SOAY SHEEP FERTILITY

METHODS

An estimate of age-specific fertility was necessary to parameterise the transition model used for simulations and in the Kalman Filter procedure. Previous analyses were not conclusive in this respect because either they did not test the influence of extrinsic factors such as population density or winter severity (Clutton-Brock et al., 1996) or they did not consider a full-age structure (Coulson et al., 2000) as the one in the transition matrix. Births occurred generally in the middle of April. A female sheep could produce up to two lambs and can give birth at their first birthday although at that stage they never twin. We analysed the data collected from 1986 to 2000 during which extensive individual-based information were available. To obtain a better description of the processes underlying fertility, we considered the number of lambs in the summer, NL, as the product of three probabilities named B, S, and $\phi 0$. Where B is the probability of giving birth, S is the probability, conditional on B, of producing a singleton and $\phi 0$, conditional on the probability of recapture, p, is the neonatal survival between May and the summer census. The three probabilities described above have been modelled using logistic regressions with a binomial error structure. On each analysis a scale parameter was used to correct for extrabinomial variation. The year-specific variation of the probability S was small and not considered. In modelling B and $\phi 0$, however, previous summer population size (POP(t-1)) and NAO were used to investigate the influence of density and winter severity on the age-specific values. In addition, the total spring rainfall from May to July recorded at the Benbecula Island station (ref?) was used as indication of spring weather condition in modelling neonatal survival. Note that in modelling survival probability and fertility the different accuracy of counts was not considered. As done in Catchpole at al. (2000), each probability was modelled by first detecting the appropriate age structure. We subsequently investigated the influence of time and covariates for each age class detected. The Akaike's Information Criterion (AIC) was used for model selection (Burnham & Anderson 1998). The model with the lowest AIC value was considered the best compromised between the deviance explained and the number of parameter used. Models with similar AIC value should be considered equivalent (Burnham & Anderson 1998). Model deviance and parameter estimates were obtained using software GENSTAT5 (Lawes Agricultural Trust, 1993).

RESULTS

Fertility

We began with detecting the age structure from the model assuming a constant parameter for each age class (Table 1). To be consistent with the survival analysis, in model notation the subscript *i* denotes the age of the mother. When a parameter spanned more age classes, the lower and upper limit of the class is reported. For example model $\{B_1, B_2, B_3, B_4,..,B_{16}\}$ considered one parameter for each of the 16 age classes, while model $\{B_1, B_2, B_{3\_7}, ..,B_{16}\}$ assumed the same parameter for 3 to 7 years old mothers. In model assuming time (noted t) and an influence of NAO (noted N), effects are in bracket. For example the model $\{B_1(t), B_2, B_3, B_4,..,B_{16}\}$ assumed a full age dependent structure *and* a time effect on the probability of giving birth for one year old female.
The age of the mother had an overall significant effect on the probability of giving birth (Fig.1, Table 1), however some age classes shared similar values. Two models, $\{B_1, B_2, B_{3_7}, B_{8_10}, B_{11_16}\}$and $\{B_1, B_2, B_{3\_8}, B_{9\_10}, B_{11\_16}\}$, scored similar AICc values (Table1) and must be considered equivalent. For the sake of simplicity we retained the model $\{B_1, B_2, B_{3\_7}, B_{8\_10}, B_{11\_16}\}$, which assumes an age-structure similar to the one detected for survival (Fig. 1). As for this parameter the influence of previous population size and weather condition interacted with age. Previous population size significantly influenced the probability of giving birth in all age classes expect the very old animals (Tab.2). Extrinsic factors were retained only for first-year mothers and 8 to 11 year old mother. In both classes the more significant variable were the NAO index (Tab.2). When retained previous population size and weather conditions had a negative effect on the probability of giving birth (Tab.2).
Twining probability was estimated for mothers between 1 and 12 years only (the two individuals observed >13 were eliminated from the analysis). On average, 85% of the mother produced a single lamb. This probability it appeared to vary as a quadratic function of age (Fig.3). In particular young and older mother are less likely to produce twins. Temporal variation was small and concerned few age-classes. Its influence on the total number of lambs in the summer was considered not considered.
We modelled survival probability of lambs assuming a recapture probability of 1.00. We tested the influence of the age of the mother, the previous population size, the NAO and the total rainfall from May to August. As for the previous two probabilities, the age of the mother influenced the newborn survival probability. The influence of mother age was similar to the one found for the probability of giving birth except that lambs born from 10 years old mothers had a greater probability of survival than those born by younger mothers (Fig. 4). As a

consequence we selected a 4-steps model. Note that the model assuming a structure a 5-step function similar to the one found for the probability of giving birth, had a similar but higher AIC value (results not shown). Spring rainfalls were not influencing lamb survival significantly in any age classes (result not shown). However, both previous population size and NAO did (Tab.3). This result is probably due to the indirect effect of these variables on food quality and mother condition.

The three probabilities were combined to predict the number of lambs alive during the summer (Fig. 4).

Table 1. Modelling age-specific probability of giving birth, B in the Soay sheep. Dev=residual deviance of the regression model, np=number of parameters in the model, AIC=Akaike's Information Criterion. The number as subscript denote the age structure considered. For example the subscript (1,2,3..16) denotes a model assuming a different parameter for each of the 16 age classes considered, while in model (1,2,3_7,..16) the age classes between 3 and 7year old were grouped together. The selected models are in bold. The scale parameter was 3.31

Model	Dev	Np	AIC	R^2	p(F)
$B_1, B_2, B_{3..}, B_{16}$	548.8	15	195.80	0.53	<0.001
$B_1, B_2, B_{3...}, B_{11\_16}$	559.3	10	188.97	0.52	<0.001
$B_1, B_2, B_{3...}, B_{10\_16}$	575.1	9	191.75	0.50	<0.01
$B_1, B_2, B_{3...}, B_{9\_10}, B_{11\_16}$	559.7	9	187.09	0.51	<0.01
$B_1, B_2, B_{3...}, B_{8\_10}, B_{11\_16}$	565.6	8	186.88	0.51	<0.01
$B_1, B_2, B_{3\_7}, B_{8\_10}, B_{11\_16}$	**567.3**	**4**	**179.39**	**0.51**	**<0.01**
$B_1, B_2, B_{3\_7}, B_{8\_16}$	613.0	3	191.20	0.47	<0.01
$B_1, B_2, B_{3\_10}, B_{11\_16}$	582.8	3	182.07	0.45	<0.01
$B_1, B_2, B_{3\_7}, B_{8\_10}, B_{11\_16}$	**562.4**	**4**	**177.91**	**0.51**	**<0.01**

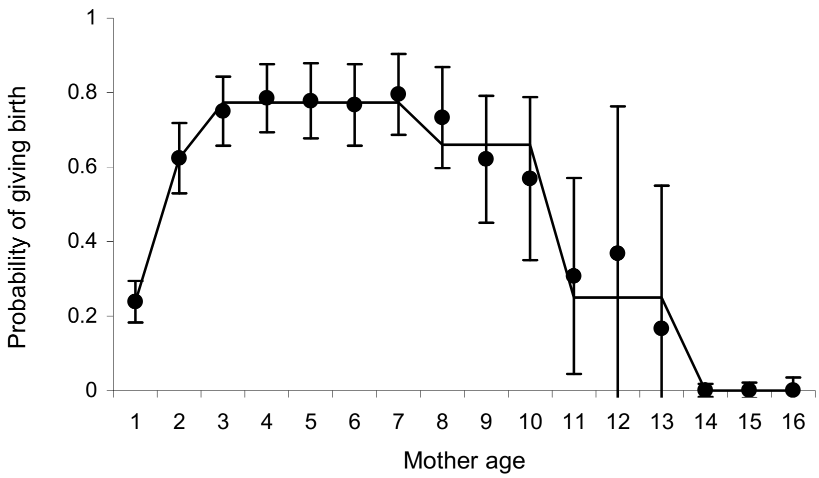

Figure 1. Age-specific probability of giving birth from the full model { $B_1, B_2, ,B_{16}$ }(●) and from the reduced model {$B_1, B_2, B_{3\_7}, B_{8\_10}, B_{11\_16}$} (—). Solid bars indicate 95% confidence interval.

Table 2 Linear predictors for the probability of giving birth and total deviance explained by the retained model. The probability of giving birth for very old mothers (>11 years old) is constant.

Mother age	1	2	3_7	8_10	11_16
CONSTANT	-0.92	0.82	1.39	1.11	-1.10
POP(t-1)	-0.38	-0.10	-0.08	-1.09	
NAO	-2.07	-2.09		-0.21	
POP(t-1).NAO				-0.81	
Total deviance	87.3%	48.4%	17.3%	46.2%	-

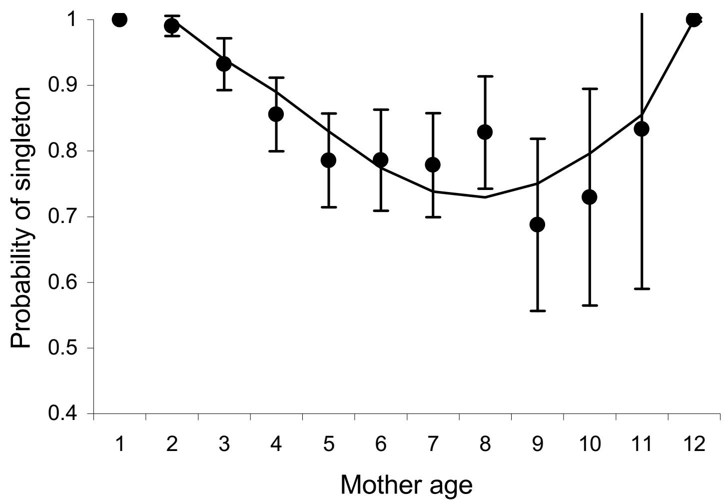

Figure 2. The probability, S, of producing a single lambs was a quadratic function of age: logit(S)=5.632-1.992Age+0.0765Age². The temporal variability was small and concerned few age classes only. Solid bars indicate 95% confidence interval.

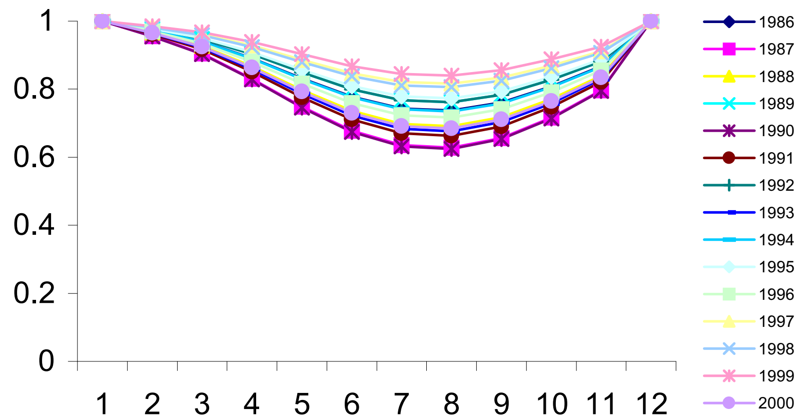

Figure 2bis. Year dependent variation on the probability, S, of producing a single lambs.Previous population size is additive (positive effect)

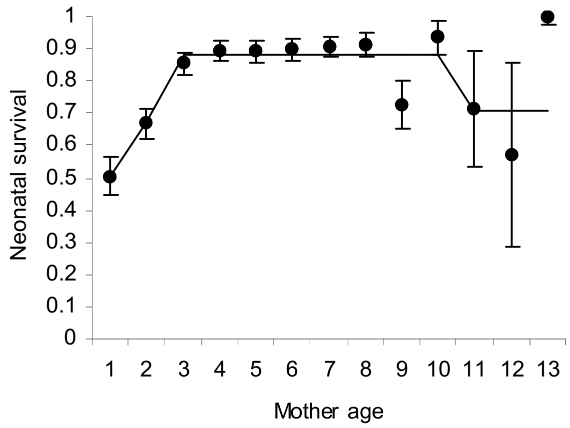

Figure 3. Neonatal survival probability, $\phi 0$, as a function of age of the mother. Estimates are from the full model { $\phi 0_1$, $\phi 0_2$, , $\phi 0_{16}$ }(●) and from the reduced model { $\phi 0_1$, $\phi 0_2$, $\phi 0_{3\_10}$, $\phi 0_{11\_16}$} (—). Solid bars indicate 95% confidence interval.

Table 3 Estimates of linear predictors for the neonatal survival. The selected age structure is slightly different to the one detected for the probability B.

Mother age	1	2	3_10	>11
CONSTANT	-0.65	1.29	2.08	0.89
POP(t-1)	-0.34	-0.23	-0.06	
NAO	-2.31	-3.55	-1.43	
POP(t-1).NAO			-0.56	
Total deviance	67.9%	45.3%	17.6%	-

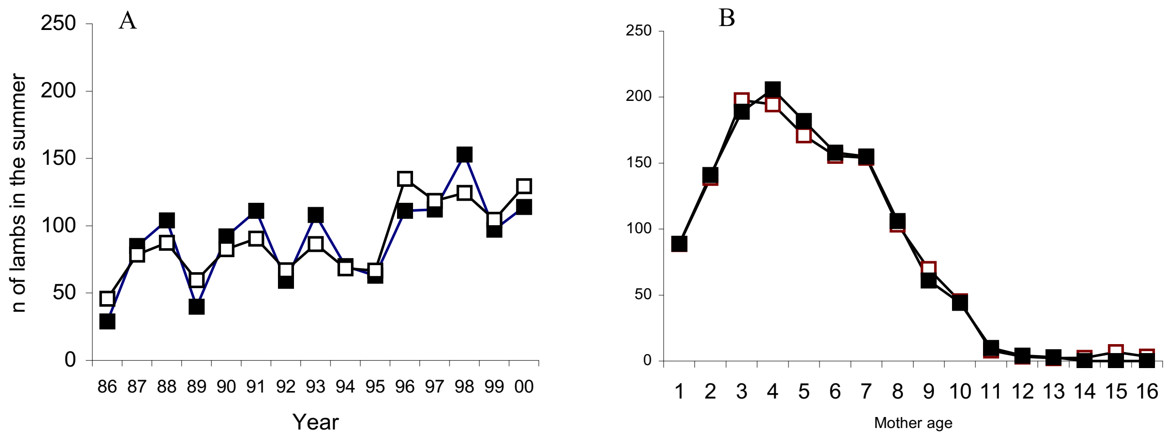

Figure 4. Observed (black square) and expected (open square) number of lambs during the summer according to time (A) and age of the mother (B)