reproduction in the next breeding season than females that did not reproduce or that failed to raise a kid.

Statistical analyses

We used multi-event capture–mark–recapture (CMR) modeling, an extension of multi-state models (Lebreton and Pradel 2002), which takes into account uncertainty

in assigning states (Pradel et al. 2005, 2008). For each year of monitoring, four resighting periods were defined, corresponding to the four seasons: summer (1 June to 31 August), when births occur; autumn (1 September to 30 November); winter (1 December to 28 February); and spring (1 March to 31 May). Each year, for each of these periods, females were classified in one of three reproductive states (Fig. 1), (1) whether the female successfully weaned a kid (state S), (2) gave birth but lost the kid during the first year (state L), or (3) did not give birth (state N). The fourth state was defined as the death of the female (state D). This modeling design allowed us to estimate state-dependent survival, state-dependent transition probabilities between states, and state-dependent recapture probabilities (Tavecchia et al. 2005, Weladji et al. 2008). Transition probabilities were denoted $\Psi(i,j)$, where i is the state in period t and j is the state in period $t + 1$. In a year when a female gave birth, the transition probability includes both female survival (ϕ_f) and kid survival (ϕ_k). For example, $\Psi(S,S) = \phi_f \times \phi_k$ and $\Psi(S,L) = \phi_f \times (1-\phi_k)$. From 1 year to the next, the transition probability includes both female survival (ϕ_f) and the probability of giving birth during the next breeding season (δi), where i is the state of the female the previous spring. Although most previous studies explored the reproductive status prior to weaning (Toïgo et al. 2002, Tettamanti et al. 2015), when breeding success is easy to assess, there could always be some uncertainty in the reliability of assessing the reproductive status from field observations in mountain ungulates, especially when overwinter survival is studied (Rughetti et al. 2015). However,

Transitions during a breeding year · Transition from the end of one breeding year to the next
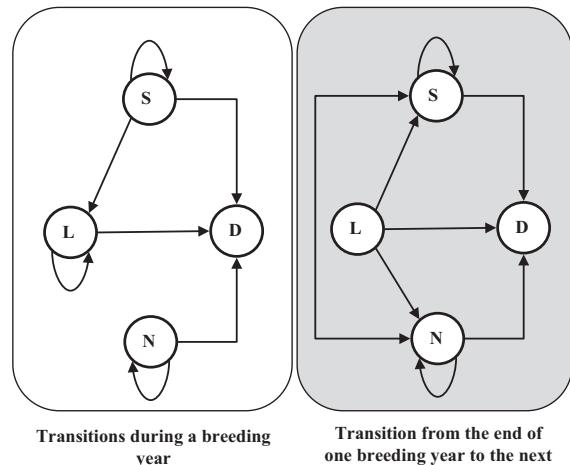
FIG. 1. Diagram showing the possible transitions between the four reproductive states of the Alpine ibex (*Capra ibex*): whether a female produced a kid and raised it successfully (S), produced a kid and lost it (L), did not produce a kid (N), or died (D). The white area represents the possible transitions during a breeding year (from summer to autumn, from autumn to winter, and from winter to spring). The gray area represents the possible transitions from the end of one breeding year (spring) to the next (summer).

this uncertainty has been neglected in most, if not all previous studies. In our study, the degree of confidence regarding the reproductive status of a female was systematically recorded for each observation in the field (see the measures of reproductive status in Table 1). The females were also observed many times during each 3-month period. From the five different codes recorded for each observation in the field (Table 1), we then defined seven possible codes by combining the successive observations of the same female during the same season (Table 2). These seven codes are named "events" in a CMR multi-event context, i.e., they represent what is recorded in the field that might not be the true state of the individuals. Using this approach, we were thus able to estimate the probability that a female recorded as being "Probably with a kid" or "Possibly with a kid" (codes of Table 2) is actually raising a kid or not. Thus this approach allows us to separate the probability of transition between two different states (e.g., from the state "weaning a kid in summer" to the state "lost its kid in winter," which indicates winter mortality of the kid) from a shift in the probability to correctly assign females to a reproductive state (i.e., to detect if the female still raises a kid or not) without any subjective decisions regarding its reproductive state. To our knowledge, this is the best approach to obtain unbiased estimates of reproductive success and survival. This approach provides an explicit estimate of the reproductive state, instead of being subjectively assigned by observers directly from the field observation. Moreover, this approach is conservative because the estimate of the reproductive state

is associated with a confidence interval so that small or spurious effects should be overwhelmed in this confidence interval.

To model between-individual heterogeneity, two methods have been proposed. One consists in using random intercept models (Cam et al. 2002, Lescroel et al. 2009). However, Gimenez and Choquet (2010) warned against using this method in CMR modeling because of methodological issues, especially when the number of individuals is low (difficulties in estimating variance of the random effect, time-consuming computation when random effects are applied to more than one parameter, and poor performance of numerical integration when variance is high). The second is the mixture approach (Pledger et al. 2003), which aims to discriminate discrete classes of individuals that have different mean values of the parameters. The latter approach adequately models continuous heterogeneity (Pledger 2005) and has been already used to study effects of senescence on survival (Péron et al. 2010) or to detect individual heterogeneity in the quality of breeding sites (Chevallier et al. 2013). Here, we used this approach to take into account a discrete hidden individual heterogeneity on the demographic parameters. Mixture models then allow assessing whether individual heterogeneity is detectable, without any a priori assumption about the factors shaping this heterogeneity. Such a mixture is expected to occur when two types of females coexist within the population, with two different combinations of survival and recruitment probabilities. We defined these two types "+" (called hereafter "good" individuals) and "−" ("poor" individuals). All individuals could thus be a posteriori attributed to one of the seven states: S−, S+, L−, L+, N−, N+, and D.

In well-established ibex populations that are close to carrying capacity, as in other large herbivores, age at primiparity is delayed compared to those of colonizing populations at low density (Gaillard et al. 2003). To account for both senescence in reproductive success and potential confounding effects between age and individual heterogeneity, we built models with two age classes (Appendix S2: Table A2): adults (4–12 yr old) and senescent adults (13 yr and older). The choice of 13 yr for the onset of actuarial senescence was justified by previous studies (Toïgo et al. 2002, Rughetti et al. 2015).

Because the epizootic occurred over a short time period and affected this ibex population only between the spring of 2007 and the summer of 2008, and in absence of any detectable change in other environmental factors at this time, we identified three periods: before epizootic (BE), during epizootic (E), and after epizootic (AE). This allowed us to assess the impact of the epizootic event without any confounding effects of other potential factors. Preliminary analyses showed that female survival did not vary according to season or in the periods before and after the disease (A. Garnier, J.-M. Gaillard, and A. Besnard, *unpublished*

TABLE 2. The seven possible events assigned to a female ibex based on repeated observation during a 3-month period (spring, summer, autumn or winter).

No.	Event	Definition
0	Unobserved female	
1	Female of unknown reproductive status	Female observed and events other than 2, 3, 4, 5, or 6
2	Female without kid	nb_obs "no breeding" >2 OR nb_obs "possible breeding" = 0
3	Female probably without kid	nb_obs "no breeding" >1 AND nb_obs "possible breeding" <2
4	Female possibly with a kid	nb_obs "probably breeding" = 1
5	Female probably with a kid	nb_obs "probably breeding" = 2
6	Female certainly with a kid	nb_obs "certainly breeding" >0 OR nb_obs "probably breeding" >2

Note: nb_obs is the number of observations with each degree of confidence (see Table 1).

data; see Appendix S1). However, we tested whether kid survival differed according to season (3S) because we expected kids to be more susceptible to dying from the end of the summer to early in autumn when weaning takes place, and over the winter when climatic conditions are harsh. To assess potential fitness costs of reproduction, we tested the effect of giving birth (GB), of kid survival (KS), and of raising a kid successfully (RK) on subsequent female survival and reproduction. We expected that females that successfully raised a kid would bear greater reproductive costs than females that gave birth but lost their kid or did not give birth.

In ibex, weaning occurs in early autumn, and direct contact between a female and her kid becomes less common from that time. In addition, observation conditions were expected to vary substantially according to season, because females use different seasonal areas and their activity depends on climatic factors (Grignolio et al. 2004). We therefore modeled season-dependent event probabilities (4S).

Model selection was performed using $QAIC_c$ (Burnham and Anderson 2004). We separately studied the demographic parameters included in the models in the following order: female survival, kid survival, and the probability that a female would give birth in the next breeding season (Appendix S2: Table A2). We first tested the effect of female heterogeneity, female age, reproductive success, and of the epizootic pneumonia on female survival. These effects were tested one at a time and we then retained those that displayed selected effects (ΔAIC <2). We then kept the selected model on female survival and tested the effects of female heterogeneity, female age class, epizootic, and season on kid survival. Finally, we kept the selected models on female survival and kid survival and tested the effects of female heterogeneity, female age class, reproductive success, and epizootic on the probability that a female would give birth. We controlled a posteriori from the best model that a female that gave birth and lost its kid had the same event probabilities as a female that did not give birth. The goodness of fit of the Cormack-Jolly-Seber model (i.e., the fully time-dependent model) was assessed using the software U-CARE 2.3.2 (Pradel et al. 2005, Choquet et al. 2009*a*). We used the program E-SURGE 1.8.5 (Choquet et al. 2009*b*) to obtain maximum likelihood estimates of the parameters and to perform model selection. All matrices used in E-SURGE are available in the Appendix S3: Table A3.

Results

Survival and reproduction patterns

According to the best model, survival of females from one season to the next was strongly influenced by age, the outbreak of the disease, and the successful raising of a kid (Appendix S2: Table A2a, model 1). Survival was similar for unsuccessful females (i.e., that either did not give birth (state N) or gave birth but lost their kid during the year (state L; Appendix S2: Table A2a, models 3, 9, 10). Before and after the epizootic, both adult and senescent survival were higher for successful females (0.994 [0.971–0.999] and 0.966 [0.762–0.996], respectively) than for unsuccessful females (0.975 [0.956–0.986] and 0.890 [0.743–0.947], respectively); values are means, with 95% confidence intervals in brackets (see Fig. 2). During the outbreak, survival patterns according to reproductive state were reversed, with much lower survival for successful than unsuccessful females (adult survival 0.642 [0.435–0.806] vs. 0.918 [0.803–0.968]; senescent survival 0.265 [0.035–0.783] vs. 0.805 [0.518–0.941]). We did not find any evidence of individual heterogeneity on survival, meaning that "good" and "poor" females discriminated by the model had similar survival probability. Kid survival from one season to the next was independent of the mother's age (Appendix S2: Table A2b). The disease outbreak led to a large decrease in kid survival. Kid survival was greater for "good" than for "poor" mothers (0.89 [0.83–0.93] vs. 0.62 [0.29–0.87] outside the epizootic period and 0.38 [0.15–0.69] vs. 0 [SE = 0] during the epizootic). There was no difference in kid survival between seasons (model 13 and model 15, $\Delta QAIC_c$ < 2). Nevertheless, kid survival outside the epizootic period tended to be lower in winter ($\phi_k = 0.77$ [0.54–0.90]) than in summer ($\phi_k = 0.91$ [0.81–0.96]), with an intermediate value in autumn ($\phi_k = 0.87$ [0.67–0.94]).

Heterogeneity in reproductive success

According to the best model, the probability of giving birth during a given year was independent of age (Appendix S2: Table A2c), but was strongly influenced by female heterogeneity. "Good" females had a high probability of giving birth whatever their reproductive success the previous year (0.66 [0.56–0.74] when successful and 0.76 [0.62–86] when unsuccessful), whereas almost no "poor" females gave birth (0 [0–0] when successful the year before, and 0.05 [0.01–0.19] when unsuccessful; values are means, with 95% CI; Fig. 3). The distribution of females among the initial states indicated that most females captured in a given year were "good" and gave birth (with kid, 0.57 [0.43–0.70]; without kid, 0.19 [0.10–0.33]). The probability for a "poor" female that had given birth was very low (with kid, 0.06 [0.02–0.20]; without kid, 0.18 [0.10–0.31]; see Fig. 3). To summarize, 76% of females showed a high probability of giving birth annually (probability between 0.66 and 0.77, depending on the previous reproductive status), whereas 24% of females showed a very low probability of giving birth annually (probability between 0 and 0.05). We did not detect any effect of
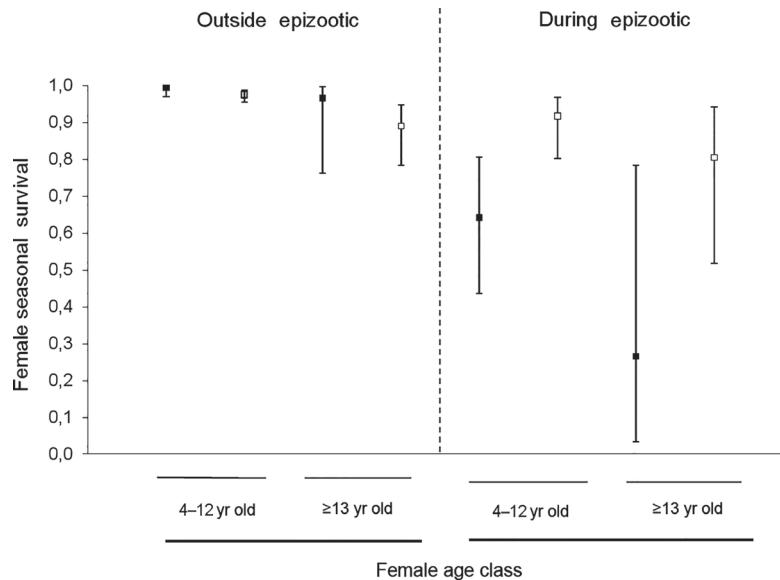
Fig. 2. Age-dependent seasonal survival of successful (solid squares) and unsuccessful (open squares) ibex females monitored in Vanoise National Park, Savoie, France, during a period with contagious pneumonia epizootic (right panel; annual sample size of 20.0 ± 4.0 females, mean ± SD) and a period without (left panel; annual sample size of 21.53 ± 5.67 females). Estimates were obtained from model 13 (see Appendix: Table A2). Bars indicate the 95% confidence interval.

the epizootic on the probability of parturition (Appendix S2: Table A2c; models 20, 22, and 23 not better than model 13).

Cost of reproduction on breeding the following season

The best models regarding the probability of parturition included the effect of the reproductive status in the previous year (Appendix S2: Table A2c, models 13 and 20). The probability that a "good" female would give birth was lower when it had successfully raised a kid the year before (0.62 [0.50–0.73]) than when it had been unsuccessful (0.76 [0.62–0.86]; values are means, with 95% CI; Fig. 3). However, the probability of giving birth in a given breeding season was similar for females that had given birth in the previous year (0.66 [0.56–0.74]) and for those that had not given birth (0.77 [0.59–0.89]). We detected the same pattern for "poor" females, although they gave birth at a much lower rate and only when they had not given birth in the previous year (0.05 [0.01–0.19]).

Resighting probability

As expected, the probability of detecting a female and assessing whether she had had a kid strongly varied between seasons (Appendix S4: Table A4), demonstrating the increasing difficulty of reliably identifying reproductive status from birth onward. The probability of observing with certainty a female raising a kid was 0.56 [0.47–0.65] in summer, but decreased

to 0.22 [0.14–0.31] the following spring, when there was a high probability of detecting a female without being able to determine its reproductive status (0.28 [0.19–0.39]; values are means, with 95% CI). In the same way, the probability of observing with certainty a female not raising a kid was 0.41 [0.32–0.50] in the summer and decreased over the following three seasons.

DISCUSSION

Our results suggest that once we accounted for overall individual differences, female ibex did not suffer survival costs associated with reproduction under "normal" environmental conditions. However, fitness consequences of reproduction were pronounced under harsh environmental conditions, when the population faced a severe pneumonia outbreak. Moreover, we detected low costs of reproduction in terms of reproduction independently of the pneumonia epizootic, whereas such costs are usually masked by individual differences in resource availability when unaccounted for (Toïgo et al. 2002).

The multi-event CMR approach that we used to quantify fitness consequences differed from that of previous studies in that it allowed us to explicitly incorporate uncertainty in determining the reproductive status of an individual into our analysis. Such an approach should be beneficial for other taxonomic groups in which it is not easy to determine the reproductive status of individuals. For example, some breeding episodes are regularly unobserved in birds.
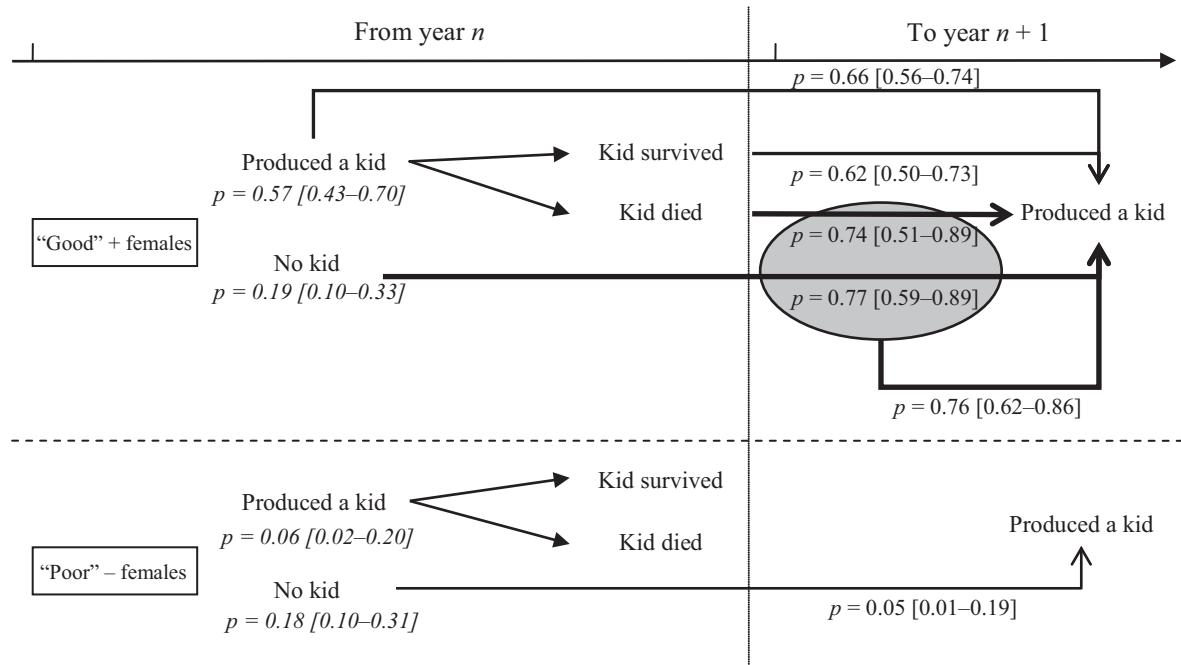
Fɪɢ. 3. Diagram showing the probability (P) of a female producing a kid in year $t + 1$ depending on its breeding success in year t, from the multi-event capture–mark–recapture analysis. Values are means, with 95% confidence intervals in brackets. The probability of a female being in the reproductive state and including heterogeneity ("good" females vs. "poor" females) is displayed in italics. The shaded area highlights probabilities that are not statistically different, and represent unsuccessful females that either failed to produce a kid or produced a kid and lost it.

This is especially the case for birds that fail early in the breeding season, which are then wrongly interpreted as individuals skipping a breeding event. Such uncertainty can now be resolved using multi-event modeling at an interannual scale (see, e.g., Pradel et al. 2012, Souchay et al. 2014). Here, we generalized previous approaches to model the reproductive status within a reproductive attempt (intra annual transitions) to estimate both the probability of a female giving birth and the probability of the kid surviving. This approach can be applied to situations when field efforts are insufficient to ascertain the reproductive status of an individual or when criteria available to determine individual reproductive status are difficult to apply (e.g., social ungulates with older offspring, species including ungulates inhabiting forested habitats where reliable observations on reproductive status are difficult to obtain).

Reproductive costs in normal environmental conditions

Before and after the occurrence of the epizootic, we did not detect any survival cost of reproduction. In fact, both adult and senescent ibex females that successfully raised a kid were more likely to survive than unsuccessful females that did not give birth or lost their kid. The absence of a trade-off between current reproduction and future survival in the normal

range of environmental conditions after having accounted for individual differences supports previous findings (Moyes et al. 2011) and indicates that females of long-lived iteroparous species are able to withstand the increased energetic demands during reproduction.

Heterogeneity in individual performance has been previously assessed using multifactorial traits, most often involving longevity, age at first and last reproduction, body mass, social rank, or breeding experience (e.g., Hamel et al. 2009b). In this study, we modeled individual heterogeneity using two discrete classes of females, without any a priori assumption about traits that capture individual heterogeneity. We showed that the ability of females to give birth each year was best accounted for by differences between "good" and "poor" individuals. "Good" females had a high probability of giving birth each year, whereas "poor" females had a much lower probability. Such heterogeneity in reproductive ability was not driven by the female's age, as neither kid survival nor the probability of giving birth was influenced by the age of adult females. This is contrary to what has been reported in seabirds when using breeding quality as an a priori proxy for individual quality (Lescroel et al. 2009). Moreover, "good" females, which reproduced more often, had kids with higher survival chances than "poor" females, suggesting that they have either higher fecundity and

better parental care or higher genotypic quality, or both. As life-history traits that define quality are positively correlated with individual fitness, quality is under selection (Wilson and Nussey 2010). Individual quality originates from interactions between genetics, variation in selection on individual and multivariate suit of traits, and of context-specific plasticity in allocation strategies (for a review, see Lailvaux and Kasumovic 2011). In large herbivores, individual heterogeneity partly comes from cohort variation (Gaillard et al. 2003), and differences in phenotypic quality may be associated with differences in reproductive success (Hamel et al. 2009b). Although data on body mass and social rank were not available for the ibex females that we monitored, we might expect females classified as "good" to be large, dominant individuals that forage in the best habitat patches. Further investigation will be required to test this hypothesis.

In capital breeders (Jönsson 1997), successful reproduction depletes body condition and thus has a negative influence on the reproductive performance at the next reproductive attempt (Festa-Bianchet et al. 1998, Testa and Adams 1998). Unexpectedly, several studies have found no evidence of gestation and lactation costs in terms of future reproduction (Toïgo et al. 2002, Weladji et al. 2008), or have detected these costs only for females a priori ranked as low quality (Hamel et al. 2009a). Accounting only for a priori measured individual heterogeneity is likely to underestimate overall individual differences, explaining why these previous studies did not detect reproductive costs. In this study, we measured reproductive costs on breeding in the following season for all females after accounting for overall individual heterogeneity in their reproductive capacity. In a given year, very few "poor" females gave birth, and they did so only when they had not given birth the previous year. The annual reproductive success of "good" females was consistently high; however, they were more likely to give birth when they were unsuccessful the previous year than when they successfully raised their kid until the spring. Such costs of reproduction on breeding in the following season are more likely to correspond to the cost of lactation and maternal care than to gestation (Festa-Bianchet et al. 1998). In capital breeders such as the ibex, we thus provide support for reproductive costs in terms of reproduction occurring for all females, even in the absence of extreme environmental conditions such as a disease outbreak in the present study of ibex.

Reproductive costs in harsh environmental conditions

The disease outbreak that affected the studied ibex population from 2007 resulted in a marked decrease in kid survival: survival was more than twofold higher before and after than during the epizootic. The ibex is an iteroparous species with a highly conservative reproductive tactic (Toïgo et al. 2007), which we would expect to involve skipping reproduction when resources are scarce or environmental conditions are harsh (Festa-Bianchet et al. 1998). Thus, during the epizootic we expected adult survival to be favored over the probability of females reproducing. However, we did not detect any change in the probability that females would reproduce during the epizootic, meaning that the disease did not affect the ability of females to allocate resources for reproduction. Our findings also showed that during the epizootic, ibex females with a kid had lower survival probability than females without a kid, revealing the existence of reproduction costs on survival during the disease outbreak for both adult and senescent females. Similar results have been reported in birds, where reproductive fitness costs were shown to be higher during an epizootic (Descamps et al. 2009). Recent studies have also reported that costs of reproduction mainly affect individuals of intermediate quality and are influenced by environmental harshness (Robert et al. 2012). In large mammals, the few studies that have explored the costs of reproduction on survival under varying conditions have detected them only during severe environmental conditions, for example, a harsh winter or a high-density population (Festa-Bianchet et al. 1998, Tavecchia et al. 2005).

In our study, the explanation for females paying a cost in terms of survival rather than skipping reproduction may be the suddenness of the disease. During the study, no change in resource availability was observed, so females in good condition could continue to give birth. However, once affected by the disease, these females could no longer cope with the energetic requirements of reproduction and the high physiological costs of immunity (Hudson et al. 2002, Schmid-Hempel 2003). Their survival probability and that of their kid consequently decreased. In contrast, during these harsh conditions, females that did not give birth had a higher survival rate. This illustrates that the costs of reproduction on survival occur in long-lived iteroparous species only when environmental conditions severely deteriorate. In such contexts, individuals that would normally have low fitness might have a selective advantage, which might explain the maintenance of individual heterogeneity in terms of investment in reproduction.

Previous studies have reported the varying intensity of reproductive costs in relation to environmental changes (Lescroel et al. 2009, Robert et al. 2012) while accounting only for individual differences in reproductive success. We provide a first demonstration that adult survival is influenced by changing environmental conditions through investment in reproduction after having accounted for overall individual heterogeneity independently of any particular assumption about what shapes such heterogeneity. Our findings show that the strength of individual differences and reproduction costs depend on the harshness of environmental conditions, such as the disease outbreak in the present study, which

markedly influence the demography and the evolution of life-history traits in long-lived iteroparous species (Le Bohec et al. 2007, Lescroel et al. 2009). Our approach offers a useful way to measure overall differences independently of a priori assumptions about its cause. Our findings reinforce the need to account for individual differences when investigating life-history responses to environmental variation by demonstrating that a sudden shift in environmental conditions, in this case a disease outbreak, allows the coexistence of different reproductive tactics within a given population.

Literature Cited

Boyd, I. L., J. P. Croxall, N. J. Lunn, and K. Reid. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. Journal of Animal Ecology 64:505–518.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference-understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. American Naturalist 159:96–105.

Chevallier, C., P. A. Crochet, N. Vincent-Martin, A. Ravayrol, and A. Besnard. 2013. Use of mixture models to characterize site quality in philopatric animals: a case study with Bonelli's eagle. Animal Conservation 16:198–206.

Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009a. U-CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32:1071–1074.

Choquet, R., L. Rouan, and R. Pradel. 2009b. Program E-SURGE: a software application for fitting multievent models. Environmental and Ecological Statistics 3:845–865.

Clutton-Brock, T. H., I. R. Stevenson, P. Marrow, A. D. MacColl, A. I. Houston, and J. M. McNamara. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. Journal of Animal Ecology 65:675–689.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20:174–184.

Descamps, S., H. G. Gilchrist, J. Bety, E. I. Buttler, and M. R. Forbes. 2009. Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. Biology Letters 5:278–281.

Festa-Bianchet, M., J. M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

Gaillard, J. M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort effects and deer population dynamics. Ecoscience 10:412–420.

Geist, V. 1966. Evolution of horn-like organs. Behaviour 27:175–214.

Gimenez, O., and R. Choquet. 2010. Individual heterogeneity in studies on marked animals using numerical integration: capture–recapture mixed models. Ecology 91:951–957.

Girard, I., D. Gauthier, and J. P. Martinot. 1998. Evolution démographique des populations de bouquetin des Alpes (*Capra ibex ibex*) présentes dans le Parc national de la Vanoise ou réintroduites à partir de celui-ci. Game and Wildlife 15:417–431.

Grignolio, S., I. Rossi, B. Bassano, F. Parrini, and M. Apollonio. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. Ethology, Ecology, and Evolution 16:255–264.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813–815.

Hamel, S., S. D. Cote, J. M. Gaillard, and M. Festa-Bianchet. 2009a. Individual variation in reproductive costs of reproduction: high-quality females always do better. Journal of Animal Ecology 78:143–151.

Hamel, S., J. M. Gaillard, M. Festa-Bianchet, and S. D. Cote. 2009b. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981–1995.

Hamel, S., S. D. Cote, and M. Festa-Bianchet. 2010. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology 91:2034–2043.

Hudson, P. J., A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson. 2002. The ecology of wildlife diseases. Oxford University Press, Oxford, UK.

Jönsson, T. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.

Lailvaux, S. P., and M. M. Kasumovic. 2011. Defining individual quality over lifetimes and selective contexts. Proceedings of the Royal Society B 278:321–328.

Le Bohec, C., M. Gauthier-Clerc, D. Gremillet, R. Pradel, A. Bechet, J. P. Gendner, and Y. Le Maho. 2007. Population dynamics in a long-lived seabird: I. Impact of breeding activity on survival and breeding probability in unbanded king penguins. Journal of Animal Ecology 76:1149–1160.

Lebreton, J. D., and R. Pradel. 2002. Multistate recapture models: modelling incomplete individual histories. Journal of Applied Statistics 29:353–369.

Lescroel, A., K. M. Dugger, G. Ballard, and D. G. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. Journal of Animal Ecology 78:798–806.

Moyes, K., B. Morgan, A. Morris, S. Morris, T. Clutton-Brock, and T. Coulson. 2011. Individual differences in reproductive costs examined using multi-state methods. Journal of Animal Ecology 80:456–465.

van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Péron, G., P. A. Crochet, R. Choquet, R. Pradel, J. D. Lebreton, and O. Gimenez. 2010. Capture–recapture models with heterogeneity to study survival senescence in the wild. Oikos 119:524–532.

Pledger, S. 2005. The performance of mixture models in heterogeneous closed population capture–recapture. Biometrics 61:868–873.

Pledger, S., K. H. Pollock, and J. L. Norris. 2003. Open capture–recapture models with heterogeneity: I. Cormack-Jolly-Seber model. Biometrics 59:786–794.

Pradel, R., O. Gimenez, and J. . D. Lebreton. 2005. Principles and interest of GOF tests for multistate capture–recapture models. Animal Biodiversity and Conservation 28:189–204.

Pradel, R., L. Maurin-Bernier, O. Gimenez, M. Genovart, R. Choquet, and D. Oro. 2008. Estimation of sex-specific sur-

vival with uncertainty in sex assessment. Canadian Journal of Statistics 36:29–42.

Pradel, R., R. Choquet, and A. Bechet. 2012. Breeding experience might be a major determinant of breeding probability in long-lived species: the case of the Greater Flamingo. PLoS ONE 7(12):e51016.

Robert, A., V. H. Paiva, M. Bolton, F. Jiguet, and J. Bried. 2012. The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. Ecology 93:1944–1952.

Rughetti, M., A. Dematteis, P. G. Meneguz, and M. Festa-Bianchet. 2015. Age-specific reproductive success and cost in female Alpine ibex. Oecologia 178:197–205.

Sadleir, R. M. F. S. 1969. The ecology of reproduction in wild and domestic animals. Methuen, London, UK.

Schmid-Hempel, P. 2003. Variation in immune defence as a question of evolutionary ecology. Proceedings of the Royal Society of London B 270:357–366.

Souchay, G., G. Gauthier, and R. Pradel. 2014. To breed or not: a novel approach to estimate breeding propensity and potential trade-offs in an Arctic-nesting species. Ecology 95:2745–2756.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Tardy, F., et al. 2012. Emergence of atypical *Mycoplasma agalactiae* strains harboring a new prophage and associated with an alpine wild ungulate mortality episode. Applied and Environmental Microbiology 78:4659–4668.

Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. D. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. Journal of Animal Ecology 74:201–213.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345–1354.

Tettamanti, F., S. Grignolio, F. Filli, M. Apollonio, and P. Bize. 2015. Senescence in breeding success of female Alpine chamois (*Rupicapra rupicapra*): the role of female quality and age. Oecologia 178:187–195.

Toïgo, C., J. M. Gaillard, D. Gauthier, I. Girard, J. P. Martinot, and J. Michallet. 2002. Female reproductive success and costs in an alpine capital breeder under contrasting environments. Ecoscience 9:427–433.

Toïgo, C., J. M. Gaillard, M. Festa-Bianchet, E. Largo, J. Michallet, and D. Maillard. 2007. Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. Journal of Animal Ecology 76:679–686.

Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. American Statistician 39:176–185.

Weladji, R. B., A. Loison, J. M. Gaillard, O. Holand, A. Mysterud, N. G. Yoccoz, M. Nieminen, and N. C. Stenseth. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156:237–247.

Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? An evolutionary perspective. Trends in Ecology and Evolution 25:207–214.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/15-0422.1/suppinfo