

Quantitative genetics of life-history traits in a long-lived wild mammal

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Quantitative genetic studies of life-history traits in wild populations are very rare, yet variance/covariance estimates of these traits are crucial to understanding the evolution of reproductive strategies. We estimated heritabilities (h^2) of several life-history traits (longevity, age and mass at primiparity, and reproductive traits) in two bighorn sheep (*Ovis canadensis*) populations, and both phenotypic (r_P) and genetic (r_A) correlations between life-history traits in one population. We included adult mass in our analyses because it is related to several life-history traits. We used the mother–daughter regression method and resampling tests based on data from long-term monitoring of marked females. Contrary to the theoretical prediction of low heritability for fitness-related traits, heritability estimates in the Ram Mountain population ranged from 0.02 to 0.81 (mean of 0.52), and several were different from zero. Coefficients of variation tend to support the hypothesis of a higher environmental influence on life-history traits. In contrast, at Sheep River we found low heritabilities of life-history traits. Phenotypic correlations varied between -0.09 and 0.95 . Several genetic correlations were strong, particularly for different reproductive traits that are functionally related, and ranged from -0.34 to 1.71 . Overall, genetic and phenotypic correlations between the same variables were similar in magnitude and direction. We found no phenotypic or genetic correlations suggesting trade-offs among life-history traits. Bighorn sheep may not form the large, outbred populations at equilibrium that are assumed by both Fisher's fundamental theorem and by theories predicting antagonistic pleiotropy between life-history traits. Alternatively, the absence of negative genetic correlations may result from genetic variation in ability to acquire resources or from novel environmental conditions existing during the study period.

Keywords: bighorn sheep, body mass, heritability, genetic/phenotypic correlations, genetic variance, longevity, *Ovis canadensis*, primiparity, reproductive success.

Introduction

The evolution of life-history traits depends upon the existence and magnitude of genetic variability, and is affected by the nature of genetic correlations among traits subject to natural selection (Lande, 1982; Falconer & Mackay, 1996; Roff, 1997). To understand evolutionary processes in natural populations, it is therefore essential to estimate patterns of variances and covariances among life-history traits. Natural selection should decrease the additive genetic variance of a character (Fisher, 1930). Since life-history traits are strongly associated with fitness, they are expected to be under strong directional selection, and therefore should exhibit little additive genetic variance (Fisher, 1930). Heritabil-

ity (h^2), defined as the ratio of additive genetic to phenotypic variance, illustrates the evolutionary potential of a character (Falconer & Mackay, 1996), and should be low or null for life-history traits. Several empirical studies have corroborated the hypothesis of low heritability of life-history traits compared to morphological characters that are only weakly associated with fitness (Gustafsson, 1986; Mousseau & Roff, 1987; Kruuk *et al.*, 2000). An alternative but not incompatible explanation is that life-history traits are generally affected by morphological or physiological characters which are themselves influenced by many genetic and environmental factors, and are thus subject to environmental influences (Price & Schluter, 1991; Houle, 1992). As a result, life-history traits may be characterized by high additive genetic variance and have the potential to evolve (Houle, 1992). Contrary to the prediction of Fisher's hypothesis, life-history traits can indeed exhibit significant heritability (Mousseau & Roff, 1987).

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Many life-history theories rest on the fundamental assumption of genetic trade-offs caused by antagonistic pleiotropy (Williams, 1957; Roff, 1992; Stearns, 1992). Antagonistic pleiotropy means that traits are genetically related so that an increase in the fitness expression of one trait decreases the fitness expression of the other (Williams, 1957; Lande, 1982). The expectation of a trade-off between traits resides in the necessity for an individual to distribute limited resources among different traits (Roff, 1992; Stearns, 1992). Trade-offs can occur at the physiological, ecological and genetic (evolutionary) level. Evolutionary biologists are mostly concerned with genetic trade-offs, since these alone are implicated in the evolution of a character (Reznick, 1985). For reasons equivalent to those predicting the erosion of genetic variance by natural selection, genetic correlations between life-history traits are expected to be low or negative (Lande, 1982; Roff, 1996). A genetic trade-off between two traits may limit the erosion of genetic variance of both traits (Lande, 1982; Roff, 1997), by inducing a response of one trait to selection pressures on the other (correlational selection; Lande & Arnold, 1983), and sometimes leading to temporary suboptimal expression of the traits (Lande, 1982).

A full understanding of the evolution of life-history traits requires the estimation of variance-covariance matrices in many populations of different species. These estimates, however, require trait measurements on many individuals of known parentage (Falconer & Mackay, 1996; Roff, 1997). Consequently, most quantitative genetic studies have been done in the laboratory, with controlled environments and breeding designs. Little is known about quantitative genetics of natural populations. Quantitative genetics may be studied in natural populations using data obtained from long-term studies of behavioural ecology (Cheverud & Moore, 1994; Réale *et al.*, 1999).

Genetic correlations (r_A) require a knowledge of pedigrees and are difficult to estimate in wild populations, but phenotypic correlations (r_P) are easier to obtain and could be used as a substitute if they are a reliable index of genetic correlations (Cheverud, 1988), as suggested by several studies (Roff, 1995, 1996; Reusch & Blanckenhorn, 1998), although others have found important differences between genetic and phenotypic correlations (Willis *et al.*, 1991; Hughes, 1995; see also Reznick, 1985; van Noordwijk & de Jong, 1986, for a discussion of the limits of using phenotypic correlations to determine evolutionary trade-offs).

We analyse long-term data sets from behavioural ecology studies of two bighorn sheep (*Ovis canadensis*) populations, collected from 1973 to 1998 at Ram Mountain and from 1981 to 1998 at Sheep River. In both populations, most individuals were marked before

they reproduced and were monitored over their lifetime. We investigate if there is significant additive genetic variance (or heritability) of life-history traits in females and also determine if the additive genetic variance of given traits is similar in the two populations. We estimate phenotypic and genetic correlations between life-history traits in the Ram Mountain population to test the hypothesis of evolutionary trade-offs between life-history traits. Finally, we compare phenotypic and genetic correlations to see if phenotypic correlations reliably estimate genetic correlations. The characters considered were age at primiparity, longevity, fecundity, weaning success, and reproductive success. We also considered body mass at primiparity and adult body mass. The fitness consequences of size at first reproduction are a fundamental concern of life-history theories (Roff, 1992; Stearns, 1992), but empirical data on the genetic variability in this trait are rare. The quantitative genetics of adult mass at Ram Mountain have already been studied (Réale *et al.*, 1999), but we included adult mass in these analyses because of its many effects on life-history traits (Jorgenson *et al.*, 1993; Festa-Bianchet *et al.*, 1998; Bérubé *et al.*, 1999). Here we did not correct body mass to control for the effects of population density, allowing a comparison with previous heritability estimates obtained after controlling for density (Réale *et al.*, 1999).

Methods

Study sites and populations

The Ram Mountain population Data used in this paper were collected between 1973 and 1998 in the bighorn sheep population at Ram Mountain, Alberta (52°N, 115°W; elevation 1082–2173 m). The 38-km² study area, at 1082–2173 m elevation, is an isolated mountainous outcrop surrounded by coniferous forest. The number of adult sheep varied from 60 to 152 during the study. From 1973 to 1981, yearly ewe removals kept the population at 30–33 adult ewes. After 1981, the population increased, peaked at 104 ewes in 1992, then declined because of density-dependent effects on reproduction and survival (Jorgenson *et al.*, 1997; Festa-Bianchet *et al.*, 1998).

Each year, sheep were captured from late May to early October in a corral trap baited with salt. All ewes have been marked since 1976. Most adult ewes were captured two to six times each year, and weighed at each capture. Body mass was adjusted to September 15 using each individual's own rate of mass gain obtained from multiple captures. By mid-September adult ewes were at or near their maximum yearly mass. Festa-Bianchet *et al.* (1996) provide more details on the capture

schedule and mass adjustments. Although carcasses were rarely recovered, during the summer each individual was observed many times and female dispersal was extremely rare (Jorgenson *et al.*, 1997), therefore ewes not observed during one year were considered dead. Ewe reproductive status was assessed by examination of the udder at the beginning of the summer and from field observation of mother–offspring associations. In most years, over 80% of the lambs that survived to a few weeks of age were captured and marked before October. All unmarked lambs that survived the winter were marked the following year as yearlings, but their mothers could not be identified. Mother–lamb relationships were determined by observing marked lambs repeatedly suckling from marked females from May to October, a reliable index of maternity since allosuckling has never been observed on Ram Mountain. Ewes always produced singleton lambs, therefore common maternal environmental effects on heritability should be reduced. Because bighorn ewes are highly philopatric, do not preferentially associate with adult kin, and all ewes in the population use the same home range, common environmental effects on heritability estimates should be very limited (Réale *et al.*, 1999).

The Sheep River population Data were collected at Sheep River between 1981 and 1998. During the study the number of adult sheep ranged from 73 to 100. Most sheep were captured only once, usually as lambs, using immobilizing drugs and a dart gun, therefore data on body mass were not available for this population. All adult ewes have been marked since 1987. Data on life-history traits were collected from May to November, using the same observation techniques as at Ram Mountain.

Measurements

For both populations, we analysed information on the following traits.

1 Age at primiparity. Females breed in late autumn, and give birth in late May. Age at primiparity (AP) is the age at which we first saw evidence of lactation. Females that died before reaching sexual maturity were not considered. The minimum age at primiparity is two years (Jorgenson *et al.*, 1993).

2 Longevity. We measured longevity (LG) as the age at death for individuals that survived to 1 year of age. Almost all ewes produced one or more lambs that died before reaching 1 year of age. Some lambs died before being marked. Including individuals that died before 1 year of age would therefore lead to a dramatic decrease in heritability of the trait, because of stochastic effects on juvenile mortality, particularly for a species

for which females produce few offspring during lifetime. Ewes younger than 9 years that were removed artificially or were still alive in 1998 were not considered in any analyses. We included females living more than 8 years because survival senescence begins at that age (Jorgenson *et al.*, 1997).

3 Indices of lifetime reproduction. We calculated three indices of lifetime reproduction for ewes surviving to at least 2 years of age: lifetime fecundity (LFEC) was the number of lambs produced; lifetime weaning success (LWS) was the number of lambs weaned, and lifetime reproductive success (LRS) was the number of lambs surviving to 1 year of age. Ewes for which lifetime reproduction was unknown or that died before 2 years of age were not considered.

4 Indices of early reproduction. Fecundity (FECE), weaning success (WSE), and reproductive success (RSE) early in life were measured between 2 and 7 years of age, including females that died before age 7. Individuals missing more than 1 year of data between 2 and 7 years of age (18 females had one missing value, or 10.4% of the total number of females for which we had data) or that died before 2 years of age were not considered. We chose 7 years of age to distinguish between early and late reproduction because senescence in ewe survival is evident from about 8 years of age in both populations (Jorgenson *et al.*, 1997).

Data for the following traits were either unavailable or insufficient for analyses for the Sheep River population, therefore their analysis was limited to the Ram Mountain population.

1 Indices of late reproduction. Fecundity (FECL), weaning success (WSL), and reproductive success (RSL) late in life were measured between 8 years of age and death. Individuals with missing data after 8 years of age were not considered (there were no females with just one year of missing data).

2 Morphological indices. We considered body mass at primiparity (BMP — mass adjusted to mid-September the year preceding first lambing, about 2 months before conception); and adult mass (ABM — mean mid-September mass between 3 and 11 years of age, corrected for age effects).

Statistical analyses

Density-related environmental factors can affect phenotypic variability in life-history traits, and population density in the Ram Mountain population increased during the study. Nevertheless, for several reasons we did not adjust the data for density effects before analyses. First, we were interested in estimating heritability in the actual conditions in the wild. Second, it was not obvious how to standardize traits such as lifetime

fecundity, given that population size doubled over some ewes' lifetime, and that the effects of population density vary with reproductive effort (Festa-Bianchet *et al.*, 1998) and probably involve time lags.

Heritability and genetic correlations were estimated with the mean-daughters/mother regression method (Falconer & Mackay, 1996). Body mass data were normally distributed (Shapiro–Wilks test; body mass at primiparity: $W=0.98$, $P=0.55$; adult body mass: $W=0.97$, $P=0.1$). For other traits we used box-cox transformation (log transformation for age at primiparity and late reproductive traits, and square-root transformation for longevity, lifetime, and early reproductive traits). Most of our data, however, were not normally distributed. We therefore conducted randomization tests (Manly, 1991) to estimate the probability associated with heritability and correlation estimates. We regressed the mean value of daughters and the value of mothers for each trait. Heritability is the slope of the regression multiplied by 2 (Falconer & Mackay, 1996). Data for daughters were then shuffled 4999 times and heritability was estimated for each new randomization trial. We tested the null hypothesis H_0 ($h^2=0$) against its alternative H_1 ($h^2 > 0$; one-tailed test). The significance level to accept H_0 is given by $(n + 1)/5000$ where n is the number of times a randomised h^2 is equal to or greater than the observed h^2 , and the additional 1 allows to account for the observed h^2 (Manly, 1991). Standard errors of heritabilities were estimated with the probability obtained from the randomization test assuming that h^2/SE was normally distributed (Roff & Bradford, 1996). Heritability estimated with the single parent–offspring method may be biased by assortative mating (Falconer & Mackay, 1996). However, due to the promiscuous mating system, strong male dominance over females, and the high intermale variance in reproductive success (Hogg & Forbes, 1997) there is no evidence that assortative mating occurs in this species. We calculated the coefficient of variation of traits when heritability estimates were positive, where the coefficient of additive genetic variation $CV_A = 100\sqrt{V_A/\bar{X}}$ and the residual coefficient of variation $CV_R = 100\sqrt{V_P - V_A/\bar{X}}$ (Houle, 1992). V_A was previously estimated by multiplying V_P by h^2 since $h^2 = V_A/V_P$ (Falconer & Mackay, 1996). We compared heritability estimates between populations using ANCOVAs and randomization tests (comparison of slopes of mother–daughters regression).

Phenotypic correlations (r_P) were the correlation coefficients between individual values of traits X and Y . All ewes for which we had both values of X and Y were used for phenotypic correlation estimations. Data for Y -values were shuffled 4999 times and r_P was estimated for each new randomization. We tested the

null hypothesis H_0 ($r_P=0$) against its alternative H_1 ($r_P \neq 0$; two-tailed test). The significance level to accept H_0 is given by $(n + 1)/5000$ where n is the number of times absolute value of h^2 estimated from randomization procedure equals or exceeds the observed h^2 . Additive genetic correlations (r_A ; genetic correlations below) were estimated from the arithmetic mean between correlation coefficients $r = \text{cov } XY / \sqrt{(\text{cov } XX \text{ cov } YY)}$, where cov_{XY} is the cross-covariance obtained from both the value of mothers for trait X on the mean value of daughters for trait Y and the value of mothers for trait Y on the mean value of daughters for trait X , and cov_{XX} and cov_{YY} were the covariances of the value of mothers on the mean value of daughters for each trait (Falconer & Mackay, 1996). We calculated covariances based on samples with all the mother/mean-daughters pairs available for that trait combination. Genetic correlations were estimated only for traits for which the null hypothesis “ $h^2=0$ ” has been rejected at $\alpha=0.1$. Data were shuffled 4999 times and r_A was estimated from the two randomised cross-covariances and as indicated above for each new randomization. We tested the null hypothesis H_0 ($r_A=0$) against its alternative H_1 ($r_A \neq 0$; two-tailed test) as described above for r_P . Values for age at primiparity were multiplied by -1 so that females that reproduced late in life had lower values than females that reproduced early in life. Therefore, a positive correlation between age at primiparity and another trait actually reflects an absence of trade-off between these two traits.

To assess whether or not phenotypic correlations are good indices of genetic correlations, we calculated the least squares regression between r_A and r_P , and we used a Mantel test (Cheverud, 1988; Roff, 1995). We calculated the average disparity D between the two matrices as:

$$D = \sum |r_{A,i,j} - r_{P,i,j}|/n,$$

where i and j are two different traits, and n is the number of correlations (Roff, 1995).

Results

Trait means and variances

For those traits available for both populations, means and phenotypic variability were very similar between populations (Table 1). Mean age at primiparity was about 3 years. Females lived up to 19 years, with a mean longevity of 7 years. Overall, ewes weaned 70% of the lambs produced during their lifetime, and about 35% of the lambs survived to one year of age. At Ram Mountain, the mean body mass at primiparity was

Table 1 Means, phenotypic variances (V_p) and ranges of life-history traits (untransformed) in bighorn ewes of the Ram Mountain (RM) and Sheep River (SR) populations, Alberta. Characters: longevity (LG), age at primiparity (AP), lifetime fecundity (LFEC), lifetime weaning success (LWS), lifetime reproductive success (LRS), fecundity between 2 and 7 years of age (FECE), weaning success between 2 and 7 years of age (WSE), reproductive success between 2 and 7 years of age (RSE), fecundity after 7 years of age (FECL), weaning success after 7 years of age (WSL), reproductive success after 7 years of age (RSL), body mass at primiparity (BMP), adult body mass (ABM)

Trait	Population	N	Mean	V_p	Range
AP (year)	RM	175	3.19	0.82	2–6
	SR	108	2.76	0.75	2–7
LG (year)	RM	218	7.06	19.08	1–19
	SR	151	7.07	21.70	1–18
LFEC (no. of lambs produced)	RM	163	5.33	14.88	0–15
	SR	103	5.25	13.95	0–13
LWS (no. of lambs weaned)	RM	163	3.74	9.26	0–14
	SR	103	3.53	9.06	0–12
LRS (no. of lambs surviving to 1 year)	RM	163	1.87	3.62	0–9
	SR	103	2.04	3.72	0–10
FECE (no. of lambs produced)	RM	174	3.40	3.47	0–6
	SR	112	3.57	3.31	0–6
WSE (no. of lambs weaned)	RM	174	2.45	2.48	0–6
	SR	112	2.49	2.58	0–6
RSE (no. of lambs surviving to 1 year)	RM	174	1.27	1.49	0–5
	SR	112	1.40	1.46	0–5
FECL (no. of lambs produced)	RM	103	3.18	5.91	0–10
WSL (no. of lambs weaned)	RM	103	2.11	3.91	0–9
RSL (no. of lambs surviving to 1 year)	RM	103	0.95	1.46	0–6
BMP (kg)	RM	130	60.4	55.2	43.0–81.0
ABM (kg)	RM	200	71.1	20.0	60.1–82.6

60 kg but individual females ranged in mass from 43 to 81 kg in the September preceding their first parturition. The variability in mass at primiparity was probably due to the wide range in age at primiparity. Some ewes did not reproduce until they reached their adult body mass. Mean adult body mass in mid-September was about 70 kg, again with considerable interindividual variability.

Heritabilities and evolvability

Heritability estimates for Ram Mountain ewes varied between 0.02 and 0.81 with a mean of 0.52 (Table 2; Fig. 1). The lowest heritabilities were for body mass at primiparity (BMP) and late fecundity (FECL). Late-life reproductive success also showed nonsignificant heritability. Heritabilities of longevity and early fecundity had probabilities between 0.05 and 0.1. Heritability estimates for all other traits were higher than 0.40 and significantly different from zero. H_0 ($h^2 = 0$) was rejected in eight of 13 cases (at $\alpha = 0.05$; Table 2). The probability of getting eight or more significant estimates of 13 just by chance, following a binomial distribution, is 4.0×10^{-8} .

Common environmental conditions between mothers and their daughters may lead to an overestimate of the heritability of some traits. For example, females delayed primiparity as population density increased (Jorgenson *et al.*, 1993). Because population density generally increased with time from 1981 to 1998, high density could lead to an increase in age of primiparity for both late-born mothers and their daughters, independently of the heritability of the trait. Most mothers, however, were born at low density before 1987 (percentage of families with mothers born before 1987; AP: 99%; LG: 85%; lifetime reproductive traits: 89%; early reproductive traits: 89%; late reproductive trait: 89%). Therefore, in most cases mothers and daughters experienced different environmental conditions.

The coefficients of genetic and of residual variation were low for body mass, intermediate for age at primiparity, and high for other life-history traits. We found higher CV s for measures of reproductive success: lifetime, early and late. CV s generally increased for reproductive traits (FEC, WS or RS) between early and late reproduction, and as reproductive traits were measured further away from birth, from fecundity to lamb survival to 1 year. For morphological traits, there

Table 2 Heritability (h^2) estimates, additive genetic (V_A) variances, and coefficients of additive genetic (CV_A) and residual (CV_R) variations of life-history traits in bighorn ewes of the Ram Mountain population. Estimates were obtained by the mother–daughters regression method on transformed data. Family size is indicated by the number (with range in brackets) of daughters per family. The probability that a heritability estimate differs from zero (one tailed tests) was obtained with randomization tests, and SEs were obtained from randomization test probabilities (see text). Character abbreviations are the same as in Table 1: AP, FECL, WSL and RSL were log transformed and LG, LFEC, LWS, LRS, FECE, WSE and RSE were square-root transformed (see text). V_A , CV_A and CV_R were calculated on transformed values

Trait	No. of families	Family size	h^2 (SE)	P	V_A	CV_A	CV_R
AP	66	1.5 (1–4)	0.53 (0.33)	0.05	0.004	10.62	10.00
LG	85	1.6 (1–5)	0.46 (0.24)	0.07	0.350	22.89	24.80
LFEC	66	1.4 (1–5)	0.66 (0.32)	0.02	0.545	33.39	23.96
LWS	66	1.4 (1–5)	0.81 (0.34)	0.004	0.506	38.09	18.45
LRS	66	1.4 (1–5)	0.62 (0.28)	0.02	0.242	36.08	28.24
FECE	72	1.5 (1–5)	0.76 (0.51)	0.07	0.264	27.78	15.61
WSE	72	1.5 (1–5)	0.74 (0.36)	0.02	0.209	28.71	17.02
RSE	72	1.5 (1–5)	0.68 (0.29)	0.02	0.158	33.41	22.92
FECL	34	1.4 (1–3)	0.05 (0.38)	0.45	0.004	11.39	49.67
WSL	34	1.4 (1–3)	0.70 (0.40)	0.05	0.057	58.43	38.25
RSL	34	1.4 (1–3)	0.40 (0.32)	0.12	0.022	67.42	82.57
BMP	41	1.4 (1–4)	0.02 (0.28)	0.48	1.104	1.74	12.18
ABM	85	1.5 (1–5)	0.41 (0.18)	0.01	8.200	4.03	4.83

was an increase in CV_A and a decrease in CV_R comparing mass at primiparity to adult body mass.

Heritability estimates at Sheep River were lower than those at Ram Mountain and not significant (Table 3). The heritabilities of age at primiparity, early fecundity and reproductive success had negative estimates. Lifetime reproductive success, lifetime and early weaning success, lifetime fecundity and longevity had low heritabilities ranging from 0.01 to 0.32. Among the traits with positive heritability estimates, lifetime weaning success and early weaning success had low CV_A , and lifetime reproductive success had a high CV_R . The highest heritability at Sheep River was for longevity (0.32). The probability that heritability estimates differed between populations was significant only for age at primiparity (Table 3). For traits for which CV s were available, lower heritability at Sheep River seemed associated with both a lower CV_A and a higher CV_R than at Ram Mountain. CV s for longevity were similar in both populations.

Phenotypic and genetic correlations among traits in the Ram Mountain population

Phenotypic correlations ranged from -0.09 to -0.95 , with a mean of absolute values of $r_P = 0.57$. Genetic correlations ranged from -0.34 to 1.71 , with a mean of absolute values $r_A = 0.80$ (Table 4). About 67% (30/45) of r_A and 80% (36/45) of r_P coefficients were significantly different from zero at $\alpha = 0.05$. Correlations between life-history traits and adult body mass were

not significantly different from zero. Estimates of genetic correlations had to be very high to be statistically different from zero, because of the moderate sample sizes (62–85 mother–daughters pairs). All the genetic and phenotypic correlations between life-history traits were positive. H_0 ($r_A = 0$) was rejected in 31 of 45 cases (at $\alpha = 0.05$; Table 4). The probability of getting 31 or more significant estimates of 45 just by chance, following a binomial distribution, is 1.8×10^{-15} .

The regression between r_A and r_P obtained with the least squares method was highly significant ($F_{1,43} = 206.284$, $P < 0.0001$, $r = 0.91$); the Mantel test produced a similar result ($P < 0.0001$). Overall, phenotypic correlations provided good estimates of genetic correlations, particularly for stronger correlations. However, despite this strong general relation between the two correlation matrices, the disparity index $D = 0.28$ indicates that individual values of r_A could be very different from the corresponding values of r_P .

Discussion

Heritability and evolvability of life-history traits in a long-lived mammal

The heritability of life-history traits in wild bighorn sheep can be substantial. As yet, very few studies have estimated quantitative genetic parameters of life-history traits in a wild mammal (Kruuk *et al.*, 2000). Heritability estimates of ewe life-history traits at Ram Mountain ranged from 0.02 to 0.81 with a mean of 0.58, but were

Table 3 Heritability (h^2) estimates, additive genetic (V_A) variances, and coefficients of additive genetic (CV_A) and residual (CV_R) variations for life-history traits in bighorn ewes of the Sheep River population. Estimates were obtained by the mother–daughters regression method on transformed data. Character abbreviations are the same as in Table 1: AP, FECL, WSL and RSL were log transformed and LG, LFEC, LWS, LRS, FECE, WSE and RSE were square-root transformed (see text). Diff is the absolute value of the difference in heritability between the two study populations (negative heritability estimates are considered equal to 0). P^* is the probability that heritability estimate from the two populations differed. Traits with negative heritability estimates were not considered for the calculation of V_A , CV_A , and CV_R . V_A , CV_A and CV_R were calculated on transformed values

Trait	Parameters for the Sheep River population							Comparison with Ram Mountain	
	No. of families	Family size	h^2 (SE)	P	V_A	CV_A	CV_R	Diff	P^*
AP	35	1.4 (1–4)	–0.42	—	—	—	—	0.53	0.04
LG	43	1.5 (1–4)	0.32 (0.42)	0.22	0.271	20.25	29.51	0.14	0.81
LFEC	29	1.4 (1–4)	0.19 (0.50)	0.35	0.148	17.46	36.05	0.47	0.44
LWS	29	1.4 (1–4)	0.05 (0.46)	0.50	0.032	9.83	42.85	0.76	0.12
LRS	29	1.4 (1–4)	0.19 (0.48)	0.36	0.076	19.44	40.14	0.43	0.42
FECE	31	1.6 (1–7)	–0.41	—	—	—	—	0.76	0.16
WSE	31	1.6 (1–7)	0.01 (0.56)	0.49	0.003	3.19	33.46	0.73	0.26
RSE	31	1.6 (1–7)	–0.10	—	—	—	—	0.68	0.14

low and not significant for the Sheep River population. The low heritability at Sheep River may have been due to the small sample size, and considering the large standard errors associated with the estimates it would be hard to find significant differences between the two populations.

There are almost no published estimates of heritability of life-history traits in long-lived species. Herskind *et al.* (1996) reported heritability around 0.25 for human longevity, and a captive population of olive baboons (*Papio hamadryas*) had high heritability (0.87) for age at primiparity (Williams-Blangero & Blangero, 1995). Kruuk *et al.* (2000) found low and nonsignificant heritability estimates for life-history traits in a wild Red deer population. The near-zero heritability estimate of body mass at primiparity is consistent with the low heritability of body mass at 2 years of age (the age at first reproduction for many ewes) found in the same population (Réale *et al.*, 1999). The heritability of adult mass of 0.41 is consistent with estimates found for morphological traits (Mousseau & Roff, 1987), and smaller than the estimate of 0.56 obtained for the same population after controlling for population density (Réale *et al.*, 1999).

Despite their importance for our understanding of the evolutionary process, estimates of (co)variance components of life-history traits in the wild are very rare (Campbell, 1997). Quantitative genetic analyses in natural populations cannot estimate all the components of phenotypic (co)variance that can be measured in the laboratory. For example, we could not separate maternal and dominance effects from environmental effects,

since we did not control mate choice and had no data on paternity. Common environment affecting both mothers' and daughters' traits, may bias heritability estimates (Falconer & Mackay, 1996). Because most mothers were born at low population density, and because many mothers reproduced under different conditions over their lifetime, common environmental effects should not strongly bias our heritability estimates.

Contrary to our expectations, life-history traits exhibited high heritability estimates at Ram Mountain. Natural selection should erode genetic variance for reproductive traits more rapidly than for weakly fitness-related traits (Fisher, 1930). Our heritability estimates were on average higher than the mean values reported for life-history traits of 0.26 by Mousseau & Roff (1987). Our results confirm that significant additive genetic variance of life-history traits can persist in natural populations (Mousseau & Roff, 1987). The alternative to Fisher's hypothesis are the hypotheses of Price & Schluter (1991) and Houle (1992), based on higher environmental effects on heritability of life-history traits than on other characters, and these hypotheses may explain our results. The lower heritability values of late vs. early reproductive traits argue against an attenuation of selection intensity with age leading to an increase in additive genetic variance for traits expressed later in life (Rose & Charlesworth, 1980; Charlesworth, 1993). However, due to small sample sizes for late reproduction these results should be interpreted with caution. Increases in CV 's suggest that late-life weaning and reproductive success were more affected by environmental conditions than early-life weaning and reproductive

Table 4 Phenotypic (r_P , below the diagonal) and genetic (r_A , above the diagonal) correlations between life-history traits in highhorn ewes of the Ram Mountain population, obtained with the mother–daughters regression method. Estimates were only done for characters that showed heritabilities with probability < 0.1 . Character abbreviations are the same as in Table 1. Probabilities (below correlations) were estimated with randomization test (two-tailed test; see text)

	LG	AP	LFEC	LWS	LRS	FECE	WSE	RSE	WSL	ABM
LG		0.32 (0.53)	1.04 (0.01)	1.04 (0.004)	1.27 (0.001)	0.69 (0.18)	1.08 (0.01)	0.83 (0.05)	1.24 (0.02)	0.34 (0.52)
AP	0.20 (0.02)		0.69 (0.12)	0.78 (0.03)	0.92 (0.02)	1.58 (0.004)	0.96 (0.02)	1.47 (0.008)	0.52 (0.24)	-0.22 (0.61)
LFEC	0.94 (0.0002)	0.50 (0.0002)		0.99 (0.002)	1.11 (0.001)	0.98 (0.02)	1.00 (0.008)	0.77 (0.03)	1.05 (0.01)	-0.0008 (0.99)
LWS	0.88 (0.0002)	0.51 (0.0002)	0.95 (0.0002)		0.89 (0.002)	1.03 (0.006)	0.88 (0.005)	0.54 (0.06)	1.32 (0.0002)	0.17 (0.62)
LRS	0.73 (0.0002)	0.58 (0.0002)	0.82 (0.0002)	0.87 (0.0002)		1.31 (0.001)	0.92 (0.005)	0.81 (0.01)	0.98 (0.02)	0.25 (0.53)
FECE	0.82 (0.0002)	0.58 (0.0002)	0.92 (0.0002)	0.87 (0.0002)	0.75 (0.0002)		0.99 (0.02)	1.00 (0.02)	1.71 (0.002)	-0.34 (0.53)
WSE	0.74 (0.0002)	0.49 (0.0002)	0.86 (0.0002)	0.91 (0.0002)	0.79 (0.0002)	0.91 (0.0002)		0.93 (0.005)	0.99 (0.02)	0.24 (0.58)
RSE	0.58 (0.0002)	0.54 (0.0002)	0.70 (0.0002)	0.75 (0.0002)	0.91 (0.0002)	0.72 (0.0002)	0.77 (0.0002)		0.61 (0.14)	0.46 (0.26)
WSL	0.82 (0.0002)	0.53 (0.0002)	0.84 (0.0002)	0.87 (0.0002)	0.69 (0.0002)	0.49 (0.0002)	0.46 (0.0002)	0.41 (0.0002)		0.51 (0.30)
ABM	0.08 (0.35)	-0.09 (0.31)	0.03 (0.74)	0.04 (0.66)	-0.07 (0.42)	0.04 (0.70)	0.01 (0.93)	-0.06 (0.52)	0.01 (0.92)	

success. These differences, however, may be partly due to the increase in population density throughout the study period. Late reproductive traits were measured on mothers and daughters while they probably experienced different environmental conditions (mothers at low density and daughters at high density). In contrast, early reproductive traits had a higher chance of being measured while mothers and daughters experienced the same population density. Changes in environmental conditions between parents and their progeny could decrease heritability (Sgrò & Hoffmann, 1998).

Phenotypic and genetic correlations, trade-offs, and the evolution of life-history traits

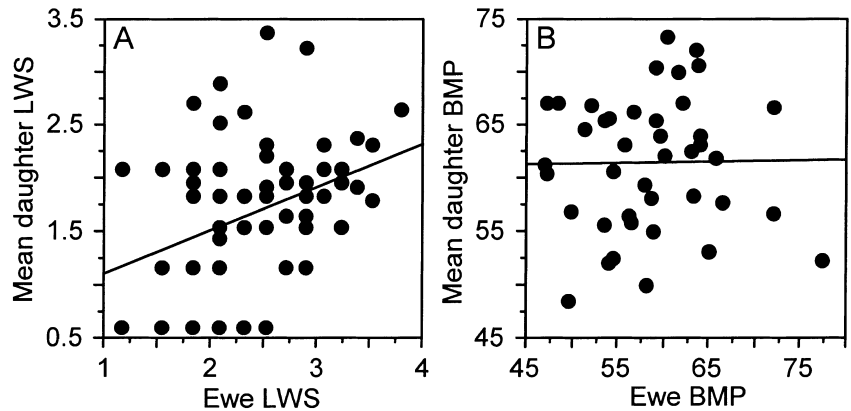
At Ram Mountain, we found no genetic or phenotypic correlations suggesting trade-offs among life-history traits. Genetic correlations between life-history traits were all positive, and several correlations were very high. Traits such as LFEC and LWS, for example, have similar h^2 estimates and such high correlations (both phenotypic and genetic) that it would be hard to consider them as two genetically different traits. It is worth noting that traits commonly assumed to be involved in evolutionary trade-offs (e.g. age at primiparity vs. longevity, age at primiparity vs. fecundity, longevity vs. fecundity, early (WSE) vs. late reproduction (WSL), or early reproduction vs. longevity; Stearns,

1992; Roff, 1992) showed positive genetic correlations, and three correlations out of six were significantly different from zero at $\alpha < 0.05$. Results of this study support previous research on the same populations that mostly reported positive phenotypic correlations among life-history traits (Festa-Bianchet *et al.*, 1995; Bérubé *et al.*, 1999). None of the genetic correlations between adult mass and life-history traits were significant. This again may be due to high sampling variance related to small sample sizes.

Our results suggest that phenotypic correlations could be used instead of genetic correlations when estimates are high, but that they were not as reliable for low correlation values, supporting previous studies (Cheverud, 1988; Roff, 1995, 1996; Reusch & Blanckenhorn, 1998; and references therein; but see references against in introduction). In general absolute values of r_A were higher than r_P (Roff, 1995; Reusch & Blanckenhorn, 1998).

According to life-history theories, genetic trade-offs among life-history traits would result from antagonistic pleiotropy, or negative correlations between traits (Williams, 1957). Quantitative genetic models of life-history evolution suggest that in large outbred populations at equilibrium the matrix of genetic (co)variances should include both negative and positive covariances among traits (Lande, 1982; Houle, 1991). Some studies, however, have found positive correlations between

Fig. 1 Examples of mean daughter on ewe regression for (A) lifetime weaning success (LWS; in number of lambs; square-root transformed), and (B) body mass at primiparity (BMP; in kg) in the Ram Mountain bighorn sheep population. Heritability estimate for lifetime weaning success was 0.86 and 0.02 for body mass at primiparity.



life-history traits, or no evidence of trade-offs between traits in both laboratory (Giesel *et al.*, 1982; Spitze *et al.*, 1991; Hughes, 1995; see also Roff, 1996) and natural populations (Mitchell-Olds, 1986; Schwaegerle & Levin, 1991; Campbell, 1997). Our results suggest the absence of trade-offs in wild bighorn sheep, and the persistence of genetic variance and (co)variance among life-history traits.

Several mechanisms could maintain genetic variance of a population (Roff, 1997). Highly positive genetic correlations between some traits at Ram Mountain (e.g. between LFEC, LWS) can just reflect redundancy. Therefore it is worth focusing on some particularly nonredundant traits or traits expected to be involved in a trade-off. Since no negative correlations were detected between traits at Ram Mountain, there is no evidence that antagonistic pleiotropy (Williams, 1957) explains the high heritabilities estimated. The Ram Mountain population is small (25–90 breeding ewes during our study) and isolated, therefore it does not satisfy the assumptions (large, outbred population at equilibrium) required for negative genetic correlations between life-history traits (Lande, 1982). Countervailing selection arising from environmental changes over time may slow the erosion of additive genetic variance (Roff, 1997). Environmental changes sufficient to induce a shift in selection pressure are probably rare; apparently none occurred during the 28-year study at Ram Mountain (Bérubé *et al.*, 1999), and much more time is needed to demonstrate the effectiveness of countervailing selection. Positive correlations may arise from genetic variation for resources acquisition (van Noordwijk & de Jong, 1986; Houle, 1991). The higher amount of resources acquired by some individuals allows them to allocate more resources to both traits. This phenomenon has been observed in ground squirrels (Dobson *et al.*, 1999). The genetic variance for the resource-acquisition trait may be maintained by mutation–selection balance (van Noordwijk & de Jong, 1986). Such a system is plausible

at Ram Mountain because the variance in body mass may reflect differences in resource-acquisition ability among individuals. Finally, the experimental manipulation of population density may have created novel environmental conditions and induced the effect of genotype-by-environment interactions (Leroi *et al.*, 1994), or the expression of new genes that may increase the genetic variance and result in the breakdown of adapted genetic covariances leading to positive correlations among traits (Service & Rose, 1985; Holloway *et al.*, 1990; Guntrip *et al.*, 1997). Low density was maintained artificially for nine years, and ewe removals may have been a selective pressure on reproductive traits, since they had the same effect as an increase in mortality rate early in life. After that, cessation of ewe removals led to a demographic explosion which was responsible for many phenotypic changes of the traits in the population (Festa-Bianchet *et al.*, 1995, 1998; Festa-Bianchet & Jorgenson, 1998; Jorgenson *et al.*, 1998).

Continued study will measure the effects of selection on morphological and life-history traits in these populations. If the novel environment effect hypothesis is true, then we should ask how often environmental conditions experienced by natural populations of large mammals correspond to theoretical conditions (i.e. large, outbred populations at equilibrium). Strong and rapid environmental changes, such as climatic incidents, habitat modifications, new epizootics or interspecific competition following introductions are common in natural populations, particularly through human influences. Therefore, we expect that future studies will confirm that genetic variability for life-history traits persists while negative genetic correlations are absent in other populations of wild mammals.

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