

Predictors of reproductive cost in female Soay sheep

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Summary

1. We investigate factors influencing the trade-off between survival and reproduction in female Soay sheep (*Ovis aries*). Multistate capture–recapture models are used to incorporate the state-specific recapture probability and to investigate the influence of age and ecological conditions on the cost of reproduction, defined as the difference between survival of breeder and non-breeder ewes on a logistic scale.
2. The cost is identified as a quadratic function of age, being greatest for females breeding at 1 year of age and when more than 7 years old. Costs, however, were only present during severe environmental conditions (wet and stormy winters occurring when population density was high).
3. Winter severity and population size explain most of the variation in the probability of breeding for the first time at 1 year of life, but did not affect the subsequent breeding probability.
4. The presence of a cost of reproduction was confirmed by an experiment where a subset of females was prevented from breeding in their first year of life.
5. Our results suggest that breeding decisions are quality or condition dependent. We show that the interaction between age and time has a significant effect on variation around the phenotypic trade-off function: selection against weaker individuals born into cohorts that experience severe environmental conditions early in life can progressively eliminate low-quality phenotypes from these cohorts, generating population-level effects.

Key-words: multistate model, recruitment, survival, trade-off function

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Introduction

Experimental and correlative studies are increasingly providing evidence to support theoretical predictions that reproduction is costly (Clutton-Brock 1984; Viallefont, Cooke & Lebreton 1995; Berube, Festa-Bianchet & Jorgenson 1996; Pyle *et al.* 1997; Festa-Bianchet, Gaillard & Jorgenson 1998; Monaghan, Nager & Houston 1998; Westendorp & Kirkwood 1998; Tavecchia *et al.* 2001; Roff, Mostowj & Fairbairn 2002 (Bérubé, Festa-Bianchet & Jorgenson 1999; Festa-Bianchet *et al.* 1995). In general, this cost is expressed as a decrease in the future reproductive value through a

decline in (i) survival, (ii) the future probability of reproduction, and/or (iii) offspring quality (Daan & Tinbergen 1997). In particular, the presence of a link between survival and reproduction is a concept underpinning the theory of life-history evolution (see Roff 1992; Fox, Roff & Fairbairn 2001). Quantitative studies of this link allow optimal behaviours and strategies to be identified as well as possible mechanisms driving the evolution of life-history tactics (McNamara & Houston 1996). Although the assumption of a trade-off between fitness components is implicit in the evolution of life-history tactics, it is not always considered in models used to explore variation in fitness or population growth rate in natural populations (van Tienderen 1995). Rather, a typical approach to explore the effects of trait variability on population growth rate, λ , is to use perturbation analyses by independently altering the probability of each fitness component. The covariation between survival and reproduction, however,

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is by definition important (Benton & Grant 1999; Caswell 2001). For example, Benton, Grant & Clutton-Brock (1995) developed a stochastic population model of red deer (*Cervus elaphus*) living on Rum and showed that stochastic variation in survival or fecundity was never able to select for an increase in fecundity. If, however, environmental stochasticity influenced the trade-off between survival and fecundity, λ became more sensitive to changes in fecundity. These empirical results are also supported by theoretical studies showing that a change in a trade-off function is more effective in promoting life-history diversity than a change in the value of a single trait (Orzack & Tuljapurkar 2001). Despite the importance of dynamic modelling of the trade-off between survival and reproduction (Roff *et al.* 2002; but see Cooch & Ricklefs 1994), empirical evidence is scarce, with most theoretical studies based on unsupported assumptions about the shape and variation of the trade-off function (Sibly 1996; Erikstad *et al.* 1998).

There are remarkably few studies where data on survival and fecundity rates exist over a sufficiently long period on a suitably large number of animals to allow detailed examination of the trade-off function (but see Bérubé, Festa-Bianchet & Jorgenson 1999; Festa-Bianchet *et al.* 1995; Berube, Festa-Bianchet & Jorgenson 1996; Festa-Bianchet *et al.* 1998, where costs of reproduction in bighorn sheep have been explored). Moreover, the computation of the trade-off function from long-term data is complicated by the fact that individuals in natural populations might breed or die undetected. The resulting 'fragmented' information can generate biases in estimates of the survival and reproductive rates of individuals (Nichols *et al.* 1994; Boulinier *et al.* 1997). Recently developed capture–recapture multistate models (Arnason 1973; Schwarz, Schweigert & Arnason 1993; Nichols & Kendall 1995) provide a robust analytical method to model and estimate the reproductive cost taking into account a detection probability (Nichols *et al.* 1994; Cam *et al.* 1998).

We applied these models to estimate the cost of reproduction in the Soay sheep (*Ovis aries*) population living on the island of Hirta in the St Kilda archipelago (Scotland) to investigate factors influencing the shape of the trade-off function. Previous work on the same population (Clutton-Brock *et al.* 1996; Marrow *et al.* 1996) has shown that the optimal reproductive strategy changes in relation to the phase of population growth, but that individuals are unable to adjust their effort to the predicted optima. This inability of females to modify their strategy to environmental cues was demonstrated by the fact that the survival of breeding females was lower than that of non-breeding females in periods of high mortality, and also varied according to the weight of the individual. Clutton-Brock *et al.* (1996) considered a model that incorporated density dependence as an environmental factor but ignored climatic effects. Recent work, however, has demonstrated that climatic effects have a substantial impact on population growth rate (Milner, Elston & Albon 1999; Catchpole *et al.* 2000; Coulson *et al.* 2001).

Clutton-Brock *et al.* (1996) estimated survival conditionally on animals that were recaptured, which reduced the amount of data available such that a full investigation of the effect of the costs of breeding for the most parsimonious age-structure was not possible. In addition, Catchpole, Morgan & Coulson (2004) showed how this kind of conditional inference can give rise to biased estimates that can lead to flawed conclusions.

In this paper we extend earlier conditional analyses to investigate further age-dependent costs of reproduction. We report significant influences of density and climate on the survival–reproduction trade-off function while taking into account the probability of recapturing or re-observing live animals. Correlative studies have been considered as unlikely systems in which to identify a trade-off between reproduction and survival (van Noordwijk & De Jong 1986; Partridge 1992; Reznick 1992) because natural selection is predicted to operate such that all individuals follow an optimal strategy for their quality or resource availability. If this were the case, any trade-off could only be shown by experimentally preventing individuals from following optimal investment strategies. In some cases, however, correlative studies have successfully detected a trade-off (Clutton-Brock 1984; Viallefont *et al.* 1995; Clutton-Brock *et al.* 1996; Pyle *et al.* 1997; Cam & Monnat 2000; Tavecchia *et al.* 2001). This is presumed to be a consequence of an individual's inability to respond to a temporally variable trade-off function, making the optimum strategy reproduction regardless of the cost. As well as reporting an environmentally determined survival–reproduction trade-off from the analysis of observational data, we also present an analysis of an experiment in which a group of randomly selected female lambs from two cohorts were artificially prevented from breeding in their first year of life through progesterone implants.

Methods

RESIGHTING DATA AND MODEL PARAMETERS

Soay sheep are a rare breed thought to be similar to domestic Neolithic sheep introduced to Britain around 5000 BC (Clutton-Brock 1999) and to the island of Soay in the St Kilda archipelago, Scotland, between 0 and 1000 BC. The studied population was moved to the island of Hirta in 1932 following voluntary evacuation of the local human population in 1930, and left unmanaged since. The data analysed in this paper were collected on female Soay sheep marked and recaptured in the Village Bay area of Hirta from 1986 to 2000. We use the term 'recaptured' to refer to those sheep that were seen in summer censuses or captured in the August catch-up, when between 50% and 90% of the sheep living in the study area are caught. All sheep were initially captured as lambs within hours of birth and uniquely marked using plastic ear tags. In successive occasions, recaptured females were released in two alternative breeding states: presence or absence of milk when

caught in the summer catch-up, or whether they were with or without lamb when resighted. Data were sorted in the form of stratified (multistate) encounter-histories according to the state in which individuals were released. Arnason (1973) and Schwarz, Schweigert & Arnason (1993), developed a model to estimate the state specific parameters from this type of data considering the multistate capture-histories as the product of three probabilities: $S_x i$, the probability that an individual in state x at occasion i , is alive at occasion $i + 1$, $\psi_{xy} i$, the probability conditional on survival that an individual is in state y at occasion $i + 1$ having been in state x at occasion i , and the state-specific probability of recapture p_x (see Brownie *et al.* 1993; Nichols & Kendall 1995). In our case, x and y are N and B, respectively, for the non-breeding and breeding state. For simplicity, because only two states are considered, ψ_{xy} is noted ψ_x . In model notation we single out juvenile survival and transition parameters (age interval from 0 to 1) noted S' and Ψ' , respectively. These probabilities do not depend on the breeding state as ewes start breeding at the earliest at 1 year of age. Ψ' is equivalent to the first-year recruitment probability. Although the date of death was known for most individuals, we did not integrate recoveries in multistate histories as it would generate numerous multiple additional parameters (see Lebreton, Almeras & Pradel 1999). The date of death, however, was considered in the conditional analysis of experimental data (see below).

AGE-, TIME-DEPENDENT PARAMETERS AND EXTERNAL COVARIATES

In a previous analysis of male and female Soay sheep survival, Catchpole *et al.* (2000) reduced model parameters by forming age-classes sharing common survival, derived from age-dependent estimates of survival probabilities. Subsequently population size and measures of winter severity were used as covariates within each sex-by-age group. In the current analysis the model complexity increases after the incorporation of the

breeding state. As a consequence, the two variables, age and/or year, had to be further combined or treated as continuous to reduce the number of possible interactions. Catchpole *et al.* (2000) and Coulson *et al.* (2001) detailed the continuous relationship between survival and external covariates; namely the previous winter population size (population size, hereafter) and three weather covariates: the North Atlantic Oscillation index (NAO hereafter; Wilby, O'Hare & Barnsley 1997), and February and March rainfall. When significant, the relationship between sheep survival and the above covariates was always negative for all groups. We are interested in describing the age-specific pattern of the trade-off, so consequently we relied on these previous results to reduce the number of parameters related to time-dependent variation by categorizing the 14 yearly intervals of the study into three groups according to the severity of environmental conditions. We combined the population size and NAO (considered a single index of winter climatic conditions) into a single variable based on their product moment correlation ($r = 0.032$). Along this gradient we identified three groups based on the values of the variable (Table 1). These groups correspond roughly to favourable (negative values; $n = 4$), severe (positive values; $n = 4$) and intermediate environmental conditions ($n = 6$), respectively (Table 1). For age, we considered 10 groups, namely from 0 to 1, from 1 to 2, etc. The last group included all animals of 9 years or older. The estimate of breeding cost concerns individuals from 1 to 9 years (9 age classes). In juveniles (from 0 to 1 year), where the breeding state is not present, we considered a full time dependence in survival probability (14 levels). A full time dependence was also assumed for the recapture probability (Catchpole *et al.* 2000) in addition to a linear effect of age as suggested by previous analyses (Tavecchia 2000).

MODEL SELECTION

To identify the most parsimonious model, we progressively eliminated effects on survival, recapture and

Table 1. NAO index and population size were combined to categorize years into three groups of similar sizes corresponding to favourable ($n = 4$), intermediate ($n = 6$) and severe ($n = 4$) environmental conditions, respectively (also see text). Note that intervals are ordered according to the combined variable

Interval	Previous summer population size	NAO index	Combined variable	Environmental conditions
1995–96	1176	-3.78	-1.807	Favourable
1986–87	710	-0.75	-1.677	Favourable
1990–91	889	1.03	-0.844	Favourable
1987–88	1038	0.72	-0.688	Favourable
1989–90	694	3.96	-0.292	Intermediate
1992–93	957	2.67	-0.239	Intermediate
1999–00	1000	2.8	-0.128	Intermediate
1996–97	1825	-0.2	0.351	Intermediate
1993–94	1283	3.03	0.414	Intermediate
1997–98	1751	0.72	0.503	Intermediate
1991–92	1449	3.28	0.766	Severe
1994–95	1520	3.96	1.089	Severe
1998–99	2022	1.7	1.25	Severe
1988–89	1447	5.08	1.302	Severe

transition parameters separately keeping the structure of other parameters as general as possible (Grosbois & Tavecchia 2003). For example, if the general model assumes age-dependent parameters we kept this effect on survival and recapture when transitions were modelled. The result of independent step-down selections, on S' , S , p , Ψ' and Ψ , would be what we term a *consensual model* including the structure selected in each parameter separately. The consensual model would provide a more parsimonious environment in which to test new factors or to re-test previously non-significant factors. This procedure was repeated until no more simplification was possible. Models were fitted using the program MARK1.9 modelling all parameters on a logit scale (White & Burnham 1998). Model selection was based on the corrected Akaike's Information Criterion (AICc; Burnham & Anderson 1998), providing a compromise between model deviance and the number of parameters used (the lowest value of AICc represents the most parsimonious model). A model selection procedure following the AICc value inevitably involves an arbitrary component. For example, Lebreton *et al.* (1992) considered as equivalent two models with a difference in AICc of 2. Burnham & Anderson (1998) suggested a higher threshold of 4 to 7. In this paper we consider models within 4 AICc values to be equivalent and among equivalent models we prefer the one with fewest parameters. Finally, all structurally estimable parameters were considered, even if their estimates were close to the boundaries of the parameter space.

MODEL NOTATION

The symbols used in model notation are summarized in Table 2. Specifically 'N' and 'B' are subscripts represent

non-breeding and breeding states, respectively; others symbols are used for factors or covariates and appear in brackets: 'y' represents year as a 14-level factor and 'e' represents year as a 3-level factor categorized according to environmental conditions; for all parameters, 'a' represents age as a 9-level factor; 'A' denotes when age is used as a continuous variable ranging from 1 to 9. A '*' always specifies the statistical interaction between main effects, a '+' when effects are additive and '.' indicates when no effects are present. Population size is denoted by 'P' and the North Atlantic Oscillation index by 'NAO'. In this paper we do not try to model S_B explicitly. Instead, we shall model S_N and a measure of the difference between S_B and S_N . Thus, we specifically denote the cost of reproduction on survival as ΔS , defined as:

$$\Delta S = \text{logit}(S_N) - \text{logit}(S_B)$$

We shall adopt linear models for $\text{logit}(S_N)$ and ΔS , as functions of covariates. We can see from the above equation that $\text{logit}(S_B)$ is then also, conveniently, a linear function of the covariates.

EXPERIMENTAL DATA

In 1988 and 1990, 37 out of the 154 female lambs released were treated with a progesterone implant to suppress oestrus in the following autumn. Implants were made by mixing 1.5 g powdered progesterone (Sigma P 0130) with 2.2 g Silastic 382 Medical Grade Elastomer and 1/3 drop of vulcanizing agent catalyst M (stannous octoate: Dow Corning, USA). The mix was then extruded into a plastic mould made from a 2-mL plastic syringe and the volume adjusted to 2.5 mL. Prior to use, implants

Table 2. Parameters modelled and symbols used in model notation (also see text)

Parameter	
S_N	Annual survival probability for an individuals released in the non-breeding state
S_B	Annual survival probability for an individuals released in the breeding state
S'	Juvenile survival probability (age interval from 0 to 1 year)
p_N	The probability of recapture or resight an individual in the non-breeding state
p_B	The probability of recapture or resight an individual in the breeding state
Ψ_N	The probability conditional on survival that an individual leaves the non-breeding state
Ψ_B	The probability conditional on survival that an individual leaves the breeding state
Ψ'	Recruitment probability at age 1
ΔS	Cost of reproduction, defined as the difference in state-specific annual survival
$\Delta S'$	Cost of reproduction at 1 year old
Effect	
a	Age (9 levels)
A	Age (continuous variable)
y	Year (14 levels)
NAO	North Atlantic Oscillation index (continuous variable)
P	Population size (continuous variable)
e	Environmental conditions (3 levels). The 14 yearly intervals are grouped in 3 classes according to the combined values of the North Atlantic Oscillation index and previous winter population size
*	Main effects and their statistical interaction
+	Main effects only (additive effect)
.	No effect considered

were soaked in 10% chlorhexidine solution for 20 min then rinsed in sterile physiological saline. Implants were implanted subcutaneously in the dorsal midline following sterile procedures after administration of 3 mL 5% lignocaine to provide local anaesthesia (see also Heydon 1991 for more details on implants). To avoid estimating recapture probability when analysing these data, we restricted the analyses to 140 of the 154 animals whose fate was known because we recovered the body in the year of death; the year of death of the 14 animals removed from the analysis was unknown (4 were from the treated group). Among the 140 animals retained for the analysis, 15 had incomplete capture histories, i.e. they were not captured or seen on one or more occasions although known to be alive. We relied on the results of the multistate analysis to 'complete' these histories and thus avoided having to model recapture probability explicitly (see Results). In the presence of a cost of reproduction, treated individuals who skipped breeding at their first opportunity, at age 1, should have a higher probability of survival than non-treated individuals that bred at their first opportunity. Moreover, if breeding decision is condition dependent, non-breeding individuals in the untreated group would be in poorer condition than average. Current reproduction and the number of previous reproductive events may have long-term or cumulative costs. In this scenario treated individuals should exhibit higher survival rates even after they have started to reproduce.

Results

CORRELATIVE DATA 10

We analysed a total of 2036 observations on 988 different females. Model selection started from the general model given below (Model 1 hereafter):

$$\text{Model 1 } S'(y)S_N(a * e)\Delta S(a * e)/\Psi'(y)\Psi_N(a * e) \\ \Psi_B(a * e)/p_N(A + y)/p_B(A + y)$$

Model 1 must be viewed as the most general model, i.e. the one with the largest number of parameters. The absence of a breeding state in juveniles' parameters, S' and Ψ' , allowed us to assume a full year effect, noted 'y' (14 levels), and test the influence of external covariates. The same was not possible for other parameters, which would depend on environmental conditions (3 levels), full age, denoted by 'a' (9 levels) and state (2 levels, denoted N and B in subscripts). Ideally we should provide a goodness-of-fit test of Model 1. Recently Pradel, Wintrebert & Gimenez (2003) proposed a method to test the fit of the Arnason-Schwarz model (Schwarz *et al.* 1993) in which all parameters are assumed to be time dependent. This requires the fit of a more general model in which recaptures depend not only on recapture occasions on the state of arrival, but on the state of departure as well (see Brownie *et al.* 1993; Pradel *et al.* 2003). In our case such a model would have to be fitted

in each cohort separately to account for the age-by-time interaction. In many cohorts, this resulted in numerical problems owing to data sparseness and consequently we were not able to correct for extra-multinomial variation, should any exist. We began to simplify Model 1 by eliminating non-significant effects from each parameter at a time. We confirmed previous findings (Catchpole *et al.* 2000) that survival probability changed according to age and environmental conditions (Table 3). In addition, we obtained the first representation of the full age-dependent pattern of the trade-off function (Fig. 1a,b). Although breeding state and environmental conditions significantly influenced survival, the evidence for variation of the breeding cost was weak at this stage (Table 3; Fig. 2). Juveniles' parameters varied significantly between years ($\Delta AICc = +262.85$ and $+63.75$, respectively). In both cases, survival and first-year transitions, the NAO and the population size, explained a significant part of the deviance (96% and 72%, respectively), but when a simpler (more constrained) environment was reached their influence was retained only for survival (see below). In contrast with previous single-site analyses, the recapture probability was not influenced by age for either state. A year effect was retained for non-breeders only ($\Delta AICc = 346.77 - 367.61 = -20.84$, Table 3). Transition probabilities after year 1 were not affected by environmental conditions. An effect of age, however, was retained for the probability of breeding after a non-breeding event.

At the end of this first simplification we retained four consensual models (Table 3) that differ by the presence of covariates in the probability of recruiting at 1 year old (Models 2 vs. 4, hereafter) and of age on the breeding cost (Models 3 vs. 5):

$$\text{Model 2 } S'(NAO * P)S_N(a * e)\Delta S(a)/ \\ \Psi'(NAO * P)\Psi_N(a)\Psi_B(\cdot)/p_N(y)p_B(\cdot)$$

$$\text{Model 3 } S'(NAO * P)S_N(a * e)\Delta S(a)/ \\ \Psi'(y)\Psi_N(a)\Psi_B(\cdot)/p_N(y)p_B(\cdot)$$

$$\text{Model 4 } S'(NAO * P)S_N(a * e)\Delta S(\cdot)/ \\ \Psi'(NAO * P)\Psi_N(a)\Psi_B(\cdot)/p_N(y)p_B(\cdot)$$

and

$$\text{Model 5 } S'(NAO * P)S_N(a * e)\Delta S(\cdot)/\Psi'(y)\Psi_N(a)\Psi_B(\cdot)/ \\ p_N(y)p_B(\cdot)$$

As expected, these consensual models including only the significant effects retained for each parameter led to a substantial decrease in the AICc value (up to 109.22 points from model 1). Model 3 had the lowest AICc but model 5 should be preferred for its similar AICc value and its lower number of parameters (Table 3). According to this model the probability of recapture of non-breeding ewes increased roughly throughout the study, ranging from 0.45 in 1987 to 1.00 in 2000. Breeding ewes were virtually always captured ($p_B = 0.999$, 95%

Table 3. Towards a first consensual model. When one parameter is modelled, the structure of the others is kept general (see text). The general model (Model 1) is $S'(y)S_N(a * e)\Delta_S(a * e)/\Psi'(y)\Psi_N(a * e)\Psi_B(a * e)/p_N(A + y)p_B(A + y)$. DEV = model deviance, np = number of structural parameters in the model, AICc = corrected Akaike's Information Criterion. $\Delta AICc$ = difference in AICc value from the general model. The consensual models are built by considering the structure retained for each parameter (marked in bold in each case). The model number is in square brackets, i.e. the general model is [1], also see text

Model [model number]			np	DEV	AICc-5000	$\Delta AICc$
<i>Juvenile survival</i>						
[1]	$S'(y)$		165	5016.88	367.61	0
	$S'(NAO * P)$		155	5028.34	356.58	-11.03
	$S'(NAO + P)$		154	5050.22	376.22	+8.61
	$S'(\cdot)$		153	5304.47	630.46	+262.85
<i>Reproductive cost</i>						
[1]	$S_N(a * e)$	$\Delta S(a * e)$	165	5016.88	367.61	0
	$S_N(a * e)$	$\Delta S(a)$	147	5032.73	343.09	-24.52
	$S_N(a * e)$	$\Delta S(\cdot)$	139	5052.66	345.25	-22.36
	$S_N(a * e)$	$\Delta S(e)$	141	5058.39	355.41	-12.20
	$S_N(a * e)$	-	150	5058.18	348.55	-19.06
	$S_N(a)$	$\Delta S(a)$	130	5242.69	515.41	+147.80
<i>Recapture</i>						
[1]	$p_N(A + y)$	$p_B(A + y)$	165	5016.88	367.61	0
	$p_N(y)$	$p_B(A + y)$	164	5019.50	367.98	+0.37
	$p_N(A + y)$	$p_B(\cdot)$	151	5029.04	348.32	-19.29
	$p_N(y)$	$p_B(\cdot)$	150	5029.72	346.77	-20.84
	$p_N(A)$	$p_B(\cdot)$	137	5069.88	358.04	-9.57
	$p_N(\cdot)$	$p_B(\cdot)$	136	5078.53	364.48	-3.13
<i>First-year recruitment</i>						
[1]	$\Psi'(y)$		165	5016.88	367.60	0
	$\Psi'(NAO * P)$		155	5043.05	371.29	+3.68
	$\Psi'(NAO + P)$		154	5043.07	369.06	+1.45
	$\Psi'(P)$		153	5050.83	374.59	+6.98
	$\Psi'(N)$		153	5105.31	429.07	+61.46
	$\Psi'(\cdot)$		152	5109.85	431.36	+63.75
<i>Transitions</i>						
[1]	$\Psi_N(a * e)$	$\Psi_B(a * e)$	165	5016.88	367.61	0
	$\Psi_N(e)$	$\Psi_B(a * e)$	141	5069.85	366.87	-0.74
	$\Psi_N(a)$	$\Psi_B(a * e)$	147	5042.51	352.86	-14.75
	$\Psi_N(\cdot)$	$\Psi_B(a * e)$	139	5070.06	362.65	-4.96
	$\Psi_N(a * e)$	$\Psi_B(e)$	141	5037.85	334.87	-32.74
	$\Psi_N(a * e)$	$\Psi_B(a)$	147	5036.89	347.25	-20.36
	$\Psi_N(a * e)$	$\Psi_B(\cdot)$	139	5045.33	337.91	-29.70
	$\Psi_N(a)$	$\Psi_B(e)$	123	5056.55	313.92	-53.69
	$\Psi_N(a)$	$\Psi_B(\cdot)$	121	5060.63	313.62	-53.99
<i>Consensual models</i>						
[2]	$S'(NAO * P)S_N(a * e)\Delta S(a)/p_N(y)p_B(\cdot) / \Psi'(NAO * P)\Psi_N(a)\Psi_B(\cdot)$		68	5124.76	264.19	-103.42
[3]	$S'(NAO * P)S_N(a * e)\Delta S(a) / p_N(y)p_B(\cdot) / \Psi'(y)\Psi_N(a)\Psi_B(\cdot)$		79	5095.76	258.39	-109.22
[4]	$S'(NAO * P)S_N(a * e)\Delta S(\cdot) / p_N(y)p_B(\cdot) / \Psi'(NAO * P)\Psi_N(a)\Psi_B(\cdot)$		60	5143.79	266.45	-101.16
[5]	$S'(NAO * P)S_N(a * e)\Delta S(\cdot) / p_N(y)p_B(\cdot) / \Psi'(y)\Psi_N(a)\Psi_B(\cdot)$		71	5115.21	260.95	-106.66

confidence limits by profile likelihood: 1.000–0.993 from model 5); this probability is therefore fixed at 1.00 in subsequent models and hereafter for simplicity omitted from model notation. Model 5 was taken as a new starting point in the model selection procedure. This model assumes the survival probability of individuals of age j in year i to be:

$$\text{Logit}(S_{Bj}) = \text{logit}(S_{Nj}) + \gamma$$

where γ is the additive effect of breeding, or 'the breeding cost' (ΔS). This additive effect could be further modelled as a quadratic function of age as:

$$\text{Logit}(S_{Bj}) = \text{logit}(S_{Nj}) + (\beta_0 + \beta_1 * A + \beta_2 * A^2)$$

where β_0 , β_1 and β_2 are the linear predictors of γ , and A is the linear age (with $1 < A < 9$). This model (Model 6, hereafter) had a lower AICc value (a decrease of 9.7 points from the consensual model; Table 4). This shows that reproduction has a negative effect on survival early and late in life even when the influence of environmental conditions is accounted for. We investigated whether the cost was interacting with environmental conditions by building a model assuming three independent parabolas describing the difference in survival between breeders and non-breeders during severe, intermediate and favourable years, respectively (Model 7, hereafter), denoted:

Model 7 $S'(NAO * P)S_N(a * e)\Delta S((A + A^2) * e) / \Psi'(y)\Psi_N(a)\Psi_B(\cdot) / p_N(y)$

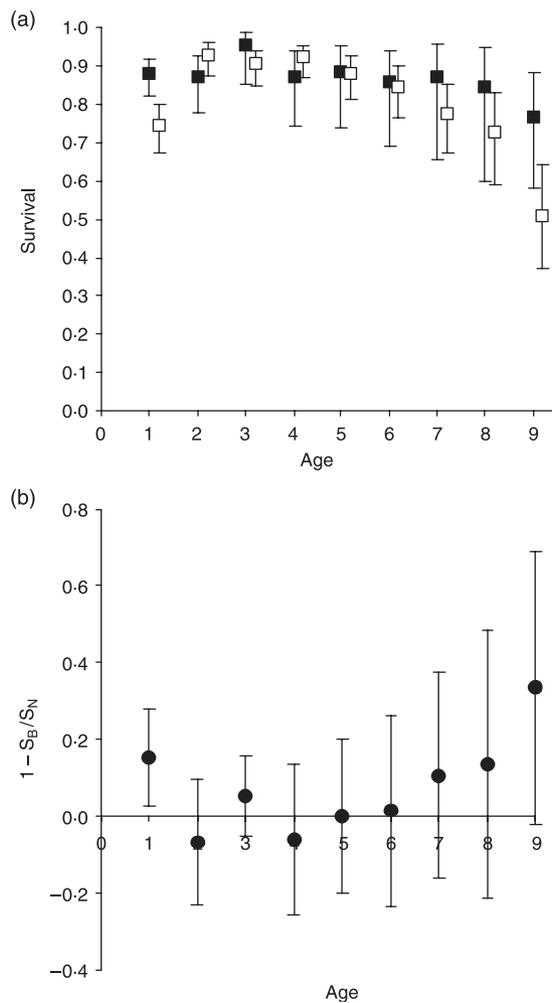


Fig. 1. (a) Age-dependent survival estimates for non-breeding and breeding ewes (■ and □, respectively) from the model $S'(y)S_N(a)\Delta_S(a)/\Psi'(y)\Psi_N(a * e)\Psi_B(a * e)/p_N(y + A)p_B(y + A)$. (b) The cost of reproduction expressed as $1 - S_B/S_N$. In both figures, bars indicate the 95% confidence interval (by δ -method in b).

Model 7 had a lower AICc than the first consensual model retained ($\Delta AICc = -8.9$), but some coefficients had unrealistic values as survival was very close to 1.00 in both states except during severe conditions (Fig. 2).

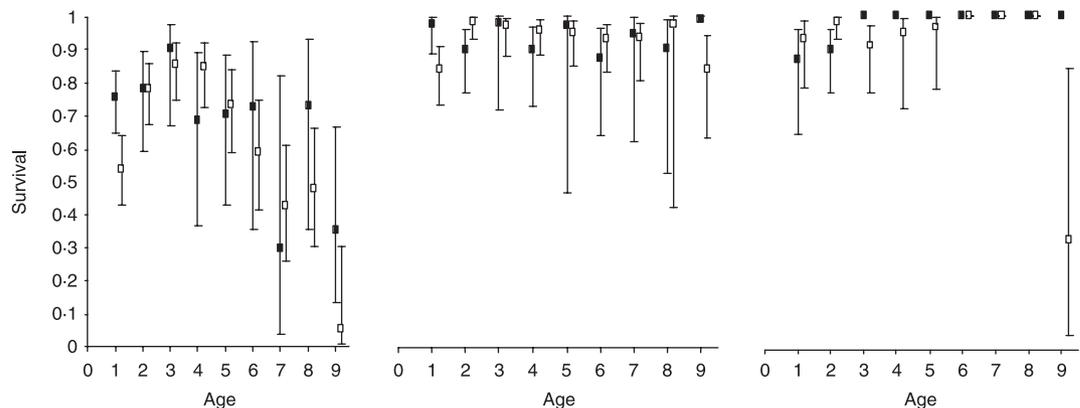


Fig. 2. Survival probability for non-breeders (■) and breeders (□) according to environmental conditions from the general model (Model 1). Bars indicate 95% confidence interval (when estimates are 1.00 confidence intervals are not plotted).

Model 6 and 7 had similar AICc values. The two models are describing the data equally well, but for reason of parsimony, the one assuming an additive effect is preferred as it has fewer parameters.

At this point we investigated the yearly variation in reproductive cost for first-year mothers only, for which the cost appeared to be greatest (Fig. 1b). As with the juvenile parameters, this restriction allowed us to consider a full year effect and directly test the influence of covariates. The model with a full year effect on 1-year-old breeders (noted Δ'_s) is noted (Model 8, hereafter):

$$\text{Model 8 } S'(NAO * P)S_N(a * e)/\Delta'_s(y)\Delta'_s(a)/p_N(y)/\Psi'(y)/\Psi_N(a)/\Psi_B(-)$$

The low AICc value of this model (Table 4) gave a clear indication of a change in the trade-off value with year (Fig. 3). Such a year variation could be decomposed into its components, namely the variation due to a density-dependent factor (noted P), winter severity (NAO) and their interaction ($P * NAO$). These covariates explained 43.3% of the yearly variation (19.3% when the interaction between the two covariates was not considered; Table 4). This set of models was built *ad hoc* to test the variation in reproductive cost in one particular age class. They are not based on a priori assumptions and will not be considered further in the analysis. We finally reduced the number of parameters of Model 7 by assuming survival to be independent of age in non-breeding animals. Such an assumption held in intermediate and favourable conditions, but did not in severe conditions where the effect of age proved to be significant regardless of the breeding state (Table 4).

The final model (Model 9; Tables 4 and 5), was therefore

$$\text{Model 9 } S'(NAO * P)S_N(a * e)\Delta_S(A + A^2)/\Psi'(y)\Psi_N(A)\Psi_B(\cdot)/p_N(y)$$

According to model 9, the probability of breeding after a non-breeding event is constant through time but decreases linearly with the age of the ewe. It is interesting to note that at a population level, old ewes appear

Table 4. Towards a final model. The consensual model of Table 3 can be simplified and/or specific effects re-tested in a more parsimonious environment. Moreover the reproductive trade-off function could be further modelled using a specific function of age. $\Delta AICc$ = difference in AICc values from the retained consensual model (Model 5; Table 3). We were not able to further simplify recapture probabilities. The model number is in square brackets

Model					Np	DEV	AICc-5000	DAICc
<i>Survival and Reproductive cost</i>								
[6]	$S_N(a * e)$	$DS(a * e)$	$Y'(y)$	$Y_N(a)$	96	5078.36	277.23	16.37
	$S_N(a * e)$	$DS(A+A^2)$	$Y'(y)$	$Y_N(a)$	73	5101.17	251.12	-9.74
[7]	$S_N(a * e)$	$DS((A + A^2) * e)$	$Y'(y)$	$Y_N(a)$	79	5089.32	251.96	-8.91
	$S_N(a * e)$	$DS(A + A^2)^1$	$Y'(y)$	$Y_N(a)$	73	5106.55	256.50	-4.36
	$S_N(a * e)^2$	$DS(\cdot)$	$Y'(y)$	$Y_N(a)$	63	5130.65	259.59	-1.28
	$S_N(a * e)^3$	$DS(\cdot)$	$Y'(y)$	$Y_N(a)$	63	5125.61	254.55	-6.32
	$S_N(a * e)^4$	$DS(\cdot)$	$Y'(y)$	$Y_N(a)$	63	5147.64	276.58	15.72
	$S_N(a * e)$	-	$Y'(y)$	$Y_N(a)$	70	5121.50	265.12	4.26
	$S_N(a * e)$	$DS(e)$	$Y'(y)$	$Y_N(a)$	73	5112.34	262.29	1.43
[8]	$S_N(a * e)$	$DS'(y)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	83	5071.30	242.42	-18.44
	$S_N(a * e)$	$DS'(NAO * P)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	74	5092.24	244.30	-16.56
	$S_N(a * e)$	$DS'(NAO + P)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	73	5101.09	251.04	-9.82
	$S_N(a * e)$	$DS'(NAO)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	72	5106.32	254.17	-6.70
	$S_N(a * e)$	$DS'(P)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	72	5106.50	254.35	-6.51
	$S_N(a * e)$	$DS'(\cdot)DS(\cdot)$	$Y'(y)$	$Y_N(a)$	71	5108.21	253.94	-6.92
<i>Transitions</i>								
	$S_N(a * e)$	$DS(\cdot)$	$Y'(y)$	$Y_N(A)$	64	5122.50	253.53	-7.33
	$S_N(a * e)$	$DS(\cdot)$	$Y'(y)$	$Y_N(\cdot)$	63	5137.57	266.51	5.65
<i>Final model</i>								
[9]	$S_N(a * e)^5$	$DS(A + A^2)$	$Y'(y)$	$Y_N(A)$	50	5128.37	230.22	-30.65

¹Breeding cost is a function of age during severe conditions only.
²Non-breeders' survival is constant during favourable conditions.
³Non-breeders' survival is constant during intermediate conditions.
⁴Non-breeders' survival is constant during severe conditions.
⁵Non-breeders' survival is constant during intermediate and favourable conditions.

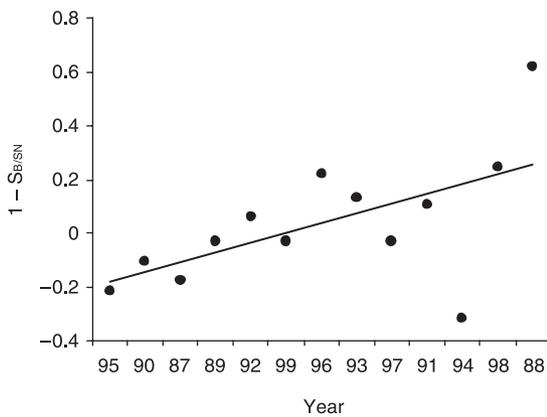


Fig. 3. Yearly variation in the reproductive cost, expressed as $1 - S_B/S_N$, of first year old ewes from Model 6. Years are ordered from left to right according to increasing values of the variable combining NAO and population size. High values correspond to severe ecological conditions. The solid line represents the trend. This relationship remains positive even when 1994 and/or 1988 are eliminated. Note that the maximum value of the y-axis is 0.8.

less likely to breed after skipping reproduction the previous year. The frequency of skipping reproduction after a breeding event is generally low (0.15), and is not influenced by environmental conditions or the age of the ewe (Tables 4 and 5). We obtained further insight on reproductive investment through the analysis of the experimental data.

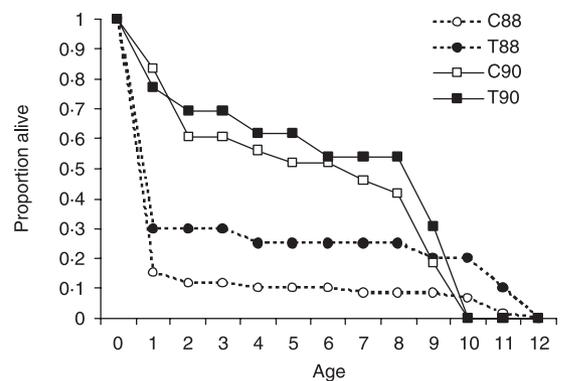


Fig. 4. Proportion of ewes alive according to age, cohort (dashed lines = 1988; solid lines = 1990) and treatment (solid symbols = treated; open symbols = untreated).

EXPERIMENTAL DATA

In the two cohorts 1988 and 1990, the proportion of ewes that survived is markedly different (Fig. 4) as a result of the interaction between age and environmental conditions on survival probability. Although results should be treated with caution because of the small sample sizes, the survival of 1-year-old ewes is lower in the untreated animals than in the treated ones. In agreement with the correlative analysis, mortality is strongly associated with breeding (Table 5). However, the survival

Table 5. Survival and breeding proportions of treated and untreated females from the 1988 and 1990 cohorts. Values for individuals that survived until age 5 and = 9 are reported as well. – denotes non-estimable

Cohort	1988		1990	
	Treated (<i>n</i> = 20)	Untreated (<i>n</i> = 59)	Treated (<i>n</i> = 13)	Untreated (<i>n</i> = 48)
<i>Age 1</i>				
Breeding proportion	–	0.20	–	0.69
Breeding cost	–	0.43	–	0.27
Mortality of non breeders	0.00	0.13	0.10	0.15
Mortality of breeders	–	0.50	–	0.38
<i>Age 5</i>				
Breeding proportion	0.40	1.00	0.80	0.75
Breeding cost	0.00	0.00	0.00	0.00
Mortality of non breeders	0.00	0.00	0.00	0.00
Mortality of breeders	0.00	0.00	0.00	0.00
<i>Age = 9</i>				
Breeding proportion	0.40	0.80	0.50	0.56
Breeding cost	0.50	0.25	0.00	0.00
Mortality of non breeders	0.00	0.00	0.00	0.00
Mortality of breeders	0.50	0.25	0.00	0.00

of treated animals is also higher than survival of non-breeding untreated animals in both cohorts. This is what we expected if breeding decisions depended on individual quality or condition. In adults, for example aged 5 years, a breeding cost was virtually absent regardless of the treatment group or the cohort. The proportion of breeding ewes in this age class was high (Table 5) suggesting that most animals were of good quality or in good body condition. Our previous results (see above and Fig. 2) suggest that breeding is costly for old animals as well as for 1-year-old ewes. This is supported experimentally only for ewes born in 1988.

Discussion

Previous evidence of a survival cost of reproduction in female Soay sheep came from the conditional analyses in Clutton-Brock *et al.* (1996) and Marrow *et al.* (1996). By directly modelling the variation in the trade-off function in a capture–recapture framework we have extended their results showing: (i) that the cost of reproduction varies as a quadratic function of the age of the mother, (ii) that it changes with both density-dependent and density-independent factors and their interaction, (iii) that these have no effect on the probability of changing reproductive state, (iv) that reproduction is condition-dependent, and (v) that an early cost of reproduction might have a key role in the selection of high quality phenotypes within cohorts. Our results should be considered in comparison to work on wild bighorn sheep living in Alberta, Canada, where costs of reproduction have been shown to be age- and mass-dependent and associated with density (Festa-Bianchet *et al.* 1998), as well as previous reproductive history (Bérubé *et al.* 1996). This is the only other detailed study of wild sheep we are aware of that permits estimates of factors influencing the costs of reproduction. Our results

show considerable similarity with the bighorn sheep work, suggesting that the costs of reproduction may typically be age-dependent and associated with environmental variation in large mammals. There is also a literature detailing the costs of reproduction in domestic sheep (e.g. Myrsterud *et al.* 2002) but given the obvious differences between the ecology of domestic and wild sheep we do not discuss this in any further detail.

ENVIRONMENTAL CONDITIONS AND THE COST OF REPRODUCTION

Correlative studies are not expected to identify a trade-off between reproduction and survival (van Noordwijk & De Jong 1986; Partridge 1992; Reznick 1992) because natural selection is predicted to operate such that all individuals follow an optimal strategy based on their quality or on resource availability (van Noordwijk, van Balen & Scha rloo 1981). When a trade-off is fluctuating in response to unpredictable environmental variation, however, the optimum strategy could be to reproduce regardless of the cost (Benton *et al.* 1995) and correlative studies could prove useful (Clutton-Brock 1984; Viallefont *et al.* 1995; Clutton-Brock *et al.* 1996; Pyle *et al.* 1997; Cam & Monnat 2000; Tavecchia *et al.* 2000). In our case, density and climate predicted reproductive cost: these covariates explained one third of the variation in reproductive cost in 1-year-old ewes, mainly through their interaction. Given such uncertainty, the payoff of a constant level of investment is probably greater than the payoff obtained by not breeding (Marrow *et al.* 1996). A fluctuating trade-off has also been found in Soay sheep rams (Stevenson & Bancroft 1995; Jewell 1997) that exhibit a cost of reproduction associated with male-male conflicts during the rut. Stevenson & Bancroft (1995) experimentally proved that early reproduction carries a survival cost in young male when population density is

high. Despite this, precocial mating is favoured owing to the high success achieved in particular years of the population cycle (Stevenson & Bancroft 1995). The low frequency of severe conditions prevents a high payoff for those individuals that skip reproduction early in life.

AGE AND COST OF REPRODUCTION

The reproductive cost varied as a quadratic function of age, being higher in young and old age classes but absent between 3 and 7 years (Fig. 1b). This pattern is common to other large herbivores: Myserud *et al.* (2002) concluded that the early onset of reproductive senescence in domestic sheep may be because of a trade-off between breeding events and litter size. An age-dependent cost of reproduction could also be a characteristic of other long-lived animals. For example, a greater cost of reproduction at a young age has been found in red deer (*Cervus elaphus*) (Clutton-Brock 1984), Californian gulls (*Larus californianus*) (Pyle *et al.* 1997), lesser snow geese (*Anas caerulescens caerulescens*) (Viallefont *et al.* 1995) and greater flamingos (*Phenicopterus ruber roseus*) (Tavecchia *et al.* 2001; but see McElligot, Altwegg & Hayden. 2002).

The association between age and the cost of reproduction could be because of natural selection progressively removes low-quality phenotypes. Results from experimental data suggest that breeding-induced mortality might act as a filter selecting against low-quality phenotypes. On average, juveniles prevented from breeding in a severe year (cohort 1988) are also less likely to breed later in life than untreated juveniles; however, this was not the case for juveniles born in 1990. One possible explanation is that low-quality individuals in the treated group were not selected against early in life. Alternatively, the effect of implants persisted beyond the first year for the 1988 cohort, but not for the 1990 cohort. Our data set is too small to distinguish between these two hypotheses. Further support for the selection hypothesis, however, comes from the survival analysis conditional on animals known to be dead, of the 1986–92 cohorts (Fig. 5) in which adult mortality is depressed

in cohorts that experienced severe conditions early in life. The selection hypothesis, however, does not explain why the cost of reproduction re-appears in old age classes. This result provides either evidence for senescence in breeding performance or of a greater investment in reproduction by those animals with lower reproductive values. The senescence-hypothesis is supported by the fact that the probability of breeding after a non-breeding event is low in older animals. A similar result was found in male fallow deer (*Dama dama*) for which reproduction probability declines with age despite an apparent absence of cost of reproduction (McElligot *et al.* 2002).

THE CAPTURE–RECAPTURE FRAMEWORK

Long-term individual-based information is often incomplete because animals might breed or die undetected and unbiased estimates can only be obtained by fitting models that include a recapture probability (Burnham *et al.* 1987; Lebreton *et al.* 1992). The number of parameters generated by these models dramatically increases with the number of states, providing limited power to test specific hypotheses with most ecological data sets (Tavecchia *et al.* 2001; Grosbois & Tavecchia 2003). Moreover, in models with large numbers of parameters, the likelihood function can encounter convergence problems, especially when estimates are near the 0–1 boundaries (see Results). These complications have probably contributed to the relative unpopularity of multistate models (Clobert 1995). In some cases researchers prefer to assume a recapture probability of 1.00 and risk biasing estimates. The magnitude of biases in parameter estimates depends on the study system (Boulinier *et al.* 1997). For example, the recapture probability of female Soay sheep was high but the assumption of a recapture probability equal to, or very close to, 1.00 only held for breeding females. In this case, avoiding a capture–recapture framework would have led to an overestimate of the breeding proportion and an underestimate of state specific survival probabilities. Recapture probabilities should be interpreted in both a biological

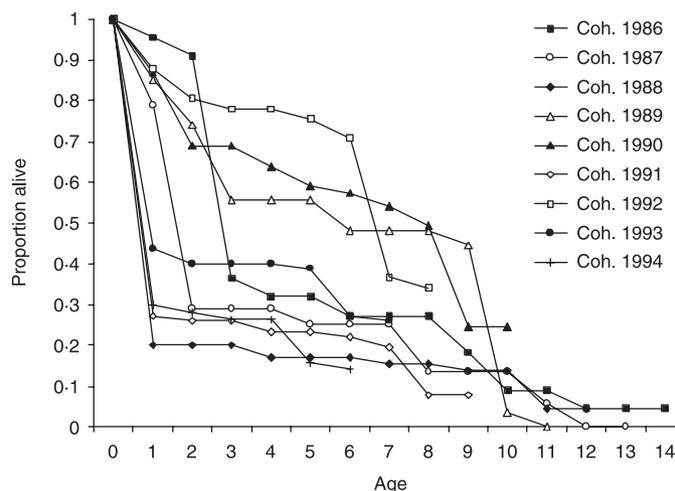


Fig. 5. Proportion of female sheep alive according to age and cohort.

Table 6. Predictors of survival, recapture, cost of reproduction and recruitment at 1 year in female Soay sheep. Estimates of linear regression parameters are from the retained model. Notation as in Table 1 except ‘^’ which denotes first order interaction between main effects in the regression

Parameter	Predictors	Effect
Juvenile survival Adult survival	Population size and NAO Environmental conditions	Logit(S') = 0.56 – 0.31(P) – 1.44(NAO) – 0.71(NAO^P) Lower during severe environmental conditions During severe conditions only (9 levels)
Cost of reproduction	Age Environmental conditions Mother age	Higher during severe conditions only Logit(S _B) = logit(S _N) – 1.56 + 0.85(A) – 0.09(A ²)
Recruitment probability at 1-year old	Time	Yearly variation mainly explained by the NAO and the P as: Logit(Y') = –0.47 – 0.24(P) – 1.30(NAO) – 0.07(NAO^P) but not retained as the only predictors Logit(Y _N) = 0.38 – 0.14(A)
Probability of breeding after a non-breeding event	Age	
Probability of non-breeding after a breeding event	–	Y _B = 0.15
Probability of recapture	Time Breeding state	In non-breeders only p _B = 1.00

and statistical setting. For example when observations are made during the reproductive period, the age-specific probabilities of recapture could provide insights on the recruitment probability (Clobert *et al.* 1994) and the pattern of reproductive skipping (Pugesek & Diem 1990; Pugesek *et al.* 1995; Viallefont *et al.* 1995). In our case, an important result was that breeding females were virtually always captured or resighted. As a consequence, when analysing the experimental data, we were able to make the assumption that all individuals known to be alive that escaped recapture were in a non-breeding state.

The analyses we report here suffer from two obvious limitations. First, although body condition is known to play an important role in breeding decisions (Marrow *et al.* 1996; Andersen *et al.* 2000), continuous time-varying covariates like weight cannot be used as predictors in a capture–recapture framework (Nichols & Kendall 1995). Moreover, individual-level processes, like experience, can also be important but cannot currently be modelled in a multistate mark–recapture framework (see Cam & Monnat 2000). A second limitation of our approach is that recoveries – information on animals found dead – cannot be included in analyses. This at first seems an important weakness of a method with the ultimate aim of estimating mortality. However, when capture probability is high, as in our case, the estimates provided by analysing recaptures alone can be expected to produce precise estimates; adding recovery information will not appreciably alter conclusions. Despite these limitations, the advantage is that recruitment, probability of reproductive skipping, state-specific survival and recapture probabilities have been modelled and estimated simultaneously (Table 6).

Conclusions

For any given trait, optimality theory predicts that evolution should select for the value that maximizes

fitness. Spatial and temporal variability in selection pressures can generate variation in the optimum trait value and lead to multiple life-history tactics within a single population or among populations (Daan & Tinbergen 1997; but see Cooch & Ricklefs 1994). Recent work has shown that a change in the trade-off function is more effective in promoting life-history diversity between and within populations than a change in the value of a single trait (Orzack & Tuljapurkar 2001; Roff *et al.* 2002) and that more attention should be focused on variation around the trade-off function. Multistate models offer the ideal framework to address these questions in natural populations. Our analysis showed that breeding is costly and that this cost changes with age and environmental conditions. A trade-off between survival and reproduction is generally expected if individuals behave in a maladaptive way. Alternatively, Clutton-Brock *et al.* (1996) concluded that the optimal strategy is to breed regardless of the cost, given that animals are not able to predict variation in mortality (see also Marrow *et al.* 1996). Our results confirmed the latter hypothesis, but demonstrated that both density-dependent and independent factors need to be considered when modelling reproductive tactics. Further work on the Soay sheep should focus on the analysis of mortality during different stages of the breeding cycle using post mortem information. It should, however, be noted that the current results reflect the ‘average’ value of the age-specific reproductive tactics. This does not necessarily mean that all individuals exhibit an ‘average’ strategy. Further work should focus on parental investment conditional to breeding decisions and on the relative cost of the different stages of the breeding cycle.

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