



## Predator-induced natural selection on temperament in bighorn ewes

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(Received 19 September 2001; initial acceptance 8 March 2002;  
final acceptance 5 June 2002; MS. number: A9166)

Temperament traits in animals may have important fitness consequences, but have received little attention from ecologists or evolutionary biologists. A few studies have linked variation in temperament with fitness, but none has measured selection on temperament traits. We estimated the strength of selection on female boldness and docility on bighorn sheep ewes, *Ovis canadensis*. The Ram Mountain population experienced little predation pressure during the first 25 years of study, then 2 years (1997 and 1998) of frequent predation by cougars, *Puma concolor*, during which adult ewe mortality almost tripled over the long-term average, to 27% a year. During years of high predation, we found moderate selection favouring bold ewes, and age-specific selection on docility. Old ewes appeared more vulnerable to predation than young ewes. In contrast, no evidence of selection on temperament traits was observed during 2 years of low predation (1996 and 1999). These results suggest predator-induced selection favouring bold and nondocile ewes. Leadership was highly correlated with age and may increase the risk of predator encounter. Leadership alone, however, could not explain the higher vulnerability of old ewes to predation. Cougar predation on bighorn sheep occurs sporadically and unpredictably, probably because individual cougars often are prey specialists. Cougar predation may have limited micro-evolutionary effects on temperament in bighorn sheep, because it mostly affects ewes near the end of their reproductive life span and because of potential countervailing selection on boldness and docility.

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The behavioural reactions of an individual to novel or challenging situations can be defined as its temperament (Wilson et al. 1994). Individuals within a population, classified along a shy/bold gradient, may react differently when faced with novelty, predation, social interactions, reproduction, habitat exploration and dispersal (Wilson et al. 1994; Wilson 1998). Temperament traits may have important fitness consequences, but have received little attention from ecologists or evolutionary biologists (Stamps 1991; Wilson et al. 1994; Wilson 1998). Very few studies have assessed whether or not temperament can be subject to natural selection, although some have shown phenotypic or genetic correlations between temperament and fitness traits. Artificial selection experiments for tameness have led to correlated changes in reproductive traits, such as earlier primiparity, larger litters or aseasonal reproduction in captive foxes, *Vulpes vulpes* (Trut 1999), and changes in timing of reproduction

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and in gestation length in mink, *Mustela vison* (Malmkvist et al. 1997). In wild yellow-bellied marmots, *Marmota flaviventris*, highly sociable females have a higher reproductive success than less sociable ones (Armitage 1986). More recently, studies of primates have revealed that levels of serotonin metabolites in cerebrospinal fluids, known to affect temperament, are correlated with fitness-related traits, such as risk of wounding during agonistic interactions (Higley et al. 1992; Mehlman et al. 1994), timing of emigration (Mehlman et al. 1995) or reproductive performance (Gerald et al. 2001). Parental care can also vary with temperament among individuals (rhesus macaques, *Macaca mulata*: Maestripieri 1993; Boissy 1995; convict cichlid, *Chiclasoma nigrofasciatum*: Budaev et al. 1999). Bolder individuals have higher growth rate, and disperse farther, than shy individuals in the freshwater killifish, *Rivulus hartii* (Fraser et al. 2001). In bighorn sheep, *Ovis canadensis*, age at primiparity has a negative phenotypic correlation with both docility and boldness, and bold ewes have a higher weaning success than shy ewes (Réale et al. 2000).

With the exception of the study by Eaves et al. (1990) on humans, no formal studies of selection on

temperament traits have been attempted. To assess whether temperament traits are subject to selection, one may estimate the strength of selection on those traits using quantitative genetic models (Lande 1979; Lande & Arnold 1983). These models use simple statistical methods to provide standardized measures of the strength of selection and can partition the direct and indirect components of selection on a set of correlated characters (Lande & Arnold 1983; Fairbairn & Reeve 2001; Kingsolver et al. 2001).

Predation may select different temperament traits. Predator-induced selection on morphological traits has been shown in several studies (Endler 1986; Janzen 1993; Gotmark et al. 1997), and predator-induced selection is assumed to have led to covariation of antipredator behaviour and temperament traits with other traits (Brodie 1992; Gotmark et al. 1997; Kotiaho et al. 1998; Hedrick 2000) and to variation in temperament among populations (Magurran 1990; Huntingford et al. 1994). In the guppy, *Poecilia reticulata*, predator inspection deters predators from attacking the inspecting individuals (Godin & Davis 1995), and mate choice by females is biased towards bolder males (Godin & Dugatkin 1996). No study, however, has used quantitative genetics to estimate selection on temperament traits.

Here we examine the strength of selection on temperament traits in wild bighorn sheep, and test whether predation can be a factor of selection on these traits. Although predators such as wolves, *Canis lupus*, black bears, *Ursus americanus*, and cougars, *Puma concolor*, were present in the study area, almost no predation on adult ewes had been documented until 1997 (M. Festa-Bianchet, personal observation). Between 1997 and 1999, an increase in mortality rate and several witnessed cougar attacks suggested that predation was an important cause of female mortality. We used survival during four winters (years of low predation: 1996 and 1999; years of high predation: 1997 and 1998) to estimate the strength of selection on docility and boldness in bighorn ewes. Ewes were classified along a shy/bold gradient, using measures of trappability, while another temperament trait, docility, was measured for ewes handled in a trap (Réale et al. 2000). These traits showed within-individual consistency in different years (Réale et al. 2000). Between-year repeatabilities of both boldness and docility were significant, and ranged from moderate (boldness:  $r=0.36$ ) to high (docility:  $r=0.86$ ). Repeatability gives the upper bound of heritability, an index of the evolutionary potential of a trait (Boake 1989), suggesting a possible response of temperament traits to selection.

Predation risk may depend on prey behaviour (Brodie 1992; Gotmark et al. 1997; Kotiaho et al. 1998; Berger et al. 2001). Variation in boldness may correspond to variation in willingness to take risks (Réale et al. 2000), such as grazing in closed habitats, where a cougar may wait in ambush. Docility is a temperament component related to reaction towards humans (Réale et al. 2000), but humans are potential predators, and variation in docility may represent variation in reactions towards other predators. Finally, individuals leading a moving group may incur higher risks of predation (Boinsky &

Garber 2000). Because bighorn ewes differed in their tendency to lead, we considered leadership in our analysis of selection. If selection on temperament reflects differential vulnerability to predation, we would expect stronger selection on temperament during years of high than of low predation rate.

## METHODS

### Study Site and Population

We observed bighorn sheep at Ram Mountain (52°N, 115°W), Alberta, Canada (Festa-Bianchet et al. 1996). Since 1972, the population has been studied each year, from late May through to October. All ewes have been individually marked since 1976. We captured sheep in a corral trap baited with salt. Details about capture and handling procedures are provided in Réale et al. (2000). More than 90% of the ewes (>1 year of age) were captured two to seven times each summer. 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 (Réale et al. 2000), which we assumed to reflect individual differences in willingness to accept the risk involved in licking the salt bait. Ewes that were rarely captured were considered shy, and ewes frequently captured were considered bold. An annual boldness index was calculated for each year from 1994 to 1998 and standardized for year effects. Mean boldness over successive years was used as the individual boldness index.

A docility score was given to each ewe at each capture during 1998 and 1999, based on her behaviour when handled (Réale et al. 2000). Docility scores varied from 0 to 7, with 7 indicating the most docile individuals. One to five scores ( $\bar{X} \pm \text{SE} = 2.24 \pm 0.09$ ;  $N=173$ ) were obtained for each ewe in 1998, and one to six scores ( $3.56 \pm 0.09$ ;  $N=133$ ) were obtained for each ewe in 1999. We calculated annual docility for each ewe as the mean of docility scores each summer. An overall docility index was calculated for each individual as the average of annual docilities. Annual docility was highly repeatable ( $r=0.81$ ), and unaffected by handler bias (Réale et al. 2000). Boldness and docility scores were normalized by a square-root transformation before statistical analyses.

To estimate an index of leadership for each female, during the summer of 1998 we observed 99 groups of ewes that changed their activity (resting, grazing) to move from one place to another. For each observation we noted the identity of the leader and the group composition. We then calculated the proportion of observations where each female was the leader over the total number of observations for that female. A 14-year-old female was the leader in 80% of the cases, before a cougar killed her on 8 August. That ewe's behaviour decreased the variation in leadership among other females. We thus

calculated leadership indices for other females from observations ( $8.56 \pm 3.09$  per female) made after 8 August. The leadership index was arcsine transformed before analyses.

### Estimating Natural Selection on Temperament Traits

Fitness was measured as survival during 4 years (1996–2000), September–September (end of the field season). These 4 years will be referred to as episodes of selection. Because female emigration is almost nonexistent (Jorgenson et al. 1997), individuals that were not seen during a summer were assumed to have died during the previous winter. Ewe survival declines with age (Jorgenson et al. 1997; Loison et al. 1999), therefore we included ewe age before each episode of selection in the model. Cougar predation appeared to start in September 1997, when the first attack was witnessed. No cougars were observed after 1998. We compared periods with high (1997 and 1998) and low predation rate (1996 and 1999) to assess age-specific predation and predator selection for temperament traits.

Although a boldness index was available for females in the population before 1998, we did not start scoring docility until 1998, and we scored leadership only in 1998. Therefore, females that died in 1997 were not classified according to docility and leadership. Leadership probably depends on the social context and its value may change from year to year, according to the population age structure. We thus ran analyses including boldness and age for the first two episodes of selection (1996 and 1997), then analyses including boldness, docility, leadership and age for 1998, and analyses including boldness, docility and age for the last episode of selection (1999). Fourteen ewes removed during the summer of 1997 for transplant elsewhere in Alberta were not considered in analyses from 1997. Only females for which all traits were measured were included. Phenotypic correlations between age, boldness, docility and leadership in 1998 were estimated with Pearson correlation coefficients. Changes in phenotypic correlations from one year to another only result from the removal of females that died between the 2 years, and therefore are not shown.

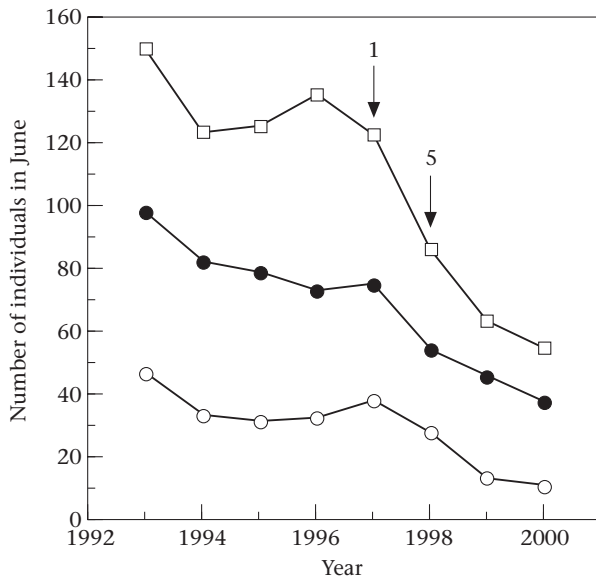
Selection on phenotypes is usually estimated following Lande & Arnold (1983; see also Fairbairn & Preziosi 1996), by regressing relative fitness ( $w'_i = w_i/\bar{w}$ ; for individual  $i$ ) values on standardized values of traits ( $z'_i = [x_i - \bar{x}]/\sigma_x$ ). Net linear (directional) selection gradients ( $\beta_1$ ) are estimated from simple linear regressions  $w'_i = a + \beta_1 z_i + e$ , where  $\beta_1$  is the coefficient of the regression of relative fitness ( $w'_i$ ) of individuals with standardized trait value  $z_i$  (Lande & Arnold 1983; Brodie et al. 1995; Fairbairn & Preziosi 1996). Nonlinear selection gradients (stabilizing or disruptive selection:  $\gamma_1$ ) are estimated from the regression model ( $w'_i = a + \beta_1 z_i + \beta_2 z_i^2 + e$ ), incorporating the main effect and its quadratic term ( $\gamma_1 = 2\beta_2$ ). For a set of two traits  $i$  and  $j$ , multivariate linear selection gradients ( $\beta_3$ ) are estimated as the partial coefficients of the multiple regression ( $w'_i = a + \beta_{3i} z_i + \beta_{3j} z_j + e$ ). Multivariate nonlinear analysis, incorporating the traits and all the quadratic

terms ( $w'_i = a + \beta_{3i} z_i + \beta_{3j} z_j + \beta_{4i} z_i^2 + \beta_{4j} z_j^2 + \beta_{5ij} z_i z_j + e$ ) allows one to estimate nonlinear ( $\gamma_{3i} = 2\beta_{4i}$  and  $\gamma_{3j} = 2\beta_{4j}$ ) and correlational selection ( $\beta_{5ij}$ ) gradients. A negative  $\gamma$  will indicate that the fitness surface is concave, and a positive  $\gamma$  suggests a convex fitness surface (Brodie et al. 1995; Fairbairn & Reeve 2001). Correlational selection gradients indicate the presence of nonlinear selection on combinations of traits (Lande & Arnold 1983; Brodie et al. 1995). Univariate selection gradients include both direct selection acting on the trait and indirect selection acting on a phenotypically correlated trait, while multivariate gradients estimate selection acting directly on the trait (Lande & Arnold 1983). Sample sizes of hundreds of individuals, however, are needed to detect nonlinear selection gradients (Lande & Arnold 1983; Brodie et al. 1995; Kingsolver et al. 2001). Although almost all the females of the population were included in the data set, population size was insufficient to estimate all of the nonlinear gradients when age, boldness, docility and leadership were considered. We therefore limited our analyses to direct linear and age-specific selection gradients; for each analysis we included the main effects (traits) and the interaction between age and the traits.

Because the binomial distribution of fitness (measured as ewe survival) violated the normality assumption of parametric models, we used logistic regressions for significance testing (Brodie et al. 1995; Janzen & Stern 1998). We were interested in selection acting directly on each trait, holding the effects of other traits constant. We therefore limited our analysis to the multivariate logistic regression. We first tested the significance of age-specific selection on the traits, in a model including the traits and interactions between age and the other traits. We then tested the significance of the main effects using a multivariate model including the traits alone (Lande & Arnold 1983). Because multivariate normality of phenotypes may not be met, we used the method proposed by Janzen & Stern (1998) for estimating selection gradients from logistic regression coefficients. Estimates of selection gradients ( $\beta_{\text{avggrad}}$ ) were obtained by multiplying the logistic regression coefficients ( $\alpha$ ) by the constant  $1/N \sum_{i=1}^N [Wz(1-Wz)]$ , where  $N$  is the number of individuals and  $Wz$  is the survival probability (obtained from the logistic regression) for an individual described by the series of traits in the analysis, and by  $1/\bar{w}$  to place gradients on a relative fitness scale (Janzen & Stern 1998). Average gradients ( $\beta_{\text{avggrad}}$ ) for main traits correspond to multivariate linear selection gradients ( $\beta_3$ ), and gradients for interactions between the traits and age to the correlational selection ( $\beta_5$ ) gradients of Lande & Arnold (1983).

## RESULTS

Before 1981, the population was controlled through yearly ewe removals. After removals were ended in 1981, the population increased, peaked in 1992, then declined. The decline was partly caused by a delay in age at primiparity (Jorgenson et al. 1993) and a decrease in lamb survival (Festa-Bianchet et al. 1998). Population



**Figure 1.** Number of bighorn sheep (adult females  $\geq 2$  years of age: ●; adult males  $\geq 2$  years of age: ○; total animals  $\geq 1$  year of age: □), at Ram Mountain between 1993 and 2000. Differences in changes from one year to the next between the total number of sheep and the number of adult males and females are due to interannual variation in recruitment. Arrows indicate the number of sightings of cougar attack and confirmed cases of cougar predation.

decline was very rapid between 1997 and 1999 (Fig. 1). Nineteen (27.1%) of 70 adult and yearling females on Ram Mountain in September 1997 had disappeared by September 1998. Fourteen (26.4%) of the 53 females alive in September 1998 disappeared before September 1999. In contrast, 16 (17.6%) of 91 and 7 (16.7%) of 42 females died during the winters of 1996/1997 and 1999/2000, respectively. During 1997 and 1998, female mortality was therefore high, compared with the average yearly mortality (about 10–15%) of adult females from 1972 to 1995 (Jorgenson et al. 1997). For the first time in 25 years of monitoring, during the summers of 1997 and 1998, four attacks by cougars were witnessed, and predation by cougars was documented on four occasions during the summer of 1998 (two attacks witnessed were successful). All attacks occurred while the sheep were foraging (3 attacks) or moving (1 attack) close to the forest edge. No cougars were seen in 1999–2001.

In 1998, docility and boldness were positively but not significantly correlated with age (Table 1). Docility and boldness tended to be negatively correlated (Réale et al. 2000). Leadership increased with age (Fig. 2) but substantial variation in leadership remained among females of the same age.

Logistic regression including ewe age, boldness and their interaction (likelihood ratio test:  $\chi^2_{3,81}=2.833$ ,  $P=0.42$ ) suggested no effect of age and boldness on survival during winter 1996, before cougar predation. A logistic regression for survival from 1997 to 1998, incorporating age and boldness and their interaction was significant ( $\chi^2_{3,60}=15.268$ ,  $P=0.002$ ). Survival was significantly higher for young than for old ewes and for bold than for shy ewes, and no significant age-specific

selection on boldness was detected (Table 2). Selection analysis between 1998 and 1999, included age, boldness, docility, leadership, and their interaction with age (Table 2). The full model was significant ( $\chi^2_{7,45}=25.387$ ,  $P<0.001$ ) indicating that at least one of the traits was related to fitness. Young females survived better than old females, and bold ewes survived better than shy ones (Table 2). The significant age\*docility interaction suggested an increase in the correlation between mortality and docility with increasing ewe age (Fig. 3a). Females that survived the period of high predation rate (1997–1999) were bolder than those that died during that period (Fig. 3b). Selection analysis between 1999 and 2000 included age, boldness, docility, and the interactions between age and boldness and docility. The model was not significant ( $\chi^2_{5,32}=3.169$ ,  $P=0.67$ ), indicating no relationship between survival and age, boldness and docility.

In summary, years of high predation suggested a strong negative relationship between age and survival, selection favouring bold ewes and age-specific selection on docility. Years of low predation rate were characterized by the absence of relationships between survival and age, boldness and docility.

## DISCUSSION

We provide evidence that temperament traits can be subject to selection in the wild. The Ram Mountain bighorn sheep population experienced high predation from 1997 to 1999 (Fig. 1). Mortality was 1.5 times as high in 1997 and 1998 than in 1996 and 1999 when no cougar observations were reported. During years of high predation, about 27% of the bighorns died, a mortality similar to that induced by cougars in other bighorn sheep populations (Wehausen 1996; Ross et al. 1997; Hayes et al. 2000). Comparisons among years with high and low predation suggest the occurrence of age-specific predation on ewes, and that predation was responsible for the covariance between temperament traits and survival.

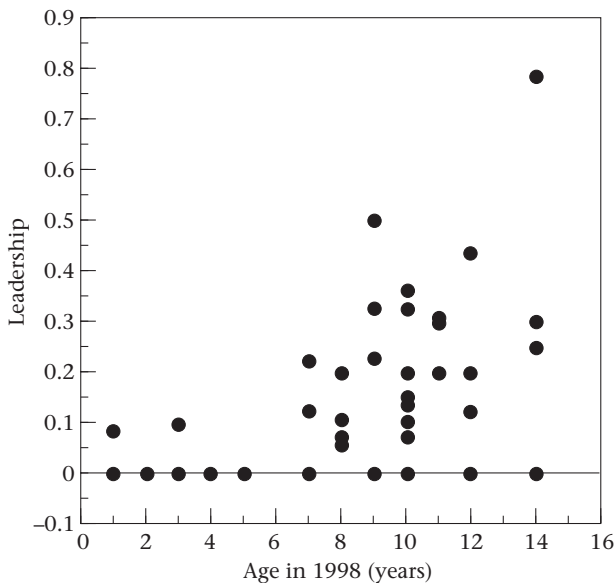
Phenotypic selection analyses require large sample sizes (Kingsolver et al. 2001), and therefore our study has limited statistical power. This may increase the risk of type II error, particularly for low estimates of selection gradients. However, we could not increase our sample size, because we considered all females in the population during the study period. Given the apparent rarity of individual cougars that specialize on sheep predation, it would have been unrealistic to wait for another predation period. We provided replicates of selection gradients on periods of high and low predation pressure, and replicates for a given trait and period were similar.

### Selection on Temperament Traits

Direct selection favoured bold ewes in years of high predation. These results, combined with the absence of selection on boldness during years of low predation, suggest predator-induced selection on boldness. During years of low predation, boldness did not seem to have a short-term selective advantage. We found age-dependent

**Table 1.** Means (nonstandardized values), phenotypic variances (within parentheses; diagonal) and phenotypic correlations (above the diagonal) between age, boldness, docility and leadership in bighorn ewes ( $N=56$ ) of the Ram Mountain population (Alberta, Canada) in 1998

	Age (years)	Boldness	Leadership	Docility
Age	7.5 (15.4)	$r=0.15, P=0.28$	$r=0.58, P<0.001$	$r=0.06, P=0.64$
Boldness		0.09 (0.06)	$r=0.00, P=0.99$	$r=-0.25, P=0.07$
Leadership			0.12 (0.03)	$r=0.13, P=0.33$
Docility				0.05 (0.90)



**Figure 2.** Relationship between female age and leadership in the Ram Mountain bighorn sheep population in 1998. Leadership was defined as the proportion of time an individual was observed leading a group over the total number of observation for that individual.

selection on docility during 1998, a year of high predation. Old docile ewes appeared to be more vulnerable to predation than less docile ones. A similar relationship could not be detected for young ewes. We measured boldness as the tendency to enter the trap, which may represent how ewes react towards a challenging situation (Réale et al. 2000). Docility, in contrast, represents the way an individual reacts to handling by humans, and may be related to reactions towards potential predators. We thus hypothesize that boldness and docility in bighorn ewes may be related to risk proneness and to antipredator behaviour. Attacks by cougars are seldom observed, however, and the mechanisms responsible for the relationship between temperament traits and survival in the presence of predators are unknown. Previous studies on temperament suggest that individuals that react boldly towards a predator are also bolder in a new and risky environment (Huntingford 1976). Because bold individuals are more prone to inspect predators, and predator inspection deters predators, bold individuals are less likely to be attacked by predators than shy individuals (Godin & Davis 1995). On some occasions, we observed ewes that stopped foraging and moved closer

to the forest edge, behaving in a way suggestive of predator inspection: they were highly vigilant, immobile, their ears pricked up, and all staring towards the forest. Unfortunately, we cannot relate these behaviours to a particular type of temperament. Our results contradict the hypothesis that bold individuals are risk prone, and may be more vulnerable to predation than shy individuals (Stamps 1991; Boissy 1995). Low docility is generally associated with fear (Boissy 1995; Grandin 1998), but no study has related docility to predator inspection or avoidance. We can also reject the hypothesis that low survival of shy or docile ewes could be due to a lower dominance rank (i.e. shy 'subordinate' ewes might be forced by bold 'dominant' ones to forage in riskier places), because neither boldness nor docility correlate with dominance (Réale et al. 2000). Further studies are needed to relate interindividual variation in temperament with the risk of predation.

### Age-specific Mortality and Predation

During years of high cougar predation, old ewes were at a greater risk of predation than young ewes. Other factors associated with age-specific mortality during years of high predation may vary, thus increasing or decreasing an individual's vulnerability to predation. For example, old females generally lead groups, and may have a higher chance of being attacked by ambush predators. In the summer of 1998, one of the oldest ewes was killed by a cougar as she entered the forest while leading a group (see above). However, leadership was not statistically related to survival in 1998, once the effect of age was removed, suggesting that contrary to what is currently assumed (Boinski & Garber 2000), leading a group does not necessarily increase the risk of predation. Cougar attacks while bighorns are travelling might represent a small proportion of all attacks. Most of the attacks witnessed occurred while bighorns were foraging close to the forest edge. We cannot reject the hypothesis that leading a group increases the risk of being killed, but leadership alone cannot explain why mortality rate increased with age in 1997 and 1998.

Higher mortality of old ewes is also caused by senescence (Loison et al. 1999), independently of predation. Our results, however, suggest that both senescence and predation affected mortality of old ewes. Senescence may also increase the risk of being killed by a cougar if older females lack stamina (Pierce et al. 2000). Although we did

**Table 2.** Logistic analysis of selection (survival) on age and temperament traits in bighorn ewes at Ram Mountain during the episode of selection 1997/1998

Variables	$\chi^2$	df	P	$\alpha$	SE	$\beta_{\text{avggrad}}$	SE
1997							
Age*Boldness	0.030	1,60	0.862	-0.076	0.433	-0.012	0.069
Age	12.558	1,61	<0.001	-1.410	0.499	-0.217	0.076
Boldness	3.562	1,61	0.059	0.651	0.347	0.100	0.054
1998							
Age*Boldness	1.365	1,45	0.243	-0.592	0.567	-0.092	0.088
Age*Docility	12.811	1,45	<0.001	-2.324	0.973	-0.360	0.152
Age*Leadership	0.198	1,45	0.656	-0.318	0.718	-0.049	0.111
Age	4.371	1,48	0.036	-0.982	0.494	-0.233	0.117
Boldness	4.244	1,48	0.039	0.774	0.382	0.184	0.091
Docility	0.796	1,48	0.379	0.309	0.350	0.073	0.083
Leadership	0.127	1,48	0.722	0.156	0.438	0.037	0.104

Traits were standardized prior to analyses. We first ran a model including age, the traits, and their interactions with age. Significance tests for the interactions were obtained with deletion procedure using likelihood ratio chi-squares. We then ran a model with main effects only, using the same significance test procedure. Selection gradients ( $\beta_{\text{avggrad}}$ ) and their approximate SEs were estimated using the average gradient method (Janzen & Stern 1998) from logistic regression coefficients ( $\alpha$ ). Relative fitness (1997:  $1/\bar{w}=1.255$ ; 1998:  $1/\bar{w}=1.395$ ). See text for more details.

not consider lambs in our analysis, cougars select both younger and older ungulates (Kunkel et al. 1999; Pierce et al. 2000). Of the 43 lambs we observed in 1997 and 1998, 81% died before 1 year of age, suggesting that they were highly vulnerable to predation.

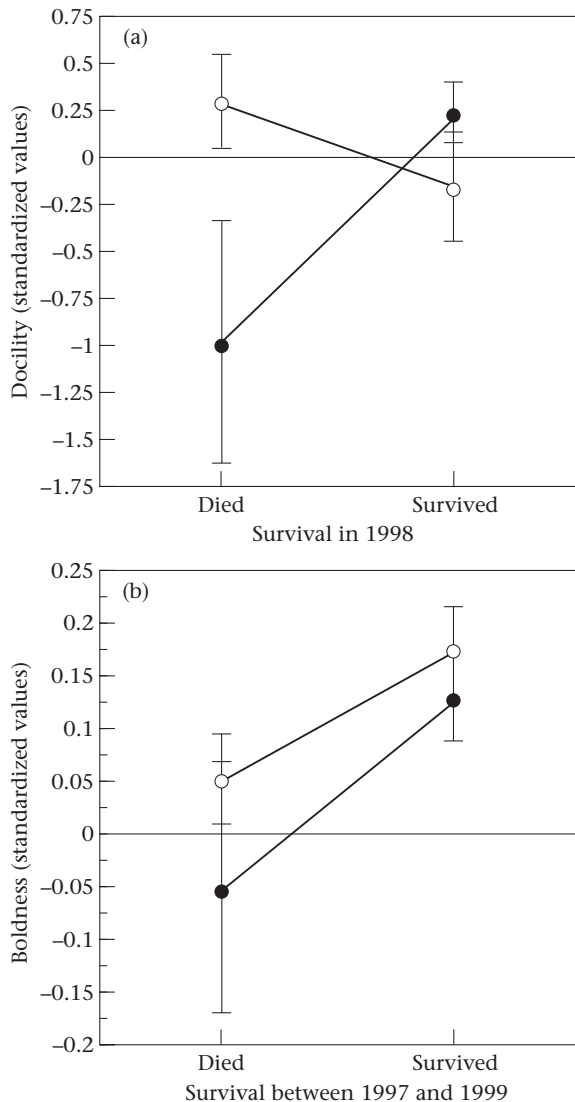
### Evolutionary Consequences of Cougar Predation

Demonstrating that predation causes evolutionary change of traits in a population is not easy. From the multivariate response equation  $\Delta\bar{z}=\mathbf{G}\beta$  (Lande 1979), the evolutionary response of a set of traits to selection ( $\Delta\bar{z}$ ; change in trait means across generations) depends on  $\mathbf{G}$ , the additive genetic variance-covariance matrix, and on  $\beta$ , the vector of multivariate selection gradients. This equation shows that selection on a trait is distinct from response to selection, and that a response of that trait to selection  $\Delta\bar{z}\neq 0$  occurs only when its additive genetic variance is different from 0. For example, age by itself is not a trait that can evolve. Selection cannot affect age, but may act on traits that vary according to age. Age-specific mortality can affect the evolution of several life-history traits (Skogland 1989).

Selection on a trait, and heritability of that trait, are both necessary for a trait to evolve. Our estimates of linear selection gradients are moderate compared to published median values (morphological traits:  $|\beta|=0.17$ ; life-history traits:  $|\beta|=0.08$ ) reviewed by Kingsolver et al. (2001). Unfortunately, estimates of selection on behavioural traits were too few (Kingsolver et al. 2001) to allow a specific comparison. Empirical evidence for heritability ( $h^2$  is the additive genetic variance relative to phenotypic variance) of temperament traits has been found in many species (Boissy 1995; Grandin 1998). Repeatability estimates of boldness and docility in the Ram Mountain bighorn population (see above) suggests that these traits should be heritable (Réale et al. 2000). It is worth noting that high repeatability of temperament in this population

may also be caused by maternal effects or permanent environmental effects (Réale et al. 2000). We are currently unable to separate these effects from purely additive genetic effects (i.e.  $h^2$ ).

Therefore, temperament traits may evolve if they are both heritable and under selection. Evolution of temperament traits because of predation by cougars, however, may be limited for several reasons. First, both correlated selection and genetic correlations between temperament traits and other traits may limit the response to selection (Lande 1979). We cannot exclude the possibility that other unmeasured traits correlated with boldness and docility are under selection (see Lande & Arnold 1983). Artificial selection on temperament often leads to correlated changes in morphological, behavioural, or life-history traits (Trut 1999), and strong selection on these traits may prevent evolution of the correlated temperament traits in natural conditions. Selection may act against ewes that are shy and docile. However, in the present study, the relationship between boldness and docility and both age at primiparity and weaning success, coupled with the rarity of nondocile ewes that were also shy, suggests the presence of other selective pressures on combinations of boldness and docility (Réale et al. 2000). Bold and docile ewes reproduced earlier than shy and aggressive ewes, and weaning success was positively related to boldness, suggesting better maternal performance by bold ewes. Second, predator-induced selection on docility may not have strong evolutionary consequences because predation mainly affects old ewes with low residual reproductive value. Finally, cougar predation on bighorn sheep appears to be sporadic, caused by individuals that specialize on bighorns (Wehausen 1996; Ross et al. 1997). Evolutionary consequences of rare selection events may therefore not be important over the long term, and temperament may be subject to different selection pressures induced by predators, such as wolves, that use different hunting techniques.



**Figure 3.** Temperament of bighorn ewes that died and survived during years of high predation (●: <7 years old; ○: >7 years old). (a) Docility (square-root transformed) in 1998 (ANOVA: survival,  $F_{1,49}=1.922$ ,  $P=0.17$ ; age,  $F_{1,49}=1.370$ ,  $P=0.25$ ; age\*survival,  $F_{1,49}=6.717$ ,  $P=0.013$ ). (b) Boldness during the period 1997–1999 (two-way ANOVA: survival,  $F_{1,60}=7.189$ ,  $P=0.009$ ; age,  $F_{1,60}=1.706$ ,  $P=0.20$ ; age\*survival,  $F_{1,60}=0.301$ ,  $P=0.59$ ).

Bighorn sheep appear to be better adapted to avoiding predation by a cursorial predator such as the wolf (Festa-Bianchet 1991) than by a stalking/ambush predator, possibly explaining the high vulnerability of bighorns to cougar predation, and the strong demographic impact of cougars on bighorn sheep (Ross et al. 1997). These results underline the need for further studies of selection on temperament traits over the long term, to evaluate the relationship between temperament traits and fitness in varying environmental circumstances.

#### Acknowledgments

We thank Jon Jorgenson and Bill Wishart for their pivotal contributions to the Ram Mountain study. Many

thanks to Pierrick Blanchard, Bruno Gallant, Achaz von Hardenberg, Mike Jokinen and Mylène Leblanc for help in collecting data on temperament. D. Réale was supported by a postdoctoral fellowship from the Fyssen Foundation (France). We are grateful for financial support from the Natural Sciences and Engineering Research Council of Canada, the Alberta Conservation Association, the Alberta Natural Resources Service, the Foundation for North American Wild Sheep, the Fonds pour la formation de Chercheurs et l'Aide à la Recherche (Québec) and the Université de Sherbrooke. The research presented here was described in Animal Utilization Proposal No. MFB01 approved on 7 May 1997 by the Université de Sherbrooke Animal Care Committee and renewed each year since. This is contribution number 154 of the Groupe de recherche en écologie, nutrition et énergétique.

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