

# Analysis of female Soay sheep recapture data (update to 2000)

## Introduction

Catchpole et al. (2000) have described the survival probability of males and females Soay sheep from 1986 to 1996 using capture and recovery information. Among other results, they showed that survival of female Soay sheep was dependent on whether condition and summer population size. However the extent and type of these relationships were changing through the different age classes considered. These new results allowed taking into account a higher level of complexity in population models that proved to better describe population dynamics (Coulson et al. 2001). Since then additional data have been collected (4 years), which increased the sample size of about one third. Including additional information inevitably increases the level of complexity in the analysis (Tavecchia et al. 2000) but whether this would significantly improve the understanding of population dynamics is not clear. The aim of this second analysis is a) to include more recent data and update the relationship between survival and environmental covariates, and b) to compare previous results with those found using program MARK1.9. In this report, I have followed the steps in Catchpole et al. 2000.

- 1) I checked **whether an increase in the data set, influences the age structure detected in previous results**
- 2) I subsequently **added more complexity** in the models by including effects such as time, age and environmental covariates **to investigate their relationship with survival parameters**

## Data

Capture histories = 1089 (females only). Note that recoveries were not considered.

Recapture occasions = 15 (1986-2000)

Cohorts or groups = 21 (1979-1999)

Individual covariates = 4 (cohort, coat, horn, id). These were implemented in the analysis, but models including them are not presented in this report.

## Goodness-of-fit of model $\{\phi_{1...15}(t)\} | \{p_{1...15}(t)\}$

Goodness-of-fit test of the general model  $\{\phi_{1...15}(t)\} | \{p_{1...15}(t)\}$  (dev.=3257.5 np=336 AICc=4005.24) was done with program U\_CARE (Choquet et al. 2000), which corrects for small sample in contingency tables and provides specific directional tests (Z-tests) for trap-dependence and transience effects.

Global test was not significant, however the directional test for trap-dependence was highly significant suggesting a trap-happiness effect (Tab.1).

Note that similar results were obtained using program RELEASE in MARK1.9, where TEST3 was not significant but TEST2 it was, however program U\_CARE should be preferred because accounts for small numbers in contingency tables.

Tab.1 Goodness-of-fit test for the general model  $\phi(AGE/TIME) P(AGE/TIME)$  including the effects of time, age and their interactions

Global $\chi^2$ -TEST number of groups =21 df =50	$\chi^2 =47.076$ p=0.59144
N(0,1) statistic for transient(>0)	Z=0.42658 p=0.66968 two-sided test p=0.33484 one-sided test for transience
N(0,1) signed for trap-dependence z<0 trap-happiness z>0 trap-shyness	Z=-3.3493 p=0.00081018 two-sided test

An insight on the effect of trap-dependence can be obtained by inspecting the cohort-specific contingency tables results (Tab.2). These suggest that the trap-happiness effect varies with time within each cohort. The pattern is however not clear. It does not seem to be associated with population size or population changes (Tab.2).

Coulson et al. (1999) have proved that population dynamics has a small-scale spatial component. This might be present also for the probability of recapture if some areas in St. Kilda are less prospected than other.

A striking pattern is that trap-dependence effects seem to disappear for animals older than 2-3 years old. In the presence of a spatial component in the probability of recapture, this would suggest that the use of particular areas are age-dependent (i.e. young animals tend to be faithful to well prospected areas).

Whether a trap-dependence effect is due to a different in the behaviour of marked animals or not, it advocates for the use of an age-dependent capture probability to partially take into account the effect of trap-happiness.

*Tab.2 Cohort-specific results for the trap-dependence test.  $I$  = cohort year,  $j$  = recapture year,  $X$  = significant trap-happiness test for cohort  $i$  in year  $j$ .  $P$  = population size in summer  $\lambda$ =population growth rate estimated by census data*

$C_i$	$j=87$	88	89	90	91	92	93	94	95	96	97	98	99
83		X											
84	X	X											
86	X	X	X										
87		X	X										
88			X	X									
89				X	X	X		X					
90					X	X							
91						X	X	X					
92								X					
93								X	X				
95											X		
96											X	X	
97													X
P	331	457	211	290	414	321	443	435	357	575	542	591	325
$\lambda$	1.57	1.38	0.46	1.37	1.43	0.78	1.38	0.98	0.82	1.61	0.94	1.09	0.55

Finally the scale parameter was taken as 1.00 cause the general test was not significant.

## Age-structure

Model selection was complicated by the fact that the number of estimable parameters in MARK1.9 is unreliable. Indeed numerical and structural problems in identifiability of parameters are confounded (parameters at the 1 boundary are considered as not-estimable). In all following tables, when the AICc values are calculated using the maximum number of estimable parameters is noted with ‘+’.

Tab.2 Detecting age structure from the simple model  $\{\phi_{1...15}\} \{p\}$ . Model 2 corresponds to the retained age-structure in in Catchpole et al. 2001. In all model  $p$  is assumed to be constant. The retained model is framed.

N	Model	deviance	np	AICc	LRT
1	$\phi_1 \dots \phi_{15}$	4208.46	16	4240.21	
2	$\phi_1, \phi_2, \phi_a(5), \phi_s$	4244.81	5	4254.83	2vs1: <b>p=0.000</b> 2vs5: <b>p=0.000</b>
3	$\phi_1, \phi_2, \phi_3(2), \phi_5, \dots \phi_{15}$	4212.14	15	4242.29	3vs1: p=0.043
4	$\phi_1, \phi_2, \phi_3(3), \dots \phi_{15}$	4212.50	14	4240.63	4vs1: p=0.095
5	$\phi_1, \phi_2, \phi_3(5), \dots \phi_{15}$	4216,79	12	4240,88	5vs1: p=0.068
6	$\phi_1, \phi_2, \phi_3(6), \dots \phi_{15}$	4237,36	11	4259.44	6vs1: <b>p=0.000</b> 6vs5: <b>p=0.000</b>
7	$\phi_1, \phi_2, \phi_3(5), \phi_8(2), \dots \phi_{15}$	4219,39	11	4241.47	7vs1: p= 0.045 7vs5: p= 0.107
8	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \dots \phi_{15}$	4221,43	10	4241.50	8vs1: p= 0.037 8vs7: p= 0.153
9	$\phi_1, \phi_2, \phi_3(5), \phi_8(4), \dots \phi_{15}$	4236,56	9	4254.61	9vs1: <b>p= 0.000</b> 9vs8: <b>p= 0.000</b>
10	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(2), \dots \phi_{15}$	4225.24	9	4243.29	10vs1: p= 0.016 10vs8: p=0.051
11	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(3), \dots \phi_{15}$	4225.25	8	4241.30	11vs1: p= 0.028 11vs10: p=0.893
12	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(4), \phi_{15}$	4229.06	7	4243.09	12vs1: p= 0.013 12vs11: p=0.051
13	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(5)$	4230.93	6	4242.96	13vs1: p= 0.011 13vs12: <b>p=0.171</b>
14	$\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(3), \phi_{14}(2)$	4229.06	7	4243.09	14vs1: p= 0.013 14vs12: p=0.051 14vs13: p=0.171
15	$\phi_A + A^2$	4366.12	4	4374.13	15vs1: <b>p= 0.000</b>
16	$\phi_{\ln(A)} + \ln(A)^2$	4239.89	4	4247.90	16vs1: p= 0.002

The model retained was:

$$\{\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(5)\} \{p\} \quad (1)$$

The 4-steps age-structure retained in the previous analyses no longer satisfying. As expected adding more data increased the power to detect differences between age-classes and in particular in the older ages. Indeed age-dependent survival can be better described by a 5-step age-structure (Fig.1). This might be important to better describing the senescence pattern in survival for female Soay sheep. Interesting the two models including a continuous relationship with age, were both rejected. This is in part because of the large flat surface of the curve corresponding to the middle age classes, but also because mortality does not seem to steadily increase with age but rather flattening off after age 10 (Fig.1).

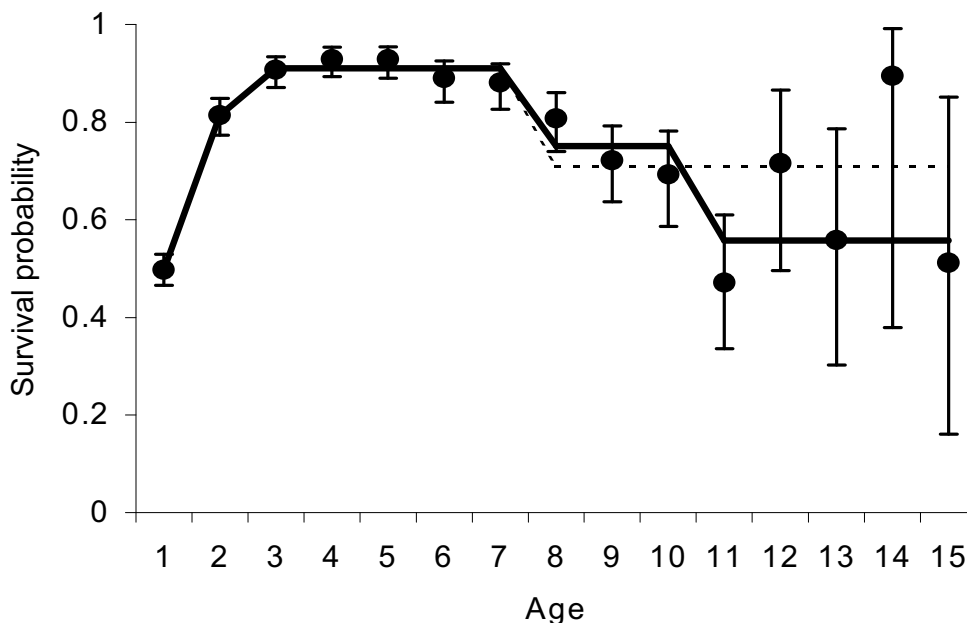


Figure 1. Age dependent survival probability. ● =  $model\{\phi_{1...15}\} \{p\}$   
 --- =  $model\{\phi_1, \phi_2, \phi_8(5)\phi_{11}(11)\} \{p\}$  (as in Catchpole et al. 2000)  
 — =  $model\{\phi_1, \phi_2, \phi_5(5)\phi_8(3), \phi_s\} \{p\}$

Age has a significant positive effect also on the probability of recapture whether survival was considered full age dependent or modelled as a 5-steps function (Tab.3).

A significant age effect on recapture probability is rather unexpected. Preliminary analysis of multisites data suggest that non breeders have a lower probability of recapture. If breeding propensity increases with age, this could likely result in an overall age effect when breeding status is not accounted for. Next step in the analysis

was to add time effect of both survival and recapture. (The 5-steps model of survival was still retained when considering a age effect on survival.)

Tab.3 Detecting age effect on the probability of recapture from model  $\{\phi_{1...15}\} \{p\}$ . Highly significant LRT are marked in bold. The retained model is framed.

N	Model	deviance	np	AICc	LRT
17	$\{\phi_{1...15}\} \{p(\cdot)\}$	4208.46	16	4240.21	
18	$\{\phi_{1...15}\} \{p_{1...15}\}$	4162.54	24	4210.91	
19	$\{\phi_{1...15}\} \{p_A\}$	4171.87	17	4206.05	19vs1: <b>p=0.000</b> 19vs18: p=0.230
20	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\} \{p\}$	4230.93	6	4242.96	
21	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\} \{p_{1...15}\}$	4184.02	15	4214.17	
22	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\} \{p_A\}$	4192.67	7	4206.70	22vs20: <b>p=0.000</b> 22vs21: p=0.373
23	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\} \{p_A^2\}$	4191.62	8	4207.67	

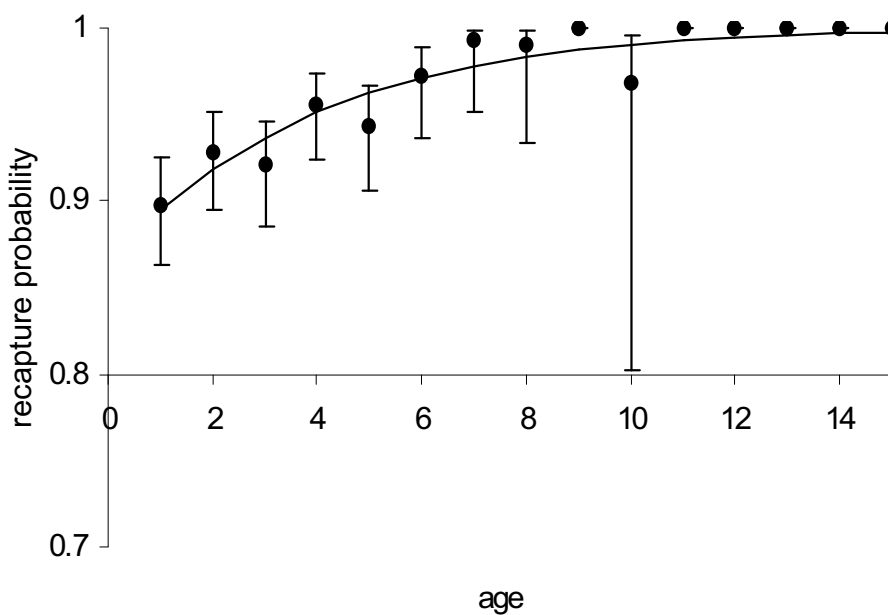


Figure 2. Age dependent recapture probability. ● = model  $\{\phi_{1...15}\} \{p_{1...15}\}$   
 — = model  $\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\} \{p_A\}$ . The regression line is  $\text{logit}(p) = 1.861 + 0.277A$

## Time

The next step was to add time effect of both survival and recapture. Contrary to age, time has been model done in a step-up procedure as in Catchpole et al. (2000). I considered the time effect for each parameter of model  $\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5) | p(A)\}$  separately. I finally built a consensual model including all the retaining parameter structure (Tab.3). I finally built a consensual model including all the retaining parameter structure (Tab.3). As found in Catchpole et al. (2000), time effect was retained in all parameters, but was more important in  $\phi_1$ . Interesting there are no evidence that survival of animals age  $>11$  ( $\phi_{11}(5)$ ) was varying over time. However this is likely to be the result of a smaller sample size and the time effect was retained the oldest animals as for the all other age classes. Interaction between age and time was not significant in the probability of recapture (i.e; recapture probability is similarly increasing with age whatever year is considered). The final consensual model was thus (Fig.3-4):

$$\{\phi_{1,(t)}\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t) | pA+t\} \quad (2)$$

Tab.4 Modelling time effect. Time effect was considered separately in each age classes and for probability of recapture. A final consensual model was than built. †=maximum number of estimable parameters.

N	Model	deviance	np	AICc	$\Delta Dev.$	$\Delta df$
22	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\}   \{pA\}$	4192.67	7	4206.70	0	0
24	$\{\phi_1(t), \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(5)\}   \{pA\}$	3901.49	20	3941.74	-291.2	13
25	$\{\phi_1, \phi_2(t), \phi_3(5), \phi_8(3), \phi_{11}(5)\}   \{pA\}$	4111.54	20	4151.79	-81.13	13
26	$\{\phi_1, \phi_2, \phi_3(5)(t)\phi_8(3), \phi_{11}(5)\}   \{pA\}$	4087.42	20	4127.78	-105.3	13
27	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3)(t), \phi_{11}(5)\}   \{pA\}$	4072.68	20	4112.94	-120	13
28	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)(t)\}   \{pA\}$	4176.18	18	4212.39	-16.49	11
29	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\}   \{pA+t\}$	4165.64	20	4125.39	-27.03	13
30	$\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)\}   \{pA*t\}$	4111.56	33	4178.25	-81.11	26
31	$\{\phi_{1,(t)}\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\}   \{pA+t\}$	3518.01	81†	3686.23	-674.7	75

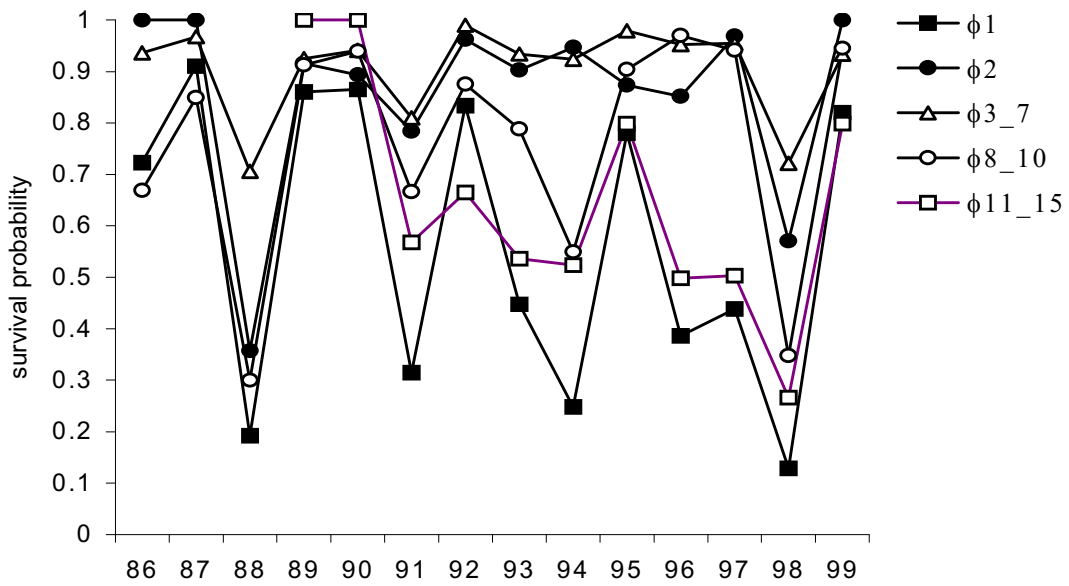


Figure 3. Age and time dependent dependent survival probability from the consensual model  $\{\phi_1(t)\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\} \{pA+t\}$ . The estimates for the period 1986-96 are identical to the ones found by Catchpole et al. 2000.

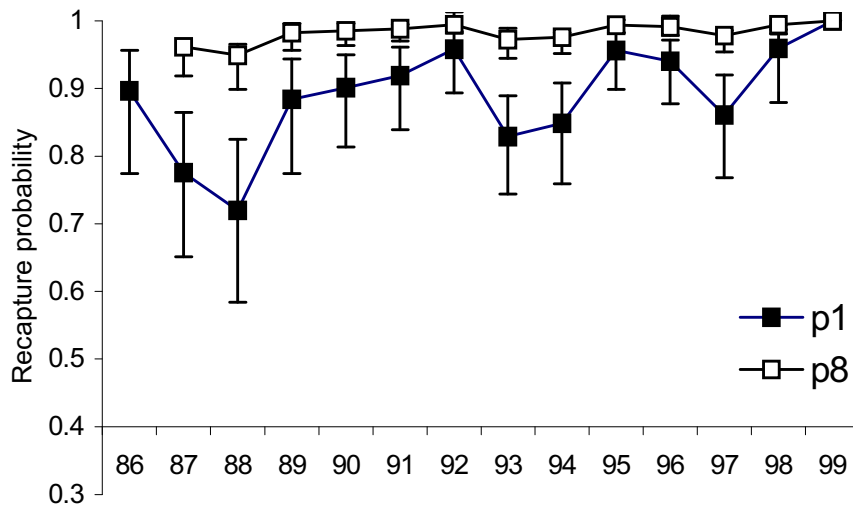


Figure 4. Time and age-dependent probability of recapture. For the sake of simplicity only the recapture probability for yearlings ( $p1$ ) and animals 8 of years old ( $p8$ ) are represented. Values for the other age classes are between following the logistic regression  $\text{logit}(p) = 1.875 + 0.483A + \beta_j$ . Where  $\beta_j$  is the linear predictor for the year  $j$  (see Appendix 1).

When each parameter is modelled separately, there is the risk of not considering some important combinations of parameter structure or of including effect retained in a too

parsimonious environment. I thus explored additional models neighbouring the consensual one. This has been done by re-testing some effects that was previously retained or dropped (Tab.4).

*Tab.4 Model neighbouring the model 31 retained as the consensual model (see Tab.3). In model notation, parallel regression is noted by writing the effect outside the brackets (i.e. in model 32 the difference between age specific survivals is constant over time) . †= maximum number of estimable parameters.*

N	Model	deviance	np	AICc	$\Delta Dev.$	( $\Delta df$ )
31	$\{\phi_1(t)\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\}   \{pA+t\}$	3518.01	82†	3686.23	0	0
32	$\{\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(5)\}   pA+t\}$	3608.75	33	3675.43	91	-49
33	$\{\phi_1(t)\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\}   \{pt\}$	3556.25	81†	3722.37	38	-1
34	$\{\phi_1(t)\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\}   \{pA\}$	3568.58	70	3711.74	51	-12
35	$\{\phi_1(t)\phi_2(t), \phi_3(5)(t)\phi_8(3)(t)=\phi_{11}(5)(t)\}   \{pA+t\}$	3548.99	71†	3694.14	31	-11

The "new" 5-steps structure on survival was still retained even when correcting for a time effect. Unexpectedly the model 32 (noted  $\{\phi_1, \phi_2, \phi_3(5)\phi_8(3), \phi_{11}(5)(t)\} | pA+t$ ) assuming a parallel regression between time and the five age-classes, was retained. This is probably an indication that the model accounting for the age, the time effects and their statistical interactions (model 31) is over-parameterised. I thus explored model including external covariates in order to reduce time parameters. This has been done by a step-down procedure as in Catchpole et al. 2000.

## External covariates

The external covariates used in the analysis are fully reported in Appendix II. Covariates were standardised as in Hilsden (1999) :

$$P = (\text{population size} - 393) / 100$$

$$N = (\text{NAO} - 0.944) / 10$$

$$F = (\text{February rainfall} - 154.8) / 100$$

$$M = (\text{March rainfall} - 142.5) / 100$$

Tab.5 Pearson's correlation coefficients between environmental variables. Two-tailed significant level in brackets. The strongest correlation is between March and NAO

	N	F	M
P	0.037 (0.901)	0.505 (0.066)	0.204 (0.485)
N		0.267 (0.356)	<b>0.676</b> <b>(0.008)</b>
F			0.493 (0.073)

The survival probability between interval  $i$  and  $i+1$  (noted as  $\phi(i)$ ) was constraint to  $P_i$ ,  $N(i+1)$ ,  $F(i+1)$  and/or  $M(i+1)$  (see Appendix I).

Ultrastructural models were compared with the full model  $\{\phi_1(t), \phi_2(t), \phi_3(5)(t), \phi_8(3)(t), \phi_{11}(5)(t)\} | \{p_{A+t}\}$  (model 31). In all age classes I fitted models with weather\*population size (population size and its interaction with weather covariates were always considered) (Tab. 6). I subsequently built a weather-consensual model with the effects suggested in each age class (even if not significant) and an AICc-consensual models considering the weather effect only where it was retained (significant) (Tab.7). Note that some of the parameters for yearlings were estimated at the boundary value of 1.00 in most of the models. This advocates for the presence of local minima despite changing the starting values of the function, did not improve model deviance.

Tab.6 Ultrastructural models including weather ( $N=NAO$ ,  $M=$ March rainfall,  $F=$ February rainfall), summer population size ( $P$ ) and their interaction (weather\*population size). In all models the probability of recapture is  $\{pA+t\}$  (as in model 31). † = maximum number of estimable parameters. Model retained in each age class are marked in bold.

N	Model	Deviance	np	AICc	$\Delta AICc$	$\Delta Dev.$	( $\Delta df$ )
31	$\{\phi_{1(t)}\phi_{2(t)}\phi_{3(5)(t)}\phi_{8(3)(t)}\phi_{11(5)(t)}\}$	3518.01	82†	3686.23	0	0	0
36	$\{\phi_{1(P+N+N.P)}\}$	3547.28	72†	3694.53	8.3	29.27	-10
37	$\{\phi_{1(P+M+M.P)}\}$	3573.79	72†	3721.04	34.81	55.78	-10
38	$\{\phi_{1(P+F+F.P)}\}$	3604.94	72†	3752.19	65.96	86.93	-10
39	$\{\phi_{2(P+M+M.P)}\}$	3566.98	72†	3714.26	28.03	48.97	-10
40	$\{\phi_{2(P+F+F.P)}\}$	3578.61	72†	3719.59	33.36	60.6	-10
41	$\{\phi_{2(P+N+N.P)}\}$	3553.88	72†	3700.84	14.61	35.87	-10
42	<b><math>\{\phi_{3(5)}(P+M+M.P)\}</math></b>	<b>3536.73</b>	72†	3683.98	<b>-2.25</b>	18.72	-10
43	$\{\phi_{3(5)}(P+F+F.P)\}$	3584.09	72†	3731.33	45.1	66.08	-10
44	$\{\phi_{3(5)}(P+N+N.P)\}$	3559.08	72†	3706.33	20.1	41.07	-10
45	$\{\phi_{8(3)}(P+M+M.P)\}$	3549.37	72†	3696.61	10.38	31.36	-10
46	$\{\phi_{8(3)}(P+F+F.P)\}$	3601.64	72†	3748.89	62.66	83.63	-10
47	<b><math>\{\phi_{8(3)}(P+N+N.P)\}</math></b>	<b>3537.69</b>	72†	3684.93	<b>-1.3</b>	19.68	-10
48	$\{\phi_{11(3)}(P+M+M.P)\}$	3521.69	75†	3675.22	-11.01	3.68	-7
49	$\{\phi_{11(3)}(P+F+F.P)\}$	3521.26	75†	3674.78	-11.45	3.25	-7
50	<b><math>\{\phi_{11(3)}(P+N+N.P)\}</math></b>	<b>3520.44</b>	75†	3672.96	-13.27	2.43	-7

Tab.7 Fitting consensual models from tab. 5. Model 52 is the one selected Coulson et al. (2001)(see also Appendix III). Model 53 is the AICc-consensual model.

N	Model	Deviance	np	AICc
51	$\{\phi_{1(N^*P)}\phi_{2(N^*P)}\phi_{3(5)(M^*P)}\phi_{8(3)(N^*P)}\phi_{11(5)(N^*P)}\}$	3623.19	35	3693.95
52	$\{\phi_{1(N^*P)}\phi_{2(F^*P)}\phi_{3(5)(M^*P)}\phi_{8(3)(N^*P)}\phi_{11(5)(N^*P)}\}$	3645.62	35	3716.39
53	<b><math>\{\phi_{1(t)}\phi_{2(t)}\phi_{3(M^*P)}\phi_{8(3)(N^*P)}\phi_{11(5)(N^*P)}\}</math></b>	<b>3558.86</b>	<b>55</b>	<b>3670.75</b>
54	$\{\phi_{1(t)}\phi_{2(t)}\phi_{3(5)}\phi_{8(3)}\phi_{11(5)}\}+M+P+M^*P$ (parallel regression)	3732.18	23	3776.48
55	$\{\phi_{1(t)}\phi_{2(t)}\phi_{3(5)}\phi_{8(3)}\phi_{11(5)}\}+N+P+N^*P$ (parallel regression)	3687.27	23	3733.61

Results showed substantial differences from the previous findings. First of all, some of the ultrastructural models had an AICc value lower than the one of the general model. This indicates that the full model is not the most parsimonious one (this was not clear after the results shown in Tab.7 in Catchpole et al. 2001). Secondly, the external variables that were retained for each age class, differed from the ones in previous

analyses. For example yearlings survival appears to vary with the NAO index and not with March rainfall as in Catchpole et al. (2000) neither with February rainfall as in Coulson et al. (2001). However, March rainfall and NAO index are highly correlated. I thus tried a parallel regression between age and weather condition but these models were not retained. Similarly, the model assuming only one class for animals >7 years old did not improve the AICc value. The linear predictors for the 'AICc'-consensual model are in Tab.8 whereas those for the 'weather'-consensual model and for the model in Coulson et al. (2001) are in Appendix III.

*Tab.8 Linear predictors of the relation between survival and external covariates from the 'AICc'-consensual model. Bold numbers are significantly different from 0.00. The weather variables considered are N, N, M, N, N for  $\phi_1, \phi_2, \phi_3(5), \phi_8(3)$  and  $\phi_{11}$ , respectively.*

Parameter	Intercept	Pop	Weather	Pop . Weather
$\phi_3(5)$	<b>2.598</b>	0.067	<b>-1.722</b>	<b>-0.575</b>
$\phi_8(3)$	<b>1.762</b>	<b>-0.981</b>	<b>-0.473</b>	<b>-1.337</b>
$\phi_{11}(5)$	<b>0.819</b>	-0.882	-0.221	-0.291

The 'AICc'-consensual model was the one with the absolute lowest AICc value. When tested in this parsimonious contest, the age effect on the probability of recapture was still highly significant ( $\chi^2_1 = 40.34$ ;  $p = 0.001$ ). The survival of the last age class does not appear to be influenced by time. As a consequence survival for animals older than 10 can be considered constant. (Note that a model assuming a parallel regression of NAO index and population size for the last two age classes was not retained). Only the 'AICc'-consensual model  $\{\phi_1(t)\phi_2(t), \phi_3(5)(M^*P), \phi_8(3)(N^*P), \phi_{11}(5)(N^*P)\} | p(A+t)$  had a lower AICc value than the one assuming a constant difference in survival between the age classes (model with parallel  $\{\phi_1, \phi_2, \phi_3(5), \phi_8(3), \phi_{11}(5)\}(t) | pA+t$ ), but the 'weather'-consensual model did not. Finally the LRT between the general model  $\{\phi_{1...15}\} | \{p_{1...15}\}$  and the 'AICc'-consensual model was not significant  $\chi^2_{281} = 301.690$   $p = 0.190$ , but it was when the 'weather'-consensual model was used instead ( $\chi^2_{301} = 366.014$   $p = 0.005$ ). In conclusions, modelling the time variation in the first two age classes would lead to a model which does not fit the data, despite the graphical evidences (Fig.6). The importance of density-dependent (DDF) and density

independent (DIF) factors are interact with the age classes. The former are more important in adults while the importance of the latter is greater for young and old animals (Tab.9).

Tab.9 Percentage of the time variation explained by each effect in the model. Time variation is not significant in the last age class. Weather variables are those in the 'weather'-consensual model  $\{\phi_1(N*P), \phi_2(N*P), \phi_3(5)(M*P), \phi_8(3)(N*P), \phi_{11}(5)(N*P)\}$

EFFECT	YEAR			
	1	2	3_7	8_10
Weather	14.8	22.7	70.0	19.4
Pop.	63.2	11.5	19.3	17.4
Weather + Pop.	80.0	54.4	74.6	55.3
Weather . Pop.	9.9	6.7	7.7	28.5
Residual Deviance	10.1	38.9	17.7	16.3

Intuitively, when the coefficient of variation is plotted over the importance of density dependent factors, it appears that selected or experienced individuals (adults) are able to 'buffer' the effect of competition. For these animals the effect of density independent factors takes place.

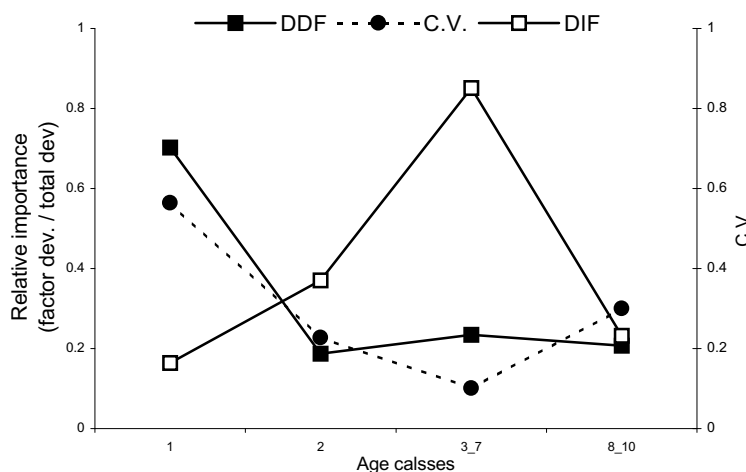


Figure 5. Changes in the relative importance of density-dependent (DDF), density-independent (DIF) factors and in the coefficient of variation of survival (CV) according to age classes in which time variation was significant. (CV is estimated as the ratio between  $\sigma^2$  of estimates from the model  $\{\phi_1(t), \phi_2(t), \phi_3(5)(t), \phi_8(3)(t), \phi_{11}(5)(t)\} \{pA+t\}$  and the constant value of model  $\{\phi_1(\cdot), \phi_2(\cdot), \phi_3(5)(\cdot), \phi_8(3)(\cdot), \phi_{11}(5)(\cdot)\} \{pA+t\}$ ).

## Conclusions

- The first result of including the latest years was that an additional class was added to the age-structure. In particular, animals  $> 7$  were no longer considered as a single group, but rather sorted into two age classes (8\_10 and 11\_15).
- Recapture probability was found to be influenced positively by age. This result is unlikely a simply numerical by-product of the analysis (i.e. difficulty in convergence) because when re-tested at several degrees of model complexity, it was always retained. Explanations for an age-dependent recapture probability in female Soay sheep are not straightforward. They might imply a different behaviour of young animals, an effect of the breeding status of individuals, and/or some spatial components in the observation effort. It is not clear to me whether an age-dependent recapture could be the result of an age-dependent trap-happiness effect (that would be even more complicated to explain). Overall, recapture probability appeared to increase over time.
- Model selection has been done using a combination of step-down and step-up procedure following Catchpole et al. (2000). This is questionable, because, for example, the age-structure was determined with models that clearly did fit the data. On the other hand, a "classical" step-down procedure would have probably selected the model including a parallel selection of time and age masking the interesting interactions among age classes. Moreover, the model selected after a mixed strategy had the lowest AICc value. When a set of *a priori* defined cannot be easily achieved, a mixed procedure is probably a good strategy. Model averaging techniques should than be considered to include model selection incertitude in the estimates.
- The influence of weather variables is different than the pattern found in previous analyses. The more striking result is that relaxing the hypothesis that lamb and yearling survival are independent from weather conditions leads to a better model.

However this would make impossible to 'predict' the population dynamic using external covariates.

- When survivals for all age classes are considered to vary with weather conditions ('weather'-consensual model), NAO index was the most important variable selected in 4 classes out of 5. The fit of this model when tested graphically (Appendix III) appeared satisfying despite the fact that the model was not retained on the base of its AICc value and that the LRT value suggested a poor fit. Why a 'new' weather variable was selected for yearling? Why local weather conditions are not better predictors? It would be interesting to investigate whether these results are due to a general increased in the information (adding more data through all age classes) or to new years being considered (a different relationship with local weather conditions). Figure 6 speculates this last point.

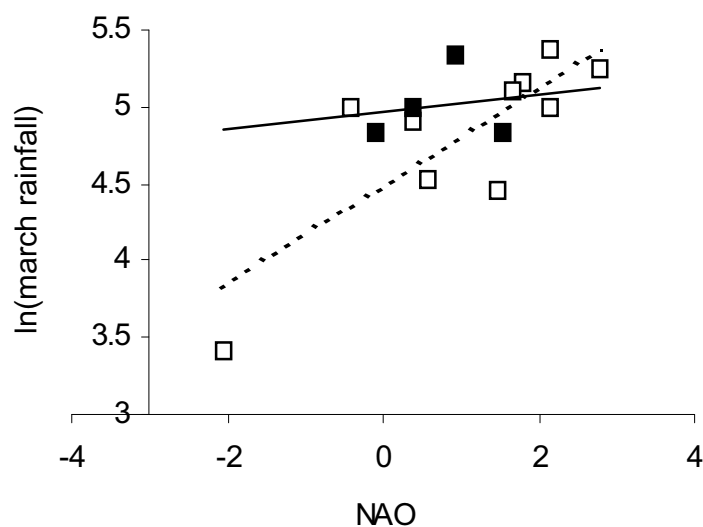


Figure 6. Value of NAO index plotted against the March rainfall (expressed in  $\ln$ ); The black square are value from 1997-2000.

## APPENDIX I

Table of  $\beta$ -values for the time dependent probability of recapture of model  $\{\phi_{1,t}\phi_2(t), \phi_3(5)(t)\phi_8(3)(t), \phi_{11}(5)(t)\} | \{pA+t\}$ .

Regression equation is  $\text{logit}(p) = 1.875 + 0.483A + \beta_j$

YEAR	$\beta$ -value	SE
1988	-0.9191793	0.5511359
1989	-1.2145854	0.5476759
1990	-0.1299525	0.6102376
1991	0.0494070	0.5935385
1992	0.2722178	0.6067723
1993	0.9713197	0.6884879
1994	-0.5819546	0.5257915
1995	-0.4371218	0.5394453
1996	0.9294131	0.6500987
1997	0.5925818	0.6045505
1998	-0.3383751	0.5550101
1999	0.9962513	0.7479431
2000	12.842940	605.42459

## APPENDIX II

Population size and weather variables used in the analysis. Note that values were standardised for the analysis (see text).

Year	Summer population size	February rainfall	March rainfall	NAO
1986	211			
1987	331	57.50	146.90	-1.353
1988	457	130.20	136.10	-0.551
1989	211	242.40	190.00	1.827
1990	290	237.50	216.30	1.216
1991	414	65.40	93.20	-0.382
1992	321	171.40	173.70	0.845
1993	443	71.30	86.00	0.513
1994	435	69.60	165.20	0.709
1995	357	130.40	148.80	1.216
1996	575	107.20	30.60	-3.005
1997	542	271.27	125.46	-1.053
1998	591	221.05	147.75	-0.551
1999	325	201.00	208.00	-0.016
2000		190.97	126.30	0.584
mean	393	154.799	142.451	0.9436

## APPENDIX III

### A) Model $\{\phi_1(N^*P)\phi_2(N^*P),\phi_3(M^*P)\phi_8(3)(N^*P),\phi_{11}(5)(N^*P)\}$ (the 'weather'-consensual model)

Linear predictors of the relation between survival and external covariates from the 'Weather'-consensual model  $\{\phi_1(N^*P)\phi_2(N^*P),\phi_3(M^*P)\phi_8(3)(N^*P),\phi_{11}(5)(N^*P)\}$ . Bold numbers are significantly different from 0.00. The weather variable considered are N, N, M, N, N for  $\phi_1,\phi_2,\phi_3(5),\phi_8(3)$  and  $\phi_{11}(5)$ , respectively.

Parameter	Intercept	Population size	Weather	Pop.weather
$\phi_1$	<b>0.405</b>	<b>-1.097</b>	<b>-0.371</b>	<b>-0.500</b>
$\phi_2$	<b>2.283</b>	<b>-0.985</b>	-0.266	<b>-0.860</b>
$\phi_3(5)$	<b>2.582</b>	0.080	<b>-1.710</b>	<b>-0.569</b>
$\phi_8(3)$	<b>1.761</b>	<b>-0.988</b>	<b>-0.469</b>	<b>-1.341</b>
$\phi_{11}(5)$	<b>0.819</b>	<b>-0.882</b>	-0.221	-0.290

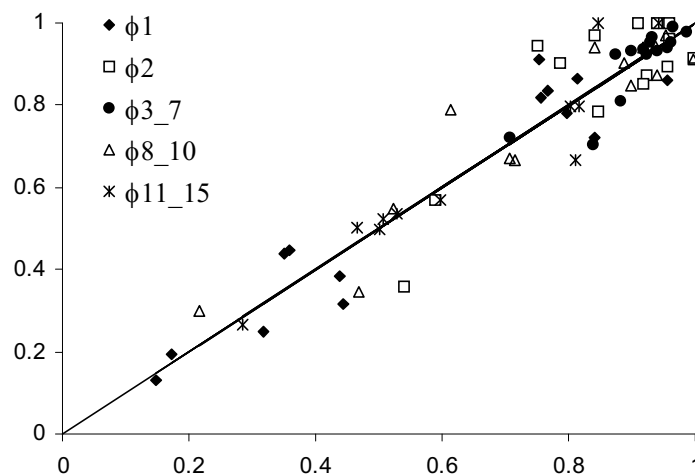


Figure 7. Estimates from the 'weather'-consensual model vs those from the full time dependent model.

Overall variance explained by the model is 90% (sum of residuals =0.204)

**B) Model  $\{\phi_1(N^*P)\phi_2(F^*P),\phi_3(M^*P)\phi_8(3)(N^*P),\phi_{11}(5)(N^*P)\}$  (the Coulson et al. 2001- model)**

Linear predictors of the relation between survival and external covariates from the model  $\{\phi_1(N^*P)\phi_2(F^*P),\phi_3(M^*P)\phi_8(3)(N^*P),\phi_{11}(5)(N^*P)\}$  in Coulson et al. 2001. Bold numbers are significantly different from 0.00. The weather variable considered are N, F, M, N, N for  $\phi_1,\phi_2,\phi_3(5),\phi_8(3)$  and  $\phi_{11}(5)$ , respectively.

Parameter	Intercept	Population size	Weather	Pop.weather
$\phi_1$	<b>0.398</b>	<b>-1.073</b>	<b>-0.373</b>	<b>-0.469</b>
$\phi_2$	<b>1.740</b>	-0.487	<b>-1.058</b>	0.679
$\phi_3(5)$	<b>2.574</b>	0.085	<b>-1.821</b>	<b>-0.498</b>
$\phi_8(3)$	<b>1.757</b>	<b>-0.977</b>	<b>-0.470</b>	<b>-1.333</b>
$\phi_{11}(5)$	<b>0.818</b>	<b>-0.882</b>	-0.221	-0.290

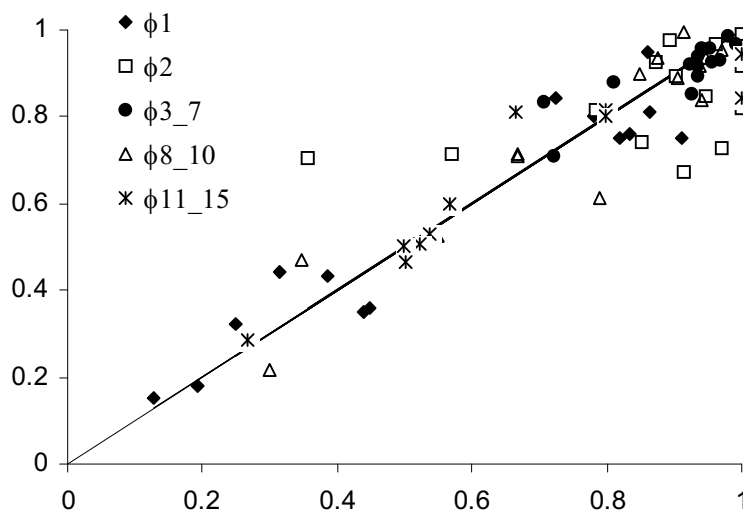


Figure 8. Estimates from the model in Coulson et al. 2001 vs those from the full time dependent model.

Overall variance explained by the model is 85% (sum of residuals =0.442)

### APPENDIX III

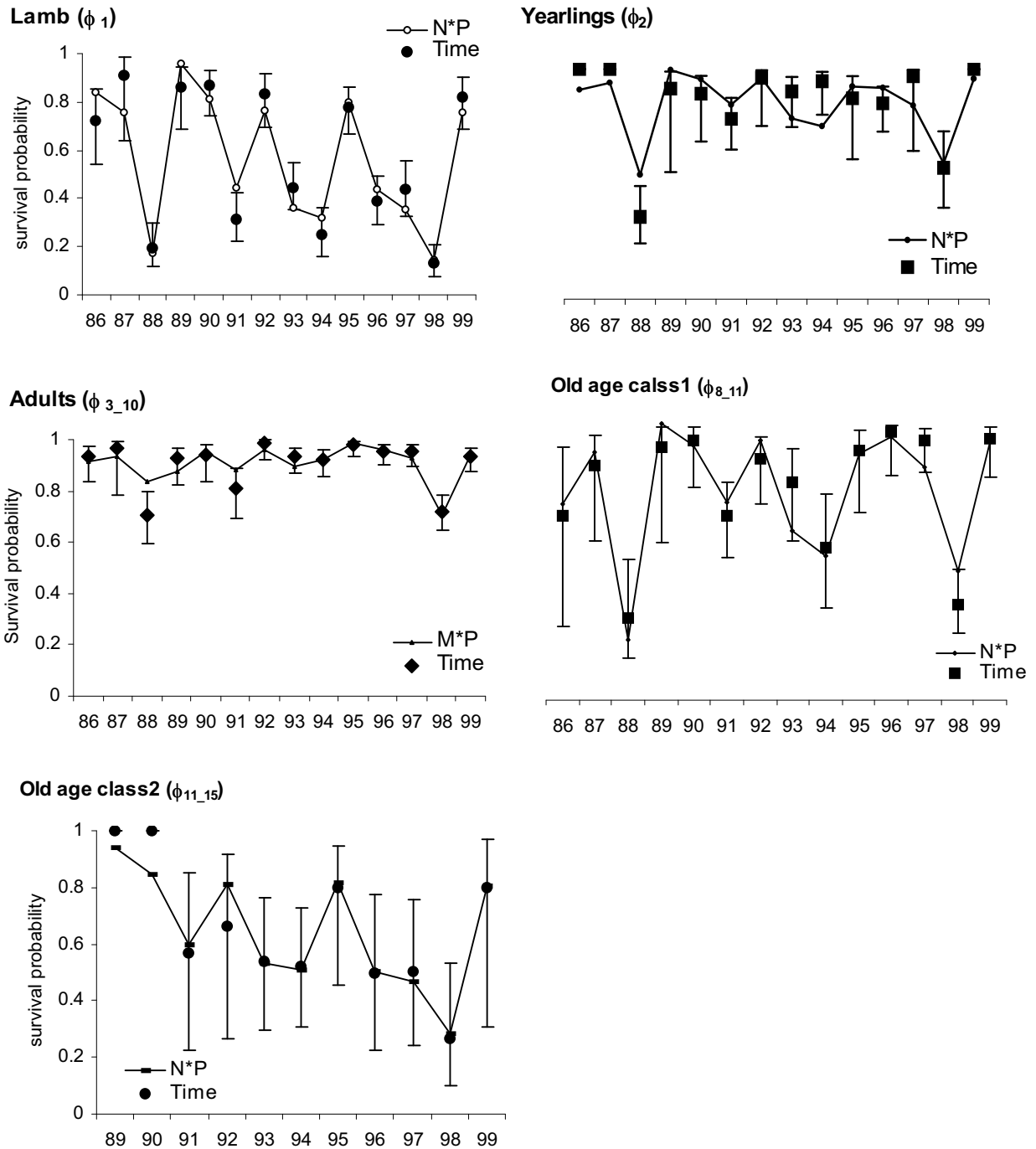


Figure 9. Estimates from the 'weather'-consensual model  $\{\phi_1(N^*P), \phi_2(N^*P), \phi_3(5)(M^*P), \phi_8(3)(N^*P), \phi_{11}(5)(N^*P)\}$  (points) vs estimates from full time-dependent model  $\{\phi_1(N^*P), \phi_2(N^*P), \phi_3(5)(M^*P), \phi_8(3)(N^*P), \phi_{11}(5)(N^*P)\}$  (continuous lines).