

Density-dependent selection on horn phenotype in Soay sheep

T. H. CLUTTON-BROCK¹, K. WILSON² AND I. R. STEVENSON²

¹Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK (thcb@cam.ac.uk)

²Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK

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SUMMARY

In the naturally regulated population of Soay sheep (*Ovis aries* L.) on Hirta (St Kilda), 12% of males and 24% of females have scurred horns. This trait reduces the competitive ability of males in the mating season but is associated with higher overwinter survival rates in both sexes (Moorcroft *et al.* 1996). In this paper, we show that scurred females also show higher conception rates and weaning rates than non-scurred ones, and that these differences are associated with heavier maternal body weight as well as higher birth weights of offspring. Selection pressures favouring scurredness in females vary with population density and are generally more pronounced among younger animals than adults. We discuss these results with reference to recent suggestions that temporal fluctuation in selection pressures may help to maintain genetic diversity within populations. We suggest that selection against scurredness operating through male mating success is opposed by selection favouring this trait, operating through the breeding success of females and the survival of both sexes.

1. INTRODUCTION

Temporal fluctuations in selection pressures have been repeatedly proposed and rejected as a possible mechanism for maintaining genetic variation in natural populations (Hedrick *et al.* 1976; Hedrick 1986; Frank & Slatkin 1990). Several recent models suggest that changing selection pressures may help to maintain genetic diversity in populations with overlapping generations where particular genotypes are sheltered from selection during some stages of the life history (Ellner & Hairston 1994). However, empirical studies that can compare selection pressures on different stages of the life history under changing environmental conditions are scarce and we currently know little about the magnitude of these changes or about the extent to which they vary throughout the lifespan.

In this paper, we describe density-dependent changes in selection on different horn phenotypes

among Soay sheep (*Ovis aries* L.) of different ages on the island of Hirta, St Kilda. This population exhibits persistent instability (Jewell *et al.* 1974; Clutton-Brock *et al.* 1991), providing an unusual opportunity to investigate density-dependent changes in selection pressures. Both sexes of sheep vary in horn morphology, ranging from polled (*P*; a total absence of horns), through scurred (*S*; the presence of small, apparently vestigial horns) to the full development of normal horns (*H*) that increase in size throughout the lifespan. The frequencies of the three horn types differ between the sexes (males: *P* = 0%, *S* = 12%, *H* = 88%; females: *P* = 41%, *S* = 24%, *H* = 35%) and horn development is known to have a significant genetic component (Ibsen 1944; Doney *et al.* 1974). Scurring appears to be modulated by genetic differences at two loci (Ibsen 1944), while the presence or absence of horns is determined by genetic differences

at one other locus (see also Dolling 1960, 1961).

Horn morphology in the Hirta population is known to be related to components of fitness. Scurred males show lower mating success than horned phenotypes (Wilson, unpublished data) while scurred animals of both sexes show significantly higher survival than horned or polled ones in years when population density and mortality are high (Moorcroft *et al.* 1996). Here, we compare the fecundity and rearing success of scurred (SC) and non-scurred (NSC) females of different ages at varying levels of population size. Since fecundity and survival are known to be related to body weight (Clutton-Brock *et al.* 1992, 1996), we also investigate whether the relationship between horn morphology and breeding success is generated by differences in body weight, offspring birth date or offspring birth weight between scurred and non-scurred animals.

2. METHODS

(a) *Study area and animals*

Soay sheep are the most primitive domestic sheep in Europe, closely resembling both the original wild species and the domestic neolithic sheep first brought to Britain in around 5000 BC (Clutton-Brock 1981). They may have been introduced to the St Kilda archipelago (57°49', 08°34' W) in the second millennium BC (Boyd & Jewell 1974) but, by historical times, were restricted to the uninhabited island of Soay (99 ha). Two years after the human population of Hirta (638 ha) was evacuated in 1930, 107 Soay sheep, some of which may have been castrated, were introduced from Soay. Numbers on Hirta increased rapidly and, in 1952, the first organized census produced an estimate of 1114 sheep. Though the sheep are distributed throughout Hirta, a relatively distinct population, comprising around 30% of the total population, uses the Village Bay area. Our analysis is based on the number of sheep using this area. Previous analyses have shown that population size in the Village Bay area is closely related to total numbers on Hirta (Jewell *et al.* 1974).

Between 1985 and 1996, the number of sheep on Hirta was counted each summer. The analyses described in this paper are based on data collected during 1985–1995. Since 1985, over 95% of lambs born in the Village Bay area have been caught and tagged each year, and the majority of adult animals using the Village Bay area have been caught in August, providing estimates of growth at different population densities. We categorize animals as juveniles from three months until the beginning of their second summer, when they are around 13 months old; as yearlings from 13 to 24 months; as two-year-olds from 25 to 36 months; and as adults after 36 months. We refer to animals less than three months old as lambs. As we have described in previous papers, a variable proportion of juveniles became pregnant in their first rut, at around seven months old.

Annual mortality was measured by systematic searches for carcasses in late winter and early spring, combined with regular censuses of tagged animals during the lambing season. Almost all animals dying in the summer months were lambs (Grubb 1974), most of which died within ten days of birth. The main peak in mortality occurred in late winter, between the end of December and the onset of lambing (Grubb 1974). Many dying animals sought shelter in the dry stone chambers (cleits) that are

scattered over the slopes of Village Bay so that a high proportion of carcasses were found and recorded. Since 1985, 84.4% of tagged animals have been recovered or are currently alive.

(b) *Variables*

Variables used in our analysis were defined as follows.

Population size: the total number of sheep alive on 1 October of a given year and regularly using the Village Bay study area. As most mortality occurs in winter (Clutton-Brock *et al.* 1997), in our analyses of the effects of population density on conception rate, weaning rate, lambing date and offspring birth weight, population size was the number of animals alive in the previous autumn whereas, in analyses of female weight, we used the number of animals alive in the same autumn.

Mother's age: the age of the mother in years, based on known birth dates or, in a minority of cases, on analysis of cementum rings in incisor teeth (Clutton-Brock *et al.* 1991). Only females up to ten years old were used in these analyses, so as to minimize the variable effects of ewe senescence.

Horn type: females were classified as horned, polled or scurred. Horned and polled animals did not differ from each other in the fitness parameters examined here and probably shared the same genotype at the locus controlling the presence of scurs (Ibsen 1944). Consequently, they were combined in our analyses and we compared scurred (SC) and non-scurred (NSC) animals.

Conception rate: the probability that a female produced one or more lambs or had one or more lambs *in utero* when dissected at death.

Weaning rate: the proportion of ewes that successfully raised at least one lamb to weaning age (six weeks); this analysis was confined to those ewes that survived to the weaning age of their lambs. The results of this analysis were unchanged by excluding ewes that produced twins.

Lambing date: defined as the Julian date of lambing (days from 1 January).

Birth weight: the residual weight of singleton lambs, calculated as a deviation from the linear regression of lamb capture weight on lamb age at capture; only lambs caught in their first ten days of life were included in the analysis.

Female weight: the weight (in kg) of the ewe in the August prior to parturition.

(c) *Analysis*

Birth and weaning rates were binomially distributed and so were analysed using logistic regression models. We used a generalized linear modelling function (McCullough & Nelder 1989) within the *Splus* statistical package (MathSoft Inc. 1993) and specified a binomial error distribution and a logit link function. Female body weight, lamb weight and birth date were all normally distributed, and so were analysed using classical linear regression models using the same package.

The aim of the analysis was to determine the effect of horn type on the relationship between female reproductive success and population density. In our initial analyses, we included population size, horn type and their interaction as independent terms in the models, whilst controlling for any effects of mother's age (see below), and refer to these as *simple* models. In subsequent analyses, we tested the significance of additional terms that might affect female reproductive success (see below) by a

method of stepwise deletion and determined the appropriate minimal models (McCullough & Nelder 1989). We refer to these as *complex* models. To avoid replication, we describe the results of the latter only when they are qualitatively different from those of the earlier analyses. In none of the models presented here was there a significant difference between polled and horned females, thus justifying the combination of these horn types.

Mother's age was a potentially important confounding variable in these analyses. Older animals were generally more fecund (Clutton-Brock *et al.* 1991). Since female survival rates differed between the horn types (Moorcroft *et al.* 1996), any relationship between horn type and fecundity could have been a consequence of the higher survival rate of scurred females. We overcame this potential problem in two ways. First, we employed analyses in which age and its interactions were included as terms in a model that included all age classes. Second, we conducted separate analyses for each of three age classes: juveniles; yearlings and two-year-olds; and adults. Yearlings and two-year-olds were combined in these analyses due to the low numbers of yearling ewes in some years.

Two characters apart from horn type are known to be related to survival in the sheep (Gulland *et al.* 1993; Moorcroft *et al.* 1996). At high population density, light-coated animals showed lower survival than dark-coated ones; and FF genotypes at the Adenosine deaminase (ADA) locus were more likely to die than SS or SF genotypes. Horn phenotype was not consistently related to coat colour ($\chi^2 = 8.45$, d.f. = 6, $p = 0.207$) or ADA genotype ($\chi^2 = 4.14$, d.f. = 4, $p = 0.387$) and we control for these effects in the complex models. We also examined the effect of including female body mass in the complex models, in order to determine whether differences in fecundity between SC and NSC animals could be explained by a difference in condition.

3. RESULTS

(a) Conception rate

When animals of all ages were combined, conception rate declined with population size and SC females conceived at a significantly higher rate than NSC ones (figure 1*a*, table 1*a*). When ewes were separated into three age classes (figure 1*b–d*, table 1*b–d*), the two youngest ones showed a similar decline in conception rate with population density, which was not observed in adults (see also Clutton-Brock *et al.* 1997). Among adult ewes, SC animals had higher conception rates than NSC ones and this difference increased as animals aged (as indicated by a significant interaction between age and horn type, table 1*d*). Among juveniles, SC females conceived at a higher rate than NSC animals at low population densities but conceived at a lower rate at high densities (figure 1*b*, table 1*b*). There was no difference in the conception rates of the two horn types among the yearling and two-year-old age class (figure 1*c*, table 1*c*).

Differences between the horn types disappeared when the condition of the ewe prior to parturition was taken into account. When mother's weight was tested for inclusion in the models, it was significant in all but the yearlings and two-year-olds and, in all

cases, the mother's horn type dropped out of the minimal model. Conception rate did not vary with coat colour in any of the age classes and only the conception rate of adults was affected by ADA genotype: FF females conceived at a higher rate than SS or SF ones (table 1*e*).

(b) Weaning rate

When animals of all ages were combined, weaning rate declined with population size and SC females showed significantly higher weaning rates than NSC animals (figure 2*a*, table 2*a*). A similar trend was found among the yearlings and two-year-olds, but not among the other age categories. When coat colour and ADA genotype were tested for inclusion in the model, only coat type in yearlings and two-year-olds proved to have a significant effect (table 2*h*) and trends with respect to horn type did not change (tables 2*e–h*). When ewe weight was added to the models, horn type retained significance only in the yearling and two-year-olds age class ($\chi^2 = 6.096$, d.f. = 1, $p = 0.0135$).

(c) Female weight

Since both survival and fecundity are commonly related to body weight in ungulates (see above), and differences between horn types generally disappeared when variation in body weight was incorporated, we investigated whether there were consistent differences in the weights of ewes belonging to different horn categories. When all females were combined, there was a significant interaction between horn type and age but, overall, SC ewes tended to be heavier than NSC ones (figure 3*a*, table 3*a*). When the data were split into three age classes, SC juveniles were significantly heavier than NSC ones across all population sizes while, among adults, the situation was reversed, though the difference was small (figure 3*b, d*, table 3*b, d*).

Inclusion of coat colour and ADA genotype had some influence on these results. The weight of adult ewes was related to ADA genotype and, when all animals were combined, there was a significant interaction between horn type and ADA genotype: in SC females, FF genotypes were significantly heavier than the other two genotypes; whereas in NSC females there was a non-significant reverse of this trend. Coat colour was significantly related to weight (figure 3*e, f*): when all animals were combined, dark ewes were significantly heavier than light ones (table 3*e*) and similar effects were found among juveniles and adults (table 3*f, h*).

The inclusion of coat colour and ADA genotype in the models strengthened the effects of horn type on weight among juveniles and adults but removed the interaction between horn and age when all animals were combined (table 3*e–h*).

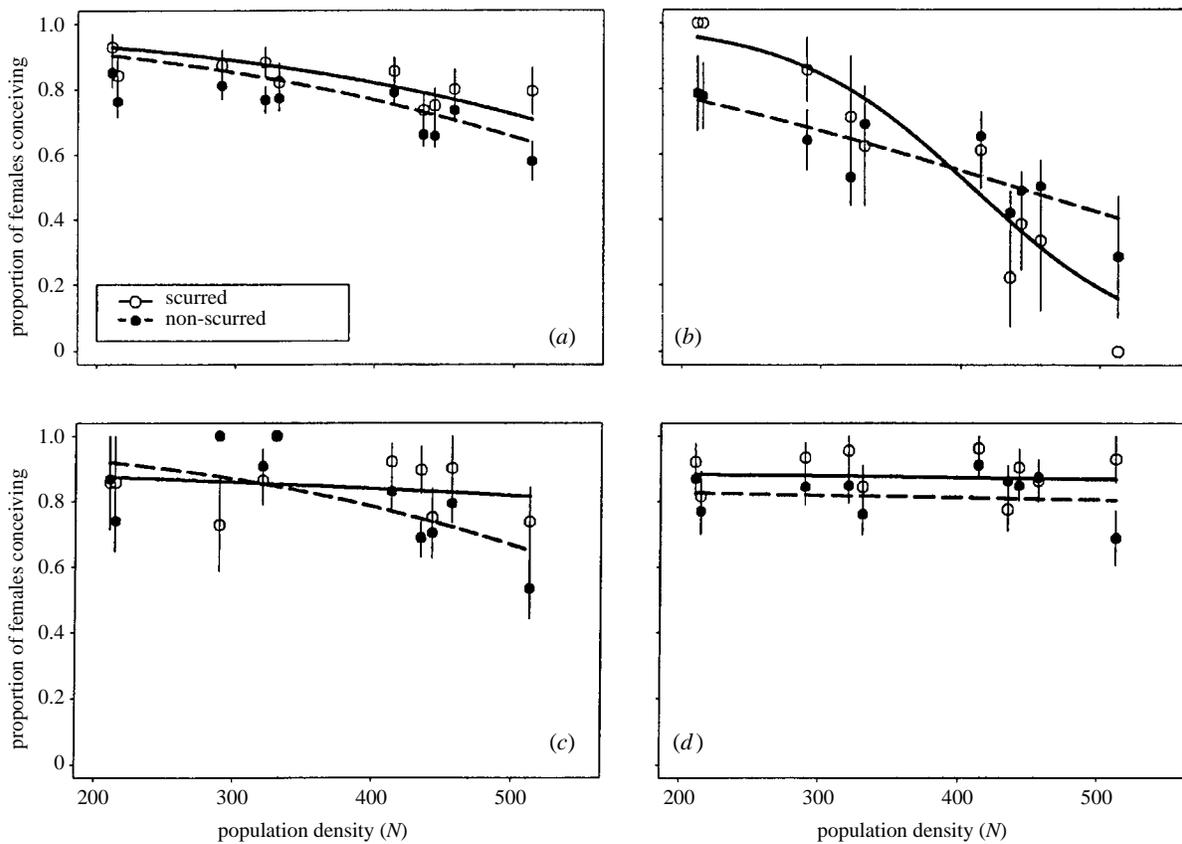


Figure 1. Proportion of SC and NSC females conceiving at different population sizes, estimated in the previous autumn: (a) all animals; (b) juveniles; (c) yearlings and two-year-olds; (d) adults. Error bars in all figures show standard errors.

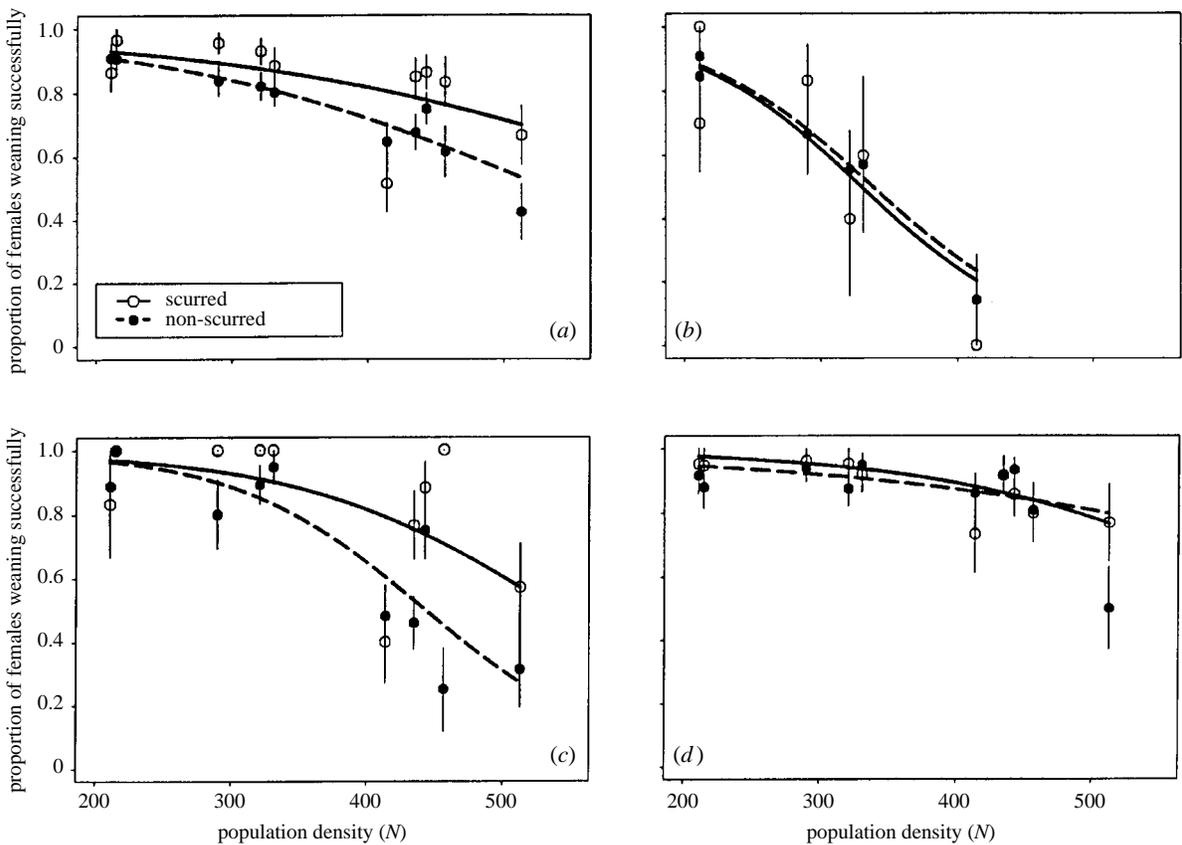


Figure 2. Proportion of SC and NSC females that produced living lambs that lost them before weaning age (6 weeks) at different population sizes (estimated in the previous autumn): (a) all animals; (b) juveniles; (c) yearlings and two-year-olds; (d) adults.

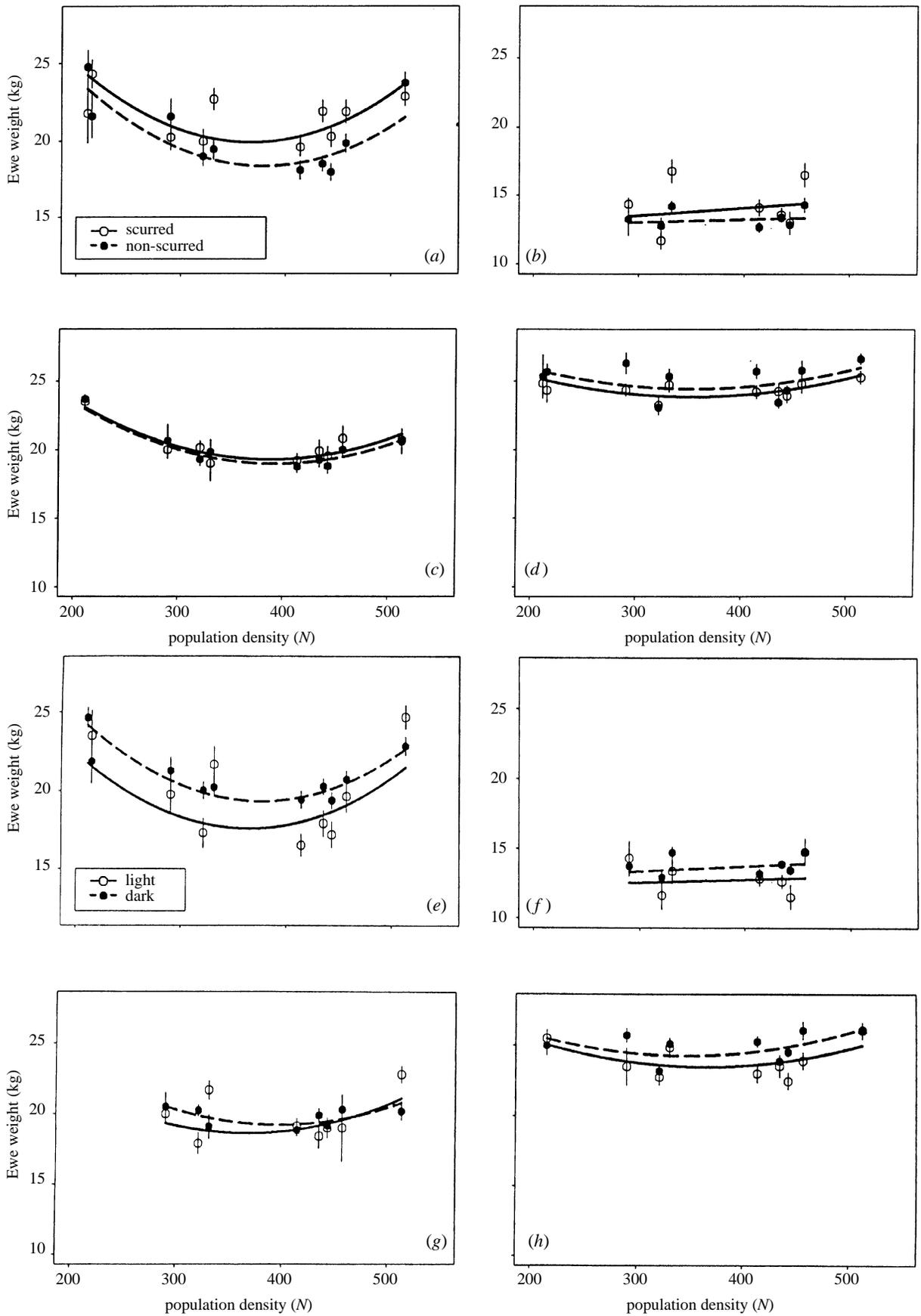


Figure 3. August live weight (in kg) of SC and NSC females (a)–(d) and of light and dark females (e)–(h) at different population sizes estimated in the same autumn: (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; (d), (h) adults.

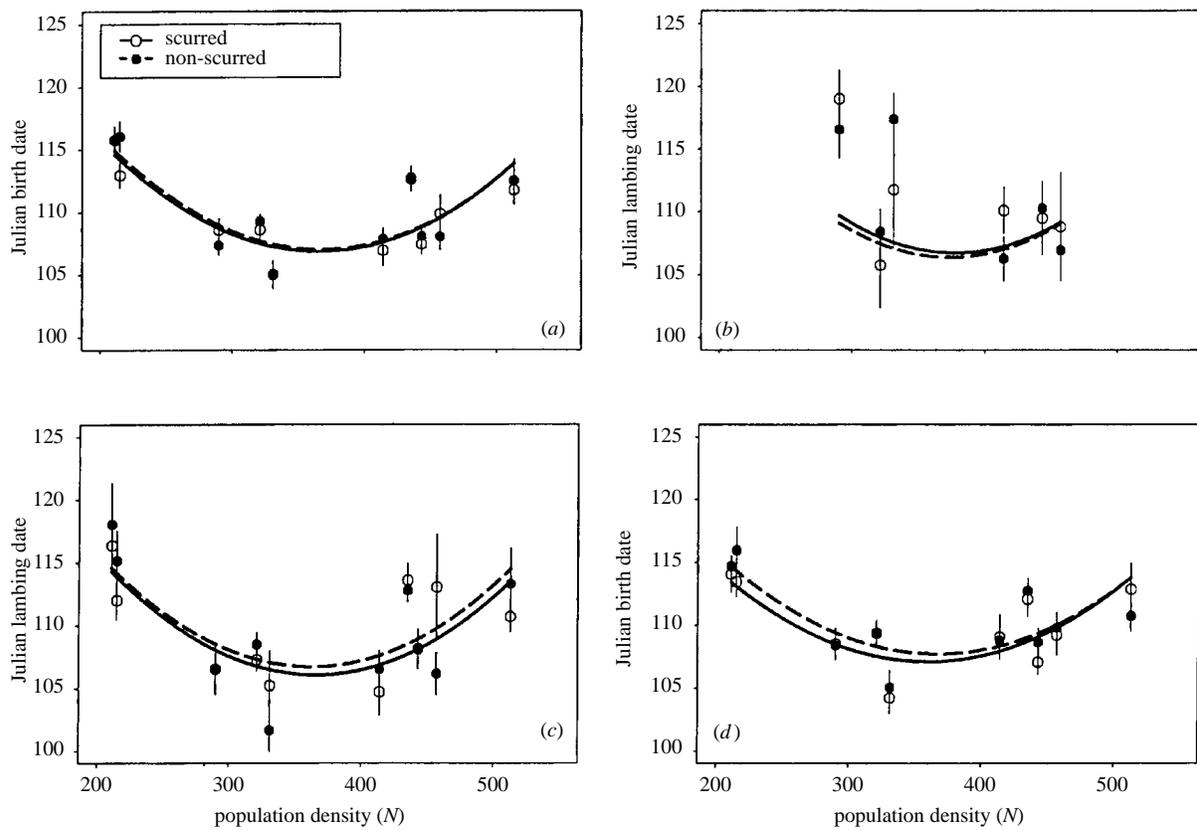


Figure 4. Julian birth date (no. in days from 1 January) of SC and NSC females at different population sizes. In this case, population size was calculated for the previous autumn, when animals conceived: (a) all animals; (b) juveniles; (c) yearlings and two-year-olds; (d) adults.

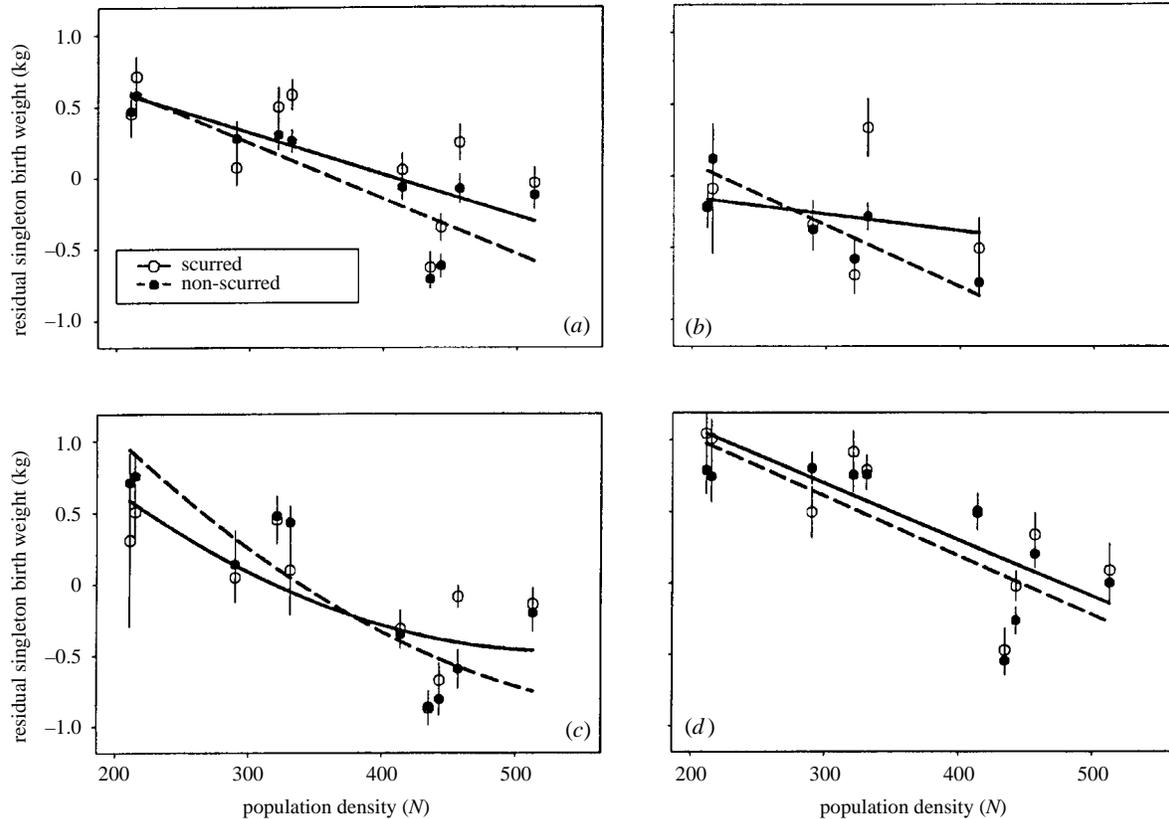


Figure 5. Birth weight of offspring born to SC and NSC females at different population sizes. Population size was estimated for the previous autumn: (a) all animals; (b) juveniles; (c) yearlings and two-year-olds; (d) adults.

Table 1. Relationship between horn type and conception rate in (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; and (d), (h) adults

(For definition of the different age classes, see the main text. Tables 1(a)–(d) illustrate the results of logistic regression analyses in which population size (POP), horn type (HORN) and their interaction are included as terms in the model, as well as ewe age (AGE) and any significant interactions involving age. Deviance values quoted are the effect of removing that term from the simple model. Tables 1(e)–(f) present minimal versions of the complex models in which coat colour (COAT) and ADA genotype (ADA) are also tested for inclusion.)

	(a) all animals simple model			(b) juveniles simple model			(c) yearlings and 2-year-olds simple model		
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>
POP	1	24.72	< 0.0001	1	30.86	< 0.0001	1	10.84	0.0009
AGE	3	96.99	< 0.0001						
HORN	1	6.21	0.0126	1	0.11	0.7378	1	2.43	0.1188
POP:AGE	3	15.82	0.0012						
POP:HORN	1	0.74	0.3879	1	8.10	0.0044	1	1.86	0.1715
null model	1732	1928.46		465	634.84		481	486.79	
fitted model	1723	1771.34		462	594.94		478	471.64	
	(d) adults simple model			(e) all animals complex model			(f) juveniles complex model		
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>
POP	1	0.27	0.6033	1	24.72	< 0.0001	1	30.86	< 0.0001
AGE	1	12.07	0.0005	3	96.99	< 0.0001			
HORN	1	4.63	0.0314	1	6.21	0.0126	1	0.11	0.7378
POP:HORN	1	0.05	0.8237				1	8.10	0.0044
POP:AGE				3	15.82	0.0012			
AGE:HORN	1	6.03	0.0140						
null model	784	701.44		1732	1928.46		465	634.84	
fitted model	779	678.39		1724	1772.08		462	594.94	
	(g) yearlings and 2-year-olds complex model			(h) adults complex model					
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>			
POP	1	12.13	0.0005						
AGE				1	0.93	0.3337			
ADA (SSSF/FF)				1	3.81	0.0506			
AGE:ADA				1	13.91	0.0001			
AGE:HORN				1	5.47	0.0193			
HORN				1	2.81	0.0931			
null model	503	515.83		700	595.57				
fitted model	502	503.69		695	568.61				

(d) Lambing date and offspring birth weight

We also investigated whether it was possible that the relationship between horn type and weaning rate was a result of relationships between the mother's horn type and the birth date or birth weight of her offspring, both of which are known to affect juvenile survival in Soay sheep (Clutton-Brock *et al.* 1992). There were no significant differences in lambing date between ewes belonging to different horn types (table 4a–d) or between ewes of different coat colour or ADA genotype (table 4e, h). However, the birth

weight of offspring varied with the mother's horn type: among all animals combined, as well as among juveniles and yearlings and two-year-olds, SC mothers tended to produce heavier lambs when population density was high, while NSC ewes tended to produce heavier lambs when it was low (figure 5b, c, d, table 5b–d). No such trends were apparent among adult ewes (figure 5d, table 5d). Offspring birth weight did not vary with coat colour (table 5e–h) and varied with ADA genotype only among adults (table 5h). When mother's weight was included in the minimal models, the interactions between horn type and pop-

Table 2. Relationship between horn type and weaning rate in (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; and (d), (h) adults

(See legend to table 1.)

	(a) all animals simple model			(b) juveniles simple model			(c) yearlings and 2-year-olds simple model		
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>
POP	1	90.14	< 0.0001	1	34.39	< 0.0001	1	55.11	< 0.0001
AGE	3	120.14	< 0.0001						
HORN	1	4.85	0.0277	1	0.07	0.7883	1	10.31	0.0013
POP:AGE	3	25.17	< 0.0001						
POP:HORN				1	0.01	0.9399	1	0.65	0.4211
null model	985	834.66		153	209.08		312	375.56	
fitted model	977	809.49		150	173.71		309	313.21	

	(d) adults simple model			(e) all animals complex model			(f) juveniles complex model		
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>
POP	1	13.77	0.0002	1	90.14	< 0.0001	1	35.29	< 0.0001
AGE	1	6.26	0.0123	3	120.14	< 0.0001			
HORN	1	0.47	0.4934	1	4.85	0.0277			
POP:HORN	1	1.07	0.2990						
POP:AGE				3	25.17	< 0.0001			
null model	518	355.10		985	834.66		153	209.08	
fitted model	514	333.51		977	809.49		152	173.78	

	(g) yearlings and 2-year-olds complex model			(h) adults complex model		
	d.f.	deviance	<i>p</i>	d.f.	deviance	<i>p</i>
POP	1	58.87	< 0.0001	1	16.94	< 0.0001
AGE				1	7.29	0.0069
HORN	1	10.59	0.0011			
COAT	1	10.68	0.0011			
null model	311	374.88		531	366.51	
fitted model	308	302.55		529	343.96	

ulation density retained significance only for all sheep combined ($\chi^2 = 3.655$, d.f. = 2, $p = 0.0266$).

4. DISCUSSION

Our results suggest that antagonistic selection operating on the two sexes affects the development of horns. Scurred males could not fight as successfully as horned males and were rarely able to maintain exclusive access to oestrous ewes for long (Stevenson & Wilson, unpublished data). Instead, they ranged widely, apparently attempting to locate receptive females before they were discovered by other males or pursuing females that have been mated and subsequently abandoned by dominant animals. However, scurred females, as well as scurred males, were more likely to survive in winter than non-scurred genotypes when population size and winter mortality were

high (Moorcroft *et al.* 1996). The analyses described in this paper show that selection for scurred phenotypes operating through survival was supplemented by selection operating through female breeding success. In contrast to males, scurred female sheep generally had higher breeding success than non-scurred animals, as measured by conception and weaning rates (figures 1 and 2).

In males, horn phenotype probably exerts a direct effect on breeding success. This appears unlikely in females. If the improved survival and breeding success of scurred females was a product of a direct effect of the absence of horns (for example, because it reduced heat loss), scurred and polled animals might be expected to show similar breeding performance and respond to changes in population density in the same way. However, polled and horned females showed similar reproductive success and similar responses to increasing population size,

Table 3. Relationship between horn type and female body weight in (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; and (d), (h) adults

(Analyses are as in table 1, except that classical linear regression models were used, and thus mean squares (m.s.) are presented rather than deviances.)

	(a) all animals simple model				(b) juveniles simple model				(c) yearlings and 2-year-olds simple model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	0.00	0.00	0.9876	1	5.73	0.93	0.3351	1	30.17	4.57	0.0334
POP2	1	90.41	14.84	0.0001					1	183.20	27.75	< 0.0001
AGE	3	6211.35	1019.68	< 0.0001								
HORN	1	1.76	0.29	0.5909	1	29.02	4.72	0.0306	1	6.68	1.01	0.3154
POP:AGE	3	16.18	2.66	0.0473								
POP:HORN					1	2.48	0.40	0.5254	1	0.40	0.06	0.8059
AGE:HORN	3	19.68	3.23	0.0218								
residuals	913	6.09			262	6.14			273	6.60		

	(d) adults simple model				(e) all animals complex model				(f) juveniles complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	6.54	0.98	0.3208	1	2.23	0.36	0.5489				
POP2	1	76.50	11.57	0.0007	1	1133.67	183.05	< 0.0001				
AGE	1	41.89	6.34	0.0122	3	5503.52	888.61	< 0.0001				
HORN	1	33.65	5.08	0.0247	1	9.06	1.46	0.2268	1	28.91	4.86	0.0283
ADA					2	6.38	1.03	0.3578				
COAT					1	76.34	12.33	0.0005	1	51.63	8.68	0.0035
POP:HORN	1	0.31	0.04	0.8296								
POP:AGE					3	17.00	2.75	0.0421				
HORN:ADA					2	31.39	5.07	0.0065				
residuals	376	6.71			805	6.19			139	5.95		

	(g) yearlings and 2-year-olds complex model				(h) adults complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	19.86	2.83	0.0905	1	6.61	1.14	0.3092
POP2	1	192.56	27.41	< 0.0001	1	83.23	13.05	0.0003
AGE					1	50.11	7.85	0.0053
HORN					1	35.73	5.60	0.0184
COAT					1	49.70	7.79	0.0055
ADA					2	44.73	3.50	0.0314
residuals	241	1692.79			364	6.39		

indicating that the relationship between horn type and breeding success was probably caused by traits associated with the genes controlling scurredness. It was possible that these operated through an influence on body condition or weight gain, for differences in survival and breeding success between SC and NSC phenotypes were partly, or totally, a consequence of differences in body weight and offspring weight between horn categories. As in other ungulates (Albon *et al.* 1983), the probability that Soay sheep would conceive was closely related to their weight (Clutton-Brock *et al.* 1996). Scurred ewes tended to be heavier than non-scurred ones and differences in weight

may have been responsible for the higher conception rates of scurred females. This was supported by evidence that horn type rarely had significant effects in models that included ewe weight as an independent variable. Similarly, lambs born at relatively low birth weights were more likely to die before weaning than heavier ones (Clutton-Brock *et al.* 1992), and the weaning rates of scurred females may have been higher because they tended to produce heavier lambs when population density was high (figure 5). Associations between horn type and weight may also have contributed to the differences in survival between scurred and non-scurred animals, for heavier

Table 4. Relationship between horn type and lambing date in (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; and (d), (h) adults

(For details of analysis, see legends to table 1 and table 3, and main text.)

	(a) all animals simple model				(b) juveniles simple model				(c) yearlings and 2-year-olds simple model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	998.22	20.71	< 0.0001	1	1369.46	21.92	< 0.0001	1	34.40	0.68	0.4118
POP2	1	5939.68	123.24	< 0.0001	1	1198.93	19.19	< 0.0001	1	2156.40	42.34	< 0.0001
AGE	3	135.23	2.81	0.0386								
HORN	1	40.39	0.84	0.3604	1	9.29	0.15	0.7002	1	30.86	0.61	0.4370
POP:AGE	3	131.89	2.74	0.0424								
POP:HORN	1	1.78	0.03	0.8475	1	1.09	0.02	0.8950	1	2.85	0.06	0.8133
residuals	970	48.24			159	62.48			290	50.92		

	(d) adults simple model				(e) all animals complex model				(f) juveniles complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	366.39	8.39	0.0039	1	1130.06	23.45	< 0.0001	1	1873.26	29.73	< 0.0001
POP2	1	2377.32	54.41	< 0.0001	1	6281.96	130.34	< 0.0001	1	1533.84	24.34	< 0.0001
HORN	1	46.87	1.07	0.3008								
AGE					3	135.23	2.80	0.0387				
POP:AGE					3	131.88	2.74	0.0424				
POP:HORN	1	18.13	0.42	0.5197								
residuals	491	43.69			972	48.19			168	63.01		

	(g) yearlings and 2-year-olds complex model				(h) adults complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	106.10	2.08	0.1504	1	403.39	9.19	0.0025
POP2	1	2386.06	46.75	< 0.0001	1	2357.21	53.73	< 0.0001
residuals	311	51.04			525	23 033.52		

adults, like heavier lambs, were more likely to survive the winter, especially when population density was high (Grenfell *et al.* 1992; Marrow *et al.* 1996; Clutton-Brock *et al.* 1997).

Our results emphasize the extent to which selection pressures vary with population density. Most of the effects demonstrated in this analysis, as well as in our previous investigation of the effects of horn type on survival, were stronger when numbers were high than when they were low, including the effects of horn type on survival (Moorcroft *et al.* 1996), weaning success (figure 2), and offspring birth weight (figure 5). In several cases, selection pressures were only apparent at high density while, in others, they changed direction as density increased (Moorcroft *et al.* 1996; see figures 1 and 5).

Several of the selection pressures we describe were restricted to particular age categories. For example, differences in conception rate, weaning success and offspring birth weight between scurred and non-scurred phenotypes were confined to juveniles and

younger ewes (figures 1, 2 and 5). Differences in offspring birth weight also varied between age categories: SC juveniles were heavier than NSC juveniles, though SC adults were lighter than NSC phenotypes.

These results emphasize the importance of investigating selection under natural conditions for where resources are abundant there is a real danger that variation in fitness may be obscured. In addition, they underline the need to analyse data separately for age or sex categories that differ in their responses to environmental conditions. Growing animals are particularly likely to be affected by adverse environments (Perrins *et al.* 1991), and phenotypic variation may be more likely to influence survival during this stage than during adulthood (Clutton-Brock 1988). In some cases, it may be sufficient to include age as a dependent variable in multifactorial analyses of the factors affecting fitness. However, in long-lived organisms where juveniles represent a relatively low proportion of the population, there is a risk that effects of phenotypic traits on juvenile survival may be

Table 5. Relationship between horn type and birth weight in (a), (e) all animals; (b), (f) juveniles; (c), (g) yearlings and two-year-olds; and (d), (h) adults

(For details of analysis, see legends to table 1 and table 3, and main text.)

	(a) all animals simple model				(b) juveniles simple model				(c) yearlings and 2-year-olds simple model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	81.89	230.44	< 0.0001	1	11.67	37.85	< 0.0001	1	49.06	143.12	< 0.0001
POP2									1	2.27	6.70	0.0101
AGE	3	36.05	101.43	< 0.0001								
HORN	1	0.54	1.53	0.2161	1	0.07	0.24	0.6263	1	0.02	0.06	0.7994
POP:HORN	1	1.52	4.29	0.0387	1	1.28	4.16	0.0433	1	2.05	6.07	0.0143
residuals	764	0.36			139	0.31			252	0.34		

	(d) adults simple model				(e) all animals complex model				(f) juveniles complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	54.25	140.33	< 0.0001	1	81.89	230.44	< 0.0001	1	11.67	37.85	< 0.0001
AGE					3	36.05	101.43	< 0.0001				
HORN	1	0.94	2.43	0.1197	1	0.54	1.53	0.2161	1	0.07	0.24	0.6263
POP:HORN	1	0.04	0.02	0.7618	1	1.52	4.29	0.0387	1	1.28	4.16	0.0433
residuals	367	141.89			764	0.36			139	0.31		

	(g) yearlings and 2-year-olds complex model				(h) adults complex model			
	d.f.	m.s.	<i>F</i>	<i>p</i>	d.f.	m.s.	<i>F</i>	<i>p</i>
POP	1	49.06	143.12	< 0.0001	1	53.28	123.04	< 0.0001
POP2	1	2.27	6.70	0.0101				
HORN	1	0.02	0.06	0.7994				
POP:HORN	1	2.05	6.07	0.0143				
ADA (SFFF/SS)					1	1.97	4.55	0.0335
residuals	252	0.34			462	200.08		

obscured by the numerical preponderance of older age categories in the analyses.

The evidence that selection pressures vary with population density and differ between categories of individuals support two of the principal assumptions of recent models of the maintenance of genetic variability through temporal fluctuations in selection pressures (Ellner & Hairston 1994). The situation that we describe in Soay sheep appears to match one of the two scenarios for the operation of a 'storage effect' suggested by Ellner & Hairston: 'The basic result, called the 'storage effect' (Chesson 1983; Warner & Chesson 1985), derives from the fact that, although an organism or a population of organisms may experience considerably reduced or even complete loss of recruitment in years favourable to its competitor, it can persist so long as there are life-history stages that are viable for periods long enough to experience the next favourable year. Such life-history stages include long-lived adults (with envi-

ronmental fluctuations affecting the success of their offspring) and dormant seeds of annual plants (with environmental fluctuations affecting the success of active individuals)' (Ellner & Hairston 1994).

It is not yet clear whether the temporal changes in selection pressures that we document in the Soay sheep of Hirta are likely to play an important role in maintaining variation in horn phenotype in this population. Other mechanisms may be involved. In particular, it would not be surprising if the relative benefits of scurred versus non-scurred phenotypes (and of the associated male mating strategies) were frequency dependent. If so, frequency dependence could play a predominant role in maintaining heritable variation in this trait. An estimate of the importance of temporal fluctuation in selection pressures on the maintenance of variation in horn development must await the results of current studies of the fitness of different male phenotypes at contrasting population densities.

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REFERENCES

- Albon, S. D., Mitchell, B. & Staines, B. W. 1983 Fertility and body weight in female red deer: a density-independent relationship. *J. Anim. Ecol.* **56**, 969–980.
- Boyd, J. M. & Jewell, P. A. 1974 The Soay sheep and their environment: a synthesis. In *Island survivors* (ed. P. A. Jewell, G. Milner & J. Morton-Boyd), pp. 360–373. London: Athlone.
- Chesson, P. L. 1983 Coexistence of competitors in a stochastic environment: the storage effect. *Lecture Notes in Biomathematics* **54**, pp. 188–198.
- Clarke, B. & Beaumont, M. A. 1992 Density and frequency dependence: a genetical view. In *Genes in ecology* (ed. R. J. Berry, T. J. Crawford & G. M. Hewitt), pp. 353–364. Oxford: Blackwell.
- Clutton-Brock, J. 1981 *Domesticated animals from early times*. London: British Museum (Natural History) and Heinemann.
- Clutton-Brock, T. H. 1988 In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 472–486. Chicago University Press.
- Clutton-Brock, T. H. & Albon, S. D. 1989 *Red deer in the highlands*. Oxford: Blackwell.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988 Reproductive success in male and female red deer. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 325–343. Chicago University Press.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer: the behavior and ecology of two sexes*. Chicago University Press.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. 1991 Persistent instability and population regulation in Soay sheep. *J. Anim. Ecol.* **60**, 593–608.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. 1992 Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* **61**, 381–396.
- Clutton-Brock, T. H., Stevenson, I. R., Marrow, P., MacColl, A., Houston, A. I. & McNamara, J. M. 1996 Population fluctuations and life history tactics in female Soay sheep. *J. Anim. Ecol.* **65**, 675–689.
- Clutton-Brock, T. H., Illius, A. I., Wilson, K., Grenfell, B. T., MacColl, A. D. C. & Albon, S. D. 1997 Stability and instability in ungulate populations: an empirical analysis. *Am. Nat.* **149**, 195–219.
- Crawley, M. J. 1993 *GLIM for ecologists*. Oxford: Blackwell.
- Dolling, C. H. S. 1960 Hornedness and polledness in sheep. I. The inheritance of polledness in the Merino. *Australian J. Agricultural Res.* **11**, 427–438.
- Dolling, C. H. S. 1961 Hornedness and polledness in sheep. IV. Triple alleles affecting horn growth in the Merino. *Australian J. Agricultural Res.* **12**, 353–361.
- Doney, J. M., Ryder, M. L., Gunn, R. G. & Grubb, P. 1974 Colour, conformation, affinities, fleece and patterns of inheritance in Soay sheep. In *Island survivors* (ed. P. A. Jewell, C. Milner & J. Morton-Boyd), pp. 88–125. London: Athlone.
- Ellner, S. & Hairston, N. G. 1994 Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* **143**, 403–417.
- Endler, J. A. 1986 *Natural selection in the wild*. Princeton University Press.
- Endler, J. A. 1990 Ecology and natural selection. *Physiol. Ecol.* **27**, 17–30.
- Frank, S. A. & Slatkin, M. 1990 Evolution in a variable environment. *Am. Nat.* **136**, 244–260.
- Grenfell, B. T., Price, O. F., Albon, S. D. & Clutton-Brock, T. H. 1992 Overcompensation and population cycles in an ungulate. *Nature* **355**, 823–826.
- Grubb, P. 1974 Population dynamics of Soay sheep. In *Island survivors* (ed. P. A. Jewell, G. Milner & J. Morton-Boyd), pp. 242–272. London: Athlone.
- Gulland, F. M. D., Albon, S. D., Pemberton, J. M., Moorcroft, P. R. & Clutton-Brock, T. H. 1993 Parasite-associated polymorphism in a cyclic ungulate population. *Proc. R. Soc. Lond. B* **254**, 7–13.
- Hedrick, P. W. 1986 Genetic polymorphism in heterogeneous environments: a decade later. *A. Rev. Ecol. Syst.* **17**, 535–566.
- Hedrick, P. W., Ginevan, M. E. & Ewing, E. P. 1976 Genetic polymorphism in heterogeneous environments. *A. Rev. Ecol. Syst.* **7**, 1–33.
- Ibsen, H. 1944 Horn and scur inheritance in certain breeds of sheep. *Am. Nat.* **78**, 505–516.
- Jewell, P. A., Milner, C. & Boyd, J. M. 1974 *Island Survivors*. London: Athlone.
- MacArthur, R. H. 1962 Some generalized theorems of natural selection. *Proc. Natn. Acad. Sci. USA* **48**, 1983–1897.
- McCullough, P. & Nelder, J. A. 1989 *Generalised linear models*, 2nd edn. London: Chapman & Hall.
- Marrow, P., McNamara, J. M., Houston, A. I., Stevenson, I. R. & Clutton-Brock, T. H. 1996 State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling. *Phil. Trans. R. Soc. Lond. B* **351**, 17–32.
- Moorcroft, P. R., Albon, S. D., Pemberton, J. M., Stevenson, I. R. & Clutton-Brock, T. H. 1996 Density-dependent selection in a fluctuating ungulate population. *Proc. R. Soc. Lond. B* **263**, 31–38.
- Perrins, C. M., LeBreton, J.-D. & Hirons, G. J. M. (eds) 1991 *Bird population studies*. Oxford University Press.
- Ryder, M. C. 1983 *Sheep and man*. London: Duckworth.
- Stevenson, I. R. & Bancroft, D. 1995 Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proc. R. Soc. Lond. B* **262**, 267–275.
- Wallace, B. 1968 Polymorphism, population size and genetic load. In *Population biology and evolution* (ed. R. C. Lewontin), pp. 87–108. New York: Syracuse University.
- Warner, R. R. & Chesson, P. L. 1985 Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* **125**, 769–787.

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