

Heterogeneity in individual quality overrides costs of reproduction in female reindeer

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Received: 10 August 2007 / Accepted: 19 December 2007 / Published online: 2 February 2008
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Abstract Reproductive allocation at one age is predicted to reduce the probability of surviving to the next year or to lead to a decrease in future reproduction. This prediction assumes that reproduction involves fitness costs. However, few empirical studies have assessed whether such costs may vary with the age at primiparity or might be overridden by heterogeneities in individual quality. We used data from 35 years' monitoring of individually marked semi-domestic reindeer females to investigate fitness costs of reproduction. Using multi-state statistical models, we compared age-specific survival and reproduction among four reproductive states (never

reproduced, experienced non-breeders, reproduced but did not wean offspring, and reproduced and weaned offspring) and among contrasted age at primiparity. We assessed whether reproductive costs occurred, resulting in a trade-off between current reproduction and future reproduction or survival, and whether early maturation was costly or rather reflected differences in individual quality of survival and reproduction capabilities. We did not find any evidence for fitness costs of reproduction in female reindeer. We found no cost of gestation and lactation in terms of future reproduction and survival. Conversely, successful breeders had higher survival and subsequent reproductive success than experienced non-breeders and unsuccessful breeders, independently of the age at primiparity. Moreover, it was beneficial to mature earlier, especially for females that successfully weaned their first offspring. Successful females at early primiparity remained successful throughout their life, clearly supporting the existence of marked among-female differences in quality. The weaning success peaked for multiparous females and was lower for first-time breeders, indicating a positive effect of experience on reproductive performance. Our findings emphasize an overwhelming importance of individual quality and experience to account for observed variation in survival and reproductive patterns of female reindeer that override trade-offs between current reproduction and future performance, at least in the absence of harsh winters.

Communicated by Hannu Ylonen.

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Keywords Fitness · Life history tactics · *Rangifer tarandus* · Reproductive cost · Reproduction

Introduction

Life history theory assumes that evolution is constrained by the presence of trade-offs among fitness components

(Roff 1992; Stearns 1992). One of the most studied trade-off is that between reproduction and survival, which predicts that reproductive allocation at a given age should reduce the probability of surviving to and/or reproducing at the next age (Williams 1966). This trade-off relies on the assumption that reproduction is “costly” (Reznick 1985), and the measurement of costs of reproduction has therefore become central in the study of life history strategies. However, the measurement of costs of reproduction (and hence trade-offs) can be difficult for several reasons (Partridge and Harvey 1985, 1988; Pease and Bull 1988; Stearns 1989; Bailey 1992).

First, the concept of trade-off is rooted in the principle of energy allocation (Cody 1966; Williams 1966) stating that, for a given amount of energy available, the energy allocated to one fitness component will lead to a decrease in the energy that can be allocated to another fitness component. Negative relationship between competing traits is thus expected to occur at the population level, but only when both the amount of energy available and the acquisition and handling capabilities of individuals are constant. However, the amount of energy available is rarely constant (except in experimental settings), so that fitness components can covary positively because some individuals have access to more resources and are able to allocate more to both reproduction and survival than others individuals (Clutton-Brock 1991). Such positive co-variations among fitness components have been commonly reported, and demonstrate that variation in energy acquisition can override any trade-off (e.g. van Noordwijk and de Jong 1986; Bize et al. 2002; Cam et al. 2002).

Second, subtle differences in estimating reproductive costs can depend upon how and when reproductive success is measured. In mammals the costs of lactation are assumed to be greater than those of gestation (Oftedal 1985; Sadleir 1987; Clutton-Brock et al. 1989). However, the relative costs of lactation may vary because of a difference in the timing of birth, in the length of the lactation period, or in individual quality (sensu McNamara and Houston 1996).

Lastly, a trade-off may involve not only reproduction and survival, but also growth in still growing individuals. The age at primiparity is therefore a critical life history trait, as selection pressure and trade-offs are expected to change markedly with maturation (Skogland 1989; Stearns 1992). Depending on the size reached at primiparity, the energy previously allocated to growth may be partly (for still-growing individuals) or totally (for fully grown individuals) allocated to the production of offspring from the age at primiparity onwards (Williams 1966). Factors determining the females’ decision to mature earlier in life are not well-understood, but empirical studies on most vertebrates have shown that good condition, large size, and good environmental conditions all favour early maturation. The bal-

ance between costs and benefits of an early or late primiparity varies among species, and according to environmental conditions (e.g. Reiter and Le Boeuf 1991; Festa-Bianchet et al. 1995). The consequences of maturing early or late can therefore have long-lasting consequences for individual fitness.

Within this setting, we can draw two extreme scenarios along the continuum of co-variations between current reproduction and future reproduction or survival. In the “cost-only” scenario, we expect to find a negative co-variation between early reproduction and both future reproduction and survival, so that females weaning a calf should have lower subsequent performance than unsuccessful females. In the “quality-only” scenario, we expect early reproduction to be a reliable indicator of good individual quality and, therefore, we expect early reproduction to be associated with high performance during a lifetime so that females weaning a calf should be more likely to wean a calf in the next year than unsuccessful females.

Based on a long-term monitoring (35 years/cohorts) of individually marked semi-domestic reindeer females, we used multi-state capture–mark–recapture (MCMR) statistical models (e.g. Nichols and Kendall 1995) to evaluate: (1) the differential costs of gestation and lactation, and (2) the costs/benefits of early maturation, as well as (3) their interaction. We assessed the costs of reproduction by comparing age-specific survival and reproductive probabilities of breeding and non-breeding individuals among contrasted age at primiparity. We were able to do that because the calving success (i.e., the probability of producing an offspring) as well as the weaning success (i.e., the probability of weaning the offspring produced) of all females was measured every year. Under the cost-only scenario, we expected females weaning the calf they produced to bear higher costs of reproduction than unsuccessful females (Clutton-Brock et al. 1983). Under the quality-only scenario, we expected females maturing later to be of below average quality (Neuhaus et al. 2004; Descamps et al. 2006) and, thereby, to have lower performance than early breeders.

Materials and methods

Study area and reindeer data

The data are from the Kaamanen Reindeer Research station in Inari, Finland (69°N, 27°E). Reindeer were free-ranging in several large-scale enclosures (encompassing about 40 km²) most of the year, excluding the calving (Eloranta and Nieminen 1986) period when they were kept in a more confined calving paddock (about 50 ha). The animals received supplemental feed only during winter (Holand

et al. 2003). The daily rations varied with snow and weather conditions from 250 to 1,200 g (2.35–11.7 MJ) concentrate per adult and day, averaging 600 g concentrate and 250 g hay per adult per day (V. Tervonen, personal communication), and accounted for about half of the estimated daily winter-energy intake (Holand et al. 2004). The herd was established in the late 1960s with about 20 males and 60 females. Since then, there has been a systematic monitoring of several aspects of their biology (e.g. life history, physiology and behaviour). The data collection procedures have been presented in details elsewhere (Eloranta and Nieminen 1986).

Newborn calves were caught by hand after the mother has licked them dry, weighed to the nearest 0.1 kg, ear marked with numbered ear-tags and sexed. The birth date of the newborns and the age and mass of their mother were also recorded. The calving area was examined daily and carcasses found were collected and examined. In this way, both the extent and cause of calf mortality were recorded (Eloranta and Nieminen 1986). Additionally, individuals were weighed in spring prior to calving and in autumn during slaughtering (mostly calves). This allowed us to have information about growth (or mass loss) for most animals, as well as their calving success and survival (neonatal, pre-weaning and adult). Removal of individuals was not based on any special selection scheme. Indeed, irrespective of their quality, a certain number of individuals have to be removed by the manager, although there may be a tendency to slaughter those in poor condition. Because the animals were gathered systematically every year both in early summer (during calf marking) and in autumn (for weighing and to determine calf survival), and all individuals were observed, capture/resighting probabilities were equal to 1. During these round-ups, missing individuals were identified and the reason for their absence assessed (usually mortality), and some of the remaining were slaughtered.

Statistical analyses

We used MCMR modelling to estimate survival and the probability of reproducing depending on age at primiparity and the reproductive states (e.g. calving success, weaning success). Although the capture/resighting probabilities were equal to 1 in our data set, we used the framework of MCMR models, which is a convenient way to deal with multinomial distributions. It allowed us to estimate state-dependent survival, state-dependent transition probabilities, and state-dependent recapture probabilities (Tavecchia et al. 2005). The transition probabilities refer to the probabilities of changing from one state to another one.

Females were classified into four possible reproductive states every year (Fig. 1), based on whether the female never reproduced (state N), failed to reproduce after having repro-

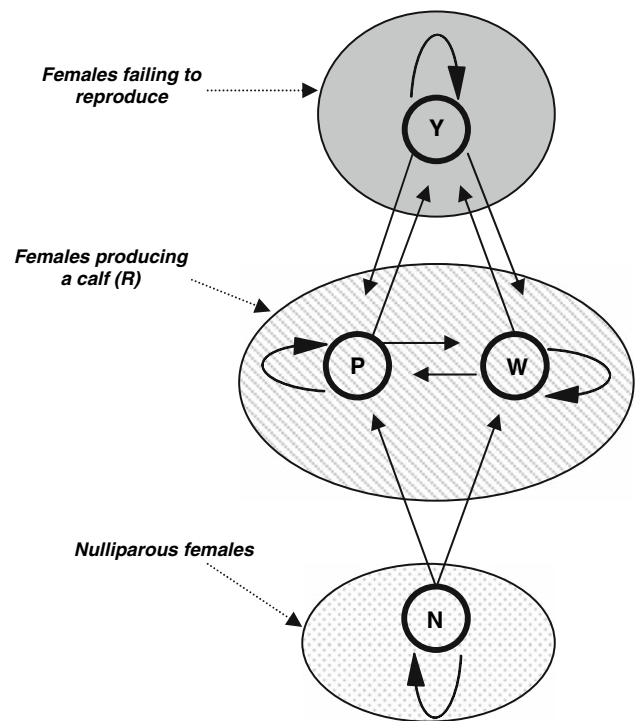


Fig. 1 Diagram explaining the transitions between the four states defining whether a female is nulliparous (N), produced a calf but lost it before weaning (P), produced a calf and weaned it (W), or failed to reproduce while it had reproduced at least once before (Y). Shaded areas group states into three simplified ones: nulliparous females, females producing a calf (R), and females failing to reproduce

duced at least once in the past (state Y), produced a calf that did not survive to weaning (state P), or produced a calf that survived until weaning (state W). The survival probabilities were denoted $S(i)_{age}$, where i designates the state (N, Y, P or W) in year t and the subscript the age class. Transition probabilities were denoted $\Psi(i, j)$, where i is the state in year t , j the state in year $t + 1$. The probability of weaning a calf given that a calf was produced was not estimated directly by the models, but could be deduced from the transition probabilities. For a state i during year t , the probability of weaning a calf during year $t + 1$ given that a calf was produced was denoted $P(WIR)^i$, and calculated as $P(WIR)^i = \Psi(i, W) / [1 - \Psi(i, Y)] = \Psi(i, W) / [\Psi(i, P) + \Psi(i, W)]$.

Analysing differential costs of gestation and lactation

To test for a differential cost of gestation and lactation, we restricted our analyses to females that reproduced (R). We thus compared $S(i)$, the probability of failing to reproduce [$\Psi(i, Y)$], or the probability of weaning successfully a calf [$\Psi(i, W)$], in year $t + 1$ of females that reproduced but failed to wean their offspring (P) and females that successfully weaned their calf (W) in year t . We expected females that weaned (i.e. that experienced both gestation and

lactation) to bear higher costs than females that produced an offspring but failed to wean it (i.e. that only experienced gestation). Only 35% of the preweaning calf mortality occurred around the calving period (Eloranta and Nieminen 1986).

Survival and transition probabilities

We considered variability of survival and transition probabilities for the four states and three age classes (see below). States P and W correspond to females that at least gave birth to a calf in a given year, and were grouped. For R females (those that at least produced a calf in a given year), the probability of reproducing is equal to being in states P or W [$P(R) = P(P) + P(W) = 1 - P(Y)$]. The conditional probability of weaning a calf given that a calf was produced in a given year was estimated as $P(W|R) = P(W)/P(R)$. For any non-nulliparous female in year t , there are three possible states for year $t + 1$ (Fig. 1) given that she survives, she may: (1) fail to reproduce, (2) reproduce without weaning her calf, (3) reproduce and wean her calf. The sum of the three transition probabilities is therefore equal to 1. We could therefore simplify our four states into three states: nulliparous females (N), females that reproduced (R), and experienced females that failed to reproduce (Y).

Because we wanted to compare the survival and transition probabilities of females with different ages at maturity, we further classified every female into three groups: females having reproduced for the first time at 2 years (primi 2), 3 years (primi 3) and 4 years of age (primi 4), respectively. We did not include in the analysis: (1) females that never reproduced because they never faced potential reproductive costs, and (2) females having reproduced for the first time at 1 year of age ($n = 6$) or later than 4 years of age ($n = 12$), because they were too few.

The age of first reproduction, the entire reproduction histories, as well as the exact age of all females were known. Age was therefore included in the models. Because multi-state models rapidly increase in number of parameters to be estimated with the number of states and age classes (Choquet et al. 2005a), we reduced the number of age classes to a biologically meaningful minimum. Variation of survival with age has now been well described from long-term data in ungulates (Loison et al. 1999; Gaillard et al. 2000, 2003), whereby prime-age females usually enjoy a high and stable survival rate, followed by a senescent stage with a lower and more variable survival rate. The age at which senescence begins depends on the species. For reindeer, we used 12 years as a cut-off point for this population, based on preliminary analyses (Weladji et al., unpublished data). Females under 12 years of age were designated as “prime-age females” and those 12 years old and above as “old females”. We assessed the age or experience effect by

comparing survival and transition probabilities of prime-aged females with those of first (primiparous) and second-breeding females.

We first performed a goodness-of-fit (GOF) test to check whether the full age-dependent model was fitted to our data. We used the Pradel et al. (2005) procedure implemented in U-CARE (Choquet et al. 2005b). As we only considered females that survived until their first breeding (i.e., no earlier than 2 years), the yearling survival was equal to 1. Note that for females primiparous at 3 years of age the survival between 2 and 3 years was also 1, as well as the survival from 3 to 4 years for females primiparous at 4 years of age. We performed the GOF test using the memory component of GOF tests (where before, where after; Pradel et al. 2005), other components (such as comparing fate of animals caught or not caught but known to be alive) being irrelevant in our case (capture probability of 1). All the other analyses were performed using MSURGE (Choquet et al. 2005a). We based our model selection on the use of the Akaike’s information criterion (AIC) as recommended by Burnham and Anderson (2002). The model with the lowest AIC was retained as the best model. When two competing models had AIC differing by less than 2, we retained the most parsimonious model. Only a priori models with biological meaning were considered (as recommended by Burnham and Anderson 2002), because of the very large number of all possible models. Parameter estimates are given with \pm SE.

Results

The fully time-dependent model provided a satisfactory fit to the data (primi-2, $\chi^2 = 43.3$, $df = 60$; primi-3, $\chi^2 = 16.2$, $df = 46$; primi-4, $\chi^2 = 1.64$, $df = 13$; all $P > 0.95$). The most general model (64 parameters and an AIC of 5,059.31) included different survival and transition probabilities among females with different ages at primiparity and reproductive status (see Tables 1, 2 for parameter estimates). The model selection (see Table 1) led us to retain a more parsimonious model (35 parameters with an AIC of 5,043.67, Tables 2, 3). The best model indicated a strong quality effect both in survival and reproduction. Female performance markedly differed according to both their age at primiparity and their previous reproductive status.

Survival patterns

The selected model clearly indicated interactive effects between the age at primiparity and subsequent breeding. Successful females (status W) in a given year exhibited a high survival rate independent of their age at maturity (Table 2; Fig. 2a). Conversely, multiparous females that failed to reproduce (status Y) in a given year showed a much

Table 1 Assessment of different biological hypotheses about variation in survival and reproduction patterns

	ΔAIC^a	Outcome ^b
Survival patterns		
Effect of age at primiparity on the survival of primiparous females	11.9	Supported
Effect of age at primiparity on the survival of multiparous females	12.6	Supported
Same survival for females that reproduced for the first time at 2 and 3 years of age	1.7	Supported
Reproduction patterns (transitions)		
Effect of age at primiparity on reproductive success of primiparous females	3.0	Not supported
Same reproductive success at primiparity for females that reproduced for the first time at 2 and 3 years of age	7.6	Supported
Effect of age at primiparity on reproductive success at second reproduction for females that lost their calf	4.69	Not supported
Effect of age at primiparity on reproductive success at second reproduction for females that weaned their calf	1.31	Not supported
Effect of reproductive success at primiparity on reproductive success at second reproduction	2.91	Not supported
Effect of age at primiparity on the reproductive success of multiparous females that weaned their calf the previous year	4.83	Not supported

^a The difference in Akaike’s information criterion (AIC) between two competing models has been used to select the best model

^b The outcome of the comparison

Table 2 Survival rates (*S*) (\pm SE) of females depending on their age at primiparity [2 years of age (*Primi 2*), 3 years of age (*Primi 3*), 4 years of age (*Primi 4*)], reproductive status during year *t* [yield (*Y*), calf produced and lost before weaning (*P*), calf weaned (*W*)], and the reproductive experience (primiparous vs. multiparous status)

	General model			Simplest acceptable model		
	Primi 2	Primi 3	Primi 4	Primi 2	Primi 3	Primi 4
(a) Following first reproduction						
S(P)	0.95 \pm 0.02	0.84 \pm 0.05	0.53 \pm 0.11	0.91 \pm 0.03		0.53 \pm 0.11
S(W)	0.95 \pm 0.02	0.97 \pm 0.02	0.92 \pm 0.05	0.95 \pm 0.01		
(b) As a prime-age multiparous						
S(Y)	0.69 \pm 0.04	0.66 \pm 0.05	0.45 \pm 0.12	0.68 \pm 0.03		0.44 \pm 0.12
S(P)	0.83 \pm 0.03	0.79 \pm 0.05	0.55 \pm 0.11	0.82 \pm 0.02		0.55 \pm 0.11
S(W)	0.94 \pm 0.01	0.98 \pm 0.01	0.92 \pm 0.03	0.95 \pm 0.01		

lower survivorship, especially for females with late age at primiparity, i.e. 4 years of age (Table 2; Fig. 2a). Multiparous females that lost their offspring (status P) in a given year showed a similar survival pattern with intermediate values. Such results strongly support the “quality-only” scenario (Table 2; Fig. 2a). The survival of unsuccessful first breeders that reproduced early was only slightly lower than the highest survival reported for females that weaned successfully. In contrast, the survival of multiparous unsuccessful breeders was lower, suggesting that the reproductive success at primiparity is not a reliable predictor of female quality. Being unsuccessful in raising a calf when multiparous (status P), on the other hand, seems to characterize poor individual quality. From these results, we did not find any evidence for reproductive costs in terms of survival.

Calving patterns

By definition, primiparous females all reproduced, so that we analysed the probability of producing a calf from the second breeding attempt. The selected model indicated that

about two-thirds of primiparous females weaned their calf, and independently of age at primiparity (Table 3; Fig. 2b). The probability of producing a calf at the second breeding attempt was independent of age at primiparity and of previous reproductive success (0.84 ± 0.02 ; Table 3; Fig. 2b). However, at later breeding attempts, the effect of age at primiparity depended on previous reproductive status. Indeed, as for survival, the age at primiparity did not have any effect on the probability of producing a calf when females weaned their previous calf (0.88 ± 0.02 ; Table 3; Fig. 2b). For unsuccessful females (status Y and P), the probability of producing a calf decreased with increasing age at maturity [except for six females which failed and that had matured at 4 years and had all reproduced (Table 3; Fig 2b)]. Among prime-age multiparous females, the probability of producing a calf at a given age at maturity was higher for females that had produced a calf the previous year than for females that had failed (e.g. 0.87 ± 0.03 vs. 0.74 ± 0.05 and 0.83 ± 0.05 vs. 0.63 ± 0.07 when age at primiparity was 2 and 3 years, respectively; Table 3), confirming the absence of reproductive costs, and supporting a marked quality effect.

Table 3 Transition probabilities (\pm SE) from one year's reproductive state (i) to the next year's reproductive state (j) denoted $\Psi(i, j)$ depending on the age at first reproduction (primi 2, primi 3 and primi 4), and the reproductive experience (primiparous/multiparous status). For other abbreviations, see Table 2

	General Model			Simplest acceptable model		
	Primi 2	Primi 3	Primi 4	Primi 2	Primi 3	Primi 4
(a) Reproductive success at first reproduction						
$\Psi(N,P)$	0.36 \pm 0.03	0.35 \pm 0.04	0.43 \pm 0.07	0.36 \pm 0.02		
$\Psi(N,W)$	0.64 \pm 0.03	0.65 \pm 0.04	0.57 \pm 0.07	0.64 \pm 0.02		
$P(R)^N$	<i>1</i>	<i>1</i>	<i>1</i>	<i>1</i>		
$P(W R)^N$	<i>0.64</i>	<i>0.65</i>	<i>0.58</i>	<i>0.64</i>		
(b) Reproductive success following first reproduction						
• If the calf did not survive to weaning						
$\Psi(P,Y)$	0.15 \pm 0.04	0.21 \pm 0.06	0.30 \pm 0.14	0.16 \pm 0.02		
$\Psi(P,P)$	0.17 \pm 0.04	0.19 \pm 0.06	0.30 \pm 0.14	0.20 \pm 0.02		
$\Psi(P,W)$	0.68 \pm 0.05	0.60 \pm 0.07	0.40 \pm 0.15	0.64 \pm 0.02		
$P(R)^P$	<i>0.85</i>	<i>0.79</i>	<i>0.70</i>	<i>0.84</i>		
$P(W R)^P$	<i>0.80</i>	<i>0.76</i>	<i>0.57</i>	<i>0.76</i>		
• If the calf survived to weaning						
$\Psi(W,Y)$	0.14 \pm 0.03	0.16 \pm 0.04	0.09 \pm 0.06	0.16 \pm 0.02		
$\Psi(W,P)$	0.27 \pm 0.04	0.14 \pm 0.04	0.21 \pm 0.09	0.20 \pm 0.02		
$\Psi(W,W)$	0.59 \pm 0.04	0.70 \pm 0.05	0.70 \pm 0.10	0.64 \pm 0.02		
$P(R)^W$	<i>0.86</i>	<i>0.84</i>	<i>0.91</i>	<i>0.84</i>		
$P(W R)^W$	<i>0.67</i>	<i>0.83</i>	<i>0.76</i>	<i>0.76</i>		
(c) Reproductive success as a prime-age multiparous						
• If no calf was produced						
$\Psi(Y,Y)$	0.26 \pm 0.05	0.37 \pm 0.07	0.00	0.26 \pm 0.05	0.37 \pm 0.07	0.00
$\Psi(Y,P)$	0.19 \pm 0.04	0.15 \pm 0.05	0.37 \pm 0.17	0.19 \pm 0.04	0.15 \pm 0.05	0.37 \pm 0.17
$\Psi(Y,W)$	0.54 \pm 0.05	0.48 \pm 0.07	0.63 \pm 0.17	0.54 \pm 0.05	0.48 \pm 0.07	0.63 \pm 0.17
$P(R)^Y$	<i>0.74</i>	<i>0.63</i>	<i>1.00</i>	<i>0.74</i>	<i>0.63</i>	<i>1.00</i>
$P(W R)^Y$	<i>0.73</i>	<i>0.76</i>	<i>0.60</i>	<i>0.73</i>	<i>0.76</i>	<i>0.60</i>
• If the calf did not survive to weaning						
$\Psi(P,Y)$	0.13 \pm 0.03	0.17 \pm 0.05	0.27 \pm 0.13	0.13 \pm 0.03	0.17 \pm 0.05	0.27 \pm 0.13
$\Psi(P,P)$	0.25 \pm 0.03	0.19 \pm 0.05	0.27 \pm 0.13	0.25 \pm 0.03	0.19 \pm 0.05	0.27 \pm 0.13
$\Psi(P,W)$	0.62 \pm 0.04	0.63 \pm 0.06	0.45 \pm 0.15	0.62 \pm 0.04	0.63 \pm 0.06	0.45 \pm 0.15
$P(R)^P$	<i>0.87</i>	<i>0.83</i>	<i>0.73</i>	<i>0.87</i>	<i>0.83</i>	<i>0.73</i>
$P(W R)^P$	<i>0.70</i>	<i>0.76</i>	<i>0.62</i>	<i>0.70</i>	<i>0.76</i>	<i>0.62</i>
• If the calf survived to weaning						
$\Psi(W,Y)$	0.11 \pm 0.01	0.13 \pm 0.02	0.17 \pm 0.05	0.12 \pm 0.01		
$\Psi(W,P)$	0.12 \pm 0.01	0.12 \pm 0.02	0.09 \pm 0.03	0.13 \pm 0.01		
$\Psi(W,W)$	0.76 \pm 0.02	0.74 \pm 0.02	0.74 \pm 0.05	0.75 \pm 0.01		
$P(R)^W$	<i>0.89</i>	<i>0.87</i>	<i>0.83</i>	<i>0.88</i>		
$P(W R)^W$	<i>0.85</i>	<i>0.85</i>	<i>0.89</i>	<i>0.85</i>		

Probabilities which are not directly estimated from multistate capture-mark-recapture models, but are based on transition estimates, are indicated in italics. Those are the probabilities of giving birth to a calf in a given year at least once [$P(R)^i$], which can be calculated for each state i as $P(R)^i = [1 - \Psi(i, Y)]$, and the probability of a female weaning her calf given that she gave birth, which was calculated as $P(W|R)^i = \Psi(i, W)/P(R)^i$

Weaning patterns

The variation in weaning patterns according to age at primiparity and previous reproductive status were very similar to

those obtained for the probability of calving. However, while there was little difference between females that weaned a calf (W) and females that only produced a calf (P) to explain the probability of reproducing [e.g. $P(R)^P = 0.87$

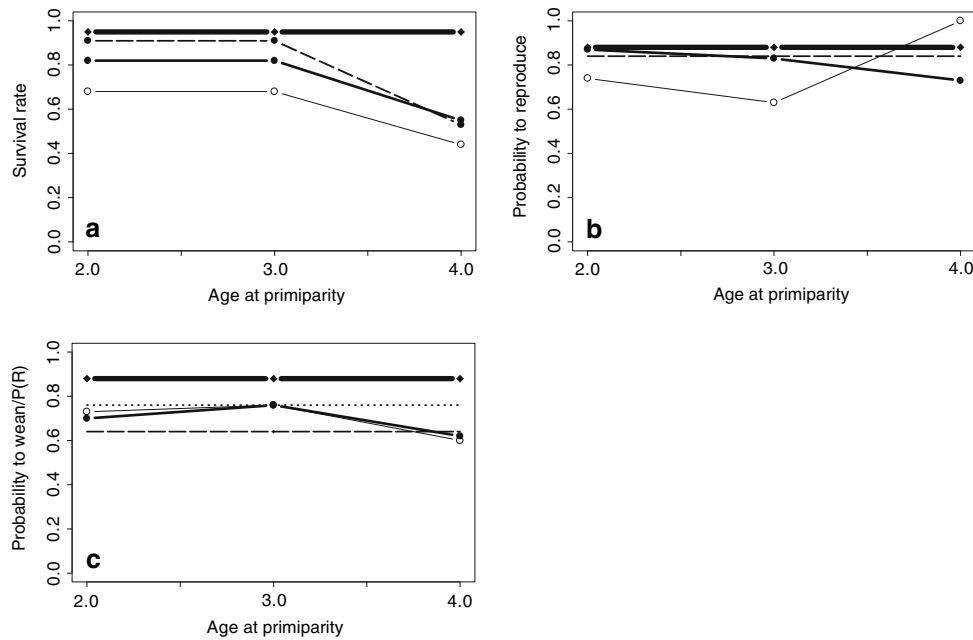


Fig. 2 Relationship between **a** survival rate, **b** probability of reproducing, and **c** probability of weaning, as a function of age at primiparity (2–4 years of age), for various reproductive statuses. *Very thick lines* indicate successful females (state W), *medium thick lines* indicate females that reproduced but lost their calf before weaning (state P), and *thin lines* indicate females that failed (state Y). **a** *Dashed line* refers to survival following the first attempt to reproduce for females that failed (status Y/N). **b** *Dashed line* refers to the probability of reproducing following the first reproductive attempt, independently of weaning success. **c** *Dashed line* refers to probability of weaning a calf at the first breeding attempt; *dotted line* refers to the probability of weaning a calf at the second reproductive attempt. *Note*: these graphs show the effect of the x-axis (the age at primiparity effect) and the effect

of the previous reproductive status. All graphs clearly show that being successful (the *very thick line*), is better than anything else, and that when successful, age at primiparity does not matter. **b** Shows that for reproduction, it is important to have reproduced before, but whether reproduction was successful or not is less important (not a large difference between the two *thickest lines*). **c** Shows that to wean a calf once a female has produced a calf, it is important to have succeeded before, and that having reproduced without weaning before does not help much (no difference between the two *thinnest lines*); there is a gradual effect showing a type of “experience effect”, when comparing the *dashed line* (success of weaning at first breeding attempt) to the *dotted line* (success of weaning at the second breeding attempt) and to the *thickest line* (success of weaning having successfully weaned before)

and $P(R)^W = 0.89$ for females that reached primiparity at age 2], the probability of weaning was higher for females that had successfully weaned a calf the previous year than for females that had not [(e.g. $P(W|R)^P = 0.70$ and $P(W|R)^W = 0.85$ for females that reached primiparity at age 2 years; Table 3; Fig. 2c, see also Fig. 3]. There was actually very little difference in reproductive success between experienced females that had failed (status Y) and females that only produced a calf (status P) the previous year [e.g. $\Psi(W, Y) = 0.11$ and $\Psi(W, P) = 0.12$ for females that reached primiparity at age 2 years; Table 3]. As previously, successfully weaning a calf when multiparous in a given year was a good predictor of doing so the year after and can therefore be interpreted as a reliable indicator of high female quality.

Effect of age

As expected from earlier analyses (Weladji et al. 2006), we found a marked effect of reproductive experience on the probability of weaning a calf. Indeed, the probability of successfully weaning a calf was lower at first reproduction

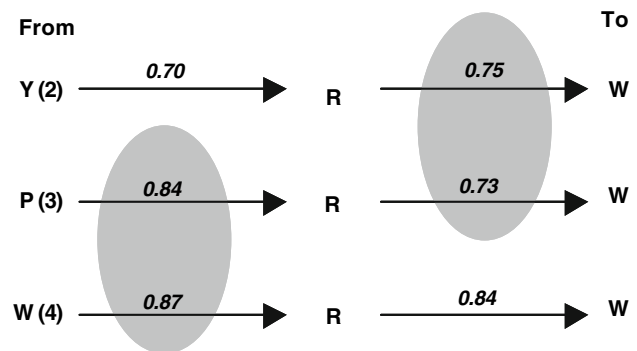


Fig. 3 Diagram showing the probability (estimated from the multi-state capture–mark–recapture analysis) of a female weaning her calf in year $t + 1$ (*To*) depending on her reproductive success in year t (*From*), decomposed into the probability of reproducing (becoming R, *first arrow*) and the probability of successfully weaning a calf given that it was produced (*second arrow*, transition from R to W). *Shaded areas* highlight probabilities that are not statistically different (see text). $Y(2)$ Y (state 2), $P(3)$ P (state 3), $W(4)$ W (state 4); see Figs. 1 and 2 for other abbreviations

(0.64) than at the second breeding attempt (0.76) and peaked for multiparous females that previously weaned a calf (0.85).

Discussion

Our results clearly supported the quality-only scenario better than the cost-only scenario. We failed to find evidence of reproductive costs in this population. In fact, there was no differential cost of gestation (i.e. females that calved, but did not wean) and lactation (i.e. females that both calved and weaned) in terms of both future reproduction and survival. Moreover, females that reproduced successfully did not show any reduced survival or reproduction in following years. Contrary to the cost-only scenario, early maturation was beneficial. Females that successfully weaned their first offspring were more successful throughout their life independently of age at maturity, and females that matured late did not have higher initial reproductive success. Also successful breeders had higher subsequent survival and reproductive success than experienced non-breeders and unsuccessful breeders, independently of the age at primiparity. In reindeer, after the age at first reproduction is reached, female ovulate (and may conceive) nearly every year in the absence of severe food limitation (Skogland 1989). On the other hand, large herbivorous females may need to reach a critical threshold body mass to be able to reproduce (Reimers 1983; Albon et al. 1986; Gaillard et al. 1992, 2000; Langvatn et al. 1996, 2004). Our results therefore support the view that individual quality matters (Beauplet et al. 2006).

Reproductive costs have been reported in several studies through a reduction of survival (Reiter and Le Boeuf 1991; Sydeman and Nur 1994; Clutton-Brock et al. 1996), a reduction of future growth and condition (e.g. Albon et al. 1983; Festa-Bianchet 1989; Rönnegård et al. 2002; Bérubé et al. 1996; Tavecchia et al. 2005; Gerhart et al. 1997) or future reproduction (Clutton-Brock et al. 1982; Clutton-Brock 1984; Huber 1987; Testa 1987; Rönnegård et al. 2002). However, the absence of trade-offs between current reproduction and both future reproduction and survival is not an exception either, as positive correlation among fitness components has been reported among a variety of mammals and birds (Millar et al. 1992; Wesolowski and Rowinski 2006; Orell et al. 1996; Beauplet et al. 2006). Indeed, detecting reproductive costs can be difficult (Festa-Bianchet and Jorgenson 1998) and may only be apparent during severe environmental conditions (e.g. Sinervo and DeNardo 1996; Doughty and Shine 1997; Festa-Bianchet et al. 1998; Mysterud et al. 2001a, b; Laaksonen et al. 2002; Tavecchia et al. 2005). In addition, costs are often measured in the short term (e.g. cost of the current reproduction on the next reproductive success), while they may have delayed effects on future fitness components (e.g. Millar 1994; Fleming et al. 1997; Jonsson 1997; Bonnet et al. 1999; Orell and Belda 2002). This is unlikely the case for reindeer in this study as we showed longevity to be posi-

tively related to fitness in this population (Weladji et al. 2006).

Subtle differences in estimating reproductive costs can also derive from how and when reproductive success is measured. In mammals, lactation is energetically more costly than gestation (Ofstedal 1985; Clutton-Brock et al. 1989). One might then expect individuals that have experienced both gestation and lactation to bear greater costs than females that only experienced gestation. However, we found no difference in reproductive probabilities or survival between females that had reproduced but did not wean their offspring (i.e. experienced only gestation costs) and females that reproduced and weaned (i.e. experienced both gestation and lactation costs) their offspring. This means that females were able to avoid the fitness cost of lactation, either because they were of above-average quality during the preweaning period or because the environmental conditions were favourable (so that the energetic costs of lactation are not large enough to translate into fitness costs). Resource availability is likely important here and females may instead have to control resource partitioning, by adequately balancing parental care (e.g. allocation of resource to growth of their offspring) with their own condition (growth, survival or future reproduction). Clutton-Brock et al. (1997) found that lactation had little effect on a mother's survival in red deer (*Cervus elaphus*) because it occurs in midsummer when resources are plentiful and ends before food supplies decline at the onset of winter. In addition, the likelihood of detecting fitness lactation costs may be prevented by the relatively low reproductive output exhibited by monotonous species such as red deer and reindeer (Robbins and Robbins 1979).

That successful and unsuccessful female reindeer had similar probabilities of surviving (see also Orell and Belda 2002) might be due to unsuccessful females being of lower quality. Low-quality females may need a reproductive pause (sensu Cameron 1994) to recover the body condition required to reproduce, while high-quality females are able to maintain an above-threshold condition to reproduce (Orell et al. 1994). Moreover, we also found female survival to decrease with delayed age at primiparity. Such a relationship is expected to occur when age at primiparity is delayed because of poor condition (Skogland 1983), given the positive relationship between body mass and age, especially among nulliparous females (Rönnegård et al. 2002; Reimers et al. 2005). Since the probability of producing a calf is closely associated with body mass in reindeer (Reimers 1983), and that age and size at maturity both determine age at primiparity of females in a given population (Roff 1992) our findings may be attributed to variation in individual quality (see also Barbraud and Weimerskirch 2005). Females maturing earlier were likely to be of above-average quality, as illustrated by their ability to show both

high survival and reproductive output right after having been successful in raising a calf. Extensive evidence for individual variation in the quality of female mammals and birds has been reported (Cobley et al. 1998; Festa-Bianchet 1998; Gaillard et al. 1998; Pomeroy et al. 1999; Crocker et al. 2001; Tavecchia et al. 2005). Early reproduction has, however, been reported to be costly in several birds (Pyle et al. 1997; Barbraud and Weimerskirch 2005), female squirrels (Descamps et al. 2006), female reindeer breeding as calves (Reimers et al. 2005), and male Soay sheep breeding as lambs (Robinson et al. 2006). We also found a marked effect of experience as the weaning success peaked for multiparous females, being lowest for first-time breeders (Forslund and Pärt 1995; Weladji et al. 2006).

The strong support we found for the individual-quality hypothesis may partly explain the lack of any cost of reproduction. In fact, among-individual differences in quality were likely underestimated in our study as managers of this reindeer population undoubtedly selected against poor-quality females. On the other hand, the decision to breed or not for the first time may not depend solely on individual quality, but also on cohort effects as well as the composition of the male segment of the population (Holand et al. 2006). Indeed, some good-quality females certainly failed to reproduce early, but once they successfully weaned a calf, they were as good as others. Our results emphasize the importance of accounting for among-individual differences in quality and experience when assessing trade-offs. An early age at primiparity and a rapid acquisition of reproductive experience are likely to be reliable predictors of female quality in long-lived vertebrates such as reindeer.

The absence of reproductive costs in this population may partly be attributed to supplemental feed during winter. Indeed, such a supplement will secure the intake of appropriate-quality feed and may reduce considerably the costs for reindeer of digging into the snow to access winter forage and locomotion costs related to searching for forage. However, we argue that such benefit from the supplement is not enough to completely compensate for possible reproductive costs. Indeed only half the female reindeer energy requirements were covered by the supplementary feed (Holand et al. 2004). Further, the animals were also affected by the delayed effects of winter on spring–summer conditions despite supplemental winter feed. By comparing domestic sheep (fed indoors during the winter in Norway) with red deer (outdoors all year round), Mysterud et al. (2001a, b) have indeed shown that the main effect of winter is a delayed effect on spring–summer environmental conditions, so that supplemental food during winter cannot alter such effects. Lastly, previous studies reported clear evidence of mass loss during the winter in this semi-domesticated reindeer population (Kumpula 2001; Holand et al. 2004), like that usually observed in most northern

free-ranging populations of large herbivores (e.g. Suttie and Webster 1995).

Acknowledgements The authors are grateful to the Finnish Game and Fisheries Research Institute and V. Tervonen and his crew at Kutuharju Reindeer Research Station for the data. Funding from the Norwegian Research Council to R. B. W. and N. G. Y., and from the Natural Sciences and Engineering Research Council of Canada to R. B. W. supported this work. The authors are also grateful to the French–Norway Network funded by CNRS and the CLIMPOP Network funded by the GICC2.

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