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State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling

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SUMMARY

Adaptive decisions concerning the scheduling of reproduction in an animal's lifetime, including age at maturity and clutch or litter size, should depend on an animal's body condition or state. In this state-dependent case, we are concerned with the optimization of sequences of actions and so dynamic optimization techniques are appropriate. Here we show how stochastic dynamic programming can be used to study the reproductive strategies and population dynamics of natural populations, assuming optimal decisions. As examples we describe models based upon field data from an island population of Soay sheep on St. Kilda. This population shows persistent instability, with cycles culminating in high mortality every three or four years. We explore different assumptions about the extent to which Soay ewes use information about the population cycle in making adaptive decisions. We compare the observed distributions of strategies and population dynamics with model predictions; the results indicate that Soay ewes make optimal reproductive decisions given that they have no information about the population cycle. This study represents the first use of a dynamic optimization life history model of realistic complexity in the study of a field population. The techniques we use are potentially applicable to many other populations, and we discuss their extension to other species and other life history questions.

1. INTRODUCTION

Theories concerning the timing of reproduction in iteroparous species have focused upon optima (Lessells 1991; Roff 1992; Stearns 1992), both in the context of the evolution of age at maturity (Gadgill & Bossert 1970; Harvey & Zammuto 1985; Stearns & Koella 1986; Charnov 1991; Kawecki & Stearns 1993; Rowe & Ludwig 1991) and of clutch or litter size (for example, Lack 1947, 1948; Mountford 1968; Charnov & Krebs 1973; Boyce & Perrins 1987; Linden & Møller 1989; Price & Liou 1989; Dhondt *et al.* 1990; Tinbergen & Daan 1990; Godfray *et al.* 1991; Liou *et al.* 1993; Rowe *et al.* 1994). However, animals change through their lifetimes and individuals vary from one another: thus optima may be expected to vary. Changing optima can be taken into account by using a state-dependent approach. State is often taken to be only the age or body size of an animal, but other components of phenotype may also be important. Evidence of maternal condition influencing clutch size and offspring quality (Guinness *et al.* 1978; Clutton-Brock *et al.* 1982; Price *et al.* 1988; Price & Liou 1989) suggests that reproductive decisions should be explained in terms of condition- or state-dependent models (Rowe & Ludwig 1991; McNamara & Houston 1992). This approach makes it clear that the choice of reproductive action an animal makes will influence the animal's future state, and thus its future actions. In this case, finding the optimal action for the current state by a process of static, or simple, optimization (Parker & Maynard Smith 1990), is inappropriate as actions cannot be considered in isolation. What is required is dynamic optimization of a sequence of actions.

McNamara & Houston (1992) introduced a dynamic approach to optimal clutch size, using stochastic dynamic programming. This was based upon the results of McNamara (1991) who showed that dynamic programming, already established in the analysis of behavioural decisions (see for example, Houston *et al.* 1988; Mangel & Clark 1988), could be used to find an optimal life history. A life history strategy specifies the reproductive decision that should be taken in each of the possible states. An optimal strategy maximizes the expected number of descendants left far into the future. McNamara (1991) assumed female demographic dominance (for example, Charlesworth 1994) and thus only considered female animals.

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To model annual reproductive decisions, we need to define four quantities. Consider an animal in state $\mathbf{x}$ which performs an action q. Then

$\alpha(\mathbf{x}, q)$ is the probability that the animal survives to the next year.

$A(\mathbf{x}, \mathbf{y}, q)$ is the probability that the animal is in state $\mathbf{y}$ next year conditional on it surviving from state $\mathbf{x}$ this year.

$\beta(\mathbf{x}, q)$ is the probability that each offspring produced survives to the next year.

$B(\mathbf{x}, \mathbf{y}, q)$ is the probability that an offspring is in state $\mathbf{y}$ next year, given that it does survive.

Thus if an animal is in state $\mathbf{x}$ and performs action q, then the expected number of descendants of this animal which are in state $\mathbf{y}$ in one years time is given by:

$$D(\mathbf{x}, \mathbf{y}, q) = \alpha(\mathbf{x}, q)A(\mathbf{x}, \mathbf{y}, q) + n(\mathbf{x}, q)\beta(\mathbf{x}, q)B(\mathbf{x}, \mathbf{y}, q), \quad (1)$$

where $n(\mathbf{x}, q)$ is the number of (female) offspring produced by an adult in state $\mathbf{x}$ performing action q. If T is a target year far into the future, then we can define $f(\mathbf{x}, t, T)$ as the maximum expected number of descendants left in this target year by an individual which is in state $\mathbf{x}$ at time t, where t is less than T. Then for each possible state $\mathbf{x}$ the following holds:

$$f(\mathbf{x}, t, T) = \max_{q} \sum_{\mathbf{y}} D(\mathbf{x}, \mathbf{y}, q) f(\mathbf{y}, t+1, T), \quad (2)$$

where the maximization is taken over all actions available in that state. The strategy given by this equation depends on both the animal's state and the time remaining until T, but as this time to go increases behaviour in a given state will tend to a limiting value. The strategy of adopting this limiting value in each state maximizes fitness and is hence the optimal life history strategy (McNamara 1991; McNamara & Houston 1992).

McNamara & Houston (1992) applied their approach to a generalized avian clutch size problem. In this paper, we use the approach to develop a model that can be compared with empirical data. Recent long-term studies of large mammal populations (Clutton-Brock *et al.* 1982, 1996*a*) provide detailed information on the life histories of individual animals in relation to phenotype, enabling empirical tests of state-dependent life history models to be made. In large mammals, which invest proportionally more resources in each offspring than do smaller species (Owens-Smith 1988; Reiss 1989), the most important question is not how many young to produce but whether or not to produce young at all. We use data on the Soay sheep (*Ovis aries* L.) population of Hirta, St Kilda, which has been intensively studied since 1959 (Jewell *et al.* 1974; Clutton-Brock *et al.* 1991).

Though relatively large animals, Soay sheep exhibit population instability that results in crashes every three to four years, a phenomenon more often associated with smaller species (Grubb 1974; Clutton-Brock *et al.* 1991, 1992, 1996*a*; Grenfell *et al.* 1992). The unstable dynamics are thought to arise from high fecundity and lack of density-dependent vegetation limitation (Clutton-Brock *et al.* 1991), leading to a population density which cannot be supported by the vegetation available in the winter. Because Soay sheep are a primitive breed of domestic sheep (Clutton-Brock 1987), and show higher fecundity than some wild sheep, and an early age of first reproduction, one explanation of the unusually high mortality is that they are not well adapted to the environment they inhabit.

Elsewhere (Clutton-Brock *et al.* 1996*b*), we examine the costs and benefits of reproduction to Soay ewes using generalized linear models to predict mortality costs. These regression relations provide parameters for a dynamic optimization model which predicts the optimal reproductive strategy of Soay ewes. By comparing the predicted optimal strategy with the observed strategies, it is possible to estimate whether the life history decisions of individuals are maladaptive or not. The study (Clutton-Brock *et al.* 1996*b*) suggests that Soay ewes are too fecund in years of population crashes, and that this could contribute to the severity of the population crashes. However, this optimal strategy assumes that ewes have perfect information about the stage of the population cycle that they are in, and there is no indication (Grubb 1974; Clutton-Brock *et al.* 1991, 1992) that Soay ewes can distinguish this. A second model discussed by Clutton-Brock *et al.* (1996*b*) attempts to take this into account by modelling a situation in which ewes optimize as if they were experiencing any stage of the population cycle with equal probability in the following year. This demonstrates that, in the absence of information about the population cycle, the strategy followed by ewes is close to optimal.

This paper outlines the optimization techniques used in detail. It shows that the optimal strategy predicted by dynamic optimization is not sufficient to allow comparison with the details of an animal's life history, but that it is also necessary to know what proportions of animals are found in certain states at each time, and thus what proportion of animals will be performing different actions. This can be calculated by following a population of animals performing the optimal strategy forwards in time.

We start by deriving the optimal strategies for Soay ewes when they have perfect or imperfect knowledge of the population cycle. Then we use the predicted strategies as bases to address two additional questions.

1. What proportion of ewes should be performing a particular reproductive action (for example, skip reproduction, conceive twins) at a given stage of the population cycle, if they conform to an optimal strategy? To do this we calculate the stable-state distribution for a given optimal strategy, which can then be compared directly with empirical data.
2. Are the population dynamics that we observe a consequence of ewes performing an optimal strategy? This involves calculating the changes in population density over time that would result from given reproductive strategies, which can then be compared with censuses of the study area population.

Finally we present several sensitivity analyses in order to confirm the robustness of our results.

In addressing the above questions we present the details of a modelling process which can be used to study adaptive life history decisions in natural populations, in combination with the statistical modelling examined in more detail by Clutton-Brock *et al.* (1996*b*). To our knowledge this is the first application of such a technique to a mammal population where such detailed data are available.

2. NATURAL HISTORY AND DATA COLLECTION

Data were collected from the population of Soay sheep on Hirta, an island in the St Kilda archipelago (57° 49′ N, 08° 34′ W). The population was formerly restricted to the adjacent island of Soay, but 107 animals were introduced to Hirta in 1932 (Boyd 1953), after the human population of the island was evacuated. The population has now dispersed over the whole island, but intensive monitoring has concentrated upon the Village Bay sub-population (for further description of the study site see Jewell *et al.* 1974, Clutton-Brock *et al.* 1991).

The Soay sheep is the most primitive domestic sheep in Europe, and may have been introduced to St Kilda as long ago as 2000 years ago (Campbell 1974). Soays are seasonal breeders, ewes going into highly synchronous oestrous and mating occurring in November. After a gestation period of about 151 days (Jewell & Grubb 1974) lambing occurs during April. This annual reproductive cycle makes it appropriate to look at reproductive strategies in Soay ewes as annual decisions. As we cannot observe behavioural decisions such as conception, and subsequent resorption or abortion of embryos, we classify the decision made several months later when animals give birth. We ignore differences of allocation between offspring because we have no means of isolating them in the field. Reproducing ewes give birth to one offspring, or sometimes to twins. Thus the life history decision is between whether to skip reproduction altogether, to produce one offspring, or to produce twins.

The population dynamics of sheep on Hirta has been monitored since 1955, but here we consider only the period from 1985 to May 1994 when detailed studies are available (for earlier studies see Boyd *et al.* 1964; Jewell *et al.* 1974). Since 1985 individual fecundity and mortality has been recorded for sheep in the Village Bay study area. Over 95% of lambs are caught and tagged each year (Clutton-Brock *et al.* 1991). Annual fecundity is estimated by monitoring of ewes during the lambing season. Mortality is determined by recovery of carcasses; from 1985 to 1991, 84.4% of mortalities occurred in accessible locations allowing recovery of the carcasses (Clutton-Brock *et al.* 1991). Most mortality occurs in winter, between February and April. Age at death can be determined either from known birthdate, for animals which have been tagged as lambs, or from counting annuli in the cementum of incisor teeth (Reimers & Nordby 1968). Population numbers are estimated from regular censuses of the study area.

We define 'juveniles' as animals in their first year from birth in April to the following March. This 'sheep year' is then used as the basis for all subsequent survival and fecundity analysis, with the sole exception that an animal's mass is assigned according to masses measured in August when many animals are caught. All animals older than one year are referred to as 'adults'; we do not distinguish a separate category of yearling as there was no significant difference found between yearlings and older animals.

The main mortality period is towards the end of the sheep year, whereas lambs are born at the start. The period of late winter mortality enables us to categorize years according to the intensity of mortality in that year. Years with very high mortality will be referred to as 'crash years'. Non-crash years can be divided into two categories because during the period of our analysis the population follows a 3-year cycle: the year preceding a crash we will describe as a 'pre-crash year', and that after a crash as a 'post-crash year'. This classification will be the basis for the incorporation of the effects of population dynamics in the life history models. This means that juveniles are born into a year counted as the next stage of the population cycle from that in which their mothers conceived.

3. DYNAMIC LIFE HISTORY MODEL

(*a*) *State variables and transition probabilities*

Individual animals in the study population were categorized, for each year of their life, by their mass, age and stage of the population cycle. One can also include previous reproductive status as a state variable in the optimization model, but it has no effect on the optimal strategy. It is useful to include previous reproductive status when following the model forwards, as this allows comparison with empirical results. It has been included here. State variables for use in optimization modelling were identified by selecting only the factors which remained significant in the minimal statistical models of adult and offspring survival (Clutton-Brock *et al.* 1996*b*). Generalized linear modelling (McCullagh & Nelder 1989), as implemented in

Table 1. *Definitions of state variables*

mass (divided into four mass classes)	
1	< 15 kg
2	$\geqslant 15$ kg, < 20 kg
3	$\geqslant 20$ kg, < 25 kg
4	> 25 kg
age (divided into two age classes)	
1	< 1 years
2	1–6 years note: a third age class of > 6 years was incorporated into the model but later excluded from the analysis due to lack of significant differences between it and age class 2
previous reproductive status (action performed in previous year)	
0	did not breed
1	conceived single offspring
2	conceived twins
stage of population cycle	
1	year before crash
2	year of population crash
3	year after crash

Table 2. *Transition probability matrix for mass as used in the dynamic programming models*

(States in which no animals were found and therefore no transitions were observed are indicated by dashes.)

action (q)	state of animal		new mass class in relation to old			
number of lambs	age class	mass class	−1	0	+1	+2
0	1	1	0.000	0.130	0.652	0.217
		2	0.000	0.500	0.500	0.000
		3	–	–	–	–
		4	–	–	–	–
	2	1	0.000	0.000	1.000	0.000
		2	0.000	0.000	1.000	0.000
		3	0.000	0.765	0.235	0.000
		4	0.111	0.889	0.000	0.000
	3	1	–	–	–	–
		2	–	–	–	–
		3	–	–	–	–
		4	0.000	1.000	0.000	0.000
1	1	1	0.000	0.083	0.694	0.194
		2	0.000	0.533	0.467	0.000
		3	–	–	–	–
		4	–	–	–	–
	2	1	0.000	0.000	1.000	0.000
		2	0.000	0.326	0.652	0.022
		3	0.022	0.789	0.189	0.000
		4	0.200	0.800	0.000	0.000
	3	1	–	–	–	–
		2	–	–	–	–
		3	0.000	0.938	0.063	0.000
		4	0.566	0.444	0.000	0.000
2	1	1	–	–	–	–
		2	–	–	–	–
		3	–	–	–	–
		4	–	–	–	–
	2	1	–	–	–	–
		2	0.000	0.000	1.000	0.000
		3	0.000	0.667	0.333	0.000
		4	0.071	0.929	0.000	0.000
	3	1	–	–	–	–
		2	–	–	–	–
		3	0.000	1.000	0.000	0.000
		4	0.167	0.833	0.000	0.000

the Genstat package (Genstat 5 Committee 1993), was used to derive logistic regression relations between adult and offspring survival probability and state variables. Logistic regression was appropriate because survival is a binary variable (Cox 1970). Further details of the logistic regression analysis, in the context of the costs and benefits of reproductive decisions, are given by Clutton-Brock *et al.* (1996*b*). For purposes of analysis (to obtain a manageable number of discrete states, and to best explain the variation in the data) animals were grouped into four mass and three age classes (see table 1). The annual probability of an individual moving between any two mass classes was estimated from empirical field data (see table 2). These probabilities were calculated for animals in every combination of states (previous reproductive status, age, and stage of cycle). In view of the importance of the population cycle in the life history of Soay sheep, it would be appropriate to have separate mass transition matrices for each stage of the population cycle; however too few animals were observed in many state combinations to make this feasible.

Of course, the age of an animal increases by one unit each year, so the probability of the transition from age class 1 to age class 2 was 1.0, but because age class 2 comprised animals in the range 1–6 years of age, the probability of subsequent transition to age class 3 was 1 in 6, or 0.167. Previous reproductive status changed, by definition, in a fully deterministic way; it was set to the previous value of q, the action.

The last component of state, the stage of the population cycle, differs from other components of state in recording an aspect of the external environment. Because the population cycle in Soay sheep has a direct effect on the mortality and reproductive success of individual animals, it is appropriate to consider it as another aspect of state. Although we assume for the sake of tractability that animals experience one of three stages of the population cycle (see table 1), these three values cover a range of population densities which in the natural population occur irregularly, although with a high degree of periodicity (Clutton-Brock *et al.* 1991, 1996*a*; Grenfell *et al.* 1992).

We start off by considering the population cycle as fully deterministic. Thus the cycle stage transition probability equals 1.0 for the transitions between cycle stages 1 → 2, 2 → 3, 3 → 1, and zero for all other transitions. As we go on to consider the limited information on population density that may be used by a ewe we will alter these assumptions.

Offspring mass class was related to that of their mother by least-squares linear regression. This was done in two stages. First the birthmass of a lamb was predicted based upon the mass and other state components of its mother. Then the birthmass was used to estimate the mass of the lamb in August of its first year. Offspring could then be assigned to adult mass classes. By definition offspring are assigned to age class 1, and previous reproductive status zero, with probability one. (Clearly new-born animals are not in a range of ages and have not previously reproduced). Offspring follow the same population cycles as adults.

(*b*) *Evaluating forwards dynamics*

As well as predicting the optimal strategy which animals should follow, our model can be used to study the dynamics of a population following a given strategy. This approach is based upon the observation that for a wide range of starting conditions the population will converge to a stationary state (the 'stable state distribution'). To follow the dynamics of a population forward we first define:

$\phi(\mathbf{x},t)$, the number of animals in state $\mathbf{x}$ at time t.

$N(\mathrm{t}) = \Sigma_{\mathrm{x}}\phi(\mathrm{x},t)$, the total number of animals at time t.

$\rho(\mathbf{x},t) = \phi(\mathbf{x},t)/N(\mathrm{t})$, the proportion of animals in state $\mathbf{x}$ at time t.

Then, from equation (1), the change in population numbers over time is given by:

$$\phi(\mathbf{y},\ t+1) = \sum_{\mathbf{x}}\phi(\mathbf{x},\ t)D(\mathbf{x},\ \mathbf{y},\ q). \tag{4}$$

If the sheep population was at a density-dependent equilibrium then one would expect $\rho(\mathbf{x},\ t)$ to tend to a limiting value $\rho(\mathbf{x})$ as t tends to infinity. The distribution $\rho(\mathbf{x})$ is the stable distribution of states and generalizes to state-structured populations the concept of a stable age distribution in an age-structured population. In fact the three-year population cycle incorporated in our model means that we obtain convergence over a three year period, so that the distribution of states in one year is the same as the distribution three years previously.

(*c*) *Alternative models considered here*

We consider two models of the consequences of cyclic population dynamics in this paper. The first, which we will refer to as the 'Perfect information' model, assumes that ewes have perfect information about the stage of the population cycle and that they can use this information in selecting the optimal strategy. We also assume that population dynamics occurs in a deterministic cycle, so the cycle state transition probability is one for the transitions between cycle stages 1 → 2, 2 → 3, 3 → 1 and zero for all other transitions.

We refer to a strategy as stage-independent if the actions taken under the strategy depend only on a ewe's age and mass, and not on the stage of the population cycle. We are interested in the best strategy in this class. This is because there is evidence that ewes do not use information about the population cycle. To obtain an approximation to this strategy, we consider a modified model that we call the 'Random years' model. In this model ewes experience successive stages of the population cycle at random with equal probability. In other words, the cycle stage transition probabilities are modified to one third for all transitions from one stage of the cycle to another. The optimal strategy for the Random years model is a stage-independent strategy, and can be regarded as an approximation to the best stage-independent strategy for the original problem in which stages cycle rather than occurring at random. Later we investigate how good this approximation is. When considering the stable state distribution and population dynamics of the Random years model, the standard deterministic population cycle, as used in the Perfect information model, is used when running the model forwards.

4. RESULTS

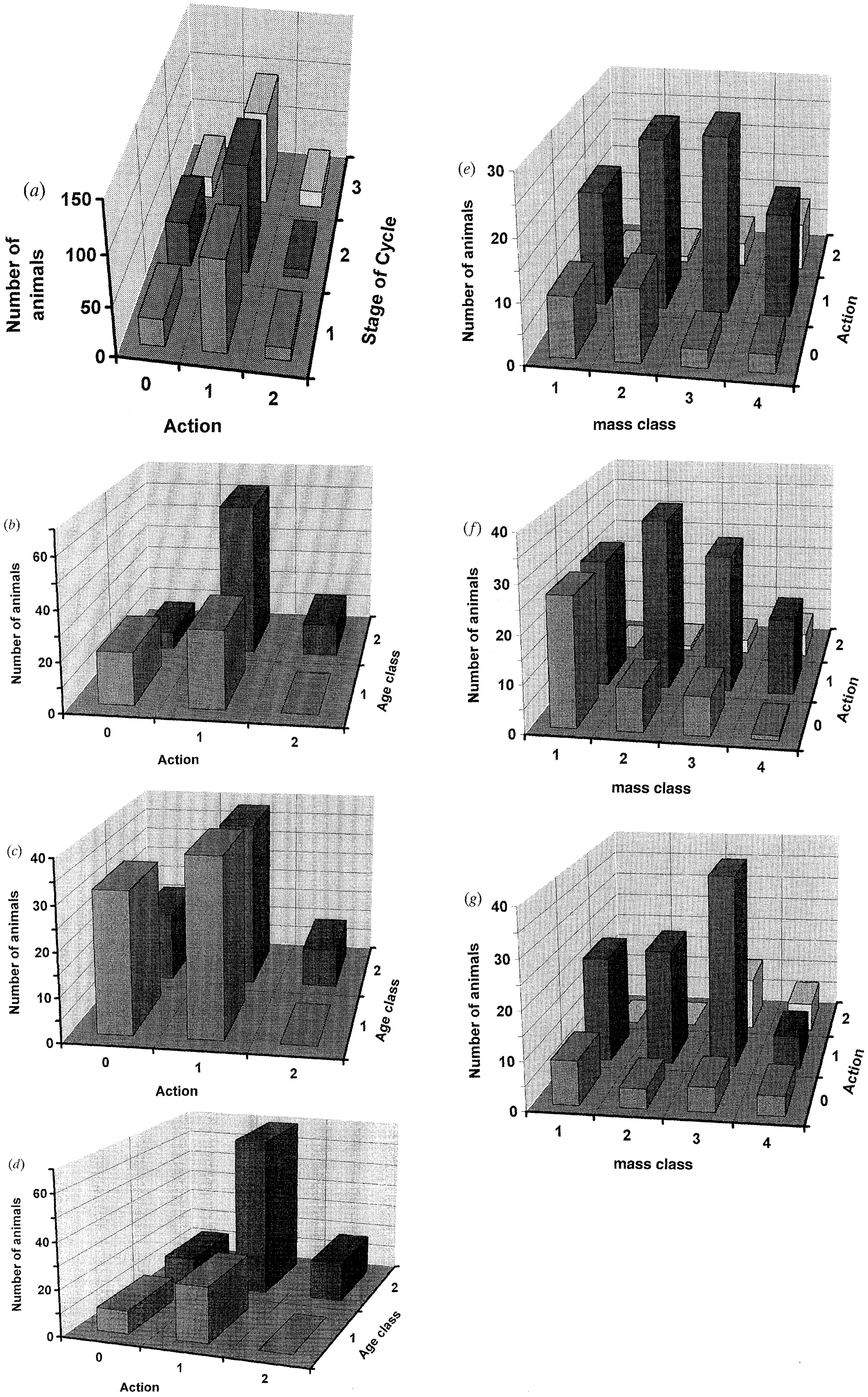
We use dynamic programming to find the optimal strategy. We then run forward using this strategy to find the stable state distribution. There are two ways in which we use this distribution to compare our results with the data. First, we examine the proportion of animals expected in different states, and the actions they should perform after convergence to the stable distribution during iteration forwards. This stable state distribution can be compared with the distribution of animals observed in field data. Second, expected numbers of animals calculated during the forwards iteration process can be used to construct a time series of the expected population dynamics that would result if all animals were following an optimal strategy, and this can be compared to the data available on the population dynamics of the Village Bay population (Clutton-Brock *et al.* 1996*a*).

Both these applications depend on being able to calculate the optimal strategy, the set of state-dependent actions that maximize animals' long-term reproductive success, but they enable us to go beyond the simple comparison of the optimal strategy with observed actions, and test hypotheses about adaptive behaviour more precisely.

(*a*) *Stable state distributions*

(*i*) *Empirical data*

As a basis from which to compare stable state distributions predicted from the models, we can examine the distribution of animals by states found in


(a)
Number of animals
150
100
50
0
0
1
2
Action
Stage of Cycle
1
2
3
(b)
Number of animals
60
40
20
0
0
1
2
Action
Age class
1
2
(c)
Number of animals
40
30
20
10
0
0
1
2
Action
Age class
1
2
(d)
Number of animals
60
40
20
0
0
1
2
Action
Age class
1
2
(e)
Number of animals
30
20
10
0
1
2
3
4
mass class
Action
0
1
2
(f)
Number of animals
40
30
20
10
0
1
2
3
4
mass class
Action
0
1
2
(g)
Number of animals
40
30
20
10
0
1
2
3
4
mass class
Action
0
1
2

the study population at various stages of the population cycle, and the actions they perform (see figure 1). Among the important features of these distributions we observe that lambs are only found in the first two mass classes (see table 2); thus predictions for mass classes 3 and 4 in age class 1 are not applicable. Also, mature ewes are very rarely found in the lowest mass class. The proportions of animals in each mass class varied significantly between years of the cycle for lambs (G-test = 12.3, 2 d.f., $p < 0.01$), but not for adult ewes (G-test = 3.2, 6 d.f., $p > 0.05$).

At each stage of the cycle, a proportion of animals skip reproduction (see figure 1*a*). These animals are distributed across all mass and age (see figure 1*b*–*g*) categories, although significantly more lambs skip reproduction than do mature ewes ($X^2 = 43.7$ with Yates' correction, 1 d.f., $p < 0.001$). The proportion of animals skipping reproduction does not, however, vary significantly between different years of the cycle ($X^2 = 5.3$, 2 d.f., $p > 0.05$). Similarly, at every stage of the cycle some animals produce twins (see figure 1*a*). Lambs never produce twins, and in mature ewes the proportion of animals twinning varies significantly across mass classes (G-test = 48.9, 2 d.f., $p < 0.001$) and tends to increase with mass, with the exception of post-crash years. The proportion of animals twinning does not vary significantly between different stages of the cycle ($X^2 = 4.7$, 2 d.f., $p > 0.05$).

(*ii*) *Perfect information*

When the Perfect information optimal strategy (given in table 3) is followed to a stationary state we obtain the results in table 4. The results are given for three years, corresponding to one complete cycle of population dynamics. Figure 2 shows the population at stable state distribution classified by state variable and action. The distribution of actions by stage of the cycle (see figure 2*a*) is clearly different from the observed situation in figure 1*a*. Animals following the perfect information optimal strategy should never skip reproduction except in crash years, and are not expected to produce twins in crash years. This is not observed in the field, and the proportions of animals performing particular actions in different stages of the cycle are significantly different in the case of perfect information from the observed proportions (G-test = 803.2, 8 d.f., $p < 0.001$). In this case, as in G-tests to follow, where proportions predicted from the model were compared with empirical data, the proportions were scaled to the total population size, in order that a valid comparison could be made (a small number was substituted in cells where the proportion was zero so that the G-test could be performed).

The proportions of lambs in different mass classes (see figure 2*e*–*g*) varied significantly between stages of

Table 3. *The optimal strategy when ewes have perfect information about the stage of the population cycle and can adjust their strategy accordingly*

(Actions are indicated by number; 0, skip reproduction, 1, produce single offspring, 2, produce twins.)

pre-crash year				
mass class	1	2	3	4
age class 1	1	1	1	1
age class 2	1	1	1	2
crash year				
age class 1	0	0	1	1
age class 2	0	0	1	1
post-crash year				
age class 1	1	1	2	2
age class 2	1	2	2	2

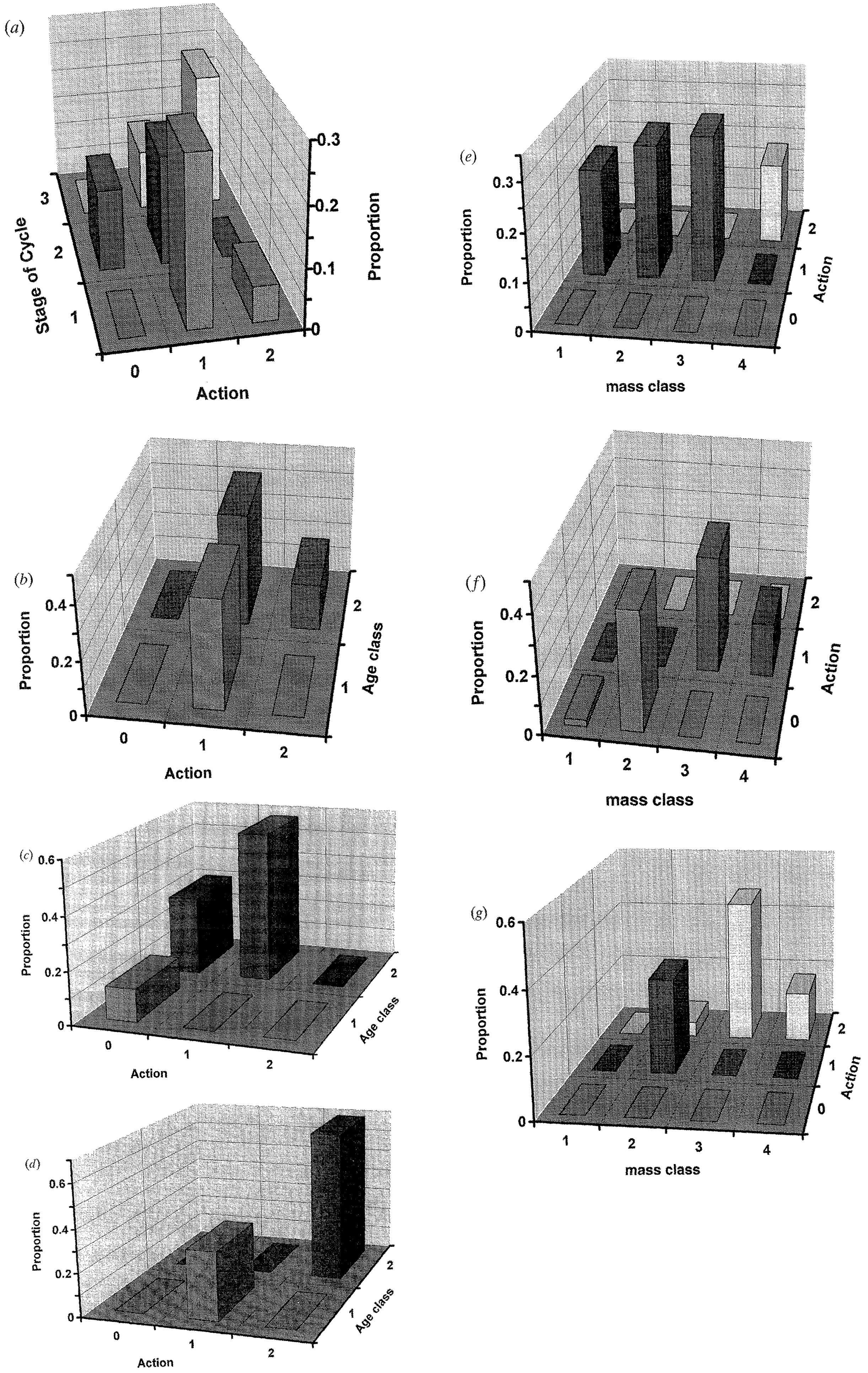
Table 4. *The stable state distribution resulting when ewes perform the Perfect information optimal strategy*

(Convergence to the stable state distribution was achieved in the first (pre-crash) year, but the following two years are shown to detail the distribution of actions over the whole population cycle. Animals in age class 3 have been excluded, and the proportions rescaled to sum to 1. PRS indicates previous reproductive status. States which are not shown are not represented in the stable state distribution.)

state of animal				
age class	mass class	PRS	proportion in state	action
year 1[a]				
1	2	0	0.312	1
2	1	0	< 0.001	1
	2	0	0.044	2
	3	0	0.228	2
2	2	1	0.006	2
	3	1	0.245	2
	4	1	0.165	2
year 2[b]				
1	1	0	0.230	1
	2	0	0.173	1
2	2	1	0.113	1
	3	1	0.099	1
2	3	2	0.211	1
	4	2	0.175	2
year 3[c]				
1	1	0	0.003	0
	2	0	0.121	0
2	1	1	0.019	0
	2	1	0.283	0
	3	1	0.382	1
	4	1	0.050	1
2	3	2	0.010	1
	4	2	0.133	1

[a] Post crash year.
[b] Pre-crash year.
[c] Crash year.

Figure 1. Observed distributions of animals, by state, in the study population. (*a*) Classified by action and stage of cycle; (*b*) classified by age class and action, in pre-crash years; (*c*) classified by age class and action, in crash years; (*d*) classified by age class and action, in post-crash years; (*e*) classified by mass class and action, in pre-crash years; (*f*) classified by mass class and action, in crash years; (*g*) classified by mass class and action, in post-crash years. Numbers of animals where not otherwise indicated include all animals in age classes 1 and 2.


(a)
Stage of Cycle
1
2
3
Action
0
1
2
Proportion
0
0.1
0.2
0.3
(b)
Proportion
0
0.2
0.4
Action
0
1
2
Age class
1
2
(c)
Proportion
0
0.2
0.4
0.6
Action
0
1
2
Age class
1
2
(d)
Proportion
0
0.2
0.4
0.6
Action
0
1
2
Age class
1
2
(e)
Proportion
0
0.1
0.2
0.3
mass class
1
2
3
4
Action
0
1
2
(f)
Proportion
0
0.2
0.4
mass class
1
2
3
4
Action
0
1
2
(g)
Proportion
0
0.2
0.4
0.6
mass class
1
2
3
4
Action
0
1
2

the cycle, as expected (G-test = 412.4, 2 d.f., $p < 0.001$), but so did the proportions of adult ewes (G-test = 145.1, 2 d.f., $p < 0.001$). This confirms previous ideas that ewes do not adjust their strategies at different stages of the cycle to the extent that the perfect information model predicts (Clutton-Brock *et al.* 1996*b*).

As a consequence of this stage-dependence, the expected proportion of animals skipping reproduction varies significantly between different stages of the cycle (G-test = 286.4, 2 d.f., $p < 0.001$), as does the expected proportion of animals producing twins (G-test = 328.4, 2 d.f., $p < 0.001$). The stable state distribution is in agreement with field data in that the expected proportion of animals producing twins varies across mass classes (G-test = 291.5, 3 d.f., $p < 0.001$), and shows some tendency to increase with mass.

In general the stable state distribution for perfect information shows a sharper dependence of reproductive strategies on density than is observed in nature, and gives support to the idea that ewe reproductive strategies have been selected in the absence of information about cycle stage.

(*iii*) *Stage-independent strategies*: *Random years*

The Random years model would seem like a better candidate to represent the observed situation. The stable state distribution when animals perform the appropriate optimal strategy (see table 5) is given in table 6 and figure 3. The distribution appears to show a similar distribution of reproductive actions in crash and non-crash years (see figure 3*a*) to that observed in the field (see figure 1*a*), and there is no significant difference in proportions performing each action between the model and the field data (G-test = 1.8, 4 d.f., $p > 0.5$).

The Random years model predicts correctly that the proportion of lambs in different mass classes will vary significantly over the population cycle (G-test = 92.0, 6 d.f., $p < 0.001$; see figure 3*b*–*d*). However the proportion of ewes in different mass classes is also predicted to vary (G-test = 46.8, 6 d.f., $p < 0.001$). Although animals follow the same strategy in all years, because animals are typically in different states in different years, actions can differ between years.

The model does predict twinning at all stages of the population cycle, and the proportion of ewes twinning does not vary with the population cycle (G-test = 1.4, 2 d.f., $p > 0.1$; see table 6), in accordance with empirical observations. The proportion of animals twinning within each year, from 13 to 17%, are close to the proportions observed (up to 16%; Clutton-Brock *et al.* 1991). These agreements between the observed and predicted distributions of animals lend further support to the view that selection upon Soay ewes in respect of reproductive strategies is mass and age, rather than density-based.

(*b*) ***Population dynamics***

The stable state distribution of the Random years model shows a good fit to the empirical state distribution. In order to verify the accuracy of the Random years optimal strategy, it is instructive to compare the population dynamics that results from a population modelled performing the optimal strategy, with the time series of the Village Bay study population (see figure 4*a*). As our model deals only with females, we also show the time series of ewe population dynamics for comparison (see figure 4*b*). Both time series show population crashes. There is no clear tendency for the long-term peak population density to increase.

An example time series of population dynamics produced by applying the Perfect information model is shown in figure 5. The population has already attained the stable state distribution, but because this incorporates changes in the proportions of animals in different states at different stages of the cycle, the population consequently fluctuates, increasing in pre- and post-crash years, and decreasing in crash years. Note that the magnitude of the crash is much lower than observed in the field, and in non-crash years the population shows a tendency to increase, which is not overcome by periodic crashes. This time series indicates the results of avoiding reproductive strategies which lead to excessively high densities and consequent density-dependent mortality in crash years. The observed time series in the field (see figure 4*a*) is consistent with a strategy where information about the population cycle is not available.

The Random years model leads to a time series (see figure 6) where once again the population declines in crash years, but the proportional decline in numbers is much lower than observed. Unlike the Perfect information model, there is no tendency for the population to increase. The population numbers in figure 6 are much lower than in figure 5 as a result. The population dynamics produced by the Random years model suggest it is a better candidate to explain the adaptive nature of ewes' reproductive decisions: the lower mortality than is observed could be due to the omission of short-term fluctuations in weather conditions.

Figure 2. Stable state distribution when animals are performing the optimal strategy given perfect information about the population cycle. The expected numbers of animals in each state class are calculated as a proportion of the total expected number of animals present in the year when convergence to the stable state distribution was achieved. Animals in age class 3 were then excluded and the proportions rescaled to sum to 1. (*a*) Classified by action and stage of cycle; (*b*) classified by age class and action, in pre-crash years; (*c*) classified by age class and action, in crash years; (*d*) classified by age class and action, in post-crash years; (*e*) classified by mass class and action, in pre-crash years; (*f*) classified by mass class and action, in crash years; (*g*) classified by mass class and action, in post-crash years. Numbers of animals where not otherwise indicated include all animals in age classes one and two.

Table 5. *The optimal strategy for the Random years model*

(The results are identical for different stages of the population cycle, so are not differentiated with respect to that variable. The action in age class 1, mass class 2 (asterisked) is not optimal in a 3 year population cycle background, where action 1 i.e. produce one offspring is optimal.)

mass class	1	2	3	4
age class 1	1	0*	2	2
age class 2	1	1	1	2

Table 6. *The stable state distribution resulting when ewes perform the Random years optimal policy, under conditions of a deterministic 3 year population cycle*

(Convergence to the stable state distribution was achieved in the year 1, but the following two years are shown to detail the distribution of actions over the whole population cycle. Animals in age class 3 have been excluded, and the proportions rescaled to sum to 1. States which are not shown are not represented in the stable state distribution.)

state of animal				
age class	mass class	PRS	proportion in state	action
year 1[a]				
1	1	0	0.030	1
	2	0	0.317	0
2	2	0	0.085	1
	3	0	0.085	1
2	1	1	0.008	1
	2	1	0.090	1
	3	1	0.236	1
	4	1	0.045	2
2	3	2	0.008	1
	4	2	0.097	2
year 2[b]				
1	1	0	0.001	1
	2	0	0.120	0
2	2	0	0.153	1
	3	0	0.153	1
2	1	1	0.003	1
	2	1	0.079	1
	3	1	0.316	1
	4	1	0.055	2
2	3	2	0.008	1
	4	2	0.110	2
year 3[c]				
1	1	0	0.136	1
	2	0	0.235	0
2	2	0	0.036	1
	3	0	0.036	1
2	1	1	< 0.001	1
	2	1	0.044	1
	3	1	0.336	1
	4	1	0.066	2
2	3	2	0.008	1
	4	2	0.102	2

[a] Pre-crash year.
[b] Crash year.
[c] Post-crash year.

(*c*) ***Sensitivity tests***

(*i*) *Canonical costs of sub-optimal actions*

One way of investigating the robustness of optimal behaviour predicted by dynamic optimization is to examine the canonical costs of various actions. Because we are considering annual decisions, we can define the payoff under an action as the expected total reproductive value of descendants produced in one year's time. Under the optimal strategy, the action taken in each state maximizes the payoff. The canonical cost of an action is the difference between the payoff under the action and the payoff under the optimal action (McNamara & Houston 1986). Thus the optimal action will always have a canonical cost of zero; a high canonical cost will indicate a clearly sub-optimal action.

Table 7 gives the canonical costs for actions for the Perfect information model, and table 8 for the Random years model. Most canonical costs are below 1.0. Also most canonical costs are not close to zero, indicating distinct fitness advantages of the optimal action relative to sub-optimal actions. However some canonical costs are very small; this suggests that environmental fluctuations of small effect or inaccuracies in parameter estimation could overwhelm the advantage of the predicted optimal strategy. In such cases we might expect different observed behaviour than was predicted (for further discussion, see Houston *et al.* 1992). However, because the instances where canonical costs are small are themselves only a small proportion of the total states animals can be in, this suggests that the overall distribution of reproductive actions by states will approximate to what is predicted, assuming that all relevant components of state have been included in the model.

(*ii*) *The best stage-independent strategy*

Our motivation for studying the Random years model is to find the best stage-independent strategy when the population density follows a regular cycle. As we have said, the optimal strategy in the Random years model should give us an approximation to this best strategy. To investigate how good this approximation is, we examine the long-term growth rate of a population that follows modifications of the Random years optimal strategy. Each modification consists of changing one of the actions taken in the Random years optimal strategy (see table 9*a*). We observe that only one deviation from the optimal strategy results in an increased growth rate, when the action corresponding to age class 1, mass class 2 is changed from 0 (skip reproduction) to 1 (produce one offspring).

To check that the resulting set of actions does in fact give the highest growth rate we examine all single-action deviations from this strategy (see table 9*b*). Excluding changes to mass classes three and four in age class 1, states in which no animals are observed in the field and are thus irrelevant, the strategy identical to the optimal strategy except in this one state is seen to give the highest growth rate. Thus we conclude that the Random years optimal strategy gives a good approximation of the strategy which will result in the highest fitness benefit when ewes have no information

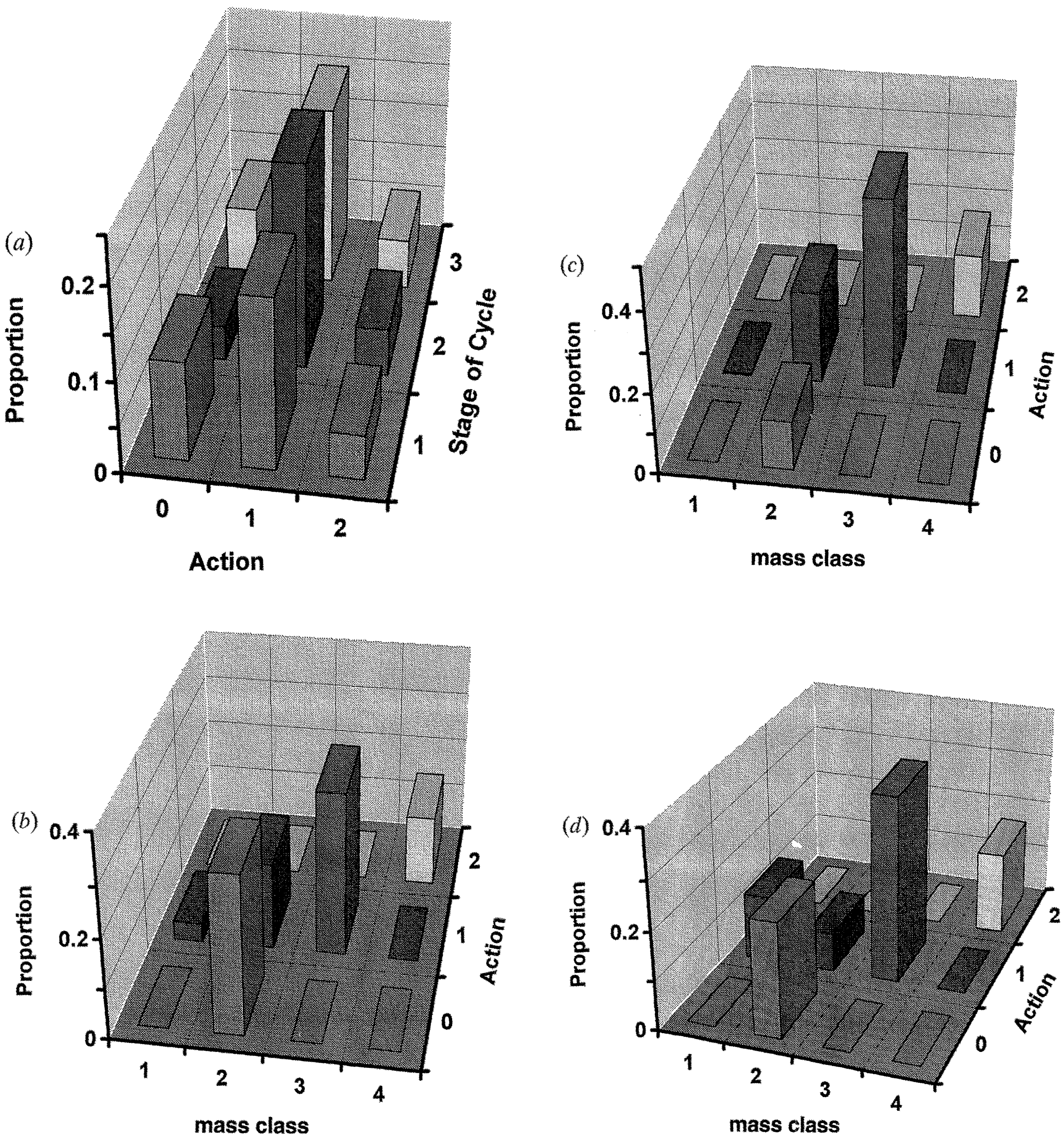


Figure 3. Stable state distribution when animals are performing the optimal strategy given that ewes experience successive stages of the population cycle at random, with equal probability. Proportions of animals in each state are calculated as in figure 2. (*a*) Classified by action and stage of cycle; (*b*) classified by mass class and action, in pre-crash years; (*c*) classified by mass class and action, in crash years; (*d*) classified by mass class and action, in post-crash years. Numbers of animals where not otherwise indicated include all animals in age classes 1 and 2.

about the population cycle. This shows the importance of environmental fluctuations in calculating optimal strategies and state dynamics.

(*iii*) *Changes in environmental fluctuations*

As a further check on the results obtained we examine the consequences of altering the frequency of crash years in the Random years model. This has the effect of making the environment relatively less favourable (if the probability of crash years is increased), or more favourable (if the probability is decreased). If the optimal strategy depends very strongly upon environmental quality as mediated through the mortality consequences of reproductive decisions, then we might expected the predicted set of actions to change as the probability of crash years is varied. In fact, for a very wide range of probabilities, this is not the case. We modified the probability of occurrence of a crash year from 0.10 to 0.75 with no effect on the optimal strategy. Changing the probability of occurrence of crash years, and consequently of non-crash years, will affect the fitness values of particular actions performed in given states, but it does not appear to affect the relative fitness values of different actions in the same state.

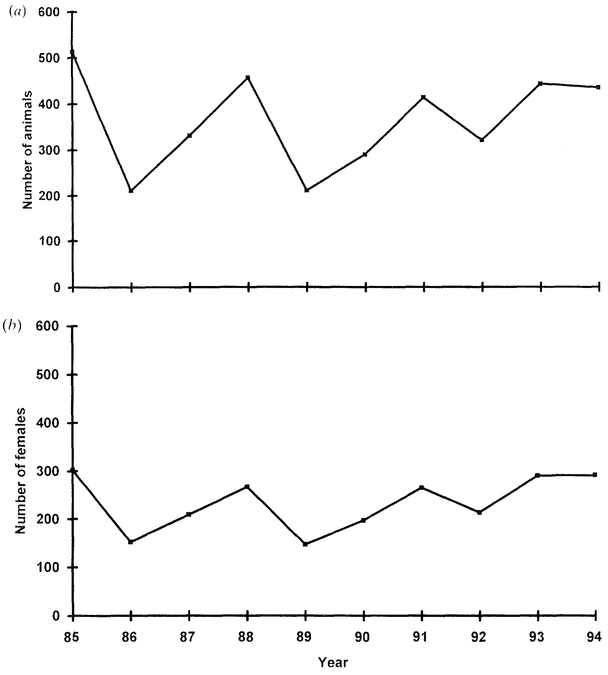


Figure 4. Time series of population dynamics of the Village Bay study population: (*a*) total population numbers; and (*b*) adult ewe numbers.

Figure 5. Population dynamics resulting from applying the optimal strategy when sheep have perfect information about the stage of the population cycle to an initial population state distribution. In this example the population was started in a pre-crash year with one animal in each state. The observed population dynamics were robust to a wide range of initial conditions. Population dynamics were evaluated based upon mortality and fecundity resulting from a three-year deterministic cycle. The total population density was evaluated over one hundred annual decisions, and the last nine iterations (each equivalent to one year) are shown.

5. DISCUSSION

In this paper we have explored the consequences of adopting an optimal reproductive strategy to a sheep population, in terms of the proportion of animals in different states and the population dynamics that would be expected. The Perfect information model is untenable given our knowledge of the field population. The optimal strategy predicts no twinning in crash years, contrary to observations, and the stable state distribution for this model shows much more dramatic changes in the proportion of animals performing different actions at different stages of the cycle than is observed. We conclude that ewes do not appear to take advantage of information about future changes in population density (see also Clutton-Brock *et al.* 1996*b*). This is consistent with the observation that density-dependent limitation on fecundity in this species does not appear to operate except at high densities (Clutton-Brock *et al.* 1991).

A model which assumes that ewes cannot predict the

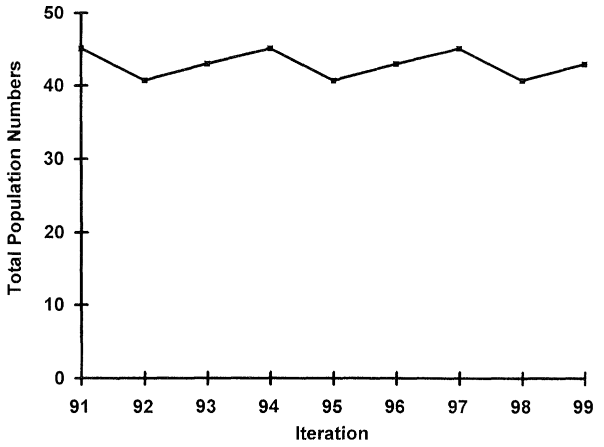


Figure 6. Population dynamics resulting from applying the optimal strategy for the Random years model to an initial population state distribution. Initial conditions, and the method of evaluating population dynamics, are as in figure 5.

Table 7. *Canonical costs of actions for the Perfect information model*

(Canonical costs were calculated as the difference between the reproductive value under the optimal action and the reproductive value under the alternative action, after convergence to the optimal strategy. Reproductive values were calculated relative to a reference state, here taken as age class 1, mass class 1. For further discussion see text.)

state of animal			canonical cost of action		
stage of cycle	mass class	age class	skip	single	twin
1	1	1	0.121	0.000	0.952
		2	0.518	0.000	0.776
	2	1	0.053	0.000	1.107
		2	0.370	0.000	0.069
	3	1	0.025	0.000	0.017
		2	0.235	0.000	0.013
	4	1	0.039	0.000	0.027
		2	0.155	0.100	0.000
2	1	1	0.000	0.237	0.409
		2	0.000	0.286	0.713
	2	1	0.000	0.429	0.924
		2	0.000	0.269	0.908
	3	1	0.178	0.000	0.075
		2	0.130	0.000	0.717
	4	1	0.302	0.000	0.124
		2	0.379	0.000	0.455
3	1	1	0.367	0.000	1.051
		2	0.889	0.000	0.920
	2	1	0.324	0.000	1.179
		2	0.753	0.122	0.000
	3	1	0.396	0.034	0.000
		2	0.598	0.038	0.000
	4	1	0.412	0.030	0.000
		2	0.603	0.585	0.000

outcome of population change seems much more realistic. The Random years model satisfies this requirement; the optimal strategy predicted under this model is closer to the observed situation, and the stable state distribution that results bears much resemblance to the observed distribution of animals. It appears that Soay ewes are selected to make reproductive decisions on the basis of current nutrition, mass and age, rather than population density. The population dynamics expected under the Random years model shows no long-term tendency to increase, and this is consistent with the observed situation, but exhibits rather less severe population crashes. As we have not included the effects of short-term fluctuations in weather conditions or of parasites in our model, it is possible that some of the differences between the predicted and observed mortality may be accounted for by these factors (Campbell 1974; Gulland *et al.* 1994; Stevenson 1994).

Table 8. *Canonical costs for alternative actions for the Random years model*

(Canonical costs were calculated as in table 7. The canonical costs are identical for given mass and age classes over different stages of the cycle, and thus are not differentiated for that variable.)

state of animal		canonical cost of action		
mass class	age class	skip	single	twin
1	1	0.180	0.000	1.680
	2	0.927	0.000	1.454
2	1	0.000	0.095	2.235
	2	0.500	0.000	0.088
3	1	0.530	0.272	0.000
	2	0.515	0.000	0.049
4	1	0.622	0.284	0.000
	2	0.779	0.580	0.000

Table 9. *Long-term growth rates of populations*

((*a*) Long-term growth rates of populations with one action different from optimal strategy from Random years model. The growth rate is calculated by comparing populations three years apart in the same state, due to the assumption of a three-year population cycle. The relative growth rate is measured by comparison to the growth rate under the optimal strategy (1.2576). (*b*) Long-term growth rates of populations performing strategies with one action different from strategy with maximal growth rate. The relative growth rate is measured by comparison to the maximal growth rate (1.2781). Note that the action performed in mass classes 3 and 4, of age class 1 does not affect the population growth rate because animals are not found in these mass classes.)

state				
age class	mass class	change in action	growth rate	relative growth rate
(*a*) one action different from optimal strategy from Random years model				
1	1	1 → 2	1.144	0.909
		1 → 0	1.230	0.978
	2	0 → 1	1.278	1.016
		0 → 2	0.790	0.628
	3	2 → 1	1.258	1.000
		2 → 0	1.258	1.000
	4	2 → 1	1.258	1.000
		2 → 0	1.258	1.000
2	1	1 → 2	1.252	0.996
		1 → 0	1.255	0.998
	2	1 → 2	1.182	0.940
		1 → 0	1.234	0.982
	3	1 → 2	1.087	0.864
		1 → 0	1.072	0.852
	4	2 → 1	1.231	0.979
		2 → 0	1.179	0.937
(*b*) one action different from strategy with maximal growth rate				
1	1	1 → 0	1.242	0.972
		1 → 2	1.115	0.872
	2	1 → 0	1.258	0.984
		1 → 2	0.790	0.618
	3	2 → 0	1.278	1.000
		2 → 1	1.278	1.000
	4	2 → 0	1.278	1.000
		2 → 1	1.278	1.000
2	1	1 → 0	1.276	0.998
		1 → 2	1.270	0.994
	2	1 → 0	1.271	0.995
		1 → 2	1.188	0.929
	3	1 → 0	1.081	0.846
		1 → 2	1.084	0.848
	4	2 → 0	1.205	0.943
		2 → 1	1.265	0.989

One of our concerns has been to find the best strategy when population density changes follow a regular cycle but the sheep do not use information about this cycle. The optimal policy in the Random years model does not necessarily give us this strategy, but it is likely to give an approximation to it. Using this strategy as a starting point, we have been able to find the best strategy by evaluating the performance of local modifications of this strategy. Finding the best strategy when animals cannot use information about cycle stage is an example of what we see as a widespread and important issue in the study of adaptive behaviour. Animals may be unable to gain information about certain aspects of their state or be constrained to use only certain variables in making a decision. The search technique that we have used is unlikely to be universally applicable, and theoretical work on general techniques is needed.

This paper develops and extends the results presented by Clutton-Brock *et al.* (1996*b*). There, optimal strategies were discussed; an optimal strategy can tell us what an animal should do but it does not tell us what we should expect to see in a natural population, that is, how many animals are in which states and thus what proportion of animals are performing particular actions. For this we need to calculate the stable state distribution. In addition, the techniques that one uses to calculate the stable state distribution can also be used to follow population dynamics forward; this is particularly useful in the case of a cyclic population such as Soay sheep on St Kilda. Where detailed records of survival and reproduction are available, many life history questions can be investigated. In the case of Soay sheep and, potentially, many other animals, this type of modelling is not restricted to annual decisions, we can also consider timing of reproduction within years, and reproductive and other life history decisions in relation to other phenotypic variables than considered here.

In the search for more realistic models, it will be of interest to include males as well as females in the model; especially in view of the very different life history of males in this population (Stevenson 1994). A two-sex model will make the strategies adopted by individuals frequency-dependent, necessitating the analysis of a stochastic dynamic game (Houston & McNamara 1987, 1988; Mangel & Clark 1988). A stochastic dynamic game may also be used to study the role of population dynamics in the reproductive decisions of animals, because the population dynamics can be modelled directly, unlike the current models. Clearly this would be a more accurate representation of the situation: our models here are intended as a first approximation.

The techniques we have described can be applied to many questions concerning the adaptive nature of life histories. Such models need not be restricted in their application: in principle a similar model could be constructed for any species where the relevant data is available. What is required is data identifying the probabilities of transition from each value of state to every other value, given a certain action, and data to establish how state and actions determine survival.

Such data requirements may be satisfied in a number of long-term studies of birds (e.g. Fitzpatrick & Woolfenden 1988; McCleery & Perrins 1988; van Noordwijk & van Balen 1988), or mammals (e.g. Clutton-Brock *et al.* 1982; Boyd *et al.* 1995). These detailed studies where individuals are known typically reveal state-dependent effects (Clutton-Brock *et al.* 1988; Finke 1988; Newton 1988; Mousseau & Dingle 1991; Schulter & Gustafsson 1993) and hence questions about the adaptive nature of life histories in these species can best be answered using stochastic dynamic programming methods. Techniques of dynamic optimization such as described here provide a useful complement to empirical investigations as more becomes known about the life histories of natural populations.

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