Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores

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Abstract. Variations among individuals in phenotypic quality and fitness often confound analyses of life-history strategies assessed at the population level. We used detailed long-term data from three populations of large herbivores with generation times ranging from four to nine years to quantify heterogeneity in individual quality among females, and to assess its influence on mean annual reproductive success over the lifetime (MRS). We also determined how environmental conditions in early life shaped individual quality and tested A. Lomnicki's hypothesis that variance in individual quality should increase when environmental conditions deteriorate. Using multivariate analyses (PCA), we identified one (in sheep and deer) or two (in goats) covariations among life-history traits (longevity, success in the last breeding opportunity, adult mass, and social rank) as indexes of individual quality that positively influenced MRS of females. Individual quality was reduced by unfavorable weather, low resource availability, and high population density in the year of birth. Early-life conditions accounted for 35–55% of variation in individual quality. In roe deer, we found greater variance in individual quality for cohorts born under unfavorable conditions as opposed to favorable ones, but the opposite was found in bighorn sheep and mountain goats. Our results demonstrate that heterogeneity in female quality can originate from environmental conditions in early life and can markedly influence the fitness of females in species located at different positions along the slow–fast continuum of life-history strategies.

Key words: bighorn sheep; cohort effects; environmental conditions; fitness; mean annual reproductive success over the lifetime; longevity; mountain goat; roe deer; ungulates.

INTRODUCTION

Within a population, individuals often display substantial heterogeneity in both phenotypic quality (e.g., mass, size) and performance (survival, reproduction), which can be associated with differences in life-history strategies, especially in long-lived species (Gross 1996, McNamara and Houston 1996). Empirical studies that included heterogeneity in phenotypic quality as a source of variation in life-history traits have revealed positive covariations among traits (Cam and Monnat 2000, Cam et al. 2002), demonstrating that analyses of life-history strategies or of population dynamics that ignore individual effects can be misleading (Clutton-Brock and Harvey 1979, Nussey et al. 2008). For example, individuals surviving to old age are unlikely to be a random sample of their cohort (Vaupel et al. 1979). Instead, longevity is often associated with performance

in other life-history traits (Service 2000, Nussey et al. 2006). Individual quality can thus be defined as a covariation among life-history traits at the individual scale. As a general rule, low-quality individuals are smaller at each stage of the life cycle, reproduce later and less frequently, give birth to and raise fewer offspring per breeding attempt, and have shorter lives than high-quality individuals. Moreover, although life-history theory predicts fitness costs of reproduction (Stearns 1992), several studies of iteroparous species reported a positive temporal autocorrelation in yearly reproductive success, as high-quality individuals consistently outperform low-quality ones (Reznick et al. 2000, Beauplet et al. 2006). In Mute Swans (*Cygnus olor*), for instance, Charmantier et al. (2006) demonstrated that more individuals had both an early first reproduction and a late last reproduction than expected at random.

Heterogeneity in individual quality can originate from numerous sources, including genetic variability (Meyers and Bull 2002, Nussey et al. 2005*a*) and environmental conditions, especially those experienced during early development (McNamara 1998). High population density, adverse weather conditions, or low resource availability may lower phenotypic quality (Albon et al.

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TABLE 1. Influence of PCA scores of individual quality on mean annual reproductive success (MRS) over the lifetime in marked females for three populations of large herbivores: mountain goats (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), and roe deer (*Capreolus capreolus*).

Species and parameter	β ± SE	F	df	P	V†
Mountain goat					
Intercept	0.61 ± 0.02				
Mass–social rank scores	0.07 ± 0.02	9.4	1, 20	0.006	27%
Longevity scores	0.06 ± 0.02	5.6	1, 20	0.02	17%
Bighorn sheep					
Intercept	0.62 ± 0.02				
Longevity scores	0.03 ± 0.02	1.8	1, 114	0.2	2%
Roe deer					
Intercept	1.23 ± 0.05				
Longevity scores	0.20 ± 0.05	13.9	1, 75	0.001	15%

Note: Scores of individual quality were based on PCA analyses on life-history traits of females (see *Statistical analyses*).

† Percentage of variance accounted for by the variable.

1987, Sæther 1997, Solberg et al. 2004), often in interaction with genotype (Coulson et al. 1998). As individuals born the same year develop under similar environmental conditions, some heterogeneity in individual quality should arise from cohort effects (Lindström 1999, Gaillard et al. 2003). Lomnicki (1978) predicted that heterogeneity in individual quality should increase when resources are scarce, because of uneven access to resources among individuals. Therefore, the variance in individual quality should increase for cohorts born under poor environmental conditions. Alternatively, unfavorable environmental conditions could reduce variability in resource access among individuals and result in lower variance in individual quality and performance (Nussey et al. 2005b). These hypotheses have seldom been tested in wild populations of long-lived species because of the difficulty of gathering the appropriate data.

Previous studies of large herbivores often reduced individual quality to a single life-history trait (for a review, see Moyes et al. [2009: Table 1]), measuring either performance (e.g., longevity; Weladji et al. 2006) or phenotypic quality (e.g., body mass; Festa-Bianchet et al. 1998). We sought a more general measure by defining multifactorial axes of individual quality. We thus performed a multivariate analysis (PCA) using life-history traits commonly used as measures of individual performance. We first tested the prediction that individual quality should be positively correlated with female reproductive success. We thus assessed the influence of individual quality on mean annual reproductive success over the lifetime (MRS). We therefore excluded any direct measures of reproductive success from our definition of individual quality. Lifetime reproductive success (LRS) is correlated with Darwinian fitness (Brommer et al. 2004) and can be partitioned into two statistically independent components: the number of reproductive attempts,

mainly affected by longevity, and MRS. MRS is thus statistically measured independently of longevity, but can be correlated with longevity if individual quality affects both MRS and longevity. Secondly, we determined how environmental conditions and life-history strategies influenced individual quality within and among populations of contrasted species. We assessed whether annual resource availability led to cohort effects in individual quality (Albon et al. 1987, Gaillard et al. 2003) and tested whether intra-cohort variance in individual quality increased when environmental conditions deteriorated. We predicted (1) that individual quality would be influenced by environmental conditions in early life, and (2) that a greater variance in individual quality should occur among cohorts born in years of poor, as opposed to good, environmental conditions (Lomnicki 1978).

We tested our predictions in three populations where known-age marked females were intensively monitored. The populations showed contrasted dynamics and varied in their position along the slow–fast continuum of life-history strategies (Gaillard et al. 1989, Bielby et al. 2007). Using generation time as a metric (Gaillard et al. 2005), mountain goats (*Oreamnos americanus*) were more than two times slower than roe deer (*Capreolus capreolus*), with generation times of 9 and 4 years, respectively. Most female mountain goats in our study population first reproduced at 4 or 5 years of age (range 3–7 years), gave birth to a single kid annually, and took reproductive pauses in about 25% of the years when adult (Festa-Bianchet and Côté 2008), whereas female roe deer typically started reproducing at 2 years of age, reproduced each year, and usually had twins (Gaillard et al. 1998a, b). Between these extremes, female bighorn sheep (*Ovis canadensis*) had a generation time of about 7 years. At low population density, they started reproducing at 2 or 3 years of age but delayed primiparity to 4 or 5 years of age at high density (Festa-Bianchet et al. 1995). They gave birth to singletons and rarely skipped reproduction (Bérubé et al. 1996). In addition, roe deer are income breeders that rely almost exclusively on available food resources for the high energetic needs of reproduction (Andersen et al. 2000), whereas bighorn sheep and mountain goats are capital breeders whose body reserves can substantially affect reproductive success (Festa-Bianchet et al. 1998, Côté and Festa-Bianchet 2001a).

METHODS

Study areas, populations, and measures of individual life-history traits

We studied mountain goats at Caw Ridge (54°03′ N, 119°23′ W), bighorn sheep at Ram Mountain (52°20′ N, 115°45′ W), both in Canada, and roe deer at the Trois Fontaines enclosed forest (48°42′ N, 4°55′ E), France. Mountain goats and bighorn sheep are medium-sized alpine species (adult female mass of 60–85 kg in late summer) inhabiting open, mountainous areas near rugged escape terrain, whereas roe deer is a small, forest-dwelling species (adult female mass of 22–26 kg).

We used longitudinal data collected between 1988 and 2006 for goats, and between 1975 and 2006 for sheep and deer. During the study, the mountain goat population gradually increased from about 80 to 160 individuals, but showed no density dependence (Festa-Bianchet and Côté 2008). The bighorn sheep population was kept at about 100 individuals until 1980 by yearly removals (Jorgenson et al. 1993), then increased to about 230 in 1992, declined rapidly in the 1990s, and has remained at ~40–50 individuals since 2000. During the increasing phase, age at first reproduction and juvenile survival were strongly density dependent (Jorgenson et al. 1993, 1997, Portier et al. 1998). During the declining phase (from 1997 onward), however, cougar (*Puma concolor*) predation contributed substantially to the population reduction (Festa-Bianchet et al. 2006). Despite no known cougar predation since 2002, the population has not recovered. In contrast, the roe deer population was kept relatively stable, between 200 and 300 individuals, through yearly removals of unmarked deer. Similarly to the goat population, it showed no density dependence (Gaillard et al. 2003). This population would have increased rapidly had it not been subjected to yearly removals of ~80–120 individuals (except between 2001 and 2005, when removals were stopped for three years). Extensive details on study areas and populations have been published elsewhere (Gaillard et al. 1998a, Festa-Bianchet et al. 2000, Côté and Festa-Bianchet 2001b).

In all populations, most females were individually marked with visual collars and color-coded ear tags (>98% for goats and sheep, and ~70% for deer). All females included in this study were of known age because they were first captured as juveniles. Mountain goats and bighorn sheep were captured between late May and October in box and corral traps, respectively. Over 95% of female sheep were recaptured and weighed each year, but female goats were only occasionally recaptured to avoid kid abandonment (Côté et al. 1998). Using electronic platform scales baited with salt, we collected additional body mass measurements of goats without capturing them, obtaining measurements for about 45% of female-years in goats. Roe deer were weighed when captured in drive nets in January–February. The annual recapture probability for female deer was ~50% (Gaillard et al. 1997). Because individual mass follows a marked seasonal cycle in sheep and goats, we adjusted it to a common date (Festa-Bianchet et al. 1996). In sheep, mass was adjusted to 15 September based on individual growth rates. In goats, however, most mass data were collected before August and included few repeated measures of the same individuals. We thus adjusted body mass to 15 July based on the average rates of mass gain for five age classes (3, 4, 5, 6 and ≥7 years). For roe deer, we used mass at capture, because body mass shows little seasonal variation in this species (Andersen et al. 2000). Mass varied with age for all species and with reproductive status in sheep and goats.

Because we sampled females at different ages, we used linear mixed models (LMM; Littell et al. 2006), with year and female identity as random effects, and reproductive status and age as covariates, to adjust body mass to the age when females reach asymptotic mass: 7 years for goats and sheep; 4 years for deer (Festa-Bianchet et al. 1996, Gaillard et al. 2000, Côté and Festa-Bianchet 2001b). Because we had more than one mass measurement for each female during its lifetime, we used the average of all age-adjusted measures for each female in all analyses. We used the last sighting or recapture to calculate longevity, because the annual resighting probability was >99% for sheep and goats, and 84% for deer (Gaillard et al. 2000).

For goats and sheep, we determined the annual reproductive status of each female from observations of nursing behavior during intensive censuses from mid-May to late September. We determined the sex of most kids and lambs by their urination posture and by observations of the vulvar patch in female kids (Festa-Bianchet and Côté 2008). The sex of lambs was also noted at capture. We calculated offspring sex ratio as the proportion of sons among offspring of known sex over a female's lifetime. For deer, intensive observations of marked females were performed in autumn to determine if they had fawns (for further details, see Gaillard et al. 1998a, 2000), but fawn sex was unknown in most cases.

In goats, most females give birth between 20 May and 1 June (Côté and Festa-Bianchet 2001a). Therefore, we intensively searched the study area every year during this period and determined kid birth dates either by direct observations of births or by daily observations of presence/absence of a kid for each female. In some cases, we estimated birth dates within 5 days based on the characteristics of the umbilical cord, and by comparing the kid's behavior and body size with that of known-age kids (Côté and Festa-Bianchet 2001a). For each female, we used the median offspring birth date as lifetime parturition date. We also determined social rank of female goats each year from observations of agonistic interactions (details in Côté 2000). Because age is highly correlated with social rank ($r > 0.9$; Côté 2000), we calculated age-specific social ranks as the residuals of the regression of rank on age. We used the average age-specific social ranks from 5 to 12 years of age for each female to estimate lifetime social rank. We also recorded every summer the approximate date when each female goat completed the molt of its winter coat, assuming that early molt indicated good body condition (Robbins 1993). We used the average molt date for each female as a measure of lifetime molt date. Offspring birth dates, social ranks, and molt dates were not available for sheep and deer.

Measure of mean annual reproductive success (MRS) over lifetime

We only considered females that reproduced at least once (we could not measure quality for females that

never reproduced; see PCA analysis) and died by 2007. We excluded bighorn ewes that died from human-related causes or received experimental contraceptive implants. We also excluded females from cohorts for which other females were still alive in 2007 to prevent biases, because survivors are likely to be of higher quality than individuals of the same cohort that died earlier (Vaupel et al. 1979). Thus, our analyses included cohorts from 1984 to 1992 for goats (23 females), from 1973 to 1991 for sheep (123 females), and from 1975 to 1990 for deer (84 females). We calculated MRS by dividing a female's LRS by its reproductive life span, i.e., the number of years between first parturition and death. LRS was the number of offspring weaned (surviving to late August [deer] or late September [sheep and goats]) during a female's lifetime. We excluded females that died after a single reproduction ($n = 0$ goats, 6 ewes, and 7 does) because MRS measured over a single year can only be 0 or 1.

Measures of environmental variation

For each cohort, we assessed how environmental conditions (population density, resource availability, and weather conditions; see Appendix) in the year of birth affected individual quality. Because all female roe deer gave birth for the first time at the same age at Trois Fontaines (Gaillard et al. 1998a), we could also assess the influence of environmental conditions at first parturition on cohort quality in this species.

For goats and deer, we measured population density as the total number of individuals in spring (only animals >1 year of age for roe deer, because estimates of fawn numbers were not available for all years). For sheep, however, the total number of individuals did not appear to adequately represent resource availability, as the population dynamic during the decline phase was affected by cougar predation independently of density (Festa-Bianchet et al. 2006). We thus used the consecutive years of the study to reflect the gradual decline in environmental conditions experienced by individuals, from good cohorts in early years that were born and lived at low density, through intermediate-quality cohorts that were born at low, but lived at high, density, and poor cohorts that were born and lived at high density, to very poor recent cohorts that were born at high density and lived during years of cougar predation (1997–2001). Because the average mass of yearling females is an index of annual resource availability in this bighorn population (Festa-Bianchet et al. 2004), we also examined the influence of average yearling female mass in September on individual quality. The average fawn mass in January–February was also used as a yearly measure of resource availability in roe deer (Pettorelli et al. 2006). Average yearling mass was not available for most cohorts in goats.

For sheep and goats, we used the November–March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994) as a global climate index for environmental conditions in winter. Winters (November–March) with high NPI values were colder and snowier than winters with low NPI (Ram Mountain: mean temperature, $r = -0.57$, $P = 0.001$, $n = 33$ years; total precipitation, $r = 0.48$, $P = 0.005$, $n = 33$ years; Caw Ridge: mean temperature, $r = -0.47$, $P = 0.03$, $n = 21$ years; total precipitation, $r = 0.41$, $P = 0.03$, $n = 27$ years). These correlations were obtained using the Environment Canada weather stations closest to each study area, namely Nordegg (~20 km from Ram Mountain) and Grande Cache (~25 km from Caw Ridge). We used NPI values for the winter prior to birth and the first winter of life. For deer, we used the Bagnoul-Gaussen Index (BGI; Dajoz 1975) for spring and summer, which was twice the mean temperature (°C) minus the mean precipitations summed over April and May for the spring index, and over June, July, and August for the summer index. High BGI values indicate drought (for previous applications on roe deer, see Gaillard et al. [1997] and Toïgo et al. [2006]).

Normalized difference vegetation index (NDVI) data from the National Oceanic and Atmospheric Administration satellites processed by the GIMMS group have been available since 1982 (Tucker et al. 2005) and reflect vegetation productivity (Pettorelli et al. 2005). These data were unavailable for sheep and deer cohorts born before 1982. We could thus only use NDVI for goats. We averaged NDVI values from the three pixels of 8×8 km that overlapped with the study area. We used the sum of the NDVI data for June (integrated NDVI; for details, see Pettorelli et al. 2005) to estimate the timing of spring, where high NDVI values represent early springs (Hamel et al., in press).

Statistical analyses

In goats and sheep, we assessed individual quality by performing a principal component analysis (PCA) on life-history traits related to individual performance, including longevity, age at first reproduction (AFR), age at last reproduction (ALR), adult mass, social rank, offspring sex ratio, average parturition date, and average molt date (not all traits were available for both species; see Appendix). Although there was a strong correlation between longevity and ALR ($r = 0.97$), we included ALR because low-quality females may be unable to reproduce in their last year of life (Weladji et al. 2006). Because we could not include reproduction in the last year of life in a PCA because it is a binomial variable, we used ALR as a surrogate for successful vs. unsuccessful reproduction in the last breeding attempt (see *Results* for the demonstration of this relation). PCA analyses objectively differentiated a set of successive covariations among traits that account independently from each other for the observed variation among those traits at the individual scale. If quality is the main structuring process of among-individual variation in traits, it should occur as the first axis (PC1) and account for a large part of observed variation in traits. Other PCs could represent additional axes of quality (if quality

is multidimensional) or trade-offs. Thus, the scores on PC1 should provide a gradient of individual quality, and the significance of other PCs should be assessed to determine whether other covariations among traits exist. We assessed the significance of PCs by the broken-stick method (i.e., sharp decline in consecutive eigenvalues; Cattell 1966). We used significant PCs that corresponded to quality indexes as measures of individual quality in all analyses.

In deer, available life-history traits included adult mass, longevity, ALR, and AFR. However, ALR was equal to longevity and AFR was 2 years for all females, leaving only two variables for this species (Appendix). We used the values of an orthogonal regression of longevity on adult mass as scores of individual quality when a positive correlation occurred between longevity and mass. This is similar to performing a PCA on two variables and using scores of the first axis. Therefore, we were not able to look for other axes of variation in individual quality in roe deer.

To assess the influence of heterogeneity in individual quality on MRS of females, we present R^2 values as measures of variance accounted for by linear models. To determine the overall variance in individual quality accounted for by cohorts, we performed ANOVAs using cohort as a fixed factor. We then assessed the influence of environmental variables associated with cohorts on individual quality (Appendix). We thus averaged scores of individual quality for each cohort and performed linear models weighted by the inverse of the variance in individual quality (Burnham et al. 1987) for each cohort. In addition, we used linear models to assess the influence of the same environmental variables (Appendix) on the variance in individual quality scores observed within cohorts. We used the Akaike Information Criterion adjusted for small sample size (AIC$_c$) to select the most parsimonious models to assess which combination of variables best explained cohort quality and variance in cohort quality (Burnham and Anderson 2002). We considered models with $\Delta AIC_c \leq 2$ to be equivalent (Burnham and Anderson 2002) and selected, in that case, the model with fewer parameters. We calculated AIC weights as a measure of statistical support for a given model, i.e., it provides the relative likelihood that a given model is the best among the set of fitted models (Burnham and Anderson 2002). We defined a set of a priori models for each species. Because sample size was fairly small (7 cohorts for goats, 16 for sheep, and 13 for deer), we used a maximum of two parameters for goats and three for sheep and deer (i.e., the intercept and one or two environmental variables, respectively) to avoid over-parameterization. Unfortunately, low sample sizes prevented us from assessing interactions between environmental variables. In sheep and deer, yearling mass and fawn mass, respectively, were correlated ($0.40 < r < 0.82$) with cohort year (sheep) and density (deer). Thus, we did not include both variables in the same models. We used a log transfor-
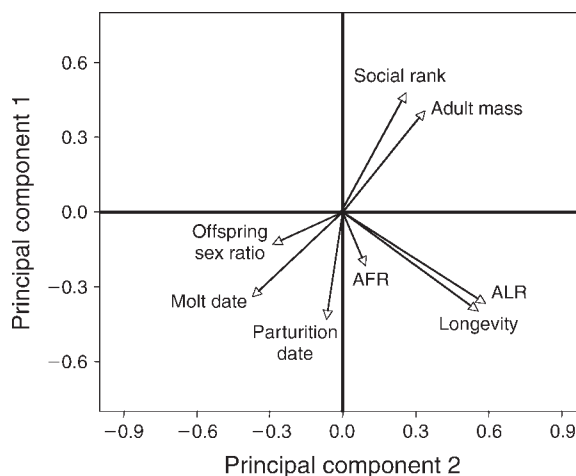

FIG. 1. Principal component analyses on life-history traits of female mountain goats (*Oreamnos americanus*). Sex ratio is the proportion of male offspring produced during a female's lifetime, birth date is the median parturition date during lifetime, AFR is age at first reproduction, and ALR is age at last reproduction.

mation to stabilize variance of parturition date (Sokal and Rohlf 1981). We standardized all variables to allow comparisons of estimates among species and performed all analyses in SAS (Littell et al. 2006).

RESULTS

Heterogeneity in life-history traits among females

For mountain goats, the two first PCs were retained (consecutive eigenvalues [% variation explained]: PC1: 2.4 [29.8%], PC2: 2.0 [24.7%], PC3: 1.2 [15.1%], PC4: 0.9 [11.4%], PC5: 0.6 [7.9%], PC6: 0.5 [5.6%], PC7: 0.4 [5.2%], PC8: 0.01 [0.1%]) and accounted for 54% of the variation observed among life-history traits at the individual level (Fig. 1). PC1 corresponded to a quality index opposing heavy and dominant individuals to light and subordinate ones (thereafter called "mass–social rank scores"; eigenvectors: social rank = 0.49, adult mass = 0.39, offspring sex ratio = −0.15, AFR = −0.20, molt date = −0.33, ALR = −0.36, longevity = −0.39, parturition date = −0.41; Fig. 1). PC2 corresponded to a second and independent quality index opposing long-lived, heavy, and dominant individuals that reproduced until the last year of life to short-lived, light, and subordinate ones that stopped reproducing as they aged (thereafter called "longevity scores"; eigenvectors: ALR = 0.57, longevity = 0.54, adult mass = 0.33, social rank = 0.25, AFR = 0.08, parturition date = −0.06, offspring sex ratio = −0.27, molt date = −0.36; Fig. 1). The positive relationship between the probability of reproducing until the last year of life and longevity scores when accounting for difference in longevity ($\beta = 1.34 \pm 0.67$, $\chi^2 = 4.0$, $P = 0.04$) demonstrates that longevity scores were not only determined by longevity. For sheep, only PC1 was retained (consecutive eigenvalues [% variation
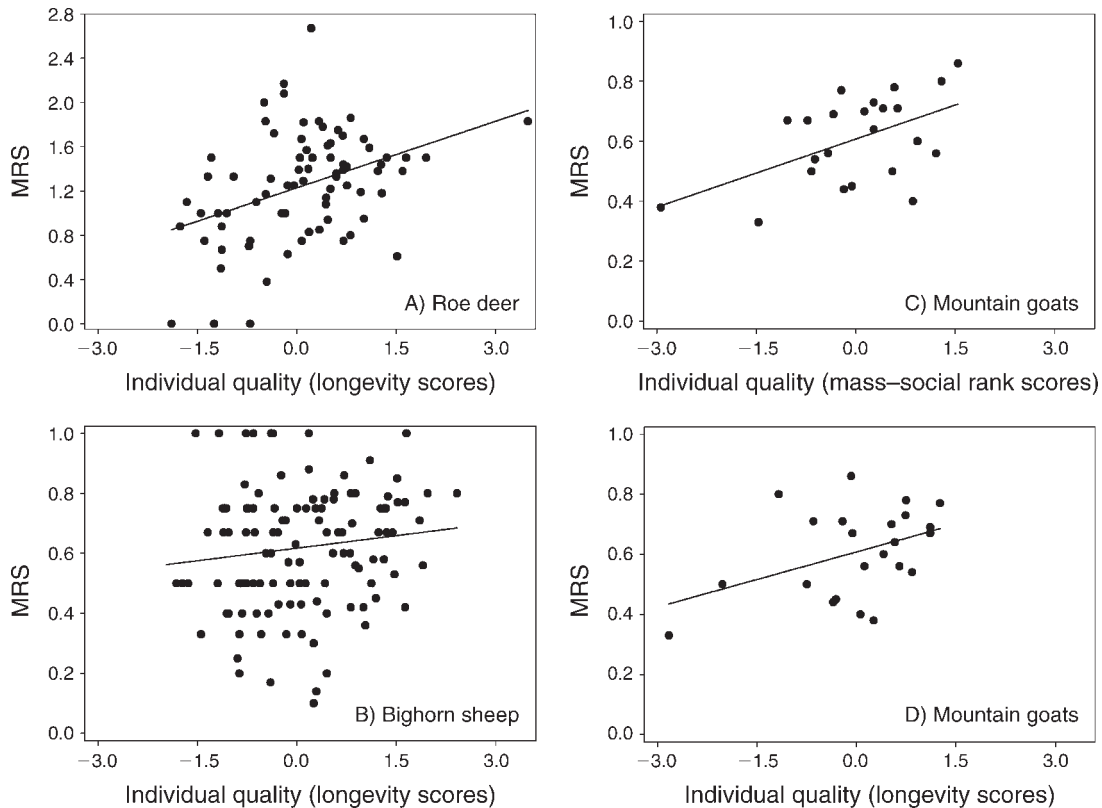
Fig. 2. Influence of individual quality, defined by (A, B, D) longevity scores and (C) mass–social rank scores (derived from orthogonal regression and PCA analyses on life-history traits; see *Statistical analyses*) on mean annual reproductive success over lifetime (MRS) in (A) female roe deer, *Capreolus capreolus*; (B) bighorn sheep, *Ovis canadensis*; and (C, D) mountain goats, *Oreamnos americanus*.

explained]: PC1: 2.0 [40.6%], PC2: 1.0 [20.8%], PC3: 1.0 [20.0%], PC4: 0.9 [18.1%], PC5: 0.03 [0.5%])]) and accounted for 41% of the total variation observed among life-history traits. PC1 corresponded to a quality index: individuals with high PC1 scores were long-lived, reproduced up to the end of their life, and tended to be heavy (eigenvectors: ALR = 0.70, longevity = 0.69, adult mass = 0.18, offspring sex ratio = 0.12, AFR = −0.10). We called this axis "longevity scores" because it was similar to PC2 in goats. There was also a positive relationship between the probability of reproducing until the year of death and longevity scores in sheep when accounting for difference in longevity ($\beta = 4.72 \pm 1.07$, $\chi^2 = 19.5$, $P < 0.001$), demonstrating that longevity scores were also not only determined by longevity in this species. In deer, the orthogonal regression between longevity and adult mass was positive ($r = 0.09$), revealing a quality index opposing females that were long-lived and heavy to females that were short-lived and light. This index was similar to PC2 in goats and PC1 in sheep; hence, we also called it "longevity scores." All indexes (PCs and orthogonal regression) described variation in individual quality, with higher values indicating higher quality. The analysis for goats included more variables than for sheep and deer.

Nevertheless, we obtained similar results when we restricted that analysis to the same variables available for sheep, except that mass was on the second, rather than on the first, axis in this analysis with fewer variables. The influence of each quality index on MRS, however, remained the same. We could not perform this comparison using only the two variables available for deer because that would inevitably result in a single axis.

Individual fitness and heterogeneity in quality

The lifetime number of weaned offspring per female (LRS; mean ± SE) was 4.7 ± 0.5 (CV = 61.9%) for goats, 4.0 ± 0.3 (CV = 77.9%) for sheep, and 7.2 ± 0.6 (CV = 86.1%) for deer. The mean MRS of females was 0.61 ± 0.03 (CV = 23.5%) for goats, 0.61 ± 0.02 (CV = 36.1%) for sheep, and 1.25 ± 0.06 (CV = 39.1%) for deer. The relation between MRS and longevity scores was positive in all species, but not significant in sheep (Table 1, Fig. 2). For goats, the mass–social rank scores also positively affected MRS (Fig. 2C), accounting for more variation than the longevity scores (Table 1). The relationship between MRS and individual quality was stronger in deer, but this model accounted for less variation in MRS compared with the model for goats (Table 1).

TABLE 2. Model selection for the influence of environmental conditions on mean individual quality scores of cohorts and variance in individual quality scores within a cohort, for (A, B) mountain goats and (C) bighorn sheep.

Models	NP	Mean scores of cohorts			Variance of scores within cohorts		
		AIC_c	ΔAIC_c	AIC_c weight	AIC_c	ΔAIC_c	AIC_c weight
A) Goats, mass–social rank scores							
I (Constant)	1	**14.2**	**0**	**0.34**	3.9	0.3	0.32
I + Density	2	15.6	1.4	0.17	5.5	1.9	0.14
I + NPI-before	2	15.8	1.6	0.15	6.6	3.0	0.08
I + NPI	2	15.6	1.4	0.17	6.8	3.2	0.08
I + NDVI	2	15.7	1.5	0.16	**3.6**	**0**	**0.37**
B) Goats, longevity scores							
I (Constant)	1	16.8	1.2	0.20	**20.0**	**0**	**0.24**
I + Density	2	17.8	2.2	0.12	20.6	0.6	0.17
I + NPI-before	2	17.1	1.5	0.18	20.5	0.5	0.18
I + NPI	2	17.8	2.2	0.12	20.2	0.2	0.21
I + NDVI	2	**15.6**	**0**	**0.37**	20.4	0.4	0.19
C) Sheep, longevity scores							
I (Constant)	1	55.7	13.6	0	22.5	3.7	0.07
I + Year	2	44.8	2.7	0.19	25.2	6.4	0.02
I + Ymass	2	58.3	16.2	0	**19.5**	**0.7**	**0.33**
I + NPI-before	2	58.1	16.0	0	25.4	6.6	0.02
I + NPI	2	55.5	13.4	0	25.2	6.4	0.02
I + Year + NPI-before	3	47.0	4.9	0.06	28.8	10.0	0
I + Year + NPI	3	**42.1**	**0**	**0.74**	28.3	9.5	0
I + Ymass + NPI-before	3	61.6	19.5	0	23.1	4.3	0.06
I + Ymass + NPI	3	59.1	17.0	0	18.8	0	0.47
I + NPI-before + NPI	3	58.8	16.7	0	28.7	9.9	0

Notes: Models in boldface were selected based on ΔAIC_c (difference in Akaike Information Criterion corrected for small sample size) and number of parameters (NP); see *Statistical analyses*. Abbreviations: I, intercept; Density, population density the year of cohort birth; NPI-before, North Pacific index value in the winter before cohort birth; NPI, North Pacific index value in the winter of cohort birth; NDVI, normalized difference vegetation index in the year of cohort birth; Year, cohort year; Ymass, average yearling mass in September in the year of cohort birth.

Because adult mass and longevity were available for all species, we performed separate analyses to compare directly the influence of each variable among species. Mass was positively correlated with MRS in all species, but its effect was not significant in sheep (for goats, $\beta = 0.018 \pm 0.005$, $F_{1,21} = 13.4$, $P = 0.002$, $R^2 = 0.39$; for sheep, $\beta = 0.005 \pm 0.004$, $F_{1,114} = 1.7$, $P = 0.2$, $R^2 = 0.02$; for deer, $\beta = 0.08 \pm 0.03$, $F_{1,75} = 9.1$, $P = 0.003$, $R^2 = 0.11$). Adult mass accounted for much of the variation in MRS in goats. Longevity was positively correlated with MRS only in deer (for goats, $\beta = 0.002 \pm 0.011$, $F_{1,21} = 0.02$, $P = 0.9$, $R^2 = 0.001$; for sheep, $\beta = 0.002 \pm 0.006$, $F_{1,114} = 0.14$, $P = 0.7$, $R^2 = 0.001$; for deer, $\beta = 0.040 \pm 0.017$, $F_{1,75} = 5.54$, $P = 0.02$, $R^2 = 0.07$). In goats and sheep, longevity scores were also representative of success in the last breeding opportunity and, in contrast to longevity, this variable affected MRS in both species (for goats, successful $= 0.65 \pm 0.03$, unsuccessful $= 0.51 \pm 0.05$, $F_{1,21} = 5.2$, $P = 0.03$, $R^2 = 0.19$; for sheep, successful $= 0.67 \pm 0.02$, unsuccessful $= 0.49 \pm 0.04$, $F_{1,114} = 36.3$, $P < 0.001$, $R^2 = 0.24$). Results were similar when we excluded the last breeding attempt in the calculation of MRS (i.e., to control for the potential overestimation of MRS in successful compared with unsuccessful individuals), although in goats the relation became nonsignificant ($P = 0.25$).

Heterogeneity in individual quality, cohort, and environmental variations

In goats, there were significant cohort effects on mass–social rank scores ($F_{8,14} = 3.6$, $P = 0.02$, $R^2 = 0.67$). For longevity scores, cohort only had a significant influence in sheep, although it accounted for a substantial amount of variation in female quality for goats (for goats, $F_{8,14} = 0.8$, $P = 0.6$, $R^2 = 0.30$; for sheep, $F_{18,103} = 2.1$, $P = 0.01$, $R^2 = 0.27$; for deer, $F_{15,68} = 0.9$, $P = 0.5$, $R^2 = 0.17$).

For goats, environmental variation at birth did not influence the mass–social rank scores of cohorts (Table 2). For longevity scores, the best model included NDVI, which accounted for 35% of variation in cohort quality (Table 2), although that model received only 1.8 times more support than the model with a constant only. Low sample size for goats might account for the apparent discrepancy between the proportion of variance explained and statistical evidence. Cohorts born in years of high NDVI (representing early springs) were of higher quality than cohorts born in years of low NDVI (Fig. 3A). For sheep, the quality of cohorts decreased over time (Table 2, Fig. 3B), but the relationship seemed mostly influenced by two particularly good cohorts in the early years of the study. Female quality was also affected by the NPI experienced by cohorts during their first winter (Table 2): cold and snowy
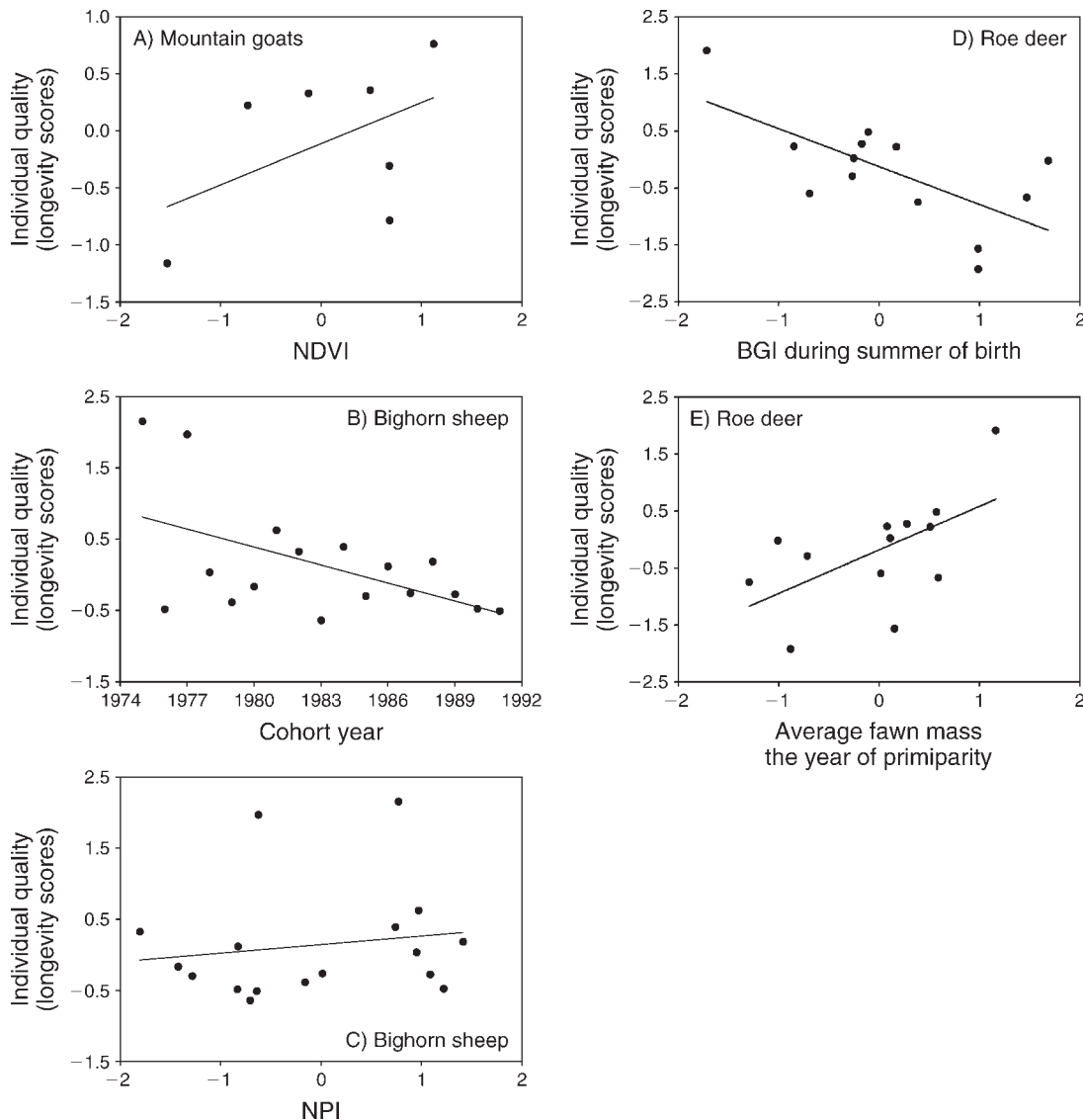
FIG. 3. Effects of environmental conditions on individual quality defined by longevity scores in (A) mountain goats, (B, C) bighorn sheep, and (D, E) roe deer. Each point is the mean individual quality computed from all individuals of a specific cohort. (A) Normalized difference vegetation index (NDVI) in the year of cohort birth, where high values represent early springs. (B) Cohort birth year, as a surrogate for the gradual increase in population density. (C) North Pacific Index values (NPI) in the winter of cohort birth, where high values represent cold and snowy winters. (D) Bagnoul-Gaussen drought index (BGI) in the summer of cohort birth, where high values represent dry summers. (E) Average fawn mass in January–February in the year of females' primiparity, where high values represent good years.

winters resulted in higher quality scores than warm and dry winters (Fig. 3C). Winter lamb survival of the cohorts we studied tended to be lower during severe winters (linear model controlling for density and its interaction with NPI: $F_{3,12} = 3.5$; $P = 0.08$, $R^2 = 0.48$, $n = 16$ years). The model including additive effects of year and NPI received three times more support than any other models. Cohort and NPI accounted for 42% and 15%, respectively, of the observed variation. For deer, four models provided a close fit (Table 3) and received three times more support than other models. Two of the best models were similarly parsimonious and had

similar statistical support. One included the BGI index of the summer of birth, which accounted for 34% of variation in female quality. Drier summers in the year of birth led to lower quality scores than summers with more precipitation (Fig. 3D). The other model included the average fawn mass in January–February (a measure of resource availability and year quality) in the year of females' primiparity (Table 3). Quality was higher for cohorts that were primiparous in years when the average fawn mass was high than when it was low (Fig. 3E), accounting for 33% of variation in female quality.

TABLE 3. Model selection for the influence of environmental conditions experienced by roe deer cohorts at birth (B) and at primiparity (P) on mean individual quality scores of cohorts and variance in individual quality scores within a cohort.

Model	NP	Mean scores of cohorts			Variance of scores within cohorts		
		AIC_c	ΔAIC_c	AIC_c weight	AIC_c	ΔAIC_c	AIC_c weight
I (Constant)	1	41.2	5.1	0.02	14.4	2.7	0.08
I + Density_B	2	44.0	7.9	0.01	15.9	4.2	0.04
I + Density_P	2	42.2	6.1	0.01	16.2	4.5	0.03
I + Fmass_B	2	41.2	5.1	0.02	17.9	6.2	0.01
I + Fmass_P	2	**37.6**	**1.5**	**0.14**	17.5	5.8	0.02
I + BGI-spring_B	2	44.4	8.3	0.00	17.8	6.1	0.01
I + BGI-summer_B	2	**37.4**	**1.3**	**0.16**	17.9	6.2	0.01
I + BGI-spring_P	2	42.4	6.3	0.01	17.9	6.2	0.01
I + BGI-summer_P	2	43.6	7.5	0.01	**11.7**	**0**	**0.30**
I + Density_B + Density_P	3	46.4	10.3	0	18.5	6.8	0.01
I + Fmass_B + Fmass_P	3	41.3	5.2	0.02	21.8	10.1	0
I + BGI-spring_B + BGI-spring_P	3	46.7	10.6	0	22.1	10.4	0
I + BGI-spring_B + BGI-summer_B	3	41.1	5.0	0.03	22.1	10.4	0
I + BGI-summer_B + BGI-summer_P	3	41.2	5.1	0.02	15.3	3.6	0.05
I + BGI-spring_P + BGI-summer_P	3	46.4	10.3	0	13.0	1.3	0.16
I + BGI-summer_B + BGI-spring_P	3	41.3	5.2	0.02	22.2	10.5	0
I + Density_B + BGI-spring_B	3	48.3	12.2	0	19.1	7.4	0.01
I + Density_B + BGI-summer_B	3	41.0	4.9	0.03	20.1	8.4	0
I + Fmass_B + BGI-spring_B	3	45.0	8.9	0	22.1	10.4	0
I + Fmass_B + BGI-summer_B	3	36.1	0	0.31	22.2	10.5	0
I + Density_P + BGI-spring_P	3	41.6	5.5	0.02	20.4	8.7	0
I + Density_P + BGI-summer_P	3	45.7	9.6	0	13.1	1.4	0.15
I + Fmass_P + BGI-spring_P	3	37.9	1.8	0.12	21.8	10.1	0
I + Fmass_P + BGI-summer_P	3	41.8	5.7	0.02	14.2	2.5	0.09

Notes: Models in boldface were selected based on ΔAIC_c (difference in Akaike Information Criterion corrected for small sample size) and number of parameters (NP); see *Statistical analyses*. Abbreviations are: I, intercept; Density, population density; Fmass, average fawn mass in January–February; BGI-spring, drought index for April–May; BGI-summer, drought index for June, July, and August.

Regarding the variance in scores of individual quality within cohorts, the model with a constant only received high statistical support for both mass–social rank scores and longevity scores in mountain goats (Table 2). Nevertheless, our analyses revealed some interesting patterns of variability described in equivalent models. The variance of mass–social rank scores within cohorts was affected by NDVI (Table 2): high NDVI values (i.e., early spring) in the year of birth resulted in higher variance than low NDVI values, accounting for 49% of observed variation (Fig. 4A). For bighorns, two models provided similar fit and received three times more support than the constant model. The most parsimonious of these two models included only average yearling mass. Variance in individual quality was higher for cohorts born in years when the average yearling mass was high than when it was low (Table 2, Fig. 4B), accounting for 29% of observed variation. In deer, three models provided similar fit (Table 3). The most parsimonious of these three models included only the BGI index during summer of primiparity, which received more than three times more statistical support than the constant model. Variance in individual quality was higher for cohorts that gave birth for the first time during dry summers than for those that did so during wet summers, accounting for 38% of observed variation (Table 3, Fig. 4C). Thus, poor environmental conditions resulted in an increase in the variance of female quality in roe deer, opposite to what we found for sheep and goats.

DISCUSSION

Using life-history traits commonly reported to influence individual performance in vertebrates, we quantified heterogeneity in quality among females in three populations of herbivores, and found that quality can be multidimensional (i.e., it can vary along more than one index), and requires multifactorial measures, where each quality index is defined as a covariation among a set of life-history traits. We provided support for the prediction that quality, defined by excluding direct measures of reproductive performance, is positively correlated with mean annual reproductive success. Body mass and social rank shaped the dominant axis of quality among female mountain goats, whereas longevity defined individual quality in all three species, as the main axis for deer and sheep and as a secondary axis in goats. Cohort effects accounted for a large amount of variance in female quality and, as we predicted, they were linked to environmental conditions in early life. In roe deer, conditions prevailing during the first reproduction could also affect individual quality. Our prediction of greater variance in individual quality for cohorts born under unfavorable than favorable conditions, however, was only confirmed in roe deer. Variance in individual quality was greater for cohorts born under good as opposed to poor conditions in both sheep and goats.
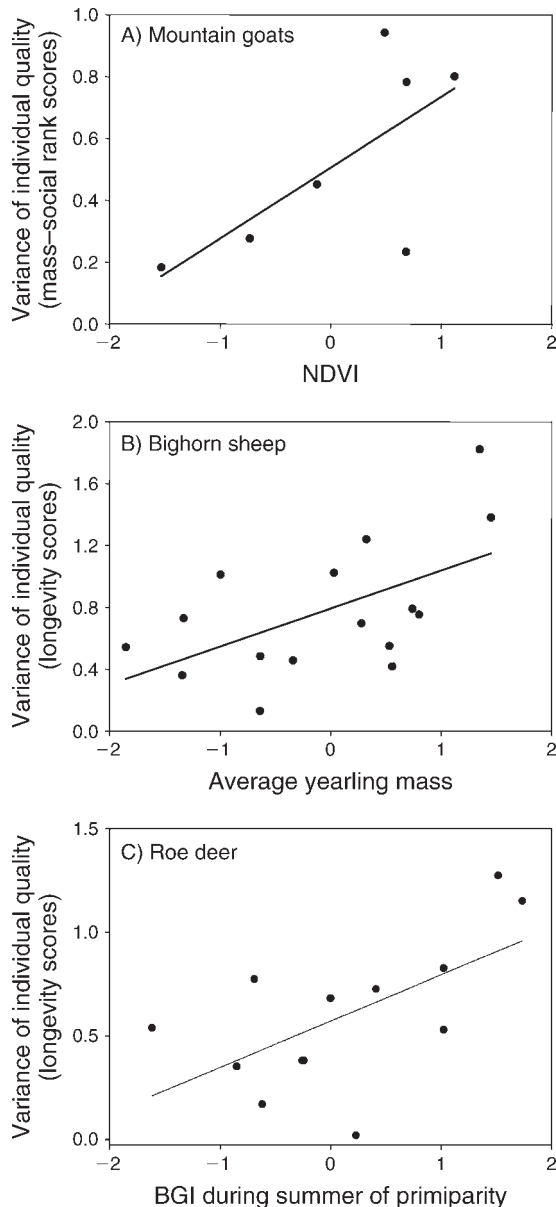
FIG. 4. Effects of environmental conditions on the variance of individual quality scores within a cohort. Individual quality is defined by mass–social rank scores in (A) mountain goats, and by longevity scores in (B) bighorn sheep and (C) roe deer. (A) Normalized difference vegetation index in the year of cohort birth, where high values represent early springs. (B) Average yearling mass in September in the year of cohort birth, where high values represent good years. (C) Bagnoul-Gaussen drought index in the summer of cohort primiparity, where high values represent dry summers.

Heterogeneity in individual quality and fitness

Weladji et al. (2006) found that the reproductive performance of short-lived female reindeer (*Rangifer tarandus*) decreased as they aged, whereas long-lived females maintained a high reproductive success until death. We also found a continuum of individual quality

opposing heavy, long-lived females that reproduced until their last breeding opportunity to light, short-lived females that stopped reproducing at least one year before death in both goats and sheep. Individual quality in deer followed a similar continuum, opposing heavy, long-lived females to light, short-lived females. Individual quality was positively related to MRS, mainly driven by body mass in goats and deer, by success in the last breeding attempt in goats and sheep, and by longevity in deer. Longevity is an appropriate measure of individual quality because it determines most of the variation in the number of breeding opportunities, a major component of lifetime reproductive success for females (Clutton-Brock 1988, Newton 1989), and it is positively related to MRS (this study). The latter correlation cannot be explained by a direct link between these traits because they are independent measures, and it provides strong support for the existence of a general quality continuum structuring individual variation in traits. In the absence of this quality continuum, we may expect a negative correlation between longevity and MRS, because high MRS during early life should lead to accelerated senescence and thus shorter lives (Hamilton 1966).

In mountain goats, the main axis of variation in quality was associated with adult mass and social rank, rather than longevity. Heavy and dominant females had greater MRS than light and subordinate ones. In sheep and deer, mass was positively correlated with longevity to define quality, but the positive relation between quality and MRS did not account for much variation in these two species. In addition, although variation in adult mass was similar among species (coefficient of variation for goats = 7.0, sheep = 7.1, deer = 8.0), mass accounted for almost half of the variation in MRS in goats, compared with only 2% and 11% in sheep and deer, respectively. These results suggest that mass has a stronger influence on the annual reproductive success of goats compared with sheep and deer. Furthermore, female goats are very aggressive toward conspecifics, in comparison with other ungulates (Fournier and Festa-Bianchet 1995), and high social rank improves reproductive success, particularly in young females (Côté and Festa-Bianchet 2001b). Dominance has a positive influence on both reproductive effort and success in other female ungulates (Clutton-Brock et al. 1986, Holand et al. 2004) and in other long-lived species (Reiter et al. 1981, Pusey et al. 1997). Nevertheless, no relationship between female dominance and reproductive success was found in about half of the studies reviewed by Ellis (1995), indicating that dominance does not have the same ecological influence in all species. Although we could not assess the influence of social rank in sheep and deer, our results suggest that social rank or other traits related to phenotypic quality may be less important for MRS in sheep and deer than in goats. Female goats have a more conservative reproductive tactic than sheep and deer (Festa-Bianchet and Côté 2008) and their body condition may be more critical for

yearly reproductive success, possibly explaining why adult female goats skipped about one in five breeding opportunities, while sheep did so rarely and roe deer almost never.

In iteroparous species, complex age-specific patterns involving trade-offs between reproduction early and late in life (Hamilton 1966) should allow individuals to develop different reproductive tactics. Variation in individual strategies should thus be greater in long-lived than in short-lived species. We should therefore expect to find a greater influence of individual quality on MRS in species at the slow end of the continuum of life-history traits (i.e., mountain goat) than in species located at the fast end (i.e., roe deer). In our study, the strength of the relationship between individual quality and MRS was greater in roe deer than in mountain goats, in opposition with this expectation. In addition, individual quality accounted for much more variation in MRS for mountain goats than for roe deer, whereas it explained almost no variation in bighorn sheep, located in between deer and goats on the life-history continuum. Therefore, our results do not support the expectation of a greater influence of variations in individual quality in slower than in faster species. One possibility is that while the three populations differed markedly in their ranking on the slow–fast continuum of life-history strategies among large herbivores, that variation was relatively small at the scale of mammalian life-history strategies. Most large herbivore species share many components of their life-history strategy (Gaillard and Yoccoz 2003), such as marked iteroparity and longevity. Therefore, even though our study species differ in life-history traits, they form a relatively homogeneous group of species that remain within the same broad life-history strategy (Gaillard et al. 1989). Future studies should evaluate if the strong and positive covariation among iteroparity, longevity, and life cycle speed usually found among strategies disappears within a specific type of life-history strategy.

Environmental conditions and cohort effects on heterogeneity in quality

Environmental conditions during early development affected individual quality in all populations, but results differed among species. Population density did not influence individual quality in goats and deer. Density dependence in life-history traits has not been observed in the goat population (Festa-Bianchet and Côté 2008) and was not expected in roe deer because of the limited variability in population size over the study (Gaillard et al. 1998b). In sheep, successive cohorts appeared to be of progressively lower quality, a likely consequence of the increase in density at Ram Mountain between 1975 and 1995, when strong density-dependent effects on juvenile survival and age at first reproduction were recorded (Jorgenson et al. 1993, 1997, Portier et al. 1998). The influence of winter conditions on cohort quality in sheep appears counterintuitive; winters with high precipitation

and cold temperature resulted in high-quality cohorts. Interestingly, winter lamb survival of the cohorts studied tended to be lower during severe winters (Portier et al. 1998). If unfavorable winters increased mortality of low-quality individuals, then cohorts experiencing mild winters as lambs would retain more low-quality individuals than those affected by severe winters. Therefore, viability selection may account for the positive effect of winter severity on cohort quality.

For roe deer, summer drought in the year of birth strongly affected individual quality. Deer have access to lower quantity and/or quality of resources during dry summers compared with wet ones (Toïgo et al. 2006). Summer drought is a critical factor for deer, affecting performance during early life (summer survival of fawns [Gaillard et al. 1997], winter fawn mass [Toïgo et al. 2006]), and with long-lasting effects on individual quality of adults (Pettorelli et al. 2002). Unfavorable conditions faced by primiparous females also influenced individual quality. Because they have not yet reached asymptotic mass (Gaillard et al. 2000), primiparous does must allocate resources to both growth and reproduction (Stearns 1992). Because roe deer do not rely on body reserves for reproduction (Andersen et al. 2000), environmental conditions in the year of primiparity should affect both the success of the first reproduction (Jönsson 1997) and the quality of a cohort throughout life, as our results suggest. In species where age at first reproduction varies, unfavorable environmental conditions in early life can delay primiparity (Bercovitch and Berard 1993), but early primiparity can reduce later reproductive success (Sydeman and Nur 1994).

Compared with bighorn sheep and roe deer, we did not find strong evidence that environmental conditions affected individual quality in mountain goats, possibly because goats have the most conservative reproductive tactic of the three populations studied. Nevertheless, heterogeneity in individual quality varied among cohorts, suggesting that environmental conditions in the year of birth affected female quality. Female goats tended to be of higher quality if they were born during early springs compared with late ones. Early springs provide good forage conditions: poor vegetation quality in early June reduced mass gain of kids of both sexes and lowered survival of female kids (Côté and Festa-Bianchet 2001a). Mass gain of kids was also lower in years of higher maximum increases in NDVI during vegetation green-up than in years of lower increases (Pettorelli et al. 2007), with high maximum increases tending to occur in late rather than in early springs (Hamel et al., in press). Kids born in years with early springs may benefit from early access to high-quality forage, and their mothers should have more resources to allocate to reproduction.

Lomnicki (1978) proposed that variance in individual quality should be low when environmental conditions are favorable, because every individual would have access to the resources needed to perform well, and

variance in individual quality would mainly result from differences in genotypes. He predicted that, as conditions deteriorate, variance should increase because some individuals could monopolize resources while others would starve. We confirmed his prediction only in roe deer, where variance in individual quality within cohorts tended to be greater during dry summers, when resource availability was restricted compared with wet summers (Toïgo et al. 2006). Nevertheless, variance could also decline if conditions become very harsh, because resources would then be limiting for all individuals and each one would perform poorly. This may explain the trends found for bighorn sheep and mountain goats. The decline of variance in individual quality found in goat and sheep cohorts as environmental conditions deteriorated suggests that these populations may be more limited by environmental conditions than the deer population. This idea is also supported by the lower ratio of lambda observed over maximum lambda in both goats and sheep compared with deer (goats, $1.01/1.30 = 0.78$; sheep [before population decline], $1.09/1.33 = 0.82$; deer, $1.28/1.40 = 0.91$) (maximum lambda for sheep, deer, and goats are, respectively, from Hass [1989], Gaillard et al. [1998a], and Williams [1999]). Furthermore, the sheep and goat populations occupy alpine habitats where they experience harsh climatic conditions throughout much of the year. The sheep population also suffered from high density and heavy cougar predation during part of the study. In contrast, the habitat of roe deer at Trois Fontaines was highly productive, with forestry practices and fertilization improving food availability (McLoughlin et al. 2007), and yearly removals of unmarked individuals maintaining the population at low density. Therefore, these results suggest that variance in individual quality may peak at intermediate environmental conditions, until conditions deteriorate to a threshold that leads to a reduction of variance among individuals.

Alternatively, roe deer might fit better with Lomnicki's prediction than do sheep and goats because they are territorial, and therefore some individuals could monopolize resources in unfavorable years (McLoughlin et al. 2007). In gregarious species such as sheep and goats, slight deterioration of environmental conditions might instead reduce the variance in access to resources and concomitantly decrease variance in individual performance. In red deer (Cervus elaphus), for example, Nussey et al. (2005b) showed that the potential for increasing birth mass in warm springs declined with increasing density for all females. A review by Charmantier and Garant (2005) suggests that harsh environmental conditions tend to lower heritability, because the proportion of environmentally induced variance in phenotypic traits increases and/or the expression of genetic variance decreases (see also Wilson et al. 2006). Therefore, both favorable and unfavorable environmental conditions could lead to greater variance in individual quality, owing to greater environmental

influences under poor conditions and to greater genetic influences under good conditions. Poor conditions during early development could also result in greater filtering of individuals, which could lead to lower variance among survivors in cohorts born under unfavorable than under favorable conditions.

Although our study is based on only three populations, it is, to our knowledge, the first empirical test of Lomnicki's prediction on the variance of individual quality in natural populations of vertebrates. Longitudinal studies on a larger number of populations experiencing a wide range of environmental conditions would be very useful to discriminate between these hypotheses. As evidence of climate change accumulates (Mann et al. 1999, Keller 2007), a better understanding of variance in life-history traits in relation to environmental variation could provide valuable insights into the fundamental consequences of an unstable climate on individual quality and life-history traits, as well as indirect consequences on population dynamics and selection processes.

Heterogeneity in individual quality and selection

Because individual quality strongly influenced fitness, life-history traits that define quality should be under selective pressure. In mountain goats, offspring mass in summer is positively related to maternal mass (Côté and Festa-Bianchet 2001a), as is often the case for large herbivores (Hewison et al. 2005). In bighorn sheep, weaning mass is positively correlated to mass as an adult (Festa-Bianchet et al. 2000), but the correlation between maternal and offspring mass at weaning is weak (Festa-Bianchet and Jorgenson 1998). Some traits affecting heterogeneity are heritable, as demonstrated by the high heritability of adult mass at Ram Mountain (Réale and Festa-Bianchet 2000, Coltman et al. 2005). The heritability estimate for longevity of bighorn ewes, however, is much lower than for body mass (Coltman et al. 2005). Life-history traits directly associated with individual fitness are generally less inheritable than morphological traits, and environmental canalization should limit selection on traits with high potential impacts on fitness (Stearns and Kawecki 1994, Pfister 1998, Gaillard and Yoccoz 2003; but see Coltman et al. 2005). This reduces the potential for selection for high-quality individuals in species where performance is not strongly correlated with phenotypic quality. Furthermore, a large amount of variance in individual quality was accounted for by cohort effects, through the influence of environmental conditions experienced early in life. Most of these effects are unpredictable and should thus contribute in maintaining heterogeneity independently of selection (Lindström and Kokko 2002, Wilson et al. 2006). Interactions between genotype and environment can also enhance heterogeneity (Endler 1995, Coulson et al. 1998), and are probably responsible for variance among individuals of the same cohort.

Our multivariate approach revealed that in each of three populations there was at least one covariation among life-history traits that defined a gradient of individual quality. We also showed that differences in individual quality can be related to several combinations of variables that are uncorrelated to each other (e.g., PC1 and PC2 in mountain goat). Because the fitness consequences of variation in one trait are often contingent upon concomitant variation of other traits, this holistic approach should provide more accurate information on selection processes, similarly to multivariate selection measures used in evolutionary studies (Blows 2007). In particular, we were able to show for the first time that between one-third and one-half of variation in individual quality in populations of large herbivores is accounted for by variation in environmental conditions during early life.

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APPENDIX

Summary of variables that were used for each population for the analyses of heterogeneity in individual quality and the influence of environmental conditions on individual quality (*Ecological Archives* E090-137-A1).