ORIGINAL ARTICLE

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Sex-ratio variation in Soay sheep

Abstract We studied the effects of ecological variables on the birth sex ratio of Soay sheep (*Ovis aries*) lambs on the island of Hirta, in the St Kilda archipelago, Scotland. Both individual- and population-level models were constructed. In the individual-based model, only population size was significantly associated with the sex of a lamb, with the probability of giving birth to a male lamb being positively associated with population size. However, this model explained a very small proportion of the variance in birth sex ratio. A multiple regression analysis of the annual population birth sex ratio also showed a slight increase in the proportion of males born in years following high autumn population density, but this result was not statistically significant. Population growth rate, Julian birthday, litter size, mother's age and weight, and the weather conditions during the gestation and neonatal period did not explain significant variation in the birth sex ratio.

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Introduction

In what has become one of the most cited references in evolutionary ecology, Trivers and Willard (1973) suggested that females in relatively good physiological condition should produce offspring of the more expensive sex, if the increased allocation is likely to benefit this offspring's fitness more than it would benefit the cheaper sex (for reviews, see Clutton-Brock and Iason 1986; Frank 1990). The three underlying assumptions of the Trivers–Willard hypothesis are that (1) the quality of young correlates with the quality of its mother, (2) these differences endure into adulthood, and (3) the reproductive success of the more expensive sex (commonly sons) is enhanced more than that of the cheaper sex by increased maternal investment because of the more intensive competition for mates (commonly among males). Ungulates provide an appealing group with which to test this hypothesis as these three assumptions are likely to be met – ungulates are commonly polygynous, display marked sexual size dimorphism, and commonly produce only one young per litter. However, published results from ungulate studies that have tested the Trivers–Willard hypothesis have been equivocal (e.g. Verme 1983; Skogland 1986; Birgersson 1998; Hewison and Gaillard 1999; Kruuk et al. 1999).

One plausible reason for the contradictory results in sex-ratio studies is that environmental conditions have an inconsistent effect on offspring sex ratio (Kruuk et al. 1999; Post et al. 1999; Mysterud et al. 2000). This, together with the fact that data are often pooled over several years, may explain why there are large within-species differences between studies (Hewison and Gaillard 1999). In addition, sample sizes in sex-ratio studies are often small. However, this is not always an adequate explanation for results at odds with expectations, as some studies with large sample sizes have also failed to detect

evidence supporting the Trivers–Willard hypothesis (Clutton-Brock 1985; Palmer 2000). Interactions between timing of sex-specific foetal growth and environmental stress on maternal condition have also been suggested as an explanation for the reported inconsistencies in sex-ratio variation in sexually size-dimorphic mammals (Forchhammer 2000). Tests for either environmentally induced or adaptive sex-ratio variation require that the preconditions for the Trivers–Willard hypothesis be met for the analysis and its interpretation to be sound (Hewison and Gaillard 1999; Cockburn et al. 2002).

The Soay sheep (*Ovis aries*) population on St Kilda provides a good system to test the Trivers–Willard hypothesis. Soay sheep are sexually size dimorphic, with males approximately 22% heavier than females at birth and 48% heavier than females as adults (Clutton-Brock et al. 1992; Milner et al. 1999; this study). The Soay sheep also satisfy the three preconditions for the Trivers–Willard hypothesis as emphasised by Hewison and Gaillard (1999). First, a high-quality mother is more likely than a mother in poor condition to wean a high-quality offspring (Clutton-Brock et al. 1996; this study). Second, conditions experienced during early development have long-lasting consequences and persist into adulthood (Coltman et al. 1999b; Forchhammer et al. 2001). Third, the variance in male mating success is likely to be higher than the variance in female mating success (Coltman et al. 1999a; unpublished data), and consequently differences in phenotypic quality may have stronger fitness consequences in males than in females.

Here we present an analysis of birth sex ratios in the Soay sheep population inhabiting the island of Hirta, in the St Kilda archipelago, Scotland (Clutton-Brock et al. 1991, 1997). Birth sex ratios based on over 2,000 newborn lambs are available for 15 years, thus enabling us to avoid the problems of small sample size common in sex-ratio studies (Palmer 2000). Furthermore, the time span covered by the data also allows us to address the question of the role of environmental variation and population size on the birth sex ratio. The Soay sheep population is naturally regulated and experiences dramatic fluctuations with up to 60% of animals dying in some years (Clutton-Brock et al. 1991). These fluctuations are strongly influenced by environmental factors and are large for a mammal of this size (Clutton-Brock et al. 1991, 1997; Grenfell et al. 1998; Milner et al. 1999). Finally, the sex-ratio data are collected within hours of birth and are therefore unbiased by differential neonatal mortality.

We tested the Trivers–Willard hypothesis and the effect of environmental variation on the birth sex ratio of Soay sheep. If mother's condition is an important determinant of offspring sex, we expect females in good condition to produce excess male offspring. Alternatively, environmental effects might operate independently of female condition and cause male-biased mortality in utero. In this case we would expect to see excess female offspring produced following years of adverse environmental conditions.

Methods

Soay sheep population of St Kilda

Soay sheep were probably introduced to the St Kilda archipelago (54°49′N, 08°34′W) in the second millennium B.C. (Boyd and Jewell 1974). Originally, they were restricted to the uninhabited island of Soay, but in 1932, 107 individuals were introduced to the island of Hirta, 2 years after the human population was evacuated. The population increased rapidly and the first census in 1952 gave an estimate of 1,114 individuals. A detailed demographic study in Hirta has been carried out since 1985 in the population of the Village Bay area, where approximately 30% of all the individuals in Hirta are found. Since 1985, over 95% of the lambs born annually have been caught and tagged shortly after birth (for a more detailed description of methods and study area, see Clutton-Brock et al. 1991), giving an estimate of the sex ratio of the cohort born each year.

Statistical analyses at the individual level

We used generalized linear mixed effect models (GLMMs) to identify sources of variation in birth weight and offspring sex. Variables included in the analyses were

- Annual autumn population size prior to the spring of birth, n_{t-1}, in the Village Bay study area
- Population growth rate [$R_t = \ln(n_t/n_{t-1})$]
- Julian birthday of each lamb
- A two-level factor indicating being born as either singleton or twin
- Mother's age (fitted alone and as a quadratic)
- Mother's weight in the previous autumn catch (fitted alone and as a quadratic)
- Mean monthly temperature (°C) for each month from October through April
- Total monthly rainfall for each month from October through April

Because maternal condition is central to the Trivers–Willard hypothesis, we fitted a set of variables that could be either a cause or a consequence of maternal condition. An individual's condition, offspring sex, and birth weight can be affected by population density (e.g. Kruuk et al. 1999; Post et al. 1999; Forchhammer et al. 2001). Therefore, annual autumn population size prior to the spring of birth, n_{t-1}, in the Village Bay study area, and population growth rate [$R_t = \ln(n_t/n_{t-1})$] were fitted. In some cases, the mother's condition affects the timing of conception, so that mothers in good condition can conceive earlier than those in poorer condition (Clutton-Brock et al. 1982). Consequently, the Julian birthday of lambs could be affected by maternal condition. Maternal condition and offspring sex ratio can also be associated with litter size (Kent 1995; Kojola 1997). In the Soay sheep approximately 85% of births are of singleton lambs, with twin births accounting for the remaining 15% (Grubb 1974; Clutton-Brock et al. 1991, 1992; Coltman et al. 1999b). Maternal age and weight in the previous autumn are condition-related factors that may affect birth weight and offspring sex (Côté and Festa-Bianchet 2001). We considered mother's age and weight as both linear and non-linear (quadratic) terms. In addition, the environmental effects of monthly mean temperature (°C) and total rainfall from October to April measured at the Benbecula weather station (80 km east of St Kilda) were fitted because they can have a significant effect on birth sex ratio in ungulates (Kruuk et al. 1999; Post et al. 1999; Mysterud et al. 2000). As the Benbecula weather station was closed in June 1996, weather variables in subsequent years were calculated using the association between Benbecula and Stornoway (ca. 150 km east of St Kilda) weather data (the average correlation between the weather variables is approximately $r=0.9$, T. Coulson, unpublished data). The number of weather variables fitted was reduced by principal component analysis (PCA) to avoid type 1 error (Sokal and

Table 1 Principal component analysis of the weather variables used in the analyses. Variable-specific loadings on the first principal components (*PC1*s) in autumn and spring are given

Variable	Loading
PC1 autumn	
October mean temperature	–0.41
November mean temperature	0.18
December mean temperature	0.52
October rainfall	–0.49
November rainfall	0.18
December rainfall	0.51
PC1 spring	
January mean temperature	0.49
February mean temperature	0.37
March mean temperature	0.40
April mean temperature	–0.11
January rainfall	0.35
February rainfall	0.47
March rainfall	0.32
April rainfall	0.07

Rohlf 1995). We used principal components to describe the weather conditions in the autumn prior to birth (October$_{t-1}$ to December$_{t-1}$) and to capture the conditions during spring (January to April in year t). This was done to assess whether the effects of environmental conditions experienced during different stages of gestation differ (e.g. Forchhammer 2000). The first principal components (PC1s) for both periods were fitted in subsequent models (Table 1). These will be referred to as Autumn and Spring for autumn and spring principal components, respectively. The first principal component for Autumn captured 33.3% of the variation in the October to December weather variables and correspondingly, Spring represents 38.4% of the variation in the spring weather (January to April, Table 1). In the birth-weight analysis age at capture (in days) was included as well.

Because the data consisted of records of multiple offspring per female across different years (1986–2000), we fitted mother's identity as a random effect. The remaining variables described above were fitted as fixed effects (Schall 1991). The model for birth weight was fitted assuming normal error structure, and the model for birth sex was fitted with a binomial error structure (0=female, 1=male offspring) and a logit link function. Statistical significance of the explanatory variables and all two-way interaction terms in both models were assessed by Wald statistics when that variable or interaction term was included last in the model. These Wald statistics follow a χ^2 distribution on the respective degrees of freedom. Altogether 1,168 lambs born to 391 mothers were included in the GLMM analysis of birth weight, and 1,229 lambs born to 406 mothers in the offspring sex model. All GLMM

analyses were performed using Genstat 5, release 4.1 using the iterative reweighted restricted maximum likelihood method (IRREML).

Statistical analyses at the population level

We also used multiple linear regression to model the annual sex ratio (proportion of males born each year) as a function of population size in the previous autumn (n_{t-1}), annual population growth rate R_t, and the weather variables Spring and Autumn for a comparable analysis at the population level. We used a forwards stepwise process with α-to-enter=0.05 and α-to-remove=0.1. This analysis was done in Systat 8.

Results

Individual-level models

The GLMM model fitted to the birth-weight data explained about 61% of the variation (Table 2). As the full-model results show, many factors contribute to offspring birth weight, sex among them demonstrating significant size dimorphism at birth (mean and standard deviation for birth weight in males: 2.18±0.68 kg, n=572; and in females: 2.08±0.63 kg, n=596). Because several of the predictor variables were correlated, we also fitted each of the explanatory variables separately as fixed effects. The only variable that did not significantly explain offspring birth weight on its own was Spring (PC1 summarising spring weather conditions), and it was therefore left out of the most parsimonious model (Table 2). None of the tested interactions were significant.

The most parsimonious model explaining offspring sex included only the population size in the previous autumn (Table 3). The model predicts an increase in the proportion of males born with increasing population size the previous autumn but reduces the model deviance only by 0.5%. None of the two-way interactions were significant. The restricted maximum likelihood estimate of variance components (e.g. Davidian and Giltinan 1995) revealed that mother's identity fitted as a random effect was not a significant term in the GLMM (variance component=0.007, SE=0.083, z=0.0063, P=0.94). In addition, we fitted both mother's identity and birth year as random factors in the GLMM but this formulation of the model did not alter the conclusions.

Table 2 Summary of the most parsimonious general linear mixed model fitting of birth weight. Parameter estimates, their standard errors (*SE*), Wald statistics, and their associated *P* values are given for each variable. Wald statistics are given for each term when fitted last in the model. *Sex* gives weight of male compared to female; *twin* gives weight of twin relative to singleton

Variable	Coefficient	SE	Wald statistic	df	P
Constant	2.303	0.017			
n_{t-1}	–0.001	0.0002	27.68	1	<0.0001
R_t	–0.466	0.049	91.56	1	<0.0001
Julian birthday	0.013	0.002	66.03	1	<0.0001
Age at capture	0.104	0.007	207.11	1	<0.0001
Sex	0.136	0.024	31.84	1	<0.0001
Twin	–0.782	0.033	547.70	1	<0.0001
Mother's age	0.269	0.025	118.87	1	<0.0001
Squared mother's age	–0.020	0.002	99.94	1	<0.0001
Mother's weight	0.211	0.025	71.46	1	<0.0001
Squared mother's weight	–0.004	0.001	44.76	1	<0.0001
Autumn	–0.017	0.008	3.85	1	0.050

Table 3 Summary of the general linear mixed model fitting of the birth sex ratios. Parameter estimates, their standard errors (*SE*), Wald statistics, and their associated *P* values (Wald statistics are given for each term when fitted last in the model) are given for the full model. A summary is given for the best-fitting model

| Variable	Coefficient	SE	Wald statistic	df	P
Full model					
Constant	–0.072	0.068			
n_{t-1}	0.002	0.001	6.41	1	0.01
R_t	–0.168	0.223	0.57	1	0.45
Julian birthday	–0.001	0.007	0.02	1	0.89
Twin	0.034	0.147	0.05	1	0.82
Mother's age	0.015	0.118	0.02	1	0.90
Squared mother's age	–0.005	0.009	0.23	1	0.63
Mother's weight	0.031	0.112	0.07	1	0.79
Squared mother's weight	–0.001	0.003	0.06	1	0.81
Autumn weather conditions	–0.035	0.042	0.71	1	0.40
Spring weather conditions	0.054	0.045	1.48	1	0.22
Best-fitting model					
Constant	–0.064	0.058			
n_{t-1}	0.002	0.001	8.33	1	0.004
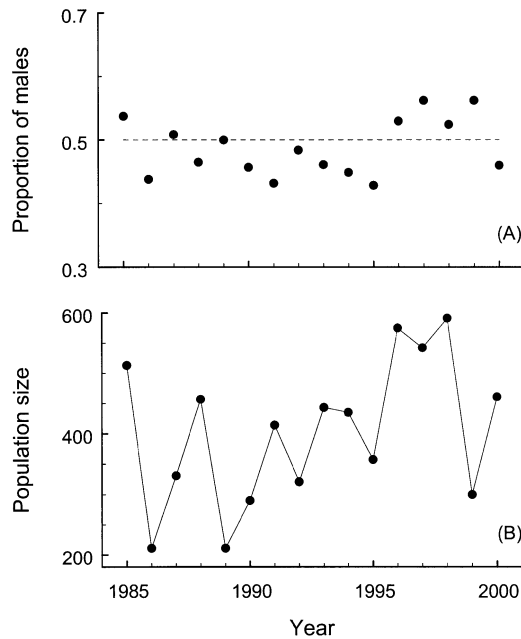
Fig. 1 A Proportion of males born and **B** population fluctuations in the Village Bay area in years 1985–2000

Population-level model

The annual population birth sex ratio fluctuated between 0.43 (1991, 1995) and 0.56 (1997, 1999; Fig. 1A). A stepwise multiple linear regression model showed that none of the explanatory terms (population size, population growth rate, Spring, and Autumn) were significant, neither as main effects nor as two-way interactions. The best fitting of these models was birth sex ratio=$0.416+0.0002\times n_{t-1}$, $P_{slope}=0.077$, $R^2=0.21$.

Discussion

Reproductive investment, in the form of birth weight, is strongly influenced by environmental factors and phenotypic terms that are likely to affect or reflect maternal condition (Table 2). In contrast, birth sex ratio is only weakly associated with population size in the year of conception, and it is not affected by other environmental factors or maternal phenotype. The individual-based (GLMM) and the population-level models showed that the proportion of male offspring increases with population size. This result is somewhat surprising as Soay sheep seem to match the preconditions of the Trivers–Willard hypothesis (Hewison and Gaillard 1999) relatively well, and we would expect maternal condition to be negatively affected by high population density. However, we did not observe any systematic relationship between traits related to maternal condition and offspring sex ratio. Our results are therefore not consistent with the Trivers–Willard hypothesis.

What factors might obscure a relationship between maternal condition and offspring sex ratio? First, there may be an interaction between environmental conditions and the mechanisms governing birth sex ratio (Kruuk et al. 1999; Post et al. 1999; Forchhammer 2000). For example, in red deer (*Cervus elaphus*), the adaptive sex-ratio variation reported by Clutton-Brock et al. (1984, 1986) disappeared at high population densities (Kruuk et al. 1999), presumably because nutritional stress at high density caused higher foetal loss in hinds carrying male foetuses. A literature survey reported in the same study showed that all positive associations between maternal quality and the proportion of male offspring produced have been found in populations below carrying capacity, usually because of artificial management. If the Hirta sheep population was never sufficiently below carrying capacity for this criterion to be met, we would expect to observe no correlation between maternal condition and an equal or perhaps female-biased sex ratio. However, we observed slightly more males born following high population densities. We also did not find evidence for an interaction between maternal condition and the timing of environmental conditions experienced during gestation, which might be expected to occur under the scenario of varying sex-specific foetal growth rates and selective

abortion (Forchhammer 2000). It seems that a potential link between high population density, reduced female condition, and increased probability of abortion of male foetuses would not explain the pattern observed in Soay sheep.

Scenarios involving sex-ratio effects mediated by maternal condition require that we are capturing the biologically meaningful part of maternal condition with the available data. This is difficult to evaluate, and age and weight may seem crude proxies. However, as indicators of condition-related variation, autumn weight and age are good predictors of over-winter survival (Milner et al. 1999), fecundity (Clutton-Brock et al. 1991), and birth weight (Table 2). Perhaps the time scale of variation in population size and weather conditions is too short and unpredictable for selection to operate on adaptive sex-ratio adjustment in Soay sheep. It has been shown that their life history strategy is close to optimal if it is assumed that the sheep have no information about the population fluctuations (Clutton-Brock et al. 1996; Marrow et al. 1996). Maybe this is also the case with sex-ratio adjustment.

In an alternative, adaptive scenario, it would be an advantage for females (especially those in good condition) to produce males after high-density years. This is because males born following high-density autumns have high postnatal survival probability (because high-density autumns are typically followed by a large crash in population size, so survivors face optimal conditions) and therefore survive to compete in many subsequent ruts and enjoy high lifetime reproductive success (Coltman et al. 1999b). This argument is close to the idea presented by West and Godfray (1997; see also Werren and Taylor 1984); if females can use the population density as a cue for recruitment likelihood of their offspring, selection would favour bias in offspring sex ratio accordingly. Their model shows that below-average recruitment can favour production of the sex with reproductive values less evenly distributed across the age classes, which would predict an increased production of males following high densities.

In conclusion, the data on Soay sheep do not support the Trivers–Willard hypothesis, nor are they consistent with environmental variation modifying birth sex ratio through effects on maternal condition. The biological significance of the relationship between population size and increased proportion of male offspring is unclear. It could be an adaptive response, however, and it could also be attributed to type I error. A mechanism for the possible adaptive explanation remains to be discovered.

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