ANALYSIS OF THE HISTORICAL DATA (female data only)

DATA

The dataset consisted in recoveries of sheep marked as a lamb and recovered between 1961 and 1984 in the village bay on the Hirta Island in the St. Kilda archipelago. Data came from the *lamb61.txt* file (Appendix 1), which list the data of birth and death from 60 until 84. Comparison with similar information on paper support (reports in box *Soays dead*) revealed few inconsistencies that at present have not been further investigated (Appendix 1). The data analysed (Tab.1) concern 1223 females released as a lamb and recovered over the period 1961-84. Although in 1973 and 1974 some recoveries are present, no new released females were recorded.

Tab.1: Recovery matrix of females Soay sheep for the period 1961-1984. i= year of release, j=year of recover.R_i*=total tags recovered from the i- cohort*

	j=	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	R
i=61	28	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
62	40		11	2	1	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
63	25			10	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	11
64	17				5	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
65	82					30	3	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	36
66	83						51	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	55
67	72							9	4	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	18
68	80								31	1	0	0	0	1	4	1	0	2	1	0	0	0	0	0	0	41
69	57									18	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	22
70	35										2	0	0	0	1	0	0	1	2	0	0	0	0	0	0	6
71	31											2	2	0	0	0	0	0	0	0	0	0	0	0	0	4
72	0												0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	43													21	1	1	0	0	0	0	0	0	0	0	0	23
74	0														0	0	0	0	0	0	0	0	0	0	0	0
75	38															16	0	0	0	0	0	0	0	0	0	16
76	48																3	3	1	0	3	0	2	1	0	13
77	51																	22	0	0	1	0	0	0	0	23
78	65																		29	0	2	0	0	1	0	32
79	63																			21	4	0	1	1	2	29
80	82																				14	1	1	0	0	16
81	81																					23	1	1	0	25
82	72																						15	0	0	15
83	69																							10	0	10
84	61																								11	11

MODEL STRUCTURE

Previous analyses that integrated recapture and recovery data collected during the decade 1986-96 showed that female survival varies according to age and time (Catchpole et al. 2000, Coulson et al. 2001). Survival could be modelled as a function of 4 age classes (Catchpole et al. 2001): *lambs* (from the birth to the 1st birthday, noted ϕ_1), *yearlings* (from the first to the second birthday, noted ϕ_2), *adult* (3 to 7, noted $\phi_3(5)$) and *senior* (8 to 15, $\phi_8(8)$). Recent results on an extended dataset suggested an additional class, 12 to 15 (Tavecchia *unpub. res.*), but given the relatively small sample size analysed this additional class was not considered. Time dependent variations could be modelled as a function of summer population density, weather conditions and the their statistical interaction. These factors interact with the age structure detected (Catchpole et al. 2000). For example lamb survival was mainly affected by population size while adult survival was mainly influenced by weather conditions (Coulson et al. 2001, Tavecchia *unpubl. res*). These results advocated for time and age recovery models and for test on the influence of external covariates.

When only date of birth and death are available, first-year parameters in full time- and age-dependent recovery models are not identifiable without additional information, i.e. live recaptures (Lakhani and Newton 1984, Brownie et al. 1985, Freeman et al. 1992). Recent studies showed that this problem could be overcome by considering the date of release (Tavecchia et. al. 2001) or by forcing the equality between some of the age classes considered (Catchpole et al. 1995, Catchpole and Morgan 1996). In the case of the current analysis, the latter method seemed the most appropriate, but it is necessary to investigate which type of constraint should be considered. Next paragraph and Appendix 2 address this point.

REDUNDANT QUANTITIES

The redundant quantities in recovery models can been investigated using the method in Catchpole and Morgan (1996). I simulated various hypothetical age- and/or time-dependent structures in recovery models and investigated how many parameters are redundant. In some cases it has been possible to detect the redundant quantities, but this was not achieved systematically. Partial derivate matrixes were calculated using MAPLEV3.0.

Results (Appendix 2) showed that in model $\{\phi_1(t),\phi_2(t),\phi_3(5)(t), \phi_8(8)(t)|\ \lambda(t)\}$, assuming 4 age-classes on survival, and time effect on both survival and recovery rate, only the parameters concerning the last occasion are not separately identifiable (Appendix 2). If the last age class is assumed to have a constant survival, all parameters become identifiable (this is also true when survival is constant but the model has a full age structure). (Note that all parameters of models $\{\phi_1(t)\ldots\ \phi_{15}(t)|\lambda(t)\}$ and $\{\phi_1(t)\ldots\phi_{14}(2)(t)|\lambda(t)\}$ are not separately identifiable). The next two paragraphs concern the influence of age and time on survival, respectively.

AGE EFFECT

Following Catchpole et al. (2000), I first analysed the variations according to age (Tab.1). Parameters after age 12 are not numerically estimable (the oldest tag recovered has 12 years old). This is shown by comparing the deviance of models 8 and 9 in Tab.1.

The retained model was:

$$\{\phi_1(.),\phi_2(.),\phi_3(5)(.),\phi_8(8)(.)|\ \lambda(t)\}$$

The age structure retained was similar to the one retained in previous analyses. Four age-classes can be detected: lamb, yearlings, adult (spanning from 3 to 7 year old) and senior (after 8). The Gompertzian model in which survival is a fonction of the logarithm of age is not adequate (model 12, Tab.1).

The only appreciable difference with previous results is that lamb survival (ϕ_1=0.24, se= 0.025) appears to be lower than the one found in recent years (ϕ_1=0.50, se=0.016) (Z=8.68,

$p<0.001$) (Tab.2). This is true also excluding neonatal mortality (those 68 lambs that died before August; $\phi_1=0.28$ se=0.05). Whether this result is due to a bias in the data (the above cited inconsistencies) or to a real lower survival has still to be proved.

Tab.1. Modelling age effect starting from the full age structure assuming 16 age classes ($\phi 1, \phi 2, \phi 3 \ldots \phi 16$).

N	Model	np	Deviance	AICc
1	**ϕ1,ϕ2,ϕ3_7,ϕ8_16**	**28**	**160.841**	**2157.865**
2	ϕ1,ϕ2_7,ϕ8_16	27	167.828	2162.760
3	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ8_16	32	157.435	2162.877
4	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ9_16	33	156.558	2164.112
5	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ10_16	34	156.068	2165.738
6	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ7_16	31	163.399	2166.731
7	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ11_16	35	155.642	2167.431
8	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ15_16	37	153.082	2169.122
9	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ13_16	37	153.082	2169.122
10	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ12_16	36	155.632	2169.545
11	ϕ1_2,ϕ3,ϕ4...,ϕ10_16	27	250.627	2245.561
12	ϕ1,ϕ2,ϕ3,ϕ4...,ϕ16 lnA	25	243.277	2231.950
13	**ϕ(LnA+lnA^2)**	**27**	**161.720**	**2156.650**
14	ϕ(A+A^2)	27	227.013	2221.940

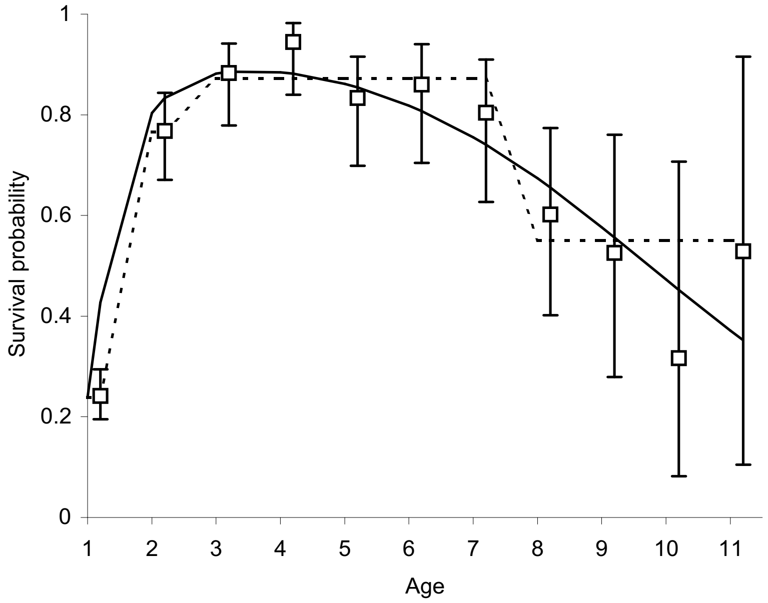


Fig.1 : Data 1961-84. □= *estimates from the full age recovery model* {$\phi_1(.),\phi_2(.),..\phi_{11}(.)| \lambda(t)$} ; --- = *estimates from the reduced model* {$\phi_1(.),\phi_2(.),\phi_3(5)(.),\phi_8(5)(.)| \lambda(t)$} ; —— = *model* {$\phi(lnA+LnA^2)| \lambda(t)$}. *Bars indicate 95% confidence interval.*

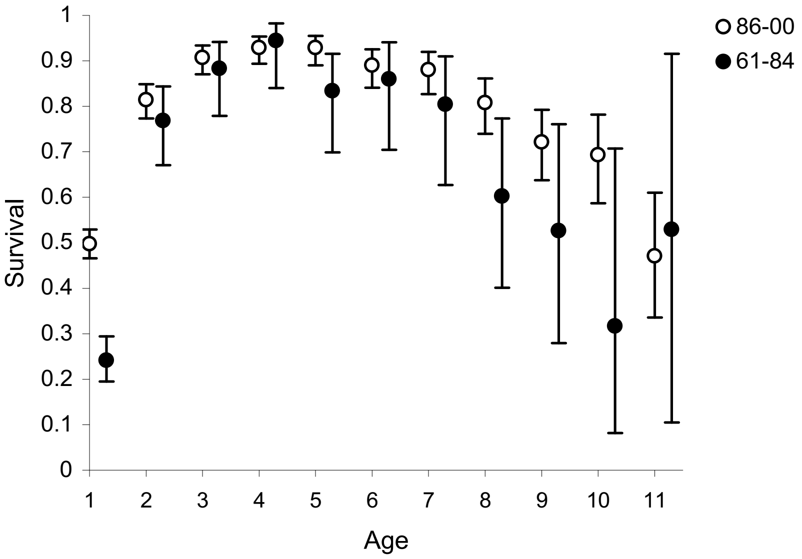


Fig.2. Full model age-dependent female Soay sheep survival estimates for period 1961-1984 (●) and 1986-2000 (○).

Tab.2. Comparing the full age model estimates for period 1961-1984 (present study) and 1986-2000 (from Tavecchia unpl. res.*). Significant (α=0.05) Z-tests are in bold.*

Parameter	1961-1984		1986-2000		Z
	Estimate	se	Estimate	se	
ϕ_1	0.497	0.026	0.241	0.025	**8.52**
ϕ_2	0.814	0.021	0.768	0.044	0.93
ϕ_3	0.907	0.018	0.883	0.040	0.54
ϕ_4	0.929	0.018	0.944	0.031	0.41
ϕ_5	0.929	0.020	0.834	0.055	1.64
ϕ_6	0.890	0.025	0.860	0.058	0.48
ϕ_7	0.881	0.028	0.804	0.072	0.99
ϕ_8	0.808	0.035	0.602	0.099	1.95
ϕ_9	0.721	0.043	0.526	0.134	1.39
ϕ_{10}	0.693	0.054	0.317	0.182	**1.98**
ϕ_{11}	0.471	0.069	0.529	0.288	0.20

TIME EFFECT

After an age-structure has been defined, I considered models with time dependent parameters as in Catchpole et al. (2000). Following the LRT results only time variation is important for all parameter but for the last age class (Tab.3). Despite this, following the AICc values non of these models should not be retained.

Tab.3 Including time variation in model $\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$*. Likelihood Ratio Test has been used to compute the significance (P) of time effect. Each model is contrasted with model* $\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$*.*

N	Model	Np	Deviance	AICc	P
13	$\{\phi 1(t), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$	51	124.47	2170.67	0.04
14	$\{\phi 1(.), \phi 2(t),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$	50	125.27	2169.29	0.03
15	$\{\phi 1(.), \phi 2(.),\phi 3\_7(t),\phi 8\_15(.) \mid \lambda(t)\}$	49	122.99	2164.83	0.01
16	$\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(t) \mid \lambda(t)\}$	44	148.33	2179.35	0.71
17	$\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(.)\}$	6	337.57	2287.28	-
18	$\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$	28	160.84	2157.87	<0.01
19	$\{\phi 1(t), \phi 2(t),\phi 3\_7(t),\phi 8\_15(t) \mid \lambda(t)\}$	109	44.75	2223.96	<0.01

This is probably due to the fact that the number of parameter used to compute AICc and LRT does not account for those parameters that are numerically not estimable (i.e. MARK1.9 estimated that only 64 on 109 structurally estimable parameters are numerically estimable this would results in an AICc value of 2119.6, the lowest of models in Tab.3, see also Appendix 3). In the next paragraph I investigate whether the use of external covariates in each age class would results in a better model.

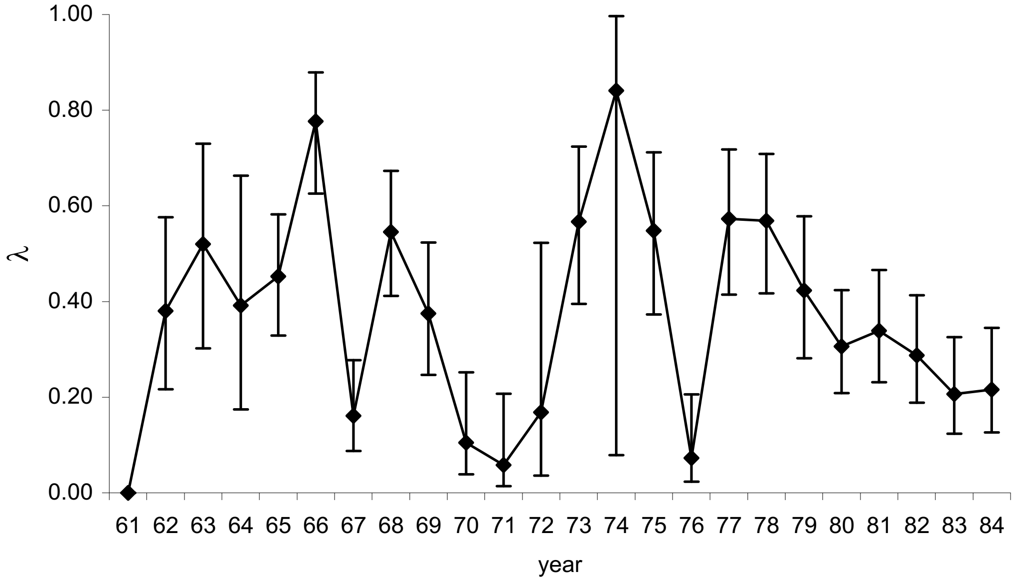


Fig.2. Recovery rate, λ*, from model* $\{\phi 1(.), \phi 2(.),\phi 3\_7(.),\phi 8\_15(.) \mid \lambda(t)\}$*. Time effect is highly significant.*

EXTERNAL COVARIATES

Previous analyses of female Soay sheep survival indicated a significant effect of both density-dependent and density-independent factors (Catchpole et al. 2000, Coulson et al. 2001, Tavecchia *unpl. res.*). External variables might be used as covariates in ultrastructural recovery models. These variables are: the North Atlantic Oscillation index (NAO), the March and February rainfall (M and F, respectively) measured at the island of Benbecula 50 Km from the study area, the total population size (P) measured as the number of sheep on the Hirta island. Note that previous analyses used the number of sheep counted on the village bay area, but this measure was not available for the period considered. However total number of sheep on Hirta in the period 1985-2000 is highly correlated with the one on village bay (Pearson's correlation coefficient =0.96, n=16).

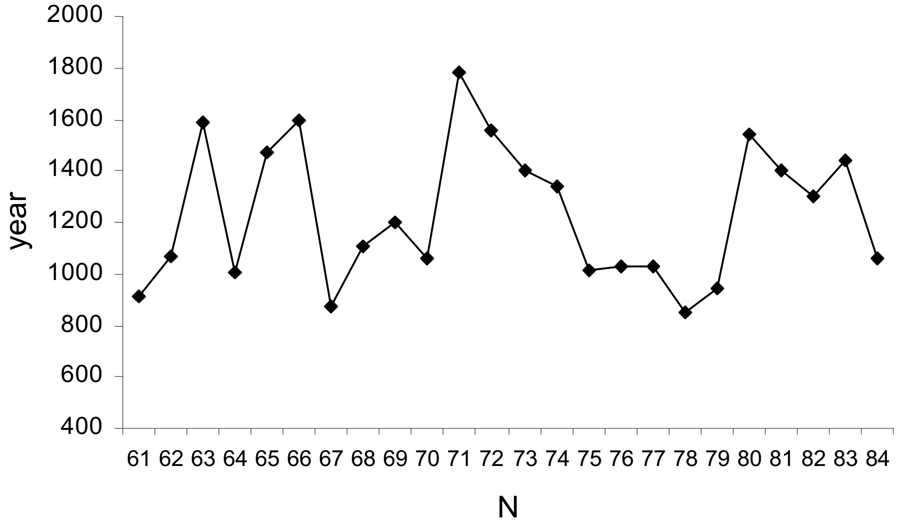


Fig.3. Total population size in Hirta from 1961 to 1984.

For most age classes, the model including NAO index as external covariates had a similar AICc than the one assuming a constant value. Only yearlings survival appeared to be influenced by February rainfall. However most of these ultrastructural models was significant (Tab. 4). I suspect problems in the function optimisation because, except for lambs, the deviance of ultrastructural models is higher than the one assuming a constant survival, which has one parameter less. An improvement in AICc was obtained by considering all the age classes affected by NAO, population size and their statistical interaction (assumed to be the product of the two variables)(Tab.4). This model was retained:

$$\{\phi_1(N*P), \phi_2(N*P), \phi_3(5)(N*P), \phi_8(6)(N*P)| \lambda(t)\}$$

(Note that a model assuming parallel regression between external covariates and age had a similar AICc). A model assuming a parallel regression, noted "//", with time could also be considered as a good candidate (model $\{\phi_1(t), \phi_2(t), \phi_3(5)(t), \phi_8(6)(t) \,//\, | \lambda(t)\}$, Appendix 3).

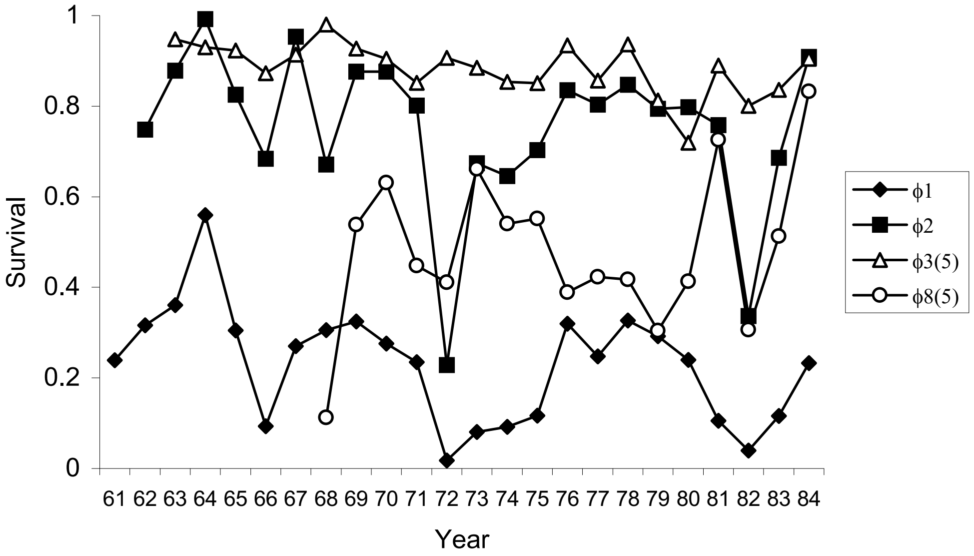


Fig.4. Survival estimates from the model assuming all age classes affected by NOA index, population size and their statistical interaction (model {$\phi_1(N*P)$, $\phi_2(N*P)$, $\phi_3(5)(N*P)$, $\phi_8(6)(N*P)| \lambda(t)$}.

Population censuses (Fig.3) suggested 6 winters of high mortality: 63/64, 66/67, 69/70, 74/75, 77/78 and 81/82. Except for the winter 66/67, the estimates of survival from the model including external covariates failed to captured these population crashes (Fig. 4). Interesting the full time dependent model (Appendix 3) captured the 63/64survival crash (i.e. in lamb survival) while the model including NAO and population size does not (in this respect the model assuming a parallel regression with time performed better, Appendix 3).

The goodness of fit of the model {ϕ_1(N*P), ϕ_2(N*P), ϕ_3(5)(N*P), ϕ_8(6)(N*P)| λ(t)} was marginally non significant (p=0.052; by bootstrap technique with 500 simulations), however when assessed graphically it appears to be poor (Fig.5).

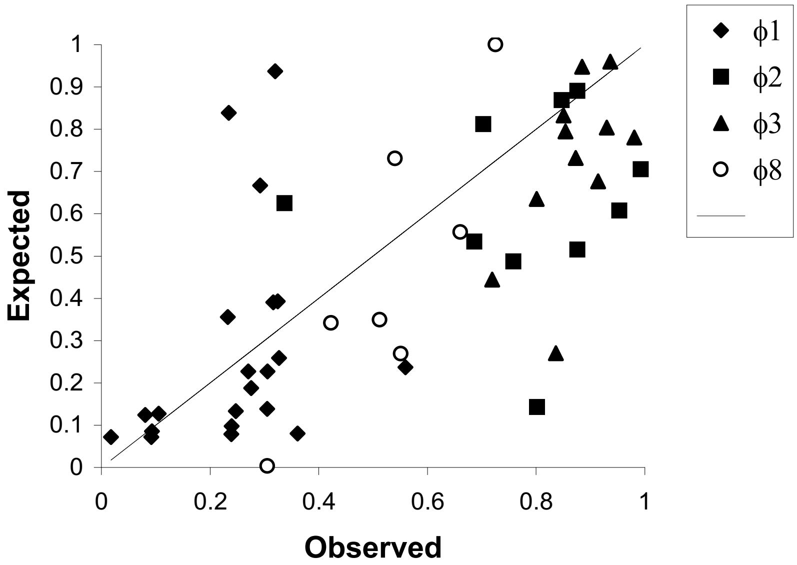


Fig.5. Goodness of fit of model {$\phi_1(N*P)$, $\phi_2(N*P)$, $\phi_3(5)(N*P)$, $\phi_8(6)(N*P)| \lambda(t)$}. Values at the 1 or 0 boundary from the full age- and time-dependent model have been eliminated.

Tab.4 Ultrastructural models including NAO index (NOA), total island population size (P), February and March rainfall (F and M, respectively). External covariates were tested in each age class at the time (all other parameters are kept constant). Bold models has been retained..

Model	AIC	Np	Deviance
ϕ_1(.)	2157.87	28	160.84
ϕ_1 (NAO)	**2154.32**	**29**	**155.19**
ϕ_1 (NAO*Pop)	**2154.74**	**31**	**151.40**
ϕ_1 (Febb)	2157.22	29	158.09
ϕ_1 (Pop)	2157.25	29	158.13
ϕ_1(Mar)	2159.56	29	160.43
ϕ_1(t)	2170.67	51	124.47
ϕ_2(.)	**2157.87**	**28**	**160.84**
ϕ_2(NAO)	2159.26	28	162.23
ϕ_2(NAO*Pop)	2160.92	31	157.58
ϕ_2(Febb)	**2158.02**	**29**	**158.89**
ϕ_2(Pop)	2159.00	28	161.98
ϕ_2(Mar)	2160.42	29	161.30
ϕ_2(t)	2169.29	50	125.27
ϕ_3(5)(.)	**2157.87**	**28**	**160.84**
ϕ_3(5) (NAO)	**2157.56**	**29**	**158.43**
ϕ_3(5) (NAO*Pop)	2158.39	31	155.06
ϕ_3(5) (Febb)	2159.89	29	169.77
ϕ_3(5) (Pop)	2161.28	29	162.15
ϕ_3(5) (Mar)	2159.25	29	162.22
ϕ_3(5)(Mar*P)	2165.30	31	161.96
ϕ_3(5) (t)	2164.83	49	122.99
ϕ_8(6)(.)	**2157.87**	**28**	**160.84**
ϕ_8(6) (NAO)	2160.36	29	161.23
ϕ_8(6) (NAO*Pop)	2163.87	31	160.54
ϕ_8(6) (Febb)	2161.41	29	162.27
ϕ_8(6) (Pop)	2159.80	29	160.67
ϕ_8(6) (Mar)	2160.56	29	161.43
ϕ_8(6) (t)	2179.35	44	148.33
ϕ_1(N*P), ϕ_2(N*P), ϕ_3(5)(N*P), ϕ_8(6)(N*P)	**2153.205**	39	132.901
ϕ_1(t), ϕ_2(t), ϕ_3(5)(t), ϕ_8(6)(t) //regression	**2156.880**	52	108.502

*Tab.5.Data 1961-84. Linear predictors (SE in brackets) of the relation between survival and NAO from the model NAO*Population size for periods 1961-84 and 1986-00 (model $\{\phi_1(N*P),\phi_2(N*P),\phi_3(5)(N*P), \phi_8(6)(N*P) \mid \lambda(t)\}$ and model $\{\phi_1(N*P),\phi_2(N*P),\phi_3(5)(M*P), \phi_8(6)(N*P) \mid p(A+t)\}$, respectively). Bold quantities are significantly different from 0.*

Parameter	Intercept	Pop	NAO	Pop . NAO
1961-84				
ϕ_1	**-1.85 (0.32)**	**-0.27 (0.12)**	**-0.60 (0.21)**	**-0.17 (0.07)**
ϕ_2	**0.87 (0.38)**	-0.18 (0.12)	**-0.77 (0.37)**	**-0.29 (0.11)**
ϕ_3(5)	**1.47 (0.32)**	0.15 (0.11)	**-0.54 (0.25)**	0.08 (0.09
ϕ_8(6)	-0.10 (0.72)	0.11 (0.24)	-0.49 (0.78)	-0.28 (0.27)
1986-00				
ϕ_1	0.41 (0.09)	**-1.10 (0.09)**	**-0.37 (0.07)**	**-0.50 (0.10)**
ϕ_2	**2.30 (0.267)**	**-1.01 (0.24)**	-0.28 (0.185)	**-0.89 (0.28)**
ϕ_3(3_7)	**2.58 (0.117)**	0.08 (0.12)	**-1.71 (0.262)**	**-0.57 (0.206)**
ϕ_8(8_11)	**1.77 (0.185)**	**-0.981 (0.15)**	**-0.469 (0.141)**	**-1.34 (0.236)**
ϕ_8(11_15)	**0.819 (0.287)**	**-0.882 (0.278)**	-0.221 (0.196)	-0.290 (0.309)

CONCLUSIONS

The pattern of age-dependent survival of female Soay sheep is similar to the one found in previous analyses. Survival probability increases sharply with age reaching a plateau at 3 years. Mortality increases again after age 7. Interesting, as found previously, mortality does not seem to increase in old ages, but rather stabilized after 8-11 years. Given this pattern, the Gompertzian model does not appear a good descriptor.

Lamb survival over the period 1961-84 seems to be lower than the one estimated by the same model over a subsequent period (1986-00).

Time dependent models appeared to have too many parameters in relation to the information available. Indeed the full model including age and time, included parameters numerically non-estimable but it was not possible to determine their exact number. The likelihood function in MARK1.9 had some difficulties to reach the optimal point in ultrastructural models (assuming the influence of density-dependent and density independent factor). This is not surprising considering the fact that the recovery of a tag is a relative “weak” information.

The final model assuming an influence of NAO index, total population size and the statistical interaction, although having a low AICc value, does not seem to adequately describe the data. This could partially due to the scarce information available, but could also suggest a real inadequacy of the covariates. Numerical difficulties make impossible to distinguish between these two hypotheses, however the fact that estimates of lamb survival from a model assuming a parallel regression between age and time do capture most of the observed population crashes, support the last hypothesis.

FURTHER WORKS

I consider that two results worth further investigation (after **all inconsistencies between paper and electronic information have been checked)**.

The first is the low survival of female lambs compared with the later period. In the current analysis I assumed that recovery rate was varying according to year only. **It would be possible to include an age structure on the recovery rate** as it has been done for survival. However this is likely to results in more redundant quantities that need to be formally identified. It is possible (although not yet proved, that lamb survival became not identifiable). Moreover, an age structure on λ would reduce the power to test the hypotheses of interest on survival probability. **It would be possible to check whether a similar low survival is found also for male lambs.**

A second point is the influence of external covariates. The results show a poor influence of time but also of external covariates. The current information available is too weak to provide high confidence in this result. More indications on this direction could be obtained by **comparing the population size expected using the current estimates with the one expected using the estimates from the previous analyses**.

APPENDIX

APPENDIX 1: *Available data on Soay sheep before 1986*

<u>*Electronic data*</u>

1 – LAMB61-83: it contains the data of birth and death of lambs marked from 1961 to 1983. Sixteen tags have been re-used. Although this has been done after a big time lag ca.10 years in one case their appear simultaneously.

2 – MORT60S: Rescued from phoenix magnetic tapes. Similar data as in LAMB61-83 (also contains some data up to 1990 that are in the popfile). It also probably contains the information about autumn recapture, but the head of columns is not clear.

3 – WTAUT60S: Some of the 1960s paper records may have information about the layout of this file. It's useful because it's got Autumn weights (oct & nov). Taken from tape LARG archive space on phoenix dated 5/9/90 (by I. Stevenson) n=258 from 1964 to 1966.

<u>*Paper support*</u>

1 – In SOAY60s REPORT box is a table of live recapture between 60-64

2 – IN SOAY LAMBING DATA and SOAY CENSUS + DATA FILE FORMAT boxes refer on the format of some of the files

3 – In SOAY DEAD box I have found some data about the recorded deaths on paper support, however the tag are coded in a different manner than the one on the electronic file. I did not found matches in both tags and number of dead sheep recorded (for example in the file there are no sheep recorded death of the 1972-cohorte, while there is at least one sheep recorded dead in the paper support).

APPENDIX 2: *Redundant quantities in age-dependent recovery model*

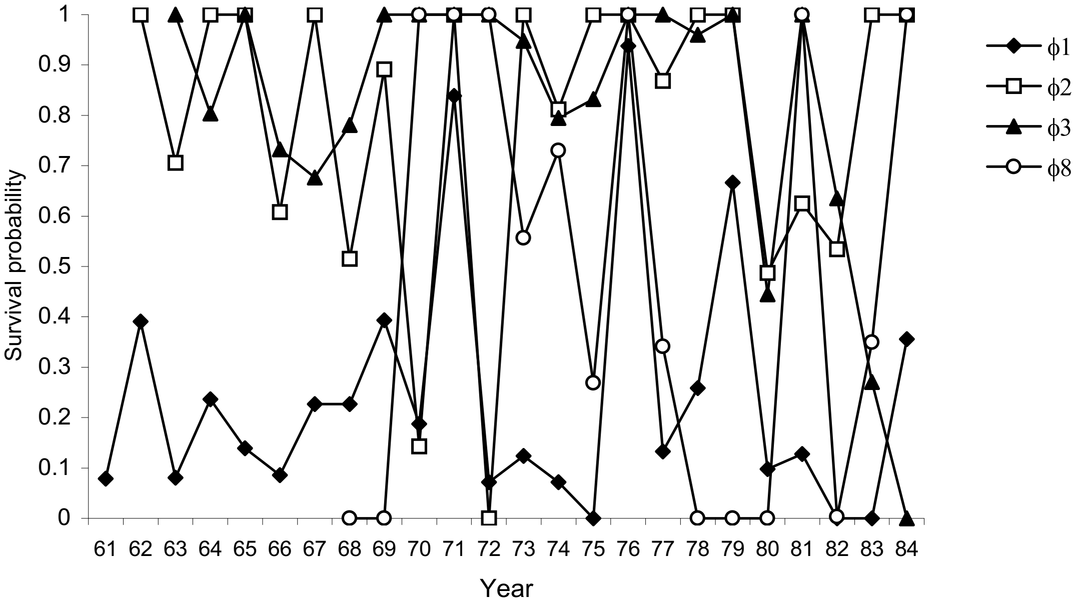
When survival is age- and time-dependent, recovery models in which recovery rate varies over time, contain redundant quantities. Counterintuitively, increasing the complexity of the model structure (adding occasions and/or age-classes) reduce the number of these quantities. The following table shows the results of the redundant quantities investigation in models differing for the degree of complexity (number of occasion, age classes, time effect).
Notation: K = number of occasions
AgeC= number of age classes
NpM = number of parameter in the models
NpR = redundant quantities

	Model notation	K	AgeC	NpM	NpR	Note
1	$\{\phi_1(t),\phi_2(t),\phi_3(t)\ldots\phi_9(t)$ $\vert\lambda(t)\}$	9	9	53	8	None is separately estimable
2	$\{\phi_1(.),\phi_2(.),\phi_3(.)\ldots\phi_9(.)$ $\vert\lambda(t)\}$	9	9	18	1	None is separately estimable
3	$\{\phi_1(t),\phi_2(t),\phi_3(3)(t),\phi_6(2)(t)\phi_8(2)(t)$ $\vert\lambda(t)\}$	9	5	39	1	Only last occasion parameters are not separately estimable
4	$\{\phi_1(t),\phi_2(t),\phi_3(3)(t),\phi_6(4)(t)$ $\vert\lambda(t)\}$	9	4	37	1	Only last occasion parameters are not separately estimable
5	$\{\phi_1(t),\phi_2(t),\phi_3(3)(t),\phi_6(4)(t)$ $\vert\lambda(t)\}$	9	5	38	0	
6	$\{\phi_1(t),\phi_2(t),\phi_3(5)(t),\phi_8(3)(t)\phi_{11}(5)(t)\vert\lambda(t)\}$	15	5	69	1	Not checked
7	$\{\phi_1(t),\phi_2(t),\phi_3(5)(t),\phi_8(3)(t)\phi_{11}(5)(.)\vert\lambda(t)\}$	15	5	66	0	
8	$\{\phi_1(t),\phi_2(.),\phi_3(3)(.),\phi_6(4)(.)$ $\vert\lambda(t)\}$	9	4	21	0	
9	$\{\phi_1(.),\phi_2(t),\phi_3(3)(.),\phi_6(4)(.)$ $\vert\lambda(t)\}$	9	4	20	0	
10	$\{\phi_1(.),\phi_2(.),\phi_3(3)(t),\phi_6(4)(.)$ $\vert\lambda(t)\}$	9	4	19	0	
11	$\{\phi_1(.),\phi_2(.),\phi_3(3)(.),\phi_6(4)(t)$ $\vert\lambda(t)\}$	9	4	16	0	

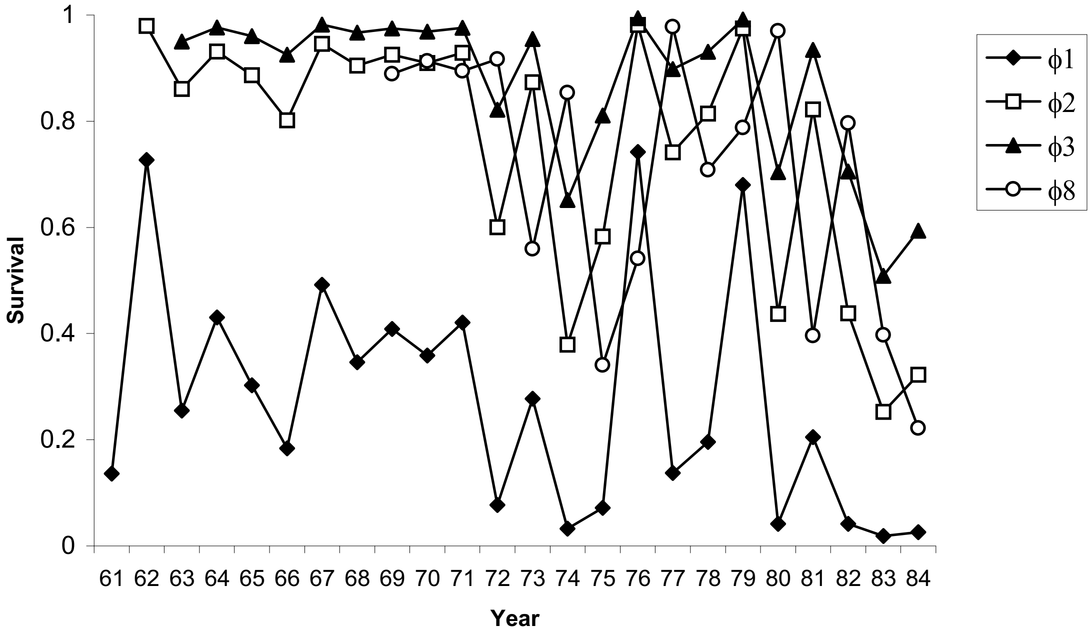
As shown by Lakhani and Newton (1984) in full age- and time-dependent models, parameters are not separately estimable (Case 1 in Table). This problem is maintained also in models with a simpler structure, i.e. assuming constant survival (Case 2).
Reducing the number of age classes would make most of the parameter separately identifiable even in the presence of a time effect (Case 3). However, the last occasion parameters are not separately estimable. This is true also no matter how the age classes are clumped (Case 4). The only way to make all parameters identifiable is to assuming a constant survival for the last age class (Case 5). A similar pattern is reproduced even for a higher number of occasions (Case 6 and 7) although for these large matrices it was not possible to determine which quantities are redundant.
In models where the time affects one age-class only, all parameters are separately identifiable (Case 8_11).

APPENDIX 3: *Full time-dependent model*

Estimates from the full time- and age-dependent model $\{\phi_1(t), \phi_2(t), \phi_3(5)(t), \phi_8(8)(t) \mid \lambda(t)\}$



Estimates from the model assuming parallel regression between age and time (no interaction) model $\{\phi_1(t), \phi_2(t), \phi_3(5)(t), \phi_8(8)(t) \mathbin{//} \mid \lambda(t)\}$



APPENDIX 4: *Age-dependent survival in males and females (1961-84)*

The age-dependent pattern of survival can be modelled using a continuous function. In particular for males (black squares), age specific survival could be modelled as a quadratic function of age (continuous line) while in females (open squares) the quadratic function should be applied to the natural logarithm of age (dotted line).

$$\phi_{\text{males}} = 1 / (1+e^{2.7062816-1.6313561*\text{Age}+0.1832299*\text{Age}^2})$$

$$\phi_{\text{females}} = 1 / (1+e^{1.1569062-5.0990014*\ln(\text{Age})+2.016894*\ln^2(\text{Age})})$$