



Consistency of temperament in bighorn ewes and correlates with behaviour and life history

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Individual differences in temperament may affect how animals react to novel situations, avoid predation, invest in reproduction and behave in a variety of social contexts. Little information is available, however, about individual differences in temperament for wild animals. For bighorn sheep, *Ovis canadensis*, ewes captured as part of a long-term study, we compared behaviour during handling to behaviour in the field and reproductive history. We considered 'bold' ewes those that were frequently trapped during the summer, and assigned to each ewe a docility index based on her behaviour during handling. Measurements of temperament for the same individual at different captures were highly consistent. Temperament was not affected by reproductive status or age, nor was it related to body mass. Correlations between behaviour at the trap and in the field were weak and mostly nonsignificant, suggesting that temperament is domain specific rather than domain general. Bold ewes tended to start reproducing earlier and have higher weaning success than shy ewes. Variability in temperamental traits in the study population could be maintained by life-history trade-offs and by yearly changes in selective pressures.

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Temperament is defined as how an individual reacts to novel or challenging situations (Wilson et al. 1994; Wilson 1998). This concept originated from child psychology (Segal & Macdonald 1998), but has recently attracted the attention of ethologists and evolutionary biologists (Clarke & Boinski 1995; Wilson 1998). Studies of how temperament varies within species, populations and individuals have implications for domestic animal husbandry (Boissy & Bouissou 1995; McCune 1995; Le Neindre et al. 1995, 1996; Wilsson & Sundgren 1998) and for conservation biology (Stone et al. 1994; Delibes & Blazquez 1998; Carlstead et al. 1999a, b). Within a population, individuals can be classified by their behaviour along a shy/bold gradient (Wilson et al. 1994): confronted by a challenging situation or facing a novel object, shy individuals will show avoidance, while bold individuals will demonstrate interest. Temperament can thus include various phenotypic traits, each expressed in a particular context.

As selection results from the covariance between a trait and fitness in a population, individual consistency in a trait and variability among individuals are essential for the evolution of the trait (Falconer & Mackay 1996; Roff 1997). Phenotypic plasticity is expected in temperamental traits (Wilson et al. 1994), as in other behaviours

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(Brodie & Russell 1999), and environmental influences on behavioural traits may limit the potential of traits to evolve (Brodie & Russell 1999). Therefore, the consistency of phenotypic expression of behaviours must be measured as a first step in the understanding of trait evolution (Hayes & Jenkins 1997; Holmes & Sherry 1997). One way to analyse interindividual trait variation is to partition phenotypic variation into additive genetic and environmental components by estimating the trait heritability (h^2), and to identify possible genetic constraints on evolution by estimating the genetic correlation between the trait in question and other traits (Boake 1994; Falconer & Mackay 1996; Roff 1997). Estimation of quantitative genetic parameters, however, requires very large sample sizes and a knowledge of pedigrees (Falconer & Mackay 1996). Because these prerequisites are rarely met in behavioural studies in the field, Boake (1989) proposed to use a trait's repeatability as an alternative approach. Repeatability is useful in two ways: it quantifies how the measurement of a particular trait is representative of an individual and it gives an upper bound to heritability.

An important unresolved issue is whether individual differences in temperament are context specific or domain general (Wilson et al. 1994). The concept of domain-general temperament as developed by psychologists (Kagan et al. 1988; Segal & Macdonald 1998) states that an individual's behaviour in a particular context

predicts how that individual will behave in other contexts. Alternatively, the context-specific temperament hypothesis (Wilson et al. 1994; Wilson 1998) predicts that the same individual could be shy in one context (such as a social interaction) and bold in another (such as when entering a new environment). Context-specific temperament may be an adaptive response to different selective pressures but requires that the expressions of temperament in different contexts be free to evolve independently of each other. Correlations between different temperamental traits or of the same trait at different ages are needed to determine whether temperament is context specific or domain general.

If individual temperaments are consistent, comparing the correlates of variation in temperament at the genetic, physiological, behavioural and ontogenetic levels with fitness consequences may reveal which selective processes affect the evolution of temperamental traits. While few studies have demonstrated the existence of a shy–bold gradient in natural populations (Armitage 1986; Coss & Biardi 1997; Coleman & Wilson 1998), even fewer have investigated the behavioural or fitness consequences of temperament (Wilson et al. 1994; Wilson 1998).

Here we examine individual variability in temperament of ewes in a wild population of bighorn sheep, *Ovis canadensis*. We measured aspects of temperament by assessing boldness and docility. Boldness was measured by the trappability of individual ewes, which we assumed to be an expression of the willingness to accept the risk of being handled in order to obtain access to a salt bait. Docility was measured by how much individuals struggled when handled. To estimate the consistency of temperament, we calculated the repeatability of docility and both the repeatability and the heritability of boldness. We then tested whether temperament varied with age and body mass. We also tested the hypothesis that temperament is context specific (Wilson et al. 1994) by estimating phenotypic correlations of boldness and docility with dominance (an expression of temperament in a social context) and with vigilance (an expression of temperament in an antipredator context). We finally assessed whether individual variation in temperament could be related to fitness, by analysing its relationship with age at primiparity and with reproductive success.

METHODS

Study Site and Population

We observed bighorn sheep at Ram Mountain (52°N, 115°W), Alberta, Canada, where they have been studied since 1971 (Festa-Bianchet et al. 1996). All ewes have been individually marked since 1976. Most of the behavioural data presented here were collected during the summer of 1998, but behaviour at the trap was also recorded in 1999. Before 1981, ewe removals maintained the population at 30–33 adult ewes. After removals were ended in 1981, the population increased, peaked at 104 ewes in 1992, then declined. At high population density, ewes experienced a delay in age of primiparity (Jorgenson et al. 1993) and decreased reproductive

success (Festa-Bianchet et al. 1998). In June 1998, the population included 57 adult ewes (mean age=7.6 years; range 2–14), three yearling ewes and 19 lambs. In June 1999, there were 41 adult ewes (mean age=7.6 years; range 2–13), three yearling ewes and 17 lambs. Large predators, including wolves (*Canis lupus*), black bears (*Ursus americanus*) and cougars (*Puma concolor*) were present in the study area. In 1998, predation by cougars was documented on four occasions.

Captures and Handling

We captured sheep in a corral trap baited with salt. The salt was removed from the trap as soon as possible after shutting the door. Sheep were caught by the horns, blindfolded and hog-tied in the trap, then dragged to a net outside the trap, where they were weighed to the nearest 250 g with a Detecto spring scale. Mass was adjusted to 15 September using each individual's rate of summer mass gain obtained from multiple captures. Festa-Bianchet et al. (1996) provide more details on mass adjustments. More than 90% of adult ewes were captured two to seven times each summer. Ewe reproductive status was assessed by examination of the udder at the beginning of the summer and from field observations of mother–offspring relationships. In most years, over 80% of lambs were captured and marked before October, and mothers of marked lambs were identified by field observations of suckling. Most adult rams were only trapped once a year and therefore were not considered in this analysis.

Temperament Indices

We classified each ewe using a boldness index based on her trappability (see Higley et al. 1996; Fairbanks et al. 1999). Sheep are attracted by salt, but those that enter the trap risk being handled. Some individuals entered the trap as soon as they arrived and spent much time licking salt, while others spent more time outside the trap, hesitated at the door, and went in and out several times. We assumed that this behavioural variability reflected individual differences in propensity to accept the risk involved in licking salt. We usually shut the door when several individuals were inside, therefore capture probability increased with time spent in the trap. Therefore, ewes that were rarely captured were considered shy, and ewes frequently captured were considered bold. We only processed individuals that had not been weighed for at least 3 weeks, and captures of ewes that were released without handling were not recorded. The number of captures reported here refers to the number of times each ewe was handled, which was almost always lower than the number of times a ewe was caught in the trap. We analysed the number of captures from 1994 to 1998. We refer to the yearly number of captures per sheep as the 'boldness score', and to the mean of boldness scores of the same sheep over several years as the 'boldness index'.

A docility score was given to each ewe at each capture, based on behaviour during handling, from when the ewe

was caught by the horns to when it was wrapped in the net for weighing. We attributed 0 points if the ewe laid down by herself when caught, and 1 point if she stood up. If she stood up, we attributed 0–2 points for the difficulty we had in wrestling her to the ground. While the ewe was lying on her side, we attributed 0–1 point for the difficulty in keeping her down, 0–1 point for the difficulty to hog-tie her, and 0–2 points for struggling while being moved to the net. We subtracted the individual score of each ewe from the maximum possible score of 7 so that docility scores varied from 0 to 7, with 7 indicating the most docile individuals. Docility scores were collected during summers 1998 and 1999. Between one and five scores ($\bar{X} \pm \text{SE} = 2.24 \pm 0.09$; $N = 173$) were obtained for each ewe in 1998, and between one and six scores ($\bar{X} \pm \text{SE} = 3.56 \pm 0.09$; $N = 133$) were obtained for each ewe in 1999. For each ewe, we calculated the mean of docility scores each summer (yearly docility), and an overall docility index (average of yearly docilities). Individual docility scores could have been affected by handler bias if handlers had formed an impression of each ewe or because large ewes were simply harder to handle than small ones. Handlers in 1999 were not the same as in 1998 and were unaware of the 1998 docility scores. Hence biases due to handlers in the estimation of docility were minimized.

To test the context specificity of temperament we used dominance rank and vigilance as other components of individual temperament. Dominance can be considered an expression of temperament in a social context. Vigilance can reflect the attitude of an individual towards the risk of predation. Data on dominance and vigilance were collected in 1998 by observing sheep with spotting scopes ($\times 20$ –45), usually at distances of over 300 m. All occurrences (Altmann 1974) of agonistic interactions ($N = 996$) between ewes were noted. Dominance is generally related to age in ungulates and most of the agonistic interactions observed were horn clashes that had no clear winner (Festa-Bianchet 1991). We therefore calculated a dominance rank for each adult female following Festa-Bianchet (1991), based on the ratio

$$(OS_D + O_U + 1) / (YS_D + Y_U + 1),$$

where OS_D is the number of ewes of the same age or older dominated by the subject, O_U is the number of older ewes with whom the subject interacted with no clear outcome, YS_D is the number of ewes of the same age or younger that dominated the subject, and Y_U is the number of younger ewes with whom the subject interacted with no clear outcome. Ewes within a cohort were ranked by individual ratios and ranks were divided by the number of ewes in the cohort (Festa-Bianchet 1991).

Vigilance behaviour of ewes was recorded from 2 June to 3 October 1998 by one of us (B.G.). From three to seven (6.77 ± 0.83 ; $N = 357$) focal samples (Altmann 1974) of 5–15 min each (12.4 ± 0.35 min) were collected on individual females. During focal samples, the majority of group members were foraging. Focal ewes were chosen so as to balance the number of observations according to group size, environmental conditions and date. For each

ewe we calculated the average proportion of time vigilant. Repeatability of vigilance from the same ewe was low but significant ($r = 0.08$, $P = 0.02$; B. Gallant & D. Réale, unpublished data).

Statistical Analyses

Boldness and docility scores were normalized by a square-root transformation before statistical analyses (Sokal & Rohlf 1981). We calculated between-year repeatability of boldness from measurements obtained in 1994–1998 for boldness scores (standardized by year; see below), following Lessels & Boag (1987). Repeatability of a trait can be estimated if a minimum of two measurements are available for each individual. To estimate repeatability, we included ewes that died before 1998, but for which we had some data since 1994, increasing the sample to 114 ewes. A repeatability of 0 would indicate that all variance is within individuals over successive measurements, and a repeatability of 1 would mean that repeated measurements of the same individual give identical estimates (Lessels & Boag 1987; Falconer & Mackay 1996). We estimated the heritability (h^2) of boldness using the parent/offspring regression method (Falconer & Mackay 1996), where heritability is twice the slope of the regression of mean boldness of daughters on the mean value for the mother, and the standard error is twice the standard error of the slope. Heritability can range from 0 to 1; low h^2 indicates that most phenotypic variance of a trait is due to environmental effects while high h^2 indicates a strong additive genetic influence on phenotypic variance. Because we used an offspring–mother regression to estimate heritability of boldness, we could not separate additive genetic influence from maternal effects in the resemblance between mother and offspring. We standardized the boldness index for year effects. This was justified because boldness was repeatable (see Results) and therefore could be considered an individual trait.

We estimated within-year repeatability (Lessels & Boag 1987) for yearly docility based on repeated docility scores obtained for each individual. We also calculated the between-year repeatability of docility as the correlation between yearly docilities for 1998 and 1999 (Falconer & Mackay 1996). We did not estimate h^2 for docility because there were too few mother–offspring pairs in the population in 1998 and 1999.

Ewes increase in mass by about 30% over the summer (Festa-Bianchet et al. 1996) and if heavy ewes were simply more difficult to handle than light ewes, docility scores should have decreased during summer. To test this possibility, we regressed docility score on capture date for 1998 and 1999. We also analysed the relationship between docility score and handling order, to check whether ewes that spent more time in the trap during capture were more likely to struggle when handled. To determine whether reproductive status affected temperament we correlated yearly docilities (1998 and 1999) and the 1998 boldness score of ewes with and without a lamb using Student's t tests. We regressed the docility index (average of the 2 years) on the square root of ewe age in 1998. To test whether boldness varied with age, we first compared

boldness scores with age for each year separately. We then performed a repeated measures analysis of covariance (ANCOVA) of boldness scores for ewes with 4 years of boldness scores and for ewes with 5 years of boldness scores (within-individuals factor), including age in 1994 as a covariate (between individuals). This analysis tested whether or not age had an effect on boldness independently of year. To test whether docility varied with age, we regressed the difference in yearly docilities between 1998 and 1999 with the square root of age in 1998. We adjusted ewe mass to mid-September 1998. Mass in September is consistent and heritable (Réale et al. 1999), therefore we regressed the docility index on September mass to test whether docility varied with ewe body size.

To assess the context specificity of temperament, we correlated boldness and docility with other behavioural traits. The dominance index and the proportion of time vigilant were arcsine transformed (Sokal & Rohlf 1981) before analyses. To adjust for age effects on vigilance, we used the residuals of the regression of vigilance on age. Dominance was measured as a rank within each cohort, and therefore, was independent of age.

We compared boldness, docility, body mass in 1998 and population density (the number of adult ewes in June) with age at primiparity using stepwise backward multiple regression. The probability level chosen to remove an independent variable from the model was $P > 0.1$. We used the residuals of the regression of mass on age to account for the effect of age on body mass. To determine whether boldness and docility were related to fitness, we correlated these indices with weaning success (i.e. the number of lambs weaned between first reproduction and 1998). Age (square-root transformed) was included in the model because the number of reproductive events increases with age and therefore weaning success was strongly age-related. Weaning success was square-root transformed before performing a stepwise backward multiple regression using boldness, docility, age and mass as covariates. Statistical tests were performed using Statview 4.02 (Abacus Concepts 1992).

RESULTS

Interindividual Variability in Boldness and Docility

The number of captures per ewe differed between years (ANOVA: $F_{4,405}=12.166$, $P < 0.001$) and ranged from a mean \pm SE of 2.97 ± 1.19 captures in 1994 to 4.57 ± 1.30 captures in 1996. The yearly boldness score for each ewe was therefore standardized as a function of the mean number of captures for a given year. Year-to-year repeatability of boldness was moderate ($r=0.36$, ANOVA: $F_{113,296}=3.059$, $P < 0.001$). The estimate of heritability for boldness was not significant ($h^2=0.21 \pm 0.23$, $N=35$ families, one-tailed Student's t test: $t_{33}=0.913$, $P=0.19$), perhaps because of the high standard error and small sample size. Differences in offspring boldness between females with more than two offspring of known boldness (ANOVA: $F_{10,11}=4.211$, $P=0.02$) suggested a genetic or maternal effect on boldness.

Docility scores increased slightly with capture date in 1998 ($r=0.15$, $F_{1,171}=4.214$, $P=0.05$) but not in 1999 ($r=0.06$, $F_{1,144}=0.680$, $P=0.41$). The docility score was not related to capture order in 1998 ($F_{1,162}=0.908$, $P=0.34$) but increased slightly with capture order in 1999 ($r=0.19$, $F_{1,144}=5.385$, $P=0.02$). Within-year repeatability of docility was high (1998: $r=0.66$, ANOVA: $F_{50,117}=6.498$, $P < 0.001$; 1999: $r=0.65$, ANOVA: $F_{38,91}=7.150$, $P < 0.001$), indicating strong within-individual consistency. Mean docility was higher in 1998 than in 1999 (paired t test: $t_{47}=3.958$; $P=0.0002$). We therefore standardized docility according to the mean value of each year. Between-year repeatability was significant and high (Pearson correlation: $r_{38}=0.86$; $P < 0.0001$; Fig. 1a). As handlers were different in the 2 years, the lower mean docility in 1999 was probably caused by a lower average score given by handlers in 1999 compared with 1998. The relative ranking of females according to behaviour at the trap was consistent from year to year.

Phenotypic Correlates of Temperament

In 1998, ewes with lambs did not differ in boldness from those without lambs (Student's t test: $t_{51}=1.049$, $P=0.40$). Boldness scores declined with age in 1994 and 1995 (Table 1), but only because of the low boldness value of a few very old ewes: when ewes aged 13 years or more were excluded, the correlations disappeared (Table 1). Repeated-measures ANCOVA on 4 years of data confirmed both the absence of an age effect ($F_{1,117}=0.874$, $P=0.36$) and the difference between years ($F_{3,117}=5.551$, $P=0.002$) in boldness scores. Similar results were obtained for the sample of ewes with 5 years of data. Ewes with lambs did not differ in docility from those without lambs (1998: $t_{51}=-0.629$, $P=0.53$; 1999: $t_{36}=-0.581$, $P=0.56$). The lack of relationship between age in 1998 and the difference between docility in 1999 and 1998 (simple regression: $F_{1,39}=0.013$, $P=0.79$; quadratic regression: $F_{2,37}=0.199$, $P=0.82$) suggested no clear pattern of variation in docility with age. Body mass corrected for age was not related to either docility ($F_{1,53}=1.998$, $P=0.16$) or boldness ($F_{1,53}=2.629$, $P=0.11$). When age was accounted for, there were no correlations between either docility or boldness and dominance or vigilance (Fig. 1c-f). There was a weak negative correlation between docility and boldness (Fig. 1b; Spearman rank correlation: $r_s=-0.31$, $N=56$ females, $P=0.02$). Less than 5% of females were shy and aggressive.

Temperament and Fitness-related Traits

For ewes that had produced at least one lamb by 1998, age at primiparity increased with population density, but primiparity occurred earlier for bold than for shy ewes (Table 2, Fig. 2b). Docile ewes tended to reach sexual maturity earlier than nondocile ewes (Fig. 2a, $P=0.06$). Light ewes tended to reach primiparity earlier than large ones, and body mass remained in the model but at a low level of probability ($P=0.08$). Bold ewes had a significantly higher weaning success than shy ewes (Table 2,

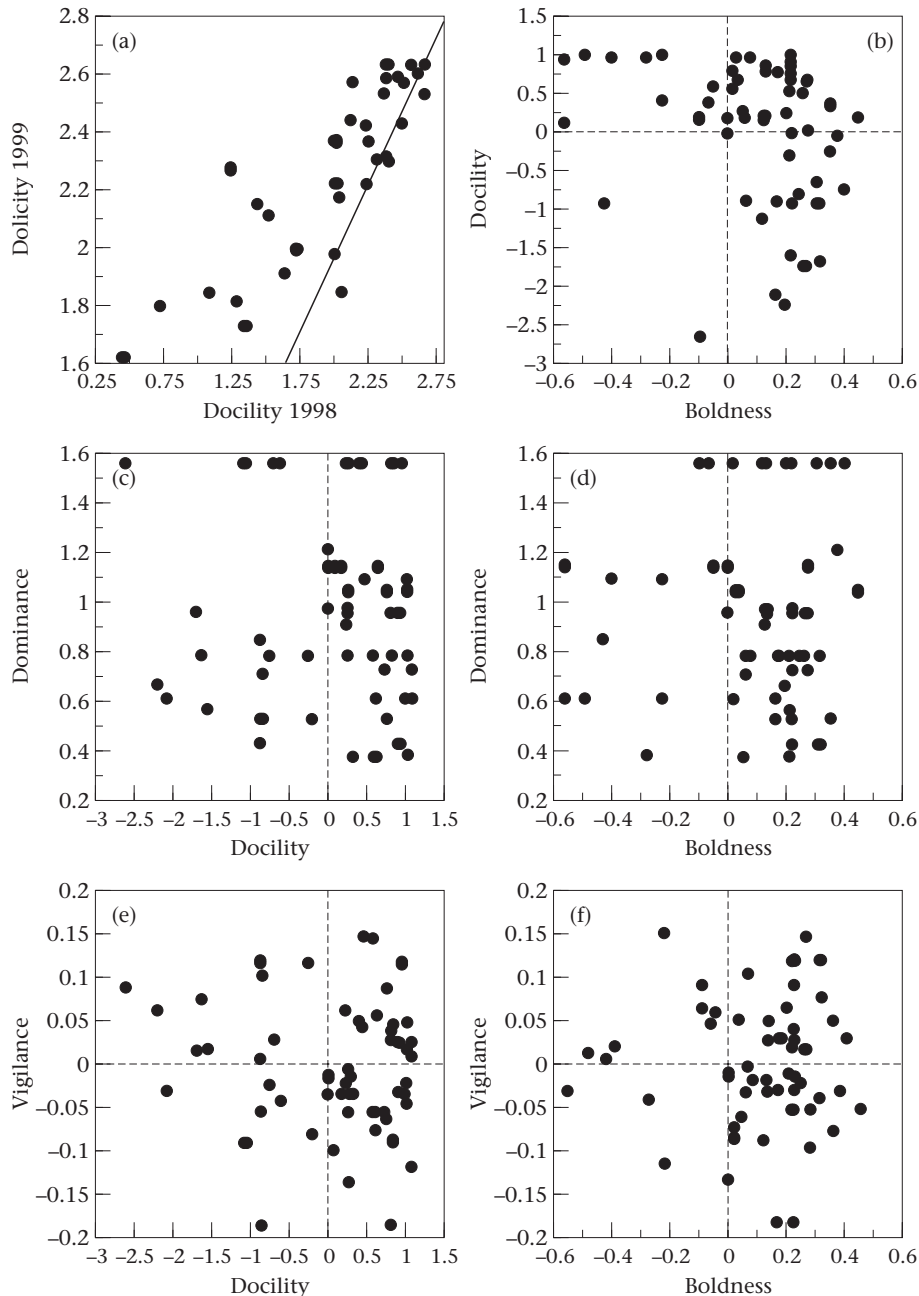


Figure 1. Relationships between temperamental traits and other behavioural variables for adult bighorn ewes at Ram Mountain, Alberta, Canada. (a) Correlation between docility indices in 1998 and 1999 for the same ewe. The solid line shows the 1:1 correlation. (b–f) Boldness is the mean value of yearly boldness scores from 1994 to 1998, while docility is the average of docility indices in 1998 and 1999. Vigilance was arcsine transformed and standardized for ewe age; dominance was square-root transformed. The relationships were tested with nonparametric Spearman's correlations with the following results: (b) $r_s = -0.31$, $N = 56$, $P = 0.02$; (c) $r_s = -0.02$, $N = 56$, $P = 0.82$; (d) $r_s = -0.02$, $N = 56$, $P = 0.88$; (e) $r_s = -0.08$, $N = 56$, $P = 0.57$; (f) $r_s = 0.01$, $N = 56$, $P = 0.93$.

Fig. 2c). Docility and mass were not significantly related to weaning success within this sample of ewes.

DISCUSSION

Interindividual Variability in Temperament

Our results show that docility and boldness were consistent within ewes in the Ram Mountain population. The

high repeatability of docility (approximately 0.65 within years and 0.86 between years) indicates that a high level of heritability is possible for this trait (Boake 1989; Falconer & Mackay 1996). Boldness was moderately repeatable and appeared to have low heritability (0.21 ± 0.23), suggesting that genetic influences on individual boldness may be weak. Small sample size, however, limited our ability to determine whether heritability of boldness differed from zero. The significant difference in

Table 1. Relationship between age and boldness score for bighorn ewes on Ram Mountain, 1994–1998

Year	Restriction	r^2	b^*	df	F	P
1994		0.096	-0.041	1,92	9.819	0.003
1994	Age <13	0.008		1,86	0.730	0.39
1995		0.096	-0.071	1,97	10.338	0.002
1995	Age <13	0.009		1,86	0.812	0.37
1996		0.000		1,84	0.001	0.99
1997		0.007		1,78	0.543	0.46
1998		0.019		1,49	0.925	0.34

*The coefficient of regression (b) is indicated for significant regressions.

boldness among families (sibling analysis) suggests that there may be additive genetic influences or maternal effects on phenotypic variation in boldness. Studies of the behaviour of domestic animals have revealed a genetic influence on docility (Boivin et al. 1994). Le Neindre et al. (1995, 1996) reported heritabilities of 0.22 and 0.28, while Morris et al. (1994) found estimates ranging from 0.22 to 0.32. Moderate heritability in boldness has been shown in both human and nonhuman primate infants (Clarke & Boinski 1995; Segal & McDonald 1998). Studies by McCune (1995) on domestic cats, and by Wilsson & Sundgren (1998) on domestic dogs indicated genetic influences on boldness. Our results suggest that some aspects of temperament in bighorn sheep have the potential to evolve.

The significant repeatability of a character may also reflect a strong environmental influence on the behaviour of each individual (Falconer & Mackay 1996). Environment early in life may affect subsequent temperament. Previous experience of handling and the frequency of handling experienced by young domestic cattle, goat and sheep can decrease boldness (Lyons et al. 1988) and increase docility during subsequent handling (Le Neindre et al. 1996). Early handling influences how domestic cats react to humans (McCune 1995). Wilsson & Sundgren

(1998) reported strong maternal effects (Mousseau & Fox 1998) or common litter effects (caused by a maternal environment shared by all the offspring of the same female) on the temperament of young puppies. The similarity in boldness among sisters suggests that maternal effects also may affect temperament in bighorn sheep. In primates, offspring of restrictive mothers are fearful and cautious when facing novel and challenging situations or when encountering strangers (Fairbanks 1996).

Docility did not seem to depend upon a greater ease of handling small compared with large ewes. Handlers in 1999 assigned lower docility scores than handlers in 1998, but the relative docility of each ewe did not vary between years. Variance in boldness was probably underestimated because one priority of the research programme was to obtain at least two captures of each sheep each year. Therefore, when ewes that were seldom captured came to the trap, observers concentrated on trying to capture those ewes. Bold ewes, on the contrary, were trapped more often than indicated during the season, but were only handled every third week. We did not keep records of how often ewes were captured and released without handling.

Reproductive status had no effect on either docility or boldness scores in 1998. Low docility, therefore, did not seem to result from a need for ewes to defend their lambs. The number of captures was not influenced by the presence of a lamb, but ewes often came to the trap without their lamb. Boldness was averaged over several years and seemed independent of age at the individual level. There was no evidence of age-related changes in docility over 2 years, suggesting that docility may be stable over an individual's lifetime.

Is Temperament Domain Specific or Domain General?

The lack of significant correlations between most temperament indices suggests that temperament in bighorn

Table 2. Multiple regression model for age at primiparity and weaning success (number of lambs weaned until 1998) as a function of age, body mass, population density, boldness and docility in parous bighorn ewes of the Ram Mountain population

Variables in the model	b	SE	F	df	P
Age at primiparity					
Population density	0.009	0.002	21.11	1,33	<0.0001
Boldness	-0.324	0.145	4.981	1,33	0.03
Docility	-0.059	0.030	3.754	1,33	0.06
Body mass	0.011	0.007	3.121	1,33	0.08
General model: $R^2=0.51$; $F_{4,33}=8.467$; $P<0.001$					
Weaning success					
Age	1.206	0.22	30.021	1,35	<0.0001
Boldness	0.989	0.35	7.804	1,35	0.008
Variables rejected					
Docility			1.737		0.20
Body mass			1.440		0.24
General model: $R^2=0.52$; $F_{2,34}=18.511$; $P<0.001$					

Age, weaning success and age at primiparity were square-root transformed, and all independent variables were corrected for age effects. b indicates coefficient of regression. P value to remove variables from the model was 0.1.

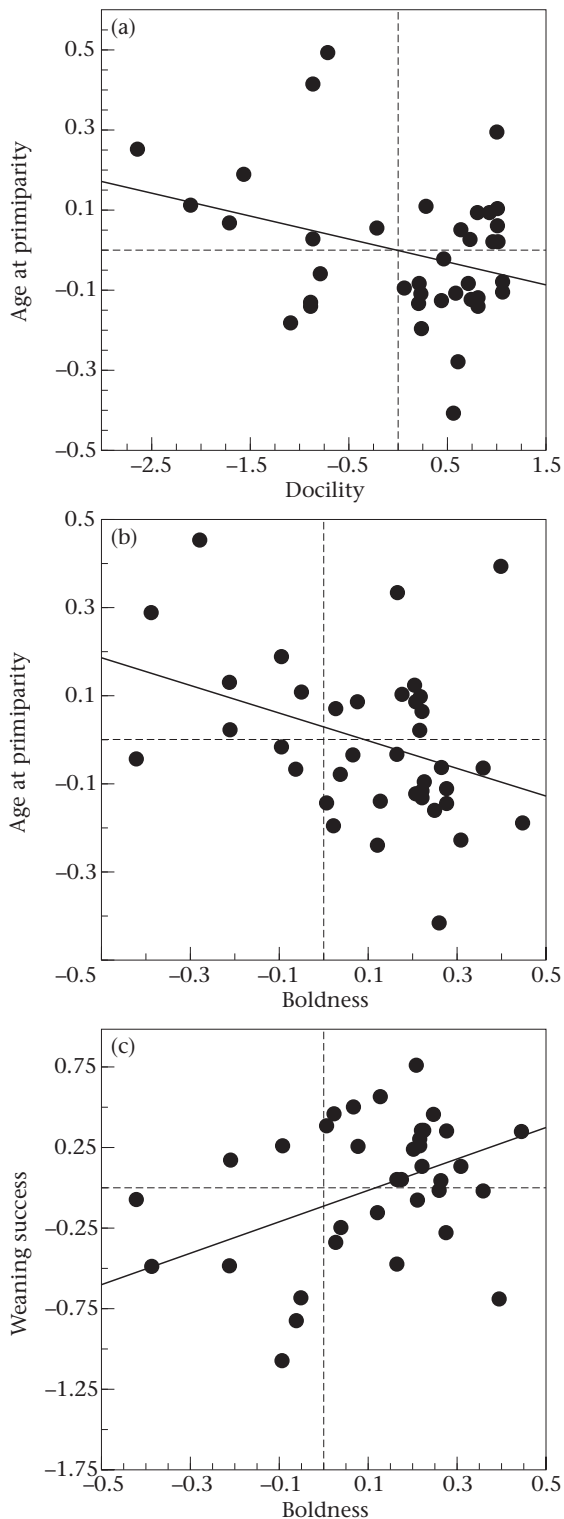


Figure 2. Relationships between temperament indices and life-history traits in bighorn ewes at Ram Mountain, Alberta, Canada. (a) Docility and age at primiparity, standardized for density, ewe mass and boldness (see Table 2). (b) Boldness and age at primiparity, standardized for density, ewe mass and docility (Table 2). (c) Boldness and weaning success, standardized by ewe age.

ewes is context specific, as proposed by Wilson et al. (1994) for other animals. Bold ewes were expected to be more docile because of more frequent experience with handling. However, shy ewes were also rarely aggressive. The association between docility and boldness suggests that some combinations of these two traits are less frequent than others in the population, possibly because of selection against particular combinations of these traits. There was no relationship between docility in the trap and dominance rank, possibly because dominance rank is not related to aggressiveness. Ewes may be mostly aggressive towards younger sheep, but those interactions were excluded from the calculation of dominance rank. Also, we could not utilize an individual frequency of agonistic interactions instead of dominance rank because the all-occurrence sampling meant that some ewes were observed more often than others.

Very few studies have addressed the question of context specificity or domain generality of temperamental traits. Tulley & Huntingford (1988) found a positive phenotypic correlation between boldness in an antipredator context and aggressiveness in a social context in sticklebacks (*Gasterosteus aculeatus*). Buirsky et al. (1978) found correlates between several social temperamental traits and dominance in chimpanzees (*Pan troglodytes*). Correlated responses to different novel situations and effects of early experience have been found in young goats (Lyons et al. 1988). On the contrary, Coleman & Wilson (1998) have shown context specificity in temperament of juvenile pumpkinseed sunfish, *Lepomis gibbosus*. Future study of interindividual variability in temperament in wild populations and of environmental effects on temperament would greatly improve our understanding of the evolution of behaviour. Temperament, if consistent, should affect fitness, because temperament affects individual reactions to predators, the way individuals explore novel environments and how they interact with conspecifics. Ewes should be selected to be bold in certain circumstances and shy in others. Context specificity in temperament would thus be advantageous compared with domain generality, and should be favoured by natural selection (Wilson 1998). Domain generality, however, could arise if different temperamental traits depended on common physiological, neural or genetic traits. For instance, studies of primates have found that low levels of serotonin metabolites in cerebrospinal fluid are associated with boldness, aggressive behaviour, risk taking, higher mortality and early emigration in young males (Mehlman et al. 1994; Higley et al. 1996; Fairbanks et al. 1999). Genetic constraints may prevent two traits from evolving independently (Arnold 1990; Falconer & Mackay 1996). The weak and not significant phenotypic correlations in our study tend to support the context specificity of temperament and the potential for different temperamental traits to evolve independently.

Relationship between Temperament and Life-history Traits

Temperament and life-history traits appeared to be related, because bold or docile ewes reproduced earlier

than shy or aggressive ewes and because boldness was positively related to a ewe's weaning success. If salt consumption affected reproductive traits in bighorn ewes, bold females would have benefited from greater access to the salt. Some laboratory experiments have shown that a salt-deficient diet affects growth or reproduction of mammals (McCree & Weeks 1993; Seynaeve et al. 1996; Woolfenden & Millar 1997). We could not estimate the amount of salt consumed by each ewe, and we do not know whether shy ewes were salt deficient. By removing the salt immediately after closing the trap door, however, we reduced between-ewe differences in salt consumption.

To our knowledge, only Armitage (1986) has explored the relationship between temperament and life-history traits. Boldness may not influence fitness directly, but rather may be correlated with life-history traits at the physiological or genetic level. Variability in temperament is assumed to be due to individual differences in neuro-endocrine activity (Boissy 1995). Hormones also affect many aspects of life-history variation in a population (Finch & Rose 1995; Ketterson et al. 1996; Sinervo & Svensson 1998). The relationship between boldness and age at primiparity supports our hypothesis that risk proneness may be simultaneously expressed in behavioural and life-history traits. Bold females appear to show precocious sexual maturity or greater maternal expenditure than shy females. For instance, the positive association between boldness, docility and fitness indices, together with the association between boldness and docility suggest that there may be a selective pressure against ewes that are both shy and aggressive. We therefore propose that future study of the relationship between temperament and life-history traits should provide clues about the evolutionary trade-offs between these characters (Stamps 1991).

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