

Male personality, life-history strategies and reproductive success in a promiscuous mammal

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Abstract

Recent theoretical work suggests that personality is a component of life history, but links between personality and either age-dependent reproductive success or life-history strategy are yet to be established. Using quantitative genetic analyses on a long-term pedigree we estimated indices of boldness and docility for 105 bighorn sheep rams (*Ovis canadensis*), born between 1983 and 1999, and compared these indices to their reproductive history from 2 years of age until death. Docility and boldness were highly heritable and negatively genetically correlated. Docile and bold rams survived longer than indocile and shy rams. Docility and boldness had a weak negative effect on reproductive success early in life, but a strong positive effect on older rams. Our findings highlight an important role of personality on reproductive success and suggest that personality could be an important component of life-history strategy.

Introduction

In many species where they compete aggressively for receptive females, males have evolved exaggerated morphological traits and developed weaponry (Andersson, 1994). Sexual selection has been measured on several secondary sexual characters, and the role of behavioural traits in mating tactics has been described in many species (Andersson, 1994; Gross, 1996). Individual behavioural variation, called personality (Dingemanse *et al.*, 2004), temperament (Réale *et al.*, 2007), behavioural syndrome (Sih *et al.*, 2004; Bell, 2007) or coping style (Koolhaas *et al.*, 1999) is receiving increasing interest in evolutionary ecology (Wilson *et al.*, 1994; Sih *et al.*, 2004; Dingemanse & Réale, 2005; Penke *et al.*, 2007; Réale *et al.*, 2007; Smith & Blumstein, 2008). Because personality affects how individuals react to challenging situations (Wilson *et al.*, 1994; Réale *et al.*, 2007), it may predict how a male competes for mates and is therefore a potential target for sexual selection.

Recent theoretical (Stamps, 2007; Wolf *et al.*, 2007) and empirical studies (Réale *et al.*, 2000; Boon *et al.*, 2007; Biro & Stamps, 2008) have shown that personality could also be related to individual variation in life-history strategies. Differences in personality within a population could be maintained if personality and risk-taking affected trade-offs between life-history traits [e.g. growth vs. mortality (Stamps, 2007; Biro & Stamps, 2008) or current vs. future reproductive success (Wolf *et al.*, 2007)], leading to coevolution between personality traits and life-history strategies. Here we use a long-term study of bighorn sheep (*Ovis canadensis*, Shaw) at Ram Mountain, Alberta, to test for possible links between personality traits and life-history strategies. In mammals with strong male-male competition, bold, aggressive males could maximize reproductive success early in life, possibly at the cost of reduced lifespan, whereas shy, nonaggressive males could survive longer, reach a high social status or a large size and enjoy greater reproductive success later in life. Therefore, differences in personality may explain some of the variation in life-history strategy among individuals of a population.

The few studies that linked male personality to reproductive success in animals (Godin & Dugatkin, 1996; Mehlman *et al.*, 1997; Smith & Blumstein, 2008)

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and humans (Linton & Wiener, 2001; Nettle, 2005) used behavioural indices of mating success. None directly estimated male reproductive success using molecular tools, or examined the link between personality, longevity and reproductive success. In the Ram Mountain bighorn sheep population, individual rams were monitored through life and paternity was determined from DNA analyses, allowing us to compare docility and boldness with survival and age-dependent reproductive success. We measured boldness and docility respectively by the tendency of individuals to enter a corral trap and by their reaction to handlers (Réale *et al.*, 2000). Bold individuals are generally considered as risk takers (Wilson *et al.*, 1994; Réale *et al.*, 2007), and individuals with low docility could be considered as pugnacious (or aggressive).

We have measured personality in bighorn ewes since 1994 (Réale *et al.*, 2000). Most rams included in this study, however, died before we started scoring personality. Furthermore, males generally come to the trap only once or twice each summer. This low number of visits limited the variance among individuals and prevented us from estimating boldness in rams. Finally, the method used to capture and handle rams are different from those used for females, which prevented us from measuring docility in males. Consequently, we could not obtain direct phenotypic measures of docility and boldness in rams. We therefore used a quantitative genetic analysis called the animal model (Cameron, 1997; Lynch & Walsh, 1998; Kruuk, 2004) to obtain predicted breeding values (PBVs) of boldness and docility based on the personality of related females in an extensive pedigree (Cameron, 1997; Lynch & Walsh, 1998; Kruuk, 2004). An individual's breeding value represents the average effect of all the genes of additive effect on a trait for that individual (Cameron, 1997). Breeding values can be obtained using best linear unbiased predictors (BLUPs) from the animal model (Kruuk, 2004), including individuals included in the pedigree but without records (Cameron, 1997). We compared longevity with PBVs of docility and boldness and analysed the relationship between yearly relative reproductive success and personality for 105 rams born between 1983 and 1999 with known lifetime reproductive histories.

Depending mostly on their social rank, bighorn rams use two main mating tactics: tending and courting (Hogg & Forbes, 1997; Coltman *et al.*, 2002). Tending rams are top-ranked males, mostly aged 7 years and older (Pelletier & Festa-Bianchet, 2006) that defend a single receptive female against other males. Courting rams are subordinates, generally aged 2–7 years, that attempt mounts after chasing the oestrous ewe away from the tending male. Courting males sire up to 40% of lambs (Hogg & Forbes, 1997; Coltman *et al.*, 2002). Boldness or docility may have different effects on the mating success of tending and courting males. Based on theory (Stamps, 2007; Wolf *et al.*, 2007) and because ram reproductive

success generally increases with age (Coltman *et al.*, 2002) we expected: (1) that docile males have a lower reproductive success early in life compared with indocile males, but survive longer, reach dominant status, and increase their reproductive success later in life; and (2) that bold males show a higher reproductive success early in life, but die younger than shy males. Shy males should therefore increase their reproductive success later in life.

Methods

Study population and personality trait

The Ram Mountain bighorn sheep population, Alberta, Canada, has been monitored since 1972 (Jorgenson *et al.*, 1993). More than 98% of the sheep are marked with ear tags or visual collars, and detailed information on their life history is available. Each year from May to September, animals are captured between one and seven times in a corral trap baited with salt. Mass, horn length and reproductive status are measured at each capture.

Data on boldness and docility were collected between 1994 and 2005 and between 1998 and 2005 respectively. We measured boldness by the frequency of captures of individual animals and docility by their reaction to handlers (Réale *et al.*, 2000). Frequency of captures reflects individual tendency to take the risk to enter the trap rather than an index of exploration, because the trap is not a novel environment (Réale *et al.*, 2000). The methodology and the justification for using such indices have been developed in previous studies (Réale *et al.*, 2000, 2007; Réale & Festa-Bianchet, 2003). Docility provides an index of resistance to handling, and is negatively related to aggressiveness, exploration and the activity of the autonomic nervous system (Koolhaas *et al.*, 1999). In 2007 and 2008 we used a stethoscope to measure heart rate at each capture of each individual after weighing the animal. We counted heart beats for 15 s, then calculated the number of beats per minute. We obtained a total of 352 heart rate measurements on 71 individuals over the 2 years.

Quantitative genetic analyses of personality traits

We calculated heritability of docility and boldness and their genetic correlation using a pedigree reconstituted from paternity analyses and mother–offspring relationships. The pedigree was essentially the same as the one in Poissant *et al.* (2008). Maternity was accurately determined for 752 individuals (224 dams) from field observations of suckling behaviour. Paternity was determined for 268 sheep (63 sires) sampled from 1988 to 2006 using approximately 30 microsatellite loci and the software CERVUS (Marshall *et al.*, 1998). The software COLONY (Wang, 2004) was also used to identify paternal half-sibs (167 individuals) sired by 38 unsampled rams. Labora-

tory and statistical methods are detailed in Coltman *et al.* (2005).

The animal model (Cameron, 1997; Lynch & Walsh, 1998; Kruuk, 2004) uses all information from the family links among individuals within a pedigree to estimate components (random effects) of the phenotypic variance (V_P) by taking into account potential confounding effects (fixed effects). We estimated additive genetic (V_A), year (V_Y), permanent environmental (V_C), maternal genetic (V_{MG}) and maternal environmental (V_{ME}) variances and tested their significance using likelihood ratio tests between nested models (Kruuk, 2004). The pedigree included 1012 identities and records on 135 females (272 records for docility and 619 records for boldness). To normalize the data, docility and boldness were square-root transformed prior to analyses. We included age as a fixed effect for models on docility, and age and year of last capture as fixed effects for models on boldness. Year of last capture allowed us to control for the fact that some females died before the end of the summer and showed a lower frequency of captures (i.e. boldness) during their last year of life. All animal model analyses used ASReml (Gilmour *et al.*, 2006).

The PBVs of docility and boldness were obtained from BLUPs (Cameron, 1997; Kruuk, 2004) of the model including V_A and V_R only (see Results), assuming an intersexual genetic correlation of 1 for each trait. Intersexual genetic correlations are generally strong and positive (Roff, 1997). We validated our estimates of ram personality by examining the correlation between PBVs of docility and boldness and individual indices of heart rate, a physiological index of coping style (Koolhaas *et al.*, 1999). First, we estimated individual heart rate from the BLUPs of a linear mixed model of heart rate as a function of sex, age, body mass, year, date and order of handling during each trapping day as fixed effects and sheep id as a random effect (results not shown). Heart rate was repeatable ($r = 0.27$, $LRT_1 = 40.05$, $P < 0.001$). High heart rate during handling reflects low activity of the parasympathetic nervous system, a characteristic of indocile, aggressive or bold individuals (Koolhaas *et al.*, 1999). We also indirectly validated PBVs of male docility and boldness by simulating individual phenotypic and genetic values of a quantitative trait (see Charmantier & Réale, 2005) in 10 populations with characteristics similar to the Ram Mountain population (i.e. Table 1: $V_A = 0.12$, $V_R = 0.06$, $V_P = 0.18$). These simulations show that on average male PBVs were positively correlated ($r = 0.58$) with true additive genetic values and with phenotypic values ($r = 0.47$) (see Appendix S1 in Supporting Information).

Effects of personality traits on longevity and reproductive success

For each male an index of horn length and body mass standardized for age was obtained using BLUPs from a

Table 1 Heritability and variance components (and SEs) of docility and boldness for bighorn sheep in the Ram Mountain population, Alberta. Records were obtained on females only but the pedigree included both sexes.

Model	V_A^*	V_C	V_{ME}	V_{MG}	V_Y	V_P	$h^2†$	c^2	me^2	mg^2	γ^2	$\log L‡$
Docility												
$V_P = V_A + V_Y + V_R$	0.118 (0.024)	-	-	-	0.011 (0.006)	0.180 (0.025)	0.65 (0.06)	-	-	-	0.06 (0.03)	181.491
$V_P = V_A + V_Y + V_C + V_R$	0.051 (0.042)	0.051 (0.036)	-	-	0.012 (0.007)	0.164 (0.023)	0.31 (0.24)	0.31 (0.22)	-	-	0.07 (0.04)	182.500
$V_P = V_A + V_Y + V_{ME} + V_R$	0.105 (0.031)	-	0.011 (0.020)	-	0.011 (0.007)	0.178 (0.025)	0.59 (0.13)	-	0.06 (0.12)	-	0.06 (0.03)	181.634
Boldness												
$V_P = V_A + V_Y + V_R$	0.075 (0.015)	-	-	-	0.019 (0.002)	0.194 (0.018)	0.39 (0.06)	-	-	-	0.10 (0.04)	292.190
$V_P = V_A + V_Y + V_C + V_R$	0.065 (0.027)	0.008 (0.018)	-	-	0.018 (0.009)	0.192 (0.018)	0.34 (0.12)	0.04 (0.10)	-	-	0.10 (0.04)	292.251
$V_P = V_A + V_Y + V_{ME} + V_R$	0.075 (0.015)	-	0.00	-	0.019 (0.009)	0.194 (0.018)	0.38 (0.08)	-	0.00	-	0.10 (0.04)	292.201
$V_P = V_A + V_Y + V_{MG} + V_R$	0.075 (0.015)	-	-	0.00	0.019 (0.009)	0.194 (0.018)	0.39 (0.06)	-	-	0.00	0.10 (0.04)	292.190

For both traits selected model 1 including only V_A and year as a random effect was selected (model 4 did not converge for docility). Results shown are for univariate analyses (bivariate analysis gave identical results). Estimates of genetic covariance ($Cov_{1,2} \pm SE = -0.034 \pm 0.015$) and genetic correlation ($r_G = -0.38 \pm 0.15$) between docility and boldness were obtained from a bivariate analysis with V_A and year as random effects.

*Variance components: V_A , additive genetic variance; V_C , permanent environmental variance; V_{ME} , maternal environmental variance; V_{MG} , maternal genetic variance; V_Y , year variance; V_P , phenotypic variance; V_R , residual variance;

†Variance components as a proportion of the phenotypic variance of the trait: h^2 , heritability; γ^2 , year effects as a proportion; c^2 , permanent environmental effects; me^2 , maternal environmental effects; mg^2 , maternal genetic effects.

‡Log likelihood of the model.

linear mixed-effect model (Pinheiro & Bates, 2000) including date of measurement (square-root transformed), age, age² as fixed effects, and identity and year of birth as random effects (for more details, see Pelletier *et al.*, 2007).

We analysed the relationship between longevity and predicted boldness and docility, horn length and body mass, year of birth and their two-way interactions, using a generalized linear model, with a log link function and a Poisson distribution (Crawley, 2007). We monitored reproductive history from 2 years of age until death for 105 males born from 1983 to 1999, who sired 187 lambs between 1987 and 2005. Male lifetime reproduction varied from 0 to 21 lambs (mean \pm SD = 1.76 ± 3.47). We calculated yearly relative reproductive success (Coltman *et al.*, 2002) as the reproductive success of a male minus the mean reproductive success of all adult males in a given year. Yearly relative reproductive success was square-root transformed [i.e. $\sqrt{(x+1)}$] to normalize the data prior to analyses. Because of potential temporal autocorrelation within each male we used an autoregressive model with corAR1 function (Pinheiro & Bates, 2000) to run the mixed models on annual relative reproductive success and on horn length. All the variables were centred on their mean prior to mixed model analyses. For each model we used a stepwise backward elimination of interactions and then main terms with a *P*-value higher than $\alpha = 5\%$.

Using a restricted sample of 97 males for which we knew the cause of death (i.e. by hunting or other causes) we finally examined the hypothesis that docility and boldness were related to selective hunting. We ran a generalized linear model on death by hunting as a function of year of birth, horn length, body mass, and predicted docility and boldness using the logit link function and a quasibinomial distribution (Crawley, 2007). Furthermore, we analysed whether docility or boldness could be related to horn length, the trait targeted by trophy hunting. For this analysis we used a linear mixed model with horn length as a function of age, age² and year of birth, docility and boldness. We allowed both intercepts and slopes of ram id as random effects in the model (Nussey *et al.*, 2007). Age, age² and year of birth, docility and boldness were centred on the mean for this analysis (see above). All the analyses were performed using R software (R Core Development Team 2006).

Results

Quantitative genetics of personality traits

We first estimated quantitative genetic parameters of docility and boldness from female records and the pedigree including both sexes. Heritability ($h^2 = V_A/V_P$) of docility and boldness were 0.65 ± 0.06 SE and 0.39 ± 0.06 , respectively, and their genetic correlation

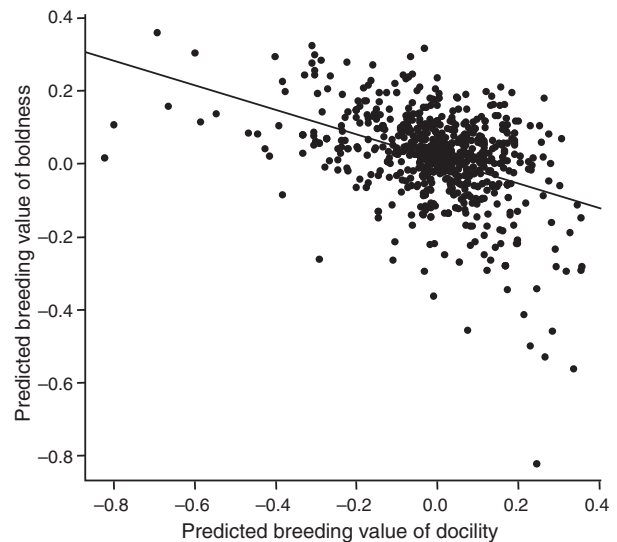


Fig. 1 Illustration of the negative genetic correlation between boldness and docility in the Ram Mountain population. Breeding values of boldness and docility were predicted from a bivariate animal model analysis with V_A and year as random effects.

was -0.38 ± 0.15 (Table 1; Fig. 1). We found a year effect on both traits but no significant permanent environmental or maternal effects. Docility increased with age (effect \pm SE = 0.015 ± 0.007 ; $F_{1,142} = 4.42$, $P = 0.038$). Boldness decreased during the year of last capture (effect \pm SE = -0.24 ± 0.04 ; $F_{1,600} = 39.12$, $P < 0.001$). We obtained male PBVs from the model including additive genetic and year effects only (Table 1).

The PBVs of docility were negatively correlated with heart rate for the two sexes combined and for females (Table 2). We observed a weak negative correlation between PBVs of docility and heart rate index for rams. Correlations between PBVs of boldness and heart rate measurement were all positive but not significant (Table 2).

Links between personality and life history

Males lived up to 14 years of age (mean \pm SD = 5.76 ± 2.61 years). Most males studied were dead by 2005, except two that were 9 and 10 years old. Docile and bold rams survived longer than indocile and shy rams (Table 3; Fig. 2a,b), because of the very low longevity of the least docile rams (none of those within the first quartile of docility survived to 10 years). Horn length had no direct effects on survival, and the negative effect of body mass on longevity (Table 3; Fig. 2c) was due to selection against large males through trophy hunting (Coltman *et al.*, 2003) and the strong phenotypic ($r = 0.74$, $t_{103} = 11.026$, $P < 0.001$) and genetic correlations of horn length and body mass (Coltman *et al.* 2005).

Table 2 Correlations between individual values of heart rate during handling and predicted breeding values (PBVs) of boldness and docility for bighorn sheep, obtained from the animal model analysis.

PBVs	Correlation	<i>t</i>	d.f.	<i>P</i>
Docility (females + males)	-0.45	-3.80	57	< 0.001
Female docility	-0.50	-3.25	31	0.003
Male docility	-0.27	-1.38	24	0.18
Boldness (females + males)	0.23	1.80	57	0.07
Female boldness	0.23	1.23	31	0.23
Male boldness	0.28	1.43	24	0.16

Table 3 Selected generalized linear model of longevity as a function of personality and other traits in bighorn rams.

	Effect ± SE*	<i>z</i>	<i>P</i>
Boldness	0.999 ± 0.476	2.10	0.03
Docility	1.274 ± 0.368	3.46	< 0.001
Body mass	-0.019 ± 0.008	-2.41	0.016
Year of birth	-0.023 ± 0.011	-2.01	0.04

We used a model with log link function and Poisson distribution. *Horn length (*z* = -0.23, *P* = 0.82) and the two-way interactions were nonsignificant (all *P* > 0.34) and were rejected from the model. †Multiple *R*² = 0.16 (calculated as the ratio of the deviance explained by the model over the null deviance).

The effect of personality on reproductive success varied with male age (Table 4; Fig. 3). Predicted docility decreased reproductive success in young males, but improved it later in life (Fig. 3a). Predicted boldness had a weak negative effect on reproductive success early in life, but increased reproductive success later in life (Table 4; Fig. 3b). Horn length was positively related to reproductive success. Shy males with short horns had very low reproductive success compared with other males (Table 4; Fig. 3c).

Death by hunting decreased with year of birth (coefficient ± SE: -0.33 ± 0.12, *t*₉₄ = -2.79, *P* < 0.001),

Table 4 Selected linear mixed model of annual relative reproductive success as a function on personality and other traits in bighorn rams.

	Effect ± SE*†	<i>z</i>	d.f.	<i>P</i>
Age	0.192 ± 0.035	5.49	1, 369	< 0.001
Boldness	0.345 ± 0.244	1.41	1, 102	0.16
Docility	0.099 ± 0.165	0.59	1, 102	0.55
Horn length	0.008 ± 0.003	2.41	1, 369	0.017
Year of birth	-0.005 ± 0.006	0.92	1, 102	0.36
Age × boldness	0.861 ± 0.374	2.30	1, 369	0.02
Age × docility	0.838 ± 0.271	3.09	1, 369	0.002
Age × year of birth	-0.035 ± 0.009	-3.71	1, 369	< 0.001
Boldness × horn length	-0.091 ± 0.036	-2.47	1, 369	0.014

Annual relative reproductive success was square root transformed. Age, body mass and horn length (both standardized by age), docility, boldness, year of birth and their two-way interactions were entered as fixed effects, and ram's identity as a random effect.

*We used an autoregressive model to take into account temporal autocorrelation in reproductive success (function corAR1; Phi = 0.14, *P* = 0.01).

†Body mass (*t*_{1,368} = 1.91, *P* = 0.06) and the other two-way interactions (all *P* > 0.08) were not significant and were rejected from the model.

and long horns increased the chance of being shot (horn length: 0.13 ± 0.06, *t*₉₄ = 2.02, *P* = 0.04). Personality had no effect on the probability of being shot (PBV docility: *t*₉₃ = -0.65, *P* = 0.52; PBV boldness: *t*₉₂ = -0.87, *P* = 0.39). Body mass was also rejected from the model (*t*₉₁ = 0.45, *P* = 0.65). Horn length increased significantly with age and its quadratic term (age: 32.18 ± 0.34, *t*₃₉₈ = 94.07, *P* < 0.001; age²: -6.72 ± 0.09, *t*₃₉₈ = -71.57, *P* < 0.001), and decreased with year of birth (-0.21 ± 0.09, *t*₁₀₄ = -2.19, *P* = 0.03). PBVs of docility and boldness were not related to horn length (docility: *t*₁₀₃ = 1.18, *P* = 0.24; boldness: *t*₁₀₂ = 0.42, *P* = 0.66).

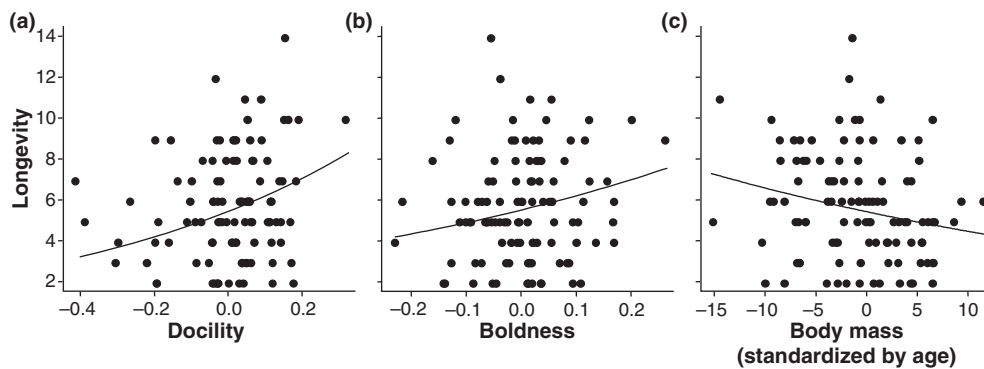


Fig. 2 Docility, boldness, body mass and longevity of bighorn rams. Longevity increases with (a) docility, (b) with boldness and decreases with (c) body mass. Docility and boldness were obtained using the predicted breeding values of a quantitative genetic model including additive genetic and year variance. Body mass was standardized by age effects.

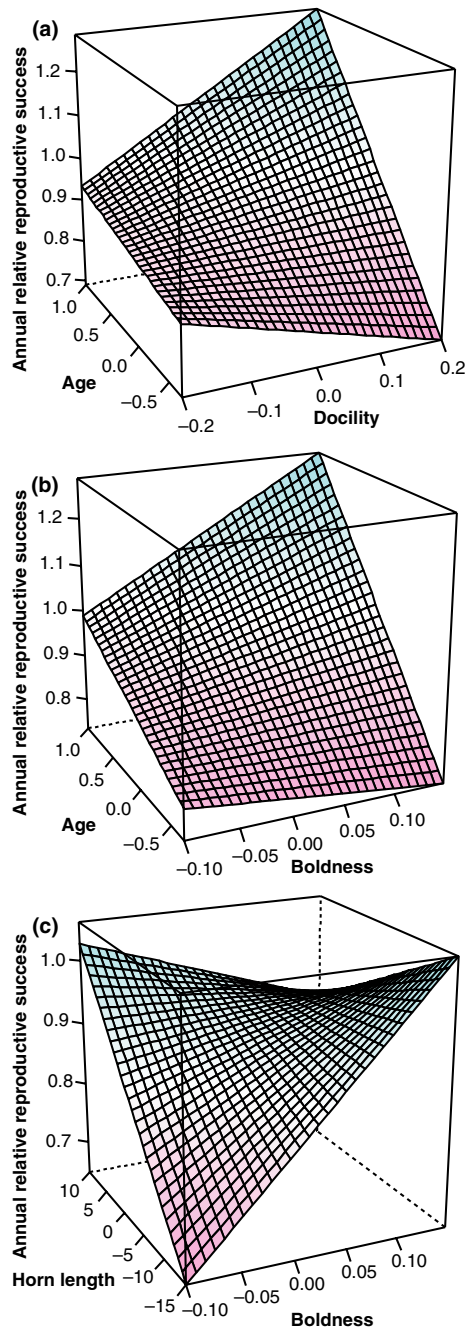


Fig. 3 Personality and age-dependent reproductive success in big-horn rams. Annual relative reproductive success as a function of the interaction between docility and age (a), boldness and age (b), and boldness and horn length (c). One hundred and five rams and 461 estimates of paternity were used for the analysis. The length of both *X* and *Y* axes is limited to the natural range of data.

Discussion

Our results support one of the assumptions of the Wolf *et al.* (2007) model that aggressiveness is linked to low

survival. A ram's pugnacity affects its life-history strategy: the least docile rams had short life expectancy and high reproductive success early in life. At the other extreme, docile rams had a longer lifespan, likely attained high dominance rank (Pelletier & Festa-Bianchet, 2006) and increased their reproductive success later in life. The Wolf *et al.* model also assumed that bold individuals should survive less than shy ones and invest in early reproduction. However, bold rams survived longer than shy ones and enjoyed higher late reproductive success. Therefore, boldness may not always be associated with risk proneness in life-history strategy. Other similar links between personality and fitness have been found in this population. Compared with shy ewes, bold ewes at Ram Mountain matured earlier and had higher weaning success (Réale *et al.*, 2000) and higher survival during a period of intense cougar (*Puma concolor*) predation (Réale & Festa-Bianchet, 2003). Our results suggest that the presence of alternative mating strategies in the population may be partly due to variance in male willingness to fight. Furthermore, because shy or indocile males were not more likely to be shot by trophy hunters, longevity and late reproductive success of bold, docile males cannot be a consequence of selective hunting (Coltman *et al.*, 2003).

To increase the sample size for rams that died before data on personality were collected, we applied a method commonly used in animal science: the prediction of breeding values for individuals without phenotypic records (Cameron, 1997). This method has been used to estimate male breeding values of clutch size in great tits (Postma & van Noordwijk, 2005) and is useful when a trait has been measured over a few generations in a population with a deep pedigree. Although PBVs are not direct phenotypic measures of the traits themselves, our results showed that heart rate, a physiological index of coping style, was negatively correlated with PBVs of docility and positively (although not significantly) with PBVs of boldness. This results could be predicted according to previous works on the link between personality traits and the response of the autonomic nervous system (Koolhaas *et al.*, 1999), and provide a biological validation for our estimates of personality traits in bighorn rams.

Predicted breeding values could be confounded by environmental effects when the underlying genetic model is not specified appropriately (Postma, 2006). For example, when significant maternal effects are not considered in the model PBVs may include some maternal effects. We assumed an intersexual genetic correlation of 1 for each trait because these correlations are generally strong and positive (Roff, 1997), including for behavioural traits (J. Poissant, A.J. Wilson & D.W. Coltman, unpublished data). A correlation lower than 1 would only increase the noise associated with the estimation of male breeding values with, as a consequence, a reduction in our power to detect any pattern

between males' docility or boldness and life-history traits. We also assumed that our quantitative genetic model, including V_A and V_R only, was appropriate. The bias caused by nonadditive genetic effects on PBVs is problematic mainly when PBVs are estimated to analyse temporal genetic trends across generations (Postma, 2006). Our purpose, however, was to obtain proxies of phenotypic values for males, that may differ in personality for genetic and nongenetic reasons. That PBVs could include nonadditive genetic effects (i.e. permanent environmental) was therefore not detrimental in our case.

Heritability estimates in this study were 0.39 and 0.65 for boldness and docility respectively. These values are similar to those generally reported for personality traits (van Oers *et al.*, 2005; Réale *et al.*, 2007), and among the highest estimates reported for behaviour traits (mean = 0.31; Stirling *et al.*, 2002). They confirm preliminary results suggesting a possible genetic basis for boldness in this population (Réale *et al.*, 2000). We did not find any significant environmental or genetic maternal effects on the phenotypic variation of these two traits. Previous quantitative genetic studies found negligible maternal effects on personality traits (van Oers *et al.*, 2004; Boissy *et al.*, 2005; Strandberg *et al.*, 2005; Beckman *et al.*, 2007; but see Forstmeier *et al.*, 2004), in contrast to experimental studies showing strong maternal effects on these traits (Groothuis & Carere, 2005). It should be noted, however, that these results are not necessarily contradictory, because maternal effects in quantitative genetic designs represent the effects of the phenotype or the environment of the mother that affects the phenotypic resemblance among her offspring, whereas experimental designs generally examine how changes in one maternal trait (e.g. androgen concentration in the yolk; Groothuis & Carere, 2005) affect offspring phenotype. Therefore, unlike the experimental approach, the quantitative genetic approach does not include in its 'maternal effects' any effects that could affect one particular offspring independent of the others. These latter effects should appear in the estimate of permanent environmental effects, which represents the permanent effects of the specific environment of an individual and nonadditive genetic effect on its phenotype (Kruuk, 2004). Although the model including permanent environmental effects provided an heritability estimate of 0.31 for docility, a large standard error was associated with this estimate, and the model was rejected in favour of a model including only additive genetic and year effects. We therefore cannot reject the possibility of permanent environmental effects on docility. The low estimate (0.04) for boldness, on the other hand, suggests that this trait is not affected by permanent environmental effects. The weak year effect on both traits could be due to the effects of population density on social structure (e.g. group size) and thus the ability of individuals to enter the trap, and/or potential differences in how field

assistants handled or scored individuals (assistants generally differed from one year to another). The increase in docility with age in bighorn ewes reflects an individual developmental trend towards higher docility as ewe grow older rather than differential survival individuals with different docility values (D. Réale & J. Martin, unpublished data).

Docility and boldness were negatively correlated at both genetic and phenotypic levels. Positive correlations between aggressiveness and boldness have been found in other species (Bell, 2007). Interestingly, the negative, boomerang-shaped, correlation between boldness and docility found both at the phenotypic (Réale *et al.*, 2000) and genetic levels in the Ram Mountain population was caused by the under-representation of individuals that were both shy and indocile (Réale *et al.*, 2000), and may be explained by selection against this personality (Réale *et al.*, 2000; Réale & Festa-Bianchet, 2003). Results on rams confirm that individuals that are both predicted to be shy and indocile probably have the lowest fitness return in the population.

In conclusion, despite our rudimentary knowledge of the strength and shape of natural selection on personality traits, some recent progress has identified the types of selection pressures that could affect these traits (Dingemanse & Réale, 2005; Boon *et al.*, 2007; Penke *et al.*, 2007; Réale *et al.*, 2007; Smith & Blumstein, 2008). Here we show that individual personality differences can influence life-history strategy (Stamps, 2007; Wolf *et al.*, 2007), and are subject to both sexual and natural selection. Studies of the relationship between personality and sexual selection are still rare, with the exceptions of recent work on extra-pair paternity in passerines (Forstmeier, 2007; van Oers *et al.*, 2008). Identical fitness returns for the different personality profiles involved in a fitness trade-off between life-history strategies is an important assumption of the models proposed to explain the long-term maintenance of variance of personality traits (Stamps, 2007; Wolf *et al.*, 2007). We provide rare empirical evidence supporting this assumption.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1 Validating our approach to obtain male PBVs.

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