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From gestation to weaning: Combining robust design and multi-event models unveils cost of lactation in a large herbivore

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Abstract

1. The cost of current reproduction on survival or future reproduction is one of the most studied trade-offs governing resource distribution between fitness components. Results have often been clouded, however, by the existence of individual heterogeneity, with high-quality individuals able to allocate energy to several functions simultaneously, at no apparent cost.
2. Surprisingly, it has also rarely been assessed within a breeding season by breaking down the various reproductive efforts of females from gestation to weaning, even though resource availability and energy requirements vary greatly.
3. We filled this gap by using an intensively monitored population of Pyrenean chamois and by expanding a new methodological approach integrating robust design in a multi-event framework. We distinguished females that gave birth or not, and among reproducing females whether they lost their kid or successfully raised it until weaning. We estimated spring and summer juvenile survival, investigated whether gestation, lactation or weaning incurred costs on the next reproductive occasion, and assessed how individual heterogeneity influenced the detection of such costs.
4. Contrary to expectations if trade-offs occur, we found a positive relationship between gestation and adult survival suggesting that non-breeding females are in poor condition. Costs of reproduction were expressed through negative relationships between lactation and both subsequent breeding probability and spring juvenile survival. Such costs could be detected only once individual heterogeneity (assessed as two groups contrasting good vs. poor breeders) and time variations in juvenile survival were accounted for. Early lactation decreased the probability of future reproduction, providing quantitative evidence of the fitness cost of this period recognized as the most energetically demanding in female mammals and critical for neonatal survival.
5. The new approach employed made it possible to estimate two components of kid survival that are often considered practically unavailable in free-ranging populations, and also revealed that reproductive costs appeared only when contrasting the different stages of reproductive effort. From an evolutionary perspective, our findings stressed the importance of the temporal resolution at which reproductive

cost is studied, and also provided insights on the reproductive period during which internal and external factors would be expected to have the greatest fitness impact.

KEYWORDS
CMR, individual heterogeneity, juvenile survival, Pyrenean chamois *Rupicapra pyrenaica pyrenaica*, reproductive success, trade-offs, ungulates

1 | INTRODUCTION

One central assumption of life-history theories is the existence of trade-offs between fitness components: growth, survival and reproduction (Stearns, 1992). These trade-offs originate from the principle of energy allocation (Stearns, 1992; Van Noordwijk & De Jong, 1986) which states that as energy is limited, the amount of energy allocated to one function cannot be used for another. Individuals should consequently allocate their resources optimally between growth, survival/maintenance and reproduction (trade-off hypothesis; Williams, 1966). Among these trade-offs, the most studied in iteroparous organisms is probably that between current reproduction and future survival or reproduction (Hamel, Gaillard, et al., 2010; Stearns, 1992). Costs of reproduction on other fitness components (negative co-variation) are expected to be strong in mammals because of high-energy requirements linked to late gestation and lactation (Clutton-Brock, 1989; Gittleman & Thompson, 1988; Oftedal, 1985; Robbins & Robbins, 1979).

The assumption of a trade-off has, however, been repeatedly questioned empirically by studies reporting the existence of positive co-variations between fitness components, with individuals seemingly able to escape the trade-offs between current reproductive effort and future survival or reproduction, i.e. enjoying both successful reproduction and high survival probability or future reproductive success (Aubry, Cam, Koons, Monnat, & Pavard, 2011; Cam, Link, Cooch, Monnat, & Danchin, 2002; Hamel, Côté, Gaillard, & Festa-Bianchet, 2009; Knape, Jonzén, Sköld, Kikkawa, & McCallum, 2011; Tavecchia et al., 2005; Weladji et al., 2008). As proposed by Van Noordwijk and De Jong (1986), such a positive co-variation can be explained if not all individuals are equal in terms of resource acquisition due to, for instance, individual differences in body mass (Festa-Bianchet & Jorgenson, 1998; Reznick, 1985) or social rank (McNamara & Houston, 1996). These differences can themselves result from genetic characteristics of individuals (Herfindal et al., 2014), environmental conditions encountered early in life (Lindström, 1999) or maternal effects (Hamel, Côté, & Festa-Bianchet, 2010). All these factors generate heterogeneity in individual quality (Wilson & Nussey, 2010), which could mask the fitness costs of reproduction that are theoretically expected at the population level, and need to be accounted for when studying the cost of reproduction.

In addition to the potentially confounding effects of individual quality, capacity to detect costs is markedly influenced by the variance in the fitness components under study as shown by Hamel, Gaillard, et al. (2010). Indeed, costs have a higher probability of being expressed in traits with higher variance, because traits with low variance have evolved to be buffered against any disruption. In ungulates characterized by a slow life history (Gaillard et al., 1989), evolutionary canalization has resulted in adult survival being particularly high and constant over time (Gaillard & Yoccoz, 2003). Conversely, fecundity and juvenile survival are usually highly variable, and responsible for the largest part of demographic variation (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toïgo, 2000). In these long-lived and iteroparous species, future reproduction and juvenile survival are thus expected to be the first affected by energy devoted to current reproduction, while adult survival should not be jeopardized.

Understanding and detection of reproductive costs would also gain from better accounting for the sequential and contrasted efforts devoted by a female throughout a reproductive event. For species inhabiting seasonal environments, energy requirements and the resources available to sustain them show great variation from gestation to weaning (Clutton-Brock, Albon, & Guinness, 1989; Gittleman & Thompson, 1988). The different stages of a reproductive occasion (gestation, early lactation and late lactation) should therefore not have the same impact on other fitness components. It follows that identifying the stage potentially leading to costs would increase understanding of which environmental variables could most affect reproductive success in a population. For instance, in capital breeders (Jönsson, 1997) inhabiting temperate environments, females rely on body reserves accumulated during the previous spring and summer to survive winter and to deal with the next gestation (Leader-Williams & Ricketts, 1982; Stephens, Boyd, McNamara, & Houston, 2009). In those species, the reproductive cost is thus expected to be maximum during lactation when a female has to produce milk for its young while building fat reserves that will affect both its survival and its next reproduction (Pelletier, Réale, Garant, Coltman, & Festa-Bianchet, 2007). Accordingly, females that only handle gestation (i.e. those that lose their young during the lactating period) should suffer lesser reproductive costs than females that wean young successfully (Clutton-Brock et al., 1989). Studying how the different stages of a reproductive occasion impact fitness components may help to better identify reproductive costs. This refinement is of great interest from an evolutionary perspective because it enables identification of critical reproductive periods of the life cycle during which selective pressure (Walther et al., 2002) would be expected to have the greatest impact.

A large number of papers have investigated reproductive costs in ungulates, with contrasted results (Tavecchia et al., 2005; Weladji et al., 2008). Hamel, Gaillard, et al. (2010) clearly recalled how results that do not include individual heterogeneity can lead to misleading patterns (e.g. a lack of observed cost when there actually is one). In addition, these studies did not necessarily focus on the costs resulting from the same reproductive effort (e.g. Tavecchia et al., 2005 focused on the cost of gestation, Toïgo et al., 2002 considered the costs of gestation and lactation, and Clutton-Brock et al., 1989 considered the cost of gestation and the cost of lactation), although these stages should lead to different costs, precluding proper comparison among studies. Difficulties with long-term empirical studies are manifold, as studying the costs of different components of reproductive effort requires teasing apart whether a female without an offspring has given birth and lost her offspring or has not given birth, and obtaining as detailed as possible observations of female-offspring in the field from shortly before birth until the offspring's first birthday. Such data are rare, but the use of recent advances in state-dependent capture–mark–recapture that allows for classification uncertainties has opened up new ways to analyse the long-term data of individually monitored animals (data that previously lacked detail), and therefore test for the existence of stage-dependent costs.

Here we performed a comprehensive study of the cost of current reproduction on survival and future reproduction in adult females of Pyrenean chamois *Rupicapra pyrenaica pyrenaica*, accounting for the different stages of the reproductive effort and for individual heterogeneity. We benefited from a population intensively monitored by capture–mark–recapture (re-sighting probability >0.98; Loison, Toïgo, Appolinaire, & Michallet, 2002; see also Results section), which offers the rare opportunity to decompose reproductive effort from gestation to weaning by distinguishing four reproductive states (Figure 1): non-reproducing females, reproducing females whose kid died during spring, died during summer or survived until weaning. We assessed the costs related to each of these states in terms of future reproductive success and survival by expanding a new methodological approach that integrates robust design in multi-event models (Souchay, Gauthier, & Pradel, 2014). Our work also presents the first application of this model to estimation of juvenile survival.

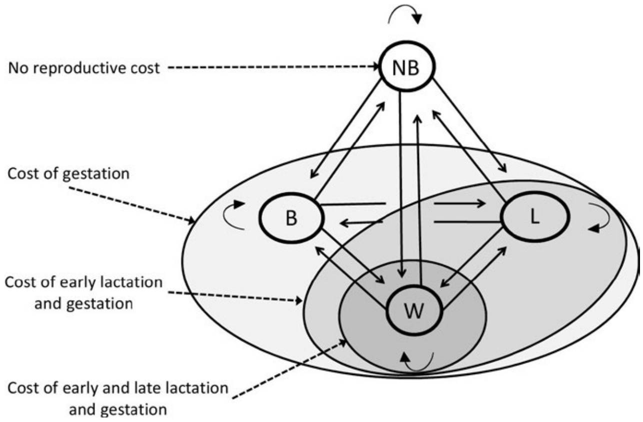

FIGURE 1 Diagram of transition between the four living states (non-breeding "NB", breeding and non-lactating "B", breeding and lactating "L" and breeding and weaning "W") with the associated reproductive cost

Focusing on the detection of individual heterogeneity and on the co-variation between fitness components, we tested three hypotheses. First, assuming the existence of trade-offs (Reznick, Nunney, & Tessier, 2000), we expected a negative relationship between previous reproductive effort and current fitness components, with increasing costs from non-reproducing females to females successfully weaning a kid (Figure 1). The costs of reproduction were expected to be higher for vital rates with a higher variance (i.e. for fecundity and juvenile survival, rather than for adult survival; Hamel, Gaillard, et al., 2010). Second, if individual heterogeneity constitutes the main factor structuring fitness components and their co-variation, we expected the existence of positive relationships between reproductive effort and subsequent reproductive success or survival. Third, if both trade-offs and individual heterogeneity shape variation between fitness components, we expected to detect costs of reproduction only once individual heterogeneity was accounted for.

2 | MATERIALS AND METHODS

2.1 | Study population and area

We studied the population of Pyrenean chamois of Bazès, located in the foothills of the French Western Pyrenees (43.00°N, 0.23°W). The study area encompasses 400 ha between 1,000 and 1,800 m a.s.l., and is mostly covered by alpine grass (*Festuca eskia*), rocks and forest (beech *Fagus sylvatica* and firs *Abies* sp.). The population originated from the release of 34 animals in the 1984 and 1985 winters, after the local disappearance of the species in the 1950s.

Since 1990, animals have been captured using traps, corrals, nets and leg-hold snares (all methods approved by the French Environment Ministry) during spring and late summer–autumn (for more details see Loison et al., 2002). For every individual, sex, age (estimated by counting horn annuli, Schröder & Von Elsner-Schak, 1985) and mass were recorded. This predator-free population experienced two contrasting demographic periods: a colonizing period with a strong population increase rate ($r = .25$; Loison et al., 2002) from the introduction to 2001, when population size peaked at *c*. 200 individuals, and a period of stabilization after 2002, with population size fluctuating between 90 and 130 individuals (Kourkgy, Garel, Appolinaire, Loison, & Toïgo, 2016). These two periods are delimited by an accidental lindane poisoning that occurred in spring 2001, and caused the death of at least 60 individuals (about one-third of the population; Gibert, Appolinaire, & SD65, 2004; Kourkgy et al., 2016).

2.2 | Reproductive data

In this population, the rut takes place between November and December, and the birth period between mid-April and mid-June, with a peak at the end of May (Kourkgy et al., 2016). The weaning process is characterized by a strong decrease in suckling success during the second month of kid life (Ruckstuhl & Ingold, 1994). This shift is accompanied by a concomitant increase in grass in the kid's diet. Lactation can thus be divided into two periods: early lactation (May–June), corresponding to the period during which the kid mostly relies on its mother, and late lactation (July–August) when the kid has a mixed (milk and grass) diet. Marked females were monitored from spring to autumn using binoculars and telescopes, during foot-surveys. The reproductive status of marked females was determined by the presence/absence of a kid at heel, on the basis of intensive field monitoring from early April to late autumn (during the study period, a female was seen on average 21 times in a given year).

2.3 | Study design

We used capture–mark–re-sighting models to estimate survival and reproductive rates, combining robust design (Pollock, 1982) and multi-event (Pradel, 2005) frameworks (Souchay et al., 2014). The principle of robust design is to consider primary and secondary occasions, where primary sessions consist in multiple secondary sampling occasions during which the system is assumed closed to migration, reproduction and death (Kendall, Nichols, & Hines, 1997). Closure is not assumed between primary sessions, creating a combination of open and closed designs that in our case enabled the estimation of survival on an annual basis for adult females, and on a monthly basis for kids.

2.4 | Multi-event models

Multi-event models are an extension of multistate models which account for uncertainty in state assessment when field observations (events) do not necessarily correspond to the underlying states (Choquet, Rouan, & Pradel, 2009). In our study, observations in the field, which correspond to the events of the multi-event model, are restricted to Not seen (0), Seen with a kid (1), or Seen without a kid (2), but we identified five different states by decomposing reproductive effort from gestation to weaning: death "D", non-breeding "NB", breeding and non-lactating "B", breeding and lactating "L", breeding and weaning "W". We focused on these four reproductive states because they are linked to different costs of reproduction (Figure 1). Non-breeding females experienced no reproductive cost. Breeding and non-lactating females produced a kid which died during spring and experienced only the cost of gestation. Breeding and lactating females produced and suckled a kid during spring but lost their kid during summer. These females experienced costs of gestation and early lactation. Finally, breeding and weaning females raised a kid to weaning and experienced the costs of gestation, early, and late lactation. All transitions between living states were permitted between primary occasions.

2.5 | Robust design

The robust design made it possible to link events with the states of interest by decomposing the period of reproduction into secondary occasions, nested within a primary occasion. Primary occasions corresponded to observations of females from April to December, and made it possible to estimate survival of adult females on an annual basis by assuming mortality to occur during winter and early spring (Jonas, Geiger, & Jenny, 2008). Secondary occasions were nested within these months, during which females are all assumed to survive, be able to breed and raise their kid.

2.6 | Secondary occasions

We defined three secondary occasions so that female reproductive success could be defined from gestation to weaning: April to June (AJ), July to August (JA) and September to December (SD). Observations conducted during AJ provide estimates for breeding probability, observations conducted during JA provide estimates for kid spring survival and observations conducted during SD provide estimates for kid summer survival (see section on "Reproductive data"). The reproductive state of a female was defined according to these three secondary occasions. A female seen without a kid on all three occasions was non-breeding "NB". A female seen with a kid only during the birth period AJ, was breeding and non-lactating "B". A female seen with a kid during the two occasions AJ and JA, but without a kid during the last occasion SD, was breeding and lactating, "L". Lastly, a female seen with a kid during these three occasions was breeding and weaning "W". From field observations, females can be not seen (secondary event: 0), seen with a kid (secondary event: 1) or seen without a kid (secondary event: 2). For each secondary occasion (AJ, JA or SD), we only kept a single observation (secondary event) with priority for females seen with a kid (1) over females seen without a kid (2). For example, for a female seen one time with a kid (1) and three times without a kid (2) during AJ, the event for this secondary occasion will be (1) (i.e. seen with a kid).

One assumption of multi-event models is to consider that the state of an individual can be imperfectly determined. We allowed detection to be imperfect during the birth period when a reproductive female could be classified without a kid because she had not yet given birth. Conversely, in the following periods (JA and SD) during which all kids were born, we assumed that the reproductive state of females was correctly determined (no misclassification error).

2.7 | Primary occasions

As recently developed by Souchay et al. (2014), we investigated the reproductive trade-offs among fitness components by integrating a robust sampling scheme within our multi-event capture–recapture framework. For this purpose, we grouped the events of the three secondary occasions in one annual event related to a primary occasion. For example, the annual event for a female observed during AJ with a kid (secondary event for AJ: 1), not observed during JA (0) and finally observed without a kid during SD (2) will be coded "102". This female produced a kid, but the kid died during spring or summer. Consequently, this female belongs to either of these two states: breeding and non-lactating "B" or breeding and lactating "L".

We specified as many primary events as there were possible combinations of secondary events and related them to biological states in the diagram of fates presented in Appendix S1.

2.8 | Estimated parameters

Multi-event models use three types of parameters: the initial state probability, the probabilities of transition between states and the probabilities of the events conditional to the underlying states. In our model, the transition probabilities correspond to adult female survival (S), breeding probability (BP), kid spring survival (SprS) and kid summer survival (SumS). Between two primary occasions, a female can survive or die with the respective probabilities S and (1-S). If a female survives, she can breed with a given probability (BP) or not, in which case the reproductive state of this female will be "NB". Then for females that breed, the kid can survive to spring (SprS) or not, in which case the female will be "B". Finally, the kid can survive to summer (SumS) for "W" females or die for "L" females. The events probabilities correspond to the probabilities of observing an individual with a kid or not during each of the three secondary occasions. The decomposed transition and event matrices are presented in Appendices S2 and S3 respectively.

2.9 | Hidden heterogeneity

We accounted for hidden individual heterogeneity in transition parameters (reproductive states and/or survival) by using finite mixture models with discrete classes of individuals as presented by Pledger, Pollock, and Norris (2003) or Pradel (2009). Capture–recapture mixture models are based on the assumption that individuals can be categorized into a finite number of heterogeneity classes (hidden states), i.e. the underlying distribution of heterogeneity is approximated by a histogram-like distribution. Multi-event models make it possible to account for such a discrete, hidden, individual heterogeneity structure in the transition parameters (Pradel, 2009). In this framework, the contribution of mixture models was to discriminate between groups of individuals that had different average values of parameters (survival or reproductive performance). Such models had already been used to study the effects of senescence on survival (Péron et al., 2010), of the quality of breeding sites on reproductive performance (Chevallier, Crochet, Vincent-Martin, Ravayrol, & Besnard, 2013) or of individual heterogeneity on survival or reproductive performance (Garnier, Gaillard, Gauthier, & Besnard, 2016; Péron et al., 2016). In our study, the hidden state of individuals corresponded to their quality ("good" or "poor") which was assumed to influence their survival and/or reproductive performance. To implement this heterogeneity, we duplicated the reproductive state to discriminate "good" (+) and "poor" (−) quality individuals. We obtained the nine following states: "NB+", "NB−", "B+", "B−", "L+", "L−", "W+", "W−" and "D". Although all transitions between reproductive states were allowed, none was allowed among quality groups, i.e. a good-quality individual remains of good quality for its entire life. We thus explicitly considered the individual heterogeneity as a fixed property: differences in performance among individuals were linked to some latent individual characteristics, and these differences were expressed in a constant (fixed) way over individuals' lifetimes (see also Bergeron, Baeta, Pelletier, Réale, & Garant, 2011; Cam et al., 2002; Péron et al., 2016). In all our models, heterogeneity was considered an additive effect of time and other covariates.

2.10 | CMR analysis

We controlled for the effects of density variation on reproductive performance by restricting the study period from 2002 to 2012 (see Kourkgy et al., 2016), when the population showed a demographic stabilization. For reproduction, three age classes are commonly used in ungulates: primiparous (2 or 3 years old for Pyrenean chamois), prime-age (4–12 years old) and senescent females (>12 years old; e.g. Ericsson, Wallin, Ball, & Broberg, 2001; Loison et al., 2002). We focused on prime-age females only because of small sample sizes in the other age classes (2 year olds, $n = 14$; 3 year olds, $n = 15$; and senescent, $n = 23$). To investigate costs of reproduction, we used the phenotypical correlation method (Reznick, 1985), and tested the effects of the reproductive effort in a given year on the performance the following year as is traditionally done in large herbivores (Clutton-Brock, Guinness, & Albon, 1983; Festa-Bianchet, Gaillard, & Jorgenson, 1998; Garnier et al., 2016; Moyes et al., 2006). The potential costs that can be linked to the different reproductive states are represented in Figure 1. The analysis was performed on 61 different females from 4 to 12 years old corresponding to 253 annual events.

We first assessed the goodness-of-fit of our multi-event model by pooling all "alive" events together, which simplified the model into a multistate model with only two states: alive or dead (see Souchay et al., 2014 for a similar approach). This procedure allowed us to test the goodness-of-fit of the Cormack–Jolly–Seber model (CJS: full-time variation on survival and capture probabilities) using U-CARE (Version 2.3.2; Choquet et al., 2009). We considered that any more complicated model will be well-fitted to the data if non-significant over dispersion was detected in the CJS model.

We performed our analysis using E-Surge (Version 1.9.0; Choquet et al., 2009). For the re-sighting probability, we estimated one parameter within each of the three secondary occasions, and did not test for time variation because of the constant intense field effort during the study period.

We conducted two distinct analyses to test the potential effect of confounding factors (time and heterogeneity) on the detection of reproductive costs. First, we investigated the costs of reproduction by testing the effect of the previous reproductive state W, L, B, NB without any other effect (individual heterogeneity or time). We used backward selection with a full model including additive effects of gestation, early lactation and late lactation on breeding probability (BP), adult female survival (S), kid spring survival (SprS) and kid summer survival (SumS). We first selected the best model for breeding probability (BP), then adult female survival (S), kid spring survival (SprS) and finally kid summer survival (SumS).

Secondly, we investigated costs of reproduction while including the effects of individual heterogeneity and time on the four parameters to control for yearly variation in population and environmental characteristics (Coulson, Milner-Gulland, & Clutton-Brock, 2000; Forchhammer, Clutton-Brock, Lindström, & Albon, 2001; Koons et al., 2012; Willisch et al., 2013). We followed a backward stepwise selection procedure from the most to the least complex models by removing one by one the least supported effects. Effect support was determined using AIC_c criteria (Akaike 1973) as recommended by Pradel (2009) for finite mixture models. An arbitrary threshold of 2 points was used (Anderson & Burnham, 2002). When a specific effect did not improve the AIC_c score above this threshold, it was removed. Among the final set of models with a difference of AIC_c <2, we discussed estimated relationships identified to be biologically relevant not only in terms of statistical significance but also in terms of effect size whether related or not to a large statistical uncertainty. We applied this selection procedure first on breeding probability (BP), then on adult female survival (S), kid spring survival (SprS) and finally on kid summer survival (SumS). The full model included additive effects of previous gestation, early lactation, late lactation, time and heterogeneity on adult survival and all reproductive components. We avoided convergence issues related to model complexity by constraining top models for step down selection as following:

- For selection on breeding probability: $BP_{\text{full model}}$, $S_{\text{full model}}$, $SprS_{\text{time}}$, $SumS_{\text{time}}$
- For selection on adult female survival: $BP_{\text{selected model}}$, $S_{\text{full model}}$, $SprS_{\text{time}}$, $SumS_{\text{time}}$
- For selection on kid spring survival: $BP_{\text{selected model}}$, $S_{\text{selected model}}$, $SprS_{\text{full model}}$, $SumS_{\text{time}}$
- For selection on kid summer survival: $BP_{\text{selected model}}$, $S_{\text{selected model}}$, $SprS_{\text{selected model}}$, $SumS_{\text{full model}}$.

For each of these four demographic parameters, we successively tested the cost of reproduction, time and individual heterogeneity effects.

3 | RESULTS

3.1 | Goodness-of-fit test

The overall goodness-of-fit test was not significant ($\chi^2 = 4.266$, *df* = 14, *p* = .99), and we detected neither transience ($\chi^2 = 3.833$, *df* = 8, *p* = .87) nor trap dependence ($\chi^2 = 0.32$, *df* = 4, *p* = .99).

3.2 | Encounter probabilities

The probability of observing a female was equal to 0.875 from April to June (the probability of not observing a female was estimated at 0.125 ± 0.02), to 0.80 ± 0.02 from July to August and to 0.87 ± 0.02 from September to December. The overall probability of observing a female without a kid during April–June while she was a breeder (i.e. classification error) was equal to 0.05 ± 0.02.

3.3 | Costs of reproduction without time and heterogeneity

We statistically detected no effect of previous reproductive effort on adult survival or reproductive performance (breeding probability and kid spring and summer survival) when not accounting for time and individual heterogeneity. Indeed, for each of these demographic parameters, the null model was among the models with the lowest AIC_c (Table 1). However, there were some biologically competing models with close AIC_c values (ΔAIC_c <1), supporting lactation effect for breeding probability (Table 1a) and breeding effect for adult survival (Table 1b). These models indicated a trend of lactating females having a lower breeding probability the next year and a trend of non-breeding females having lower probability of surviving to the next year (Table 2). No marked trend was detected on kid spring and summer survival (Tables 1c, d and 2).

Overall, adult survival was estimated at 0.91 ± 0.02 (*M* ± *SE*), breeding probability at 0.90 ± 0.03, kid spring survival at 0.52 ± 0.04 and kid summer survival at 0.84 ± 0.04.

3.4 | Costs of reproduction with time and heterogeneity

As a second step, we tested costs of reproduction while taking into account time and individual heterogeneity.

For breeding probability, the model with the lowest AIC_c included the effects of individual heterogeneity and previous early lactation, and all other models had much less support (ΔAIC_c >3; Table 3a). The selected model contrasted “poor” and “good” breeders with an overall probability of breeding each year respectively of 0.69 ± 0.10 and 0.95 ± 0.03, and highlighted a cost of previous lactation on breeding probability in both classes of individuals (Figure 2a; Appendix S4). Among “good” breeders, all females who did not incur the cost of lactation the previous year bred successfully, while the probability of breeding was 0.91 ± 0.04 for females who had lactated. Among “poor” breeders who lactated the previous year, none bred successfully. The group of “good” breeders represented 89 ± 4% of all females.

For female adult survival, three competing models had ΔAIC_c <0.36: the null model, the model with an effect of previous gestation, and the model with an effect of previous gestation and individual heterogeneity (Table 3b). We chose to keep the latter because of biological relevant differences in effect sizes related to individual heterogeneity and previous gestation (Appendix S4), and to be consistent with the model selected for breeding probability. All “poor” breeders survived until age 12 and had thus the highest survival rate (=1). Among “good” breeders, contrary to what would have been expected if costs were expressed, the females that did not breed the previous year had a lower survival rate (0.65 ± 0.14) than breeding ones (0.92 ± 0.02) (Figure 2b).

For kid spring survival, the model with the lowest AIC_c included the effects of time, individual heterogeneity and previous early lactation (Table 3c). Subsequent models were nested and included time effect only, or time effect and individual heterogeneity. We retained the model with the lowest AIC$_c$ to be in accordance with the model selected for breeding probability and because of the marked difference of effect sizes related to selected effects (Appendix S4). Kid spring survival varied markedly from year to year: from 0 ± 0 to 0.75 ± 0.14 (CV = 0.42). Kids born to "poor" breeders had a markedly lower spring survival rate (0.23 ± 0.14) compared to those born to "good" breeders (0.53 ± 0.12). Previous lactation incurred a cost on next kid spring survival: kids born to females who did not lactate the previous year had a spring survival of 0.70 ± 0.13, compared to 0.46 ± 0.12 for kids of mothers who had lactated a young the previous year (Figure 2c).

Finally, for kid summer survival, the model with the lowest AIC$_c$ was the null model (Table 3d). The second best model included an effect of previous gestation (ΔAIC$_c$ = 1.17), but this effect was not present in the next five models, and the effect size was low (Appendix S4), so we did not retain it. Kid summer survival was estimated at 0.84 ± 0.04 regardless of the quality group and of preceding reproductive success.

TABLE 1 Model selection testing for the effects of reproductive costs (Figure 1) without time and heterogeneity on (a) breeding probability (BP), (b) adult female survival (S), (c) kid spring survival (SprS) and (d) kid summer survival (SumS) during step 1. Np: number of parameters; ΔAIC$_c$, difference in AIC$_c$ between the tested model and the model with the lowest AIC$_c$, and AIC$_c$ weight (W$_i$) of the tested models are provided. The null model appears in bold

Model	NP	Deviance	AIC$_c$	ΔAIC$_c$	W$_i$
(a) Breeding probability (BP)					
Null	**20**	**1,385.94**	**1,429.28**	**0.00**	**0.22**
Early lact + Late lact	22	1,381.36	1,429.41	0.13	0.21
Early lact	21	1,383.99	1,429.67	0.39	0.18
Full	23	1,379.96	1,430.39	1.12	0.13
Gest + Early lact	22	1,382.97	1,431.02	1.74	0.09
Late lact	21	1,385.84	1,431.53	2.25	0.07
Gest	21	1,385.92	1,431.60	2.32	0.07
Gest + Late lact	22	1,385.77	1,433.81	4.54	0.02
(b) Adult survival (S)					
Gest	18	1,387.94	1,426.64	0.00	0.26
Null	**17**	**1,390.45**	**1,426.85**	**0.21**	**0.23**
Gest + Late lact	19	1,387.10	1,428.10	1.46	0.13
Gest + Early lact	19	1,387.76	1,428.76	2.12	0.09
Early lact	18	1,390.33	1,429.02	2.39	0.08
Late lact	18	1,390.43	1,429.12	2.48	0.08
Full	20	1,385.94	1,429.28	2.64	0.07
Early lact + Late lact	19	1,388.51	1,429.52	2.88	0.06
(c) Spring kid Survival (SprS)					
Null	**14**	**1,391.18**	**1,420.81**	**0.00**	**0.41**
Gest	15	1,390.96	1,422.83	2.03	0.15
Late lact	15	1,391.14	1,423.01	2.20	0.14
Early lact	15	1,391.17	1,423.03	2.23	0.13
Early lact + Late lact	16	1,390.75	1,424.88	4.07	0.05
Gest + Early lact	16	1,390.87	1,424.99	4.19	0.05
Gest + Late lact	16	1,390.96	1,425.09	4.28	0.05
Full	17	1,390.45	1,426.85	6.05	0.02
(d) Summer kid Survival (SumS)					
Null	**11**	**1,391.83**	**1,414.84**	**0.00**	**0.38**
Early lact	12	1,391.42	1,416.62	1.78	0.16
Gest	12	1,391.59	1,416.79	1.95	0.14
Late lact	12	1,391.69	1,416.89	2.05	0.14
Early lact + Late lact	13	1,391.26	1,418.66	3.82	0.06
Gest + Early lact	13	1,391.34	1,418.75	3.91	0.05
Gest + Late lact	13	1,391.54	1,418.94	4.10	0.05
Full	14	1,391.18	1,420.81	5.97	0.02

4 | DISCUSSION

Our main results showed that (1) in agreement with expectations for a long-lived iteroparous large herbivore, adult survival was high and constant (Gaillard & Yoccoz, 2003), while juvenile survival was much lower and variable (Gaillard et al., 1998, 2000), especially during the first 2 months of life; (2) significant individual heterogeneity structured the fitness components opposing good- and poor-quality individuals; (3) the effort devoted during early lactation, more than during gestation or late lactation, negatively impacted the next probability both of giving birth and raising the young (once born) during the stage of early lactation; (4) this cost of early lactation was unveiled only when temporal variation in juvenile survival and individual heterogeneity were taken into account. These results underline the fact that detecting reproductive costs is complex in long-lived mammals and can be impaired by neglecting environmental variability or individual quality (Hamel, Yoccoz, & Gaillard, 2014), or by focusing on the wrong reproductive event. Overall our study indicates that trade-offs, along with individual heterogeneity, shape the relationship between current investment in reproduction and future survival and reproductive success, and that the phase of early lactation was among the costliest.

By combining robust design with multi-event capture–recapture modelling, we estimated two components of kid survival that are reputed hard to estimate in free-ranging populations (Reed et al., 2015), and also revealed that the cost of reproduction appeared only when contrasting the different stages of reproductive effort (from gestation to weaning). With the exception of small intensively monitored populations (e.g. Bighorn in Ram Mountain: Festa-Bianchet & Jorgenson, 1998; Portier, Festa-Bianchet, Gaillard, Jorgenson, & Yoccoz, 1998; Red deer on Rum Island: Guinness, Albon, & Clutton-Brock, 1978; Soay sheep on the island of Soay: Clutton-Brock et al., 1996; Reindeer in Inari, Finland, Holand et al., 2003; Weladji et al., 2008) or experimental approaches, which are difficult to implement in ungulates (Gélin, Wilson, Coulson, & Festa-Bianchet, 2015; Tavecchia et al.,

State	S	BP	SprS	SumS
Non-breeding	0.81 ± 0.09	0.84 ± 0.10	0.50 ± 0.14	0.89 ± 0.14
Breeding and non-lactating	0.94 ± 0.03	0.96 ± 0.04	0.52 ± 0.07	0.87 ± 0.06
Breeding and lactating	1.00 ± 0.00	0.65 ± 0.14	0.46 ± 0.18	0.74 ± 0.22
Weaning	0.91 ± 0.03	0.89 ± 0.05	0.53 ± 0.06	0.82 ± 0.07

TABLE 2 Estimates for the model including effects of the previous reproductive states on survival (S), breeding probability (BP), kid spring survival (SprS) and kid summer survival (SumS). The mean estimates ± *SE* are provided

2005), teasing apart the different components of reproduction and juvenile survival remains problematic due to incomplete information or difficulties in determining reproductive status. The use of robust design and multi-event capture–recapture modelling could help overcome some inference limitations and make it possible to re-analyse datasets to better understand among which trait component trade-offs really occur (Pardo, Barbraud, & Weimerskirch, 2014).

The adult female survival rate was high, and within the range of survival rates usually found for chamois (Corlatti, Lebl, Filli, & Ruf, 2012; Loison, Festa-Bianchet, Gaillard, Jorgenson, & Jullien, 1999; Loison et al., 2002; Tettamanti, Grignolio, Filli, Apollonio, & Bize, 2015) and other ungulates (Gaillard et al., 2000; Toïgo et al., 2007). This parameter was constant over time, and did not suffer any cost from previous reproductive efforts. All these results are in agreement with the evolutionary canalization of adult survival in female ungulates (Gaillard & Yoccoz, 2003): all females maximize their survival, decreasing reproductive effort rather than jeopardizing survival (e.g. Festa-Bianchet & Jorgenson, 1998). However, we found a positive relationship (i.e. no cost) between previous reproductive success and survival among good breeders: females who did not reproduce had a lower probability of surviving. This can suggest that individuals that failed to conceive were in poorer condition than breeding females, and therefore had a lower survival probability (e.g. in red deer; Moyes, Morgan, et al., 2011). Juvenile survival during the first months of life showed strong temporal variability as expected (Feder, Martin, Festa-Bianchet, Bérubé, & Jorgenson, 2008; Festa-Bianchet et al., 1998; Simard, Huot, de Bellefeuille, & Côté, 2014), and decreased when the mother had lactated a young the previous year. Juvenile summer survival, however, was constant over time, relatively high (0.84) and affected neither by the mother's previous reproductive success nor by her quality, suggesting that environmental conditions experienced during early life, rather than mothers' attributes, shaped this parameter (Adams, 2005; Andersen & Linnell, 1997; Forchhammer et al., 2001).

Reproductive costs came out as a negative relationship between early lactation, when the kid mainly relies on milk production, and the female probability of giving birth at the next occasion and raising her kid during the next spring. This result is consistent with the fact that lactation is the most energy-demanding component of maternal care in mammals (Gittleman & Thompson, 1988). In addition, in capital breeders, such as Pyrenean chamois, inhabiting highly seasonal environments, like mountain or northern environments, early lactation takes place at a time when females are depleted after winter and have to build reserves for their own survival and the next reproductive attempt. All these factors contribute to making milk production costly for the mother. As such, environmental conditions during spring, which determine forage quality and quantity during early lactation, have repeatedly been proven instrumental for mountain ungulates' demographic parameters (Loison, Jullien, & Menaut, 1999; Pettorelli, Pelletier, Von Hardenberg, Festa-Bianchet, & Côté, 2007). As compared to lactation, giving birth to a kid that does not survive the neonatal period (i.e. dealing with gestation only) did not lead to any cost on the next reproductive success, which is consistent with the fact that gestation is much less energy-demanding than lactation in mammals (Oftedal, 1985). Similarly, lactating until weaning did not incur supplemental cost compared to early lactation only, suggesting that lactation in summer, when food resources for the mother are abundant and the kid has a mixed diet, is an easier task.

Studies investigating trade-offs provided mixed results, with some finding the expected negative correlations between fitness components (Clutton-Brock et al., 1996; Moyes et al., 2006; Tavecchia et al., 2005; Testa, 2004), while others found positive correlations that the authors generally explained by individual heterogeneity in quality, e.g. in reindeer (Weladji et al., 2006, 2008); bighorn sheep (Hamel, Côté, et al., 2009) or female fur seals (Beauplet et al., 2006). The phenotypical correlation method (Reznick, 1985) used alone does not allow us to test these two mechanisms simultaneously, but only what process overrides the other (Weladji et al., 2008) without information about the magnitude of each of the mechanisms. Studies with positive correlation hypothesize that trade-offs are masked by individual heterogeneity, and conversely for studies with negative correlation (Van Noordwijk & De Jong, 1986). In the same way, a study with no correlations concludes either that heterogeneity compensates for reproductive costs, or that the two mechanisms are not in play. However, both mechanisms act simultaneously (Wilson & Nussey, 2010) and should therefore be tested as such. Our methodological approach with discrete groups to take heterogeneity into account (Pledger et al., 2003) has the advantage of allowing us to test simultaneously for heterogeneity and reproduction costs without the measurable trait of quality. Once confounding factors (individual heterogeneity and temporal variation in neonatal survival) were taken into account, reproductive cost could be detected in both quality groups: good and poor breeders. This suggests that in studies where individual heterogeneity was not taken into account, trade-offs may have occurred at the individual level without being detected at the population level. This presence of two different types of females supports the individual quality hypothesis (Wilson & Nussey, 2010) which states that in a population some individuals consistently out-compete others.

Here, low-quality females ($n = 7$) represented only a very small part of the monitored females (11%) suggesting that successful females with high breeding probability are the rule in this population.

TABLE 3 Model selection testing for the effects of reproductive costs (Figure 1), time and heterogeneity on (a) breeding probability (BP), (b) adult female survival (S), (c) kid spring survival (SprS) and (d) kid summer survival (SumS) during step 2. Np: number of parameters; ΔAIC_c, difference in AIC_c between the tested model and the model with the lowest AIC_c, and AIC_c weight (W_i) of the tested models are provided. The selected model appears in bold

Model	Effect on BP	NP	Deviance	AIC_c	ΔAIC_c	W_i
(a) Breeding probability (BP)						
BP_9	**Early Lact + H**	**45**	**1,320.75**	**1,428.99**	**0.00**	**0.82**
BP_10	H	44	1,326.91	1,432.28	3.29	0.16
BP_12	Null	43	1,334.34	1,436.86	7.87	0.02
BP_11	Early Lact	44	1,332.44	1,437.81	8.82	0.01
BP_6	time + Early Lact + H	54	1,312.15	1,447.40	18.41	0.00
BP_8	time + H	53	1,316.91	1,449.05	20.05	0.00
BP_2	time + Gest + Early Lact + H	55	1,312.09	1,450.48	21.49	0.00
BP_4	time + Early Lact + Late Lact + H	55	1,312.31	1,450.70	21.70	0.00
BP_5	time + Gest + H	54	1,315.89	1,451.14	22.14	0.00
BP_7	time + Late Lact + H	54	1,316.09	1,451.34	22.35	0.00
BP_1	time + Gest + Early Lact + Late Lact + H	56	1,310.61	1,452.17	23.17	0.00
BP_3	time + Gest + Late Lact + H	55	1,315.18	1,453.57	24.58	0.00
BP_13	time + Early Lact	53	1,327.89	1,460.03	31.03	0.00
(b) Adult survival (S)						
S_11	Gest	32	1,335.95	1,408.75	0.00	0.31
S_13	Null	31	1,338.52	1,408.76	0.01	0.31
S_9	**Gest + H**	**33**	**1,333.72**	**1,409.11**	**0.36**	**0.26**
S_12	H	32	1,337.94	1,410.74	1.99	0.12
S_10	time + Gest	41	1,325.14	1,422.05	13.30	0.00
S_5	time + Gest + H	42	1,322.62	1,422.33	13.58	0.00
S_2	time + Gest + Early Lact + H	43	1,322.60	1,425.12	16.37	0.00
S_8	time + H	41	1,328.35	1,425.26	16.51	0.00
S_6	time + Early Lact + H	42	1,326.61	1,426.31	17.56	0.00
S_3	time + Gest + Late Lact + H	44	1,322.36	1,427.73	18.98	0.00
S_1	time + Gest + Early Lact + Late Lact + H	45	1,320.75	1,428.99	20.24	0.00
S_4	time + Early Lact + Late Lact + H	44	1,324.72	1,430.09	21.34	0.00
S_7	time + Late Lact + H	43	1,327.95	1,430.48	21.73	0.00
(c) Spring kid survival (SprS)						
SprS_6	**time + Early Lact + H**	**35**	**1,327.92**	**1,408.55**	**0.00**	**0.32**
SprS_13	time	33	1,333.72	1,409.11	0.56	0.24
SprS_8	time + H	34	1,332.22	1,410.22	1.67	0.14
SprS_10	time + Early Lact	34	1,332.97	1,410.97	2.42	0.10
SprS_2	time + Gest + Early Lact+ H	36	1,327.86	1,411.15	2.60	0.09
SprS_5	time + Gest + H	35	1,331.75	1,412.39	3.84	0.05
SprS_8	time + Late Lact + H	36	1,330.08	1,413.37	4.82	0.03
SprS_4	time + Early Lact + Late Lact + H	37	1,327.73	1,413.70	5.15	0.02
SprS_3	time + Gest + Late Lact + H	37	1,329.93	1,415.89	7.34	0.01
SprS_1	time + Gest + Early Lact + Late Lact + H	38	1,327.67	1,416.34	7.79	0.01
SprS_14	Null	24	1,364.99	1,417.82	9.28	0.00
SprS_11	H	25	1,364.62	1,419.89	11.34	0.00
SprS_12	Early Lact	25	1,364.97	1,420.24	11.69	0.00
SprS_9	Early Lact + H	26	1,364.19	1,421.89	13.35	0.00

(Continues)

TABLE 3 (Continued)

Model	Effect on BP	NP	Deviance	AIC$_c$	ΔAIC$_c$	W$_i$
(d) Summer kid survival (SumS)						
SumS_14	**Null**	**27**	**1,335.73**	**1,395.90**	**0.00**	**0.37**
SumS_11	Gest	28	1,334.41	1,397.07	1.17	0.21
SumS_12	Early Lact	28	1,334.87	1,397.52	1.62	0.17
SumS_13	Late Lact	28	1,335.26	1,397.92	2.02	0.14
SumS_9	H	28	1,335.54	1,398.19	2.29	0.12
SumS_10	time	35	1,327.92	1,408.55	12.65	0.00
SumS_8	time + H	36	1,327.87	1,411.16	15.26	0.00
SumS_5	time + Gest + H	37	1,327.05	1,413.01	17.11	0.00
SumS_6	time + Early Lact + H	37	1,327.59	1,413.56	17.66	0.00
SumS_7	time + Late Lact + H	37	1,327.87	1,413.84	17.94	0.00
SumS_4	time + Early Lact + Late Lact + H	38	1,326.83	1,415.49	19.59	0.00
SumS_2	time + Gest + Early Lact + H	38	1,326.94	1,415.61	19.71	0.00
SumS_3	time + Gest + Late Lact + H	38	1,327.01	1,415.68	19.78	0.00
SumS_1	time + Gest + Early Lact + Late Lact + H	39	1,326.19	1,417.58	21.68	0.00

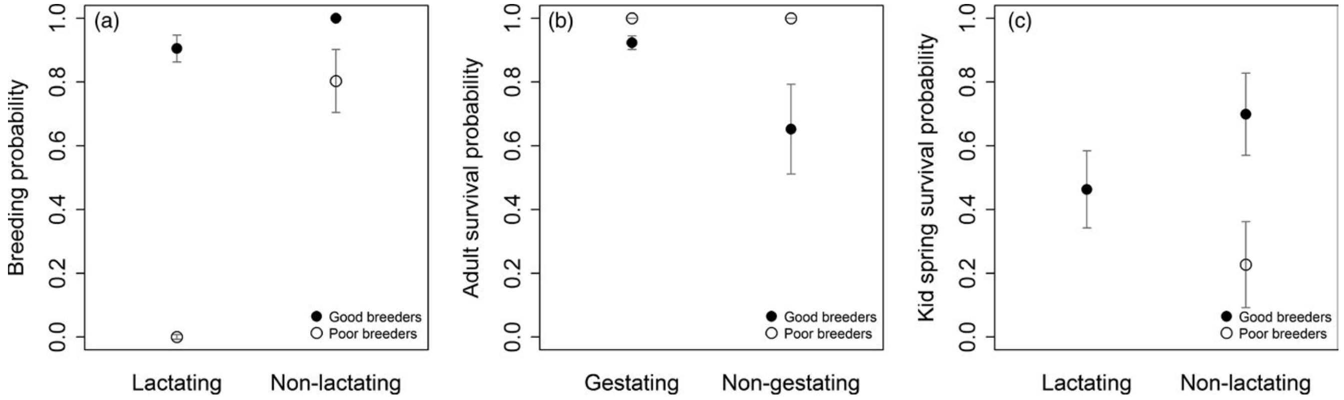

FIGURE 2 (a) Breeding probability, (b) adult survival and (c) spring kid survival of Pyrenean chamois depending on previous reproductive effort (non-gestating vs. gestating females for adult survival and non-lactating vs. lactating females for breeding probability and spring kid survival) and quality groups (good vs. poor breeders; 89% of females belong to the “good” quality group) according to the selected models. For spring kid survival, estimate is given for a median year (year 2010). The vertical line corresponds to the standard error

In large herbivores, individual quality is often associated with phenotypic features like body weight (e.g. Clutton-Brock, Albon, & Guinness, 1988; Festa-Bianchet et al., 1998), horn length (e.g. Bonenfant, Pelletier, Garel, & Bergeron, 2009; Toïgo, Gaillard, & Loison, 2013) or social rank (e.g. Côté & Festa-Bianchet, 2001; Von Holst et al., 2002). Looking more closely, we did not find any differences in terms of body weight, horn length or cohort between the poor- and the good-quality females. This suggests that morphological characteristics may not always be helpful in distinguishing quality groups, though they have previously been used in similar studies (e.g. in bighorn sheep, mountain goat and roe deer, Hamel, Gaillard, Festa-Bianchet, & Côte, 2009). Moreover, in the presence of such extremely low-performing individuals, even in low proportion, assuming normal distribution may lead to poor estimates at the population level, as reported in Alpine ibex (Garnier et al., 2016). Our results confirm the utility of mixed models in ecology to account for and measure variability between individuals within a population (Hamel, Yoccoz, & Gaillard, 2017).

Despite the high re-sighting probability ($p > .85$ within 2-month periods), our study was based on 61 females. This limited sample size might affect the detection of some relationships related to gestation, with 23 events coded “non-breeder”, and late lactation, with 21 events coded “lost the kid during summer”. In addition, sample sizes decrease throughout the reproductive stages. This may explain why, although the reproductive cost on summer kid survival had a similar effect size as when tested on breeding probability, the related uncertainty of kid survival in summer prevents the appearance of any statistical effect. For these reasons, we cannot firmly conclude that only the cost of lactating was in play in our population.

Our results support the fact that females of long-lived and iteroparous species, such as ungulates, maximize adult survival at the expense of reproduction to maximize the occasions of reproduction and consequently fitness (Festa-Bianchet & Jorgenson, 1998; Gaillard & Yoccoz, 2003). Pyrenean chamois females bear a cost of lactation on future reproduction, but no cost in terms of survival. Such cost became apparent only when taking into account individual heterogeneity, temporal variation in juvenile survival, and the different states of maternal effort: gestation, early lactation and late lactation. Our study suggests that individual quality and trade-offs are not mutually exclusive hypotheses (Wilson & Nussey, 2010), and should be systematically assessed simultaneously in studies on the cost of reproduction. Our work also stressed the central role of environmental conditions encountered in spring for juvenile survival and future reproduction (Garel et al., 2011; Portier et al., 1998; Simard, Coulson, Gingras, & Côté, 2010; Tveraa, Stien, Bårdsen, & Fauchald, 2013). In the context of global climate change, this finding is important to our understanding of the long-term fitness consequences of changes in spring vegetation phenology, particularly as females in this population have shown low adaptive potential to such changes (Kourkgy et al., 2016; see also Moyes, Nussey, et al., 2011 for red deer and Plard et al., 2014 for roe deer).

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AUTHORS' CONTRIBUTIONS

Q.R., C.T., A.L. and M.G. conceived the ideas; Q.R. designed methodology and conducted the analyses; J.A. collected the data; and Q.R., C.T., A.L. and M.G. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used within this manuscript are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.217v8 (Richard, Toïgo, Appolinaire, Loison, & Garel, 2017).

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