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Population fluctuations, reproductive costs and life-history tactics in female Soay sheep

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Summary

1. Though models of life-history decisions are traditionally based on age-related changes in the costs and benefits of reproduction, in nature both costs and benefits vary with individual differences in phenotype as well as with environmental changes.
2. Using long-term records of individual reproduction and survival in the Soay sheep of St Kilda, we show that the costs and benefits of breeding to animals of different weight categories vary with population density.
3. Subsequently, we use stochastic dynamic programming to predict the optimal fecundity of animals belonging to each category at high and low population density. Optimal strategies of fecundity vary with population density as well as between different weight categories of sheep. However, there is no evidence that the sheep track density-related changes in optimal fecundity. Instead, their behaviour approximates to an average, weight-related optimum that is well adapted to the range of conditions that they encounter.

Key-words: evolution, fecundity, life histories, ungulates.

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Introduction

Traditional models of life-history decisions are based on the assumption that the costs and benefits of breeding change only with age (Roff 1992; Stearns 1992). However, in nature, both the costs and benefits of breeding commonly vary with other aspects of an individual's phenotype, including its weight, condition, dominance and reproductive history (Clutton-Brock, Guinness & Albon 1983; Alberts & Altmann 1995; McNamara & Houston 1992). Moreover, they are also likely to vary with environmental factors: for example, in red deer, *Cervus elaphus* L., the costs of breeding increase in years when autumn rainfall is heavy (Albon, Clutton-Brock & Guinness 1987; Gomendio *et al.* 1990) or population density is high (Albon *et al.* 1987; Clutton-Brock *et al.* 1983; Clutton-Brock, Albon & Guinness 1987a, b). Environmental effects may interact with phenotypic vari-

ation, accentuating or, sometimes, reducing its effects (Albon *et al.* 1987; Clutton-Brock *et al.* 1987a, b).

Variation in the costs or benefits of breeding is likely to lead to changes in optimal reproductive strategies and several recent studies suggest that animals modify their reproductive decisions in relation to their phenotypic or environmental state. For example, in dung flies, *Scatophaga stercoraria* L., the optimal duration of copulation is shorter for large individuals than small ones and observations show that copulation durations vary with body size in the predicted manner (Parker & Simmons 1994). Similarly, parasitic wasps are more likely to lay eggs in suboptimal hosts under environmental conditions likely to cause high mortality among adults (Fletcher, Hughes & Harvey 1994; Roitberg *et al.* 1993). And, in white-footed mice, *Peromyscus leucopus* Rafinesque, juveniles from unusually large litters produced by small females show very low survival, reducing the optimal litter size for small females (Morris 1996).

Evidence of adaptive responses of this kind raises the possibility that density-dependent changes in fecundity among vertebrates (which have been widely documented but are usually interpreted as non-adapt-

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ive consequences of resource shortage) may sometimes represent adaptive adjustments to changing optima. Studies of ungulates provide some evidence that is consistent with this view. For example, in red deer, the fecundity of animals of the same body weight is lower in populations where density is high than where it is low (Albon, Mitchell & Staines 1983). Breeding costs increase with population density in red deer (Clutton-Brock *et al.* 1983) while the relative survival of light-born calves falls (Clutton-Brock *et al.* 1987a, b). Since female weight falls at high density and light mothers produce light calves, the optimal weight at which females should conceive may increase when population density is high. Similarly, in bighorn sheep, 2-year-old females of a given body weight are less likely to rear young at high than low population density (Jorgenson *et al.* 1993).

In this paper, we use detailed records of reproduction and survival in Soay sheep *Ovis aries* L. to calculate the costs and benefits of breeding for animals of different body weight in years of high and low population density. This is possible because our study population of Soay sheep on Hirta (St Kilda) fluctuates widely in size every 3–4 years as a result of heavy, over-compensatory, density-dependent mortality (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992). Records of individual variation in reproductive success and survival collected since 1985 (Clutton-Brock *et al.* 1991) provide a basis for estimating the costs of reproduction to different categories of animals in years of high and low density. We subsequently use these data to predict the optimal actions of different categories of animals at contrasting population densities using stochastic dynamic programming (Bellman 1957), and compare these estimates with records of the animals' behaviour. We use stochastic dynamic programming because each optimal decision depends on decisions at other stages of the life-history and this technique provides a way of incorporating successive decisions without having to evaluate each of the vast numbers of possible sequences of behaviour that could make up an animal's life-history. Most previous uses of dynamic programming to estimate life-history decisions (e.g. McNamara & Houston 1992) have tended to be no more than schematic because the detailed data required for parameterisation of the models have not been available. The unusual resolution of the reproductive data available for the sheep provides an opportunity to examine life-history decisions of more realistic complexity.

Materials and methods

STUDY POPULATION

Soay sheep *Ovis aries* L. are the most primitive domestic sheep in Europe, closely resembling both the original wild species and the domestic neolithic sheep first brought to Britain around 5000 BC (J. Clutton-

Brock 1981; Ryder 1983). Soay sheep may have been introduced to the St Kilda archipelago (57°49', 08°34'W) in the second millennium BC (Boyd & Jewell 1974) but, by historical times, were restricted to the uninhabited island of Soay (99 ha). Two years after the human population of Hirta (638 ha) was evacuated in 1930, 107 Soay sheep, some of which may have been castrated, were introduced from Soay (Boyd 1953; Boyd *et al.* 1964). Numbers on Hirta increased rapidly and, in 1952, the first organized census produced an estimate of 1114 sheep. Neither on Soay nor on Hirta have the sheep been managed in historical times and numbers are regulated by food availability and parasite load (Clutton-Brock *et al.* 1991; Gulland *et al.* 1993; Illius *et al.* 1995). On Hirta, population crashes, when 40–60% of all animals die, occur every 3–4 years (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992). The population is known to have been unstable for at least 30 years (Grubb 1974). The growth and reproductive parameters of Soay sheep resemble those of other primitive domestic sheep (Grubb 1974): most offspring are conceived in November and born in April and the majority of females become pregnant in their first year of life. Subsequently, virtually all ewes conceive each year, with between 10 and 30% producing twins (see Table 1). Body weight increases rapidly during the first year of life and more slowly thereafter: both lambs and yearlings are lighter than older ewes in August (Grubb 1974). In all four categories of females, body weight is highest in pre-crash years but differences between years are small.

DATA

We categorize females as juveniles from their birth in April until the beginning of their second summer when they are 12 months old; as yearlings from 13 to 24 months; and as adults over 24 months. Since the relationship between fecundity and body weight does not differ between yearlings and older ewes, we combine these categories in some analyses and refer to these combined categories as 'ewes'. Data used in this analysis were collected from the Village Bay sub-population of Hirta between 1986 and 1993. During this period, the population showed high mortality every third year and crashes occurred in 1986, 1989 and 1992 (Clutton-Brock *et al.* 1991, unpublished data). We categorized years as pre-crash, crash and post-crash: in pre-crash years, birth weights, neonatal survival and over-winter survival are all high; in crash years, birth weights and neonatal survival are high, while up to 50% of adults, 70% of yearlings and 90% of juveniles die in late winter (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992); and in post-crash years, ewes have recently passed through a period of acute food shortage, the birth weights of their offspring are reduced and neonatal mortality is high (Clutton-Brock *et al.* 1992) though food is abundant and subsequent survival of juveniles and adults is high (Clut-

Table 1. Percentage fecundity of different categories of Soay sheep, 1986–1993 in different categories of years. Weight categories refer to weight the previous August

Weight class in previous August: No. offspring produced	< 15 kg			15–20 kg			20–25 kg			≥ 25 kg		
	0	1	2	0	1	2	0	1	2	0	1	2
Pre-crash years (<i>n</i> = 160)												
Age (years)												
< 1 (<i>n</i> = 52)	36%	64%	0%	46%	54	0%	–	–	–	–	–	–
1–6 (<i>n</i> = 82)	–	–	–	6%	88%	6%	8%	81%	11%	10%	61%	29%
> 6 (<i>n</i> = 26)	–	–	–	–	–	–	–	81%	19%	14%	50%	36%
Crash years (<i>n</i> = 199)												
Age (years)												
< 1 (<i>n</i> = 72)	50%	50%	0%	28%	72%	0%	–	–	–	–	–	–
1–6 (<i>n</i> = 90)	–	–	–	14%	82%	4%	19%	73%	8%	4%	73%	23%
> 6 (<i>n</i> = 37)	–	–	–	–	–	–	9%	73%	18%	14%	53%	33%
Post-crash years (<i>n</i> = 160)												
Age (years)												
< 1 (<i>n</i> = 34)	27%	73%	0%	–	–	–	–	–	–	–	–	–
1–6 (<i>n</i> = 98)	–	–	–	8%	92%	0%	9%	71%	20%	24%	41%	35%
> 6 (<i>n</i> = 28)	–	–	–	–	–	–	17%	59%	24%	37%	25%	38%

–, < 5 animals of that age observed in that weight class.

ton-Brock *et al.* 1991). Where there were no significant differences in survival or fecundity between pre- and post-crash years, we combine these in a 'non-crash' category.

Virtually all animals using the study area are ear-tagged at birth so that their ages are known. In a minority of cases, individuals are tagged as adults and analysis of cementum rings in incisor teeth is used to estimate age after death (Clutton-Brock *et al.* 1991). Mortality is measured by systematic searches for carcasses in winter and early spring (Clutton-Brock *et al.* 1991) combined with regular censuses of tagged animals during the lambing season. Almost all animals dying in the summer months are new-born lambs (Grubb 1974), most of which die within 10 days of birth. A second peak in mortality occurs in late winter, between the end of December and the onset of lambing (Grubb 1974). Many dying animals seek shelter in the dry stone chambers (cleits) that are scattered over the slopes of Village Bay so that a high proportion of carcasses can be found and recorded. Since 1985, 84.4% of animals tagged have been recovered or are currently known to be alive.

Fecundity is measured from records of the number of lambs born in April and May. Each year, around 95% of lambs are caught and weighed within 3 days of birth (Robertson *et al.* 1992). In addition, all animals dying in winter are autopsied and the numbers of foetuses present are counted. A proportion of individuals are caught and weighed each August (Clutton-Brock *et al.* 1992) and these age-specific weights are used in the statistical models as a measure of condition. This reduces the sample sizes in these analyses since only 40–50% of study area sheep are caught annually.

STATISTICAL ANALYSIS

We use multiple linear regression to examine the factors affecting the summer weights of ewes and the birth weights of lambs, combining a set of all likely explanatory variables and interactions between them as terms in a maximal regression model. Terms are dropped until the model includes only those whose elimination would significantly decrease the explanatory power of the model. Any of the explanatory terms may be correlated, so the importance of some terms may be masked by the inclusion of others. We subsequently test whether any of the terms eliminated previously could improve the model. When a model is achieved where no term can be dropped and no term can be added, the analysis is complete.

To determine which factors affected the viability of juveniles, we use logistic regression models (Cox 1970). This technique fits a logistic probability curve through binary data and has been used to investigate the factors affecting fertility and survival in red deer (Albon *et al.* 1986; Clutton-Brock *et al.* 1987a, b; Mitchell & Brown 1974) and Soay sheep (Clutton-Brock *et al.* 1992). Continuous variations (such as body weight) can be included in these models.

The logistic curve has the form

$$P(y = 1) = \frac{\exp(G)}{1 + \exp(G)}$$

where $P(y = 1)$ is the probability that an individual will die; G is analogous to a standard regression equation and is

$$G = A + B_1X_1 + \dots + B_{iN}X_{iN}$$

where A is constant; X_{i1} , X_{iN} are the first and i th

independent terms in the model; B_1 , B_N are the coefficients for the first and n th terms of the model; and $i = 1, 2, 3, 4 \dots N$ (individual sheep).

The parameters of the logistic model are estimated by maximum likelihood, which provides a convenient index of goodness-of-fit of a model including a particular set of parameters and can be used to determine whether the inclusion of extra parameters in the model significantly improves the fit. This is done by comparing the difference between the 'deviance' values of the model before and after the parameter was added to the model. Deviance is analogous to the F ratio in standard regression analysis but is distributed approximately as chi-square with degrees of freedom equal to the difference in the number of degrees of freedom between the model with and without the test term(s). A final model for neonatal mortality, lamb winter mortality and yearling winter mortality is decided upon from a full set of possible terms using the same method of elimination described above for multiple regression (see Table 4). The column '% total deviance' provides an index of the goodness-of-fit of the term compared to a hypothetical model that explained all of the variation in the dependent variable. Within factors, separate levels are compared by dividing the difference in coefficient estimates by the standard error of this difference (Sokal & Rohlf 1981). This test of coefficient homogeneity is distributed as t , with degrees of freedom equal to the residual in the model. GENSTAT 5 was used throughout (GENSTAT 5 Committee 1987).

Since survival is a binary response, we have summarized these data in graphs as mean survival within contiguous classes of the explanatory variable. It is important to note that these means are not the data upon which the logistic regressions are based, and may in some cases provide a poor representation of these data. In analyses, confounding variables are held constant in order to examine a specific relationship, thus utilizing information from the full dataset. However, in plotting the figures, there is no way to control for such variables and so we must display a subset of the data, classified by these factors. This inevitably results in small sample sizes on which to base the class means. And, since we are dealing with binary data, these are often heavily skewed by the influence of single points. Thus, while the relationships may accurately reflect the raw binary data there may, in some cases, be an apparent mismatch with the summarised data.

MODELLING OPTIMAL LIFE-HISTORY TACTICS

To model the reproductive tactics of ewes, we use stochastic dynamic programming (Bellman 1957), treating reproduction as a state-dependent life-history decision, following McNamara (1991). Animals are assumed to choose between alternative

decisions on an annual basis. The alternative decisions we considered were:

1. to avoid breeding in the current year;
2. to produce one offspring;
3. to produce twins.

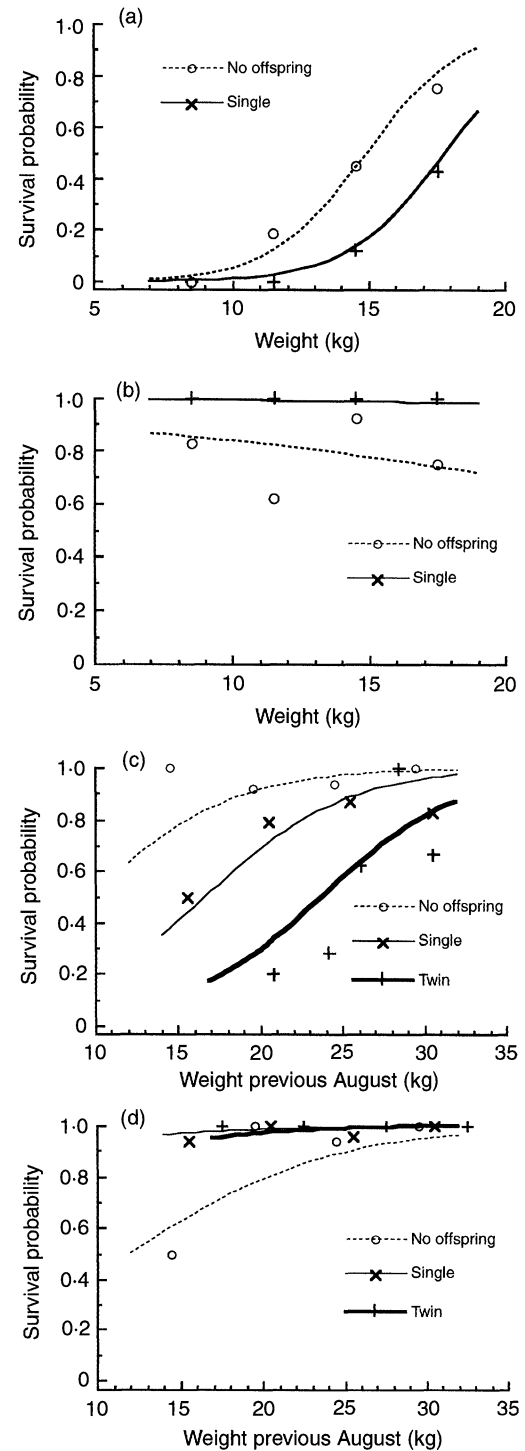


Fig. 1. Effects of breeding on survival for animals of different weight (measured the previous August): (a) juveniles in crash years; (b) juveniles in non-crash years; (c) ewes in crash years; (d) ewes in non-crash years. Symbols show the proportion of animals in different categories that survived. Survival probability is standardized for all significant terms in Models 1 and 2 (Table 5).

Although the actual decision is whether or not to conceive one or two offspring, it is not possible to observe this in the field and thus we inferred decisions several months later, when offspring were born. We consider only females, so we assume that there are sufficient males present to fertilize all females, and thus we do not have to consider their life histories separately (we assume female demographic dominance, e.g. Charlesworth 1980). In the model, yearlings are amalgamated with adults since relationships between body weight and survival do not differ in slope or intercept between these two groups. Animals of ≥ 7 years of age are treated as a separate category since survival declines after the age of 6 years (Grubb 1974).

State variables

Animals vary in state, both between individuals and over each animal's lifetime. The state of an animal is described by a number of variables, which represent relevant phenotypic characters. Although many phenotypic characters that we wish to consider will be continuous, we group them into discrete classes for the purposes of the optimization modelling. In this study the state variables are as follows.

1. *Weight measured in the most recent August catch-up.* Animals are grouped into one of four weight-classes: < 15 kg, > 15 kg but < 20 kg, > 20 kg but < 25 kg and > 25 kg.
2. *Age measured during the rut.* Animals are assigned to one of three age-classes: < 1 year (lambs), 1–6 years old (adults), and > 6 years old (old animals).
3. *Previous reproductive status.* This variable has one of three values: (i) did not breed, (ii) produced one offspring, or (iii) produced twins.
4. *Stage of the population cycle.* Though this is an aspect of the external environment rather than part of the state of an animal, it can be considered in the same way as a state variable. We classify years according to the level of mortality in each, and then define the years with highest mortality as crash years, and the preceding and following years as pre- and post-crash years (since we observe a 3-year population cycle). All animals then take the appropriate value of this variable for the year they are in.

Expected number of descendants

In order to determine the optimal reproductive decisions that females should take, we need to calculate the expected number of descendants that an animal in each state taking each of the decisions will produce. For each reproductive decision (number of offspring produced) taken in a given state descendant numbers can be found from the following four quantities.

1. The survival probability of the animal to the next year, given its initial state.
2. For each possible new state next year, the probability that the animal is in the new state, given that it survives from its initial state in this year.
3. The probability that each offspring produced survives until the next year.
4. For each possible new state next year, the probability that an offspring is in the new state, given that it survives.

State change rules and survival probabilities

The survival probabilities of animals are derived directly from the field data using generalized linear

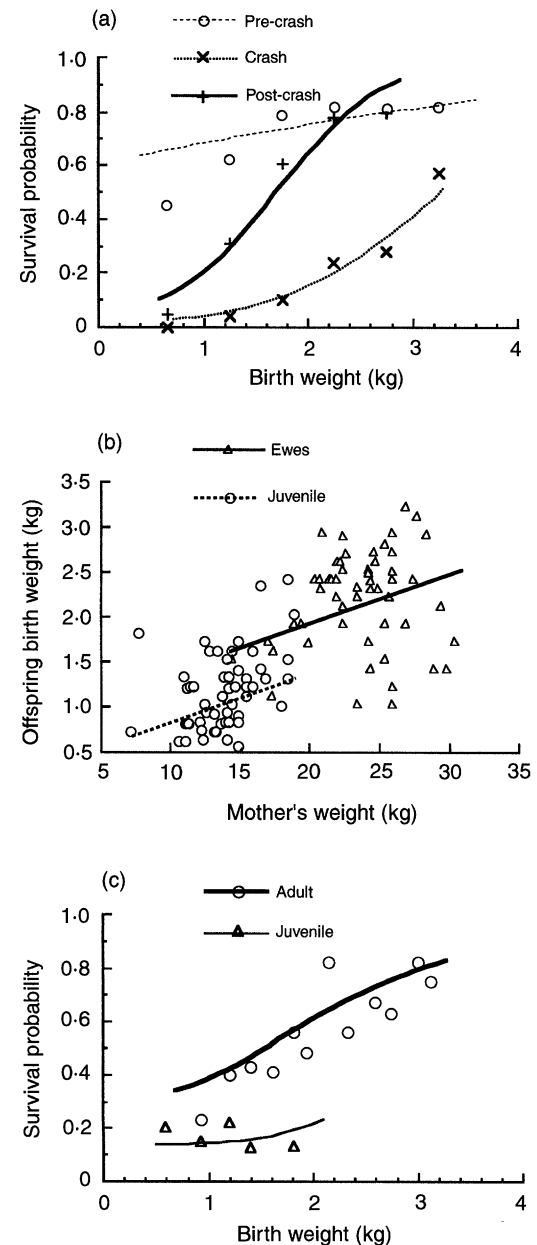


Fig. 2. Relationships between (a) juvenile survival and birth weight, (b) birth weight and mother's weight the previous August, (c) juvenile survival and birth weight, for lambs born to different categories of mothers (plotted for female offspring, averaged across the cycle).

modelling as described above (Fig. 2). To control for quality differences among females other than those caused by weight and age, which result in lower survivorship of non-breeders than breeders in non-crash years (Fig. 2b, d), we modify the survival probability parameters so that the number of offspring a female produces does not affect its survival in non-crash years. We do this by setting the parameter for non-reproducing females' survival in pre-crash years to the value of the parameter for females producing one offspring at the same stage of the cycle. Parameters for females producing twins and for survival in post-crash years are zero, as a consequence of the statistical modelling process, and thus are not changed.

For changes in weight, a matrix for transitions between weight-classes is derived by comparing field data between years for individual animals. For age, the transition probabilities between the three age-classes reflects the sizes of the age-classes and the annual time-scale of decisions. Thus, the transition from the first to the second age-class occurs with probability 1.0, at the end of the first year. The transition from the second to the third age class occurs with probability 0.167, since animals will remain in this age-class for 6 years. Hence, with probability 0.833, animals that start in the second age class will remain in it. Clearly, animals in the third age class will remain in it with probability 1.0.

For previous reproductive status, the new value of the state variable is set to the previous decision, with probability 1.0. Finally, for the stage of the population cycle we adopt two sets of transition rules. The first, intended to represent the situation where females use information about the population cycle assumes that different stages of the cycle follow each other in sequence, pre-crash year, crash year, post-crash year, etc. The second set represents a situation where females have no information about the population cycle. Here we assume that stages of the cycle succeed each other at random, so the probability of transition from any stage of the cycle to any other is 0.333. Clearly this does not represent the situation we observe, but it may be a useful attempt to represent what females perceive.

Offspring state

The states that offspring are assigned to depend upon the state of their mothers. Survival probabilities for offspring were calculated from a logistic regression on lamb birthweight (Fig. 3a). Each offspring is assigned to a weight class based upon a linear regression of birthweight on adult weight from the study population. Clearly, each offspring must start in the first age class. Since no offspring has previously reproduced, the initial value of the previous reproductive value state variable is set to zero (did not reproduce). Offspring follow the same population cycles as adults.

Calculating optimal strategies

Having calculated the above quantities, we are in a position to evaluate optimal reproductive strategies. A strategy specifies the reproductive decision that is taken in each state. An optimal strategy maximizes the number of descendants left far into the future. This strategy can be found by an iterative process using dynamic programming – see Marrow *et al.* (1996) for details.

Evaluating optimality results

We can compare the optimal strategy with observed fecundity patterns in order to determine whether ewes perform optimal behaviour. Although this means we use part of the same dataset both to construct and to test the model, the optimization results are independent of the observed reproductive behaviour since they depend upon the observed survival trends and weight changes of the animals, and not upon the observed reproductive behaviour. In the optimization process we test all possible patterns of fecundity, and not merely those observed.

In comparing behaviour predicted by the optimal strategy with observed behaviour it is not possible to test the similarity of the predictions with the data directly using statistical tests, since the optimal strategy gives no information about the proportions of animals that are expected in different states. However, we can gain a clear qualitative impression of the resemblance from the optimal strategy results.

To allow direct comparison between the optimization results and data we can use the state-change rules and survival probabilities to follow a population forwards as it performs some given set of decisions. We do not do this here because we concentrate upon the optimal strategy, but we use this approach elsewhere (see Marrow *et al.* 1996).

Results

COSTS OF PREGNANCY

In non-crash years, over-winter survival is high and does not differ between age categories. In contrast, in crash years, the survival of juveniles and ewes > 6 years old is lower than that of 1–6 year olds (see Tables 3a and 4). Probability of survival increases with body weight (Table 4, Model 1).

In crash years, the costs of pregnancy to juveniles are very high. Despite low overall levels of survival, juveniles pregnant with a single offspring are around half as likely to survive as those that are not pregnant (Fig. 1a; Table 4, Model 1). In non-crash years, when the survival of all age categories is high, there are no obvious costs of pregnancy to juvenile survival: pregnant juveniles are rather more likely to survive the winter than non-pregnant animals, presumably

because of superior weight and condition in autumn (Fig. 1b; Table 4, Model 1).

Among ewes, too, pregnancy in crash years has substantial costs to lighter animals. Relative to their weight the previous August, non-pregnant ewes show higher survival in crash years than those carrying single offspring, while ewes carrying twins have lower survival than those carrying singletons (Fig. 1c; Table 4, Model 1). These differences again disappear in non-crash years and non-pregnant animals show lower survival than pregnant ones (Fig. 1d; Model 1).

COSTS OF REARING OFFSPRING

As in bighorn sheep, *Ovis canadensis* (Festa-Bianchet 1989; Festa-Bianchet *et al.* 1995), there is no evidence that lactation reduces a ewe's fecundity or the survival of her subsequent offspring. Both among juveniles and among ewes, individuals that avoid the costs of lactation because they fail to rear offspring successfully are no more likely to survive to the next year (whether this is a crash or a non-crash year) than individuals that raise offspring successfully (Table 3b; Table 4, Model 2). Nor is there any evidence that lactation reduces fecundity in the subsequent breeding season: both among juveniles and ewes, females that fail to breed one year produce fewer offspring the following year than those that raise singletons or twins (Table 4, Model 3).

The absence of any reduction in the fecundity of ewes that breed successfully is probably related to their ability to regain body weight lost during lactation by the beginning of winter. Though there are significant differences in body weight in August among ewes that have raised different numbers offspring that year (Table 2b; Table 4, Model 4), differences are relatively small and vary between age classes: among juvenile mothers, those that have raised single offspring are slightly heavier in August than those that have failed to do so ($t_{456} = 2.11$, $P < 0.05$); among yearlings, there are no significant differences in weight between those that have bred successfully and those that have failed to breed ($t_{456} = 0.268$, NS); and, among older females, individuals that have raised single offspring are lighter than those that have either failed to breed or raised twins ($t_{456} = 2.57$, $P < 0.025$; $t_{456} = 3.675$, $P < 0.001$).

RELATIVE BENEFITS OF BREEDING

The benefits of producing offspring at different stages of the cycle vary with the mother's body weight. At all ages, heavier females give birth to heavier offspring (Table 5, Model 5). Both in post-crash years (when neonatal mortality is high) and in crash years (when many juveniles die in winter) the survival of juveniles is positively related to their birth weight, though no relationship is apparent in the relatively good conditions of pre-crash years (Fig. 2a; Table 4, Model 6).

Table 2 (a) Mean August (live) weights (kg) of female sheep at different stages of the cycle calculated directly from the data. Standard errors and sample sizes are also shown. (b) Mean August live weights (kg) of female sheep comparing mothers that gave birth to 0, 1 or 2 lambs. Figures are derived from data collected in all years and control for the stage of the population cycle (Table 5, Model 4)

(a)

Age	Pre-crash	Crash	Post-crash
Juvenile	14.4 ± 0.26	13.8 ± 0.26	12.3 ± 0.42
<i>n</i>	69	110	38
Yearling	19.4 ± 0.44	19.1 ± 0.25	18.3 ± 0.53
<i>n</i>	31	81	20
2–6 years	25.2 ± 0.31	23.9 ± 0.28	23.1 ± 0.27
<i>n</i>	59	131	97
> 6 years	25.4 ± 0.55	25.1 ± 0.43	23.8 ± 0.57
<i>n</i>	27	47	28

Using multiple linear regression to estimate fixed effects in an unbalanced dataset: age $F_{3,732} = 713.2$, $P < 0.001$; year $F_{2,732} = 19.8$, $P < 0.001$.

(b)

Age	Number of offspring born		
	0	1	2
Juvenile	17.6 ± 0.46 (<i>n</i> = 30)	18.7 ± 0.29 (<i>n</i> = 92)	–
Yearling	22.2 ± 0.87 (<i>n</i> = 9)	21.6 ± 0.35 (<i>n</i> = 52)	–
> 2 years	26.0 ± 0.43 (<i>n</i> = 33)	24.2 ± 0.18 (<i>n</i> = 201)	25.7 ± 0.31 (<i>n</i> = 63)

Table 3 (a) Mean survival of ewes by age in different years. (b) Effects of reproductive status in previous breeding season on survival in crash and non-crash years. Estimates are shown ± SE

(a)

Age of female	Pre-crash	Crash	Post-crash
Juveniles	0.87 ± 0.033	0.25 ± 0.038	0.91 ± 0.029
<i>n</i>	107	130	100
1–6 years	0.97 ± 0.013	0.75 ± 0.025	0.96 ± 0.012
<i>n</i>	179	297	267
> 6 years	0.91 ± 0.039	0.54 ± 0.057	0.95 ± 0.029
<i>n</i>	55	77	58

(b)

Age of female	Previous breeding status	Non-crash	Crash
Yearling	Single	0.98 ± 0.014	0.76 ± 0.11
	Twin	0.98 ± 0.014	0.74 ± 0.84
	None	0.98 ± 0.013	0.75 ± 0.10
2–6 years	Single	0.98 ± 0.010	0.74 ± 0.06
	Twin	0.98 ± 0.013	0.77 ± 0.09
	None	0.95 ± 0.030	–
> 6 years	Single	0.94 ± 0.023	0.53 ± 0.08
	Twin	0.95 ± 0.031	0.57 ± 0.13

Table 4. Logistic models of factors affecting (1) female over-winter survival (2) female over-winter survival incorporating effects of previous year's fecundity (3) fecundity of ewes (4) weight of ewes at the end of the summer (5) the birth weight of lambs (6) survival to one year. The division of years into 'crash or non-crash' was more parsimonious, and did not entail a significant loss of information, than a classification of 'pre-crash, crash and post-crash': $\chi^2 = 5.1$, 4 d.f., NS

1. Analysis of deviance table for model of over-winter survival in ewes.

Terms	d.f.	Deviance	% deviance	<i>P</i>
Weight	1	26.7	4.5	< 0.001
Pop-cycle				
(crash/non-crash)	1	33.2	5.6	< 0.001
No-offspring (0, 1, 2)	2	6.0	1.0	0.05
Age (0, 1-6, > 6)	2	8.9	1.5	< 0.025
No-offspring, pop-cycle	2	32.9	5.6	< 0.001
Weight.pop-cycle	1	22.4	3.8	< 0.001
Weight.age	2	6.2	1.1	< 0.05
Residual	565	326.8		
Total	576	592.7		

2. Analysis of deviance for female over-winter survival, including the previous year's fecundity leading to reduced sample size. Although previous fecundity is not significant, the interaction with the pop-cycle apparently is significant. However, the overall effect of previous fecundity (including the main effect plus interaction) is not significant and both terms are excluded ($\chi^2 = 6.6$, 4 d.f., NS).

Terms	d.f.	Deviance	% deviance	<i>P</i>
Weight	1	20.7	7.1	< 0.001
No-offspring (0, 1, 2)	2	5.2	1.8	NS
Age (1, 2-6, > 6)	2	5.9	2.0	0.06
Pop-cycle				
(crash/non-crash)	1	58.3	20.0	< 0.001
No-offspring, pop-cycle	2	11.0	3.8	< 0.005
Residual	344	192.4		
Total	352	291.6		
Excluded terms				
Previous fecundity	2	0.1	NS	
Prev-fecundity, pop-cycle	2	6.5	< 0.05	

3. Analysis of deviance for model examining association between previous and current fecundity.

Terms	d.f.	Deviance	% deviance	<i>P</i>
Prev-fecundity	2	27.0	8.3	< 0.005
Residual	777	299.3		
Total	779	326.3		
Excluded terms				
Pop-cycle	2	0.9	NS	
Prevfecundity, pop-cycle	4	2.0	NS	

Table 4 (continued)

4. Terms included in the model examining the weight of ewes in August following lambing.

Terms	d.f.	<i>F</i>	% variance	<i>P</i>
Age (0, 1, > 1)	2	211.09	42.5	< 0.001
No-lambs (0, 1, 2)	2	6.74	1.3	< 0.01
Pop-cycle				
(pre,crash,post)	2	2.89	0.6	NS
Age.pop-cycle	4	4.21	1.6	< 0.01
No-lambs.age	3	5.50	1.6	< 0.01
Residual	456			
Total	469			

5. Terms included in model examining birth weight.

Terms	d.f.	<i>F</i>	% variance	<i>P</i>
Lamb-sex	1	5.28	0.7	< 0.05
No-offspring (1, 2)	1	131.54	17.9	< 0.001
Pop cycle				
(pre, crash, post)	2	71.09	19.7	< 0.001
Mother's age (0, > 0)	1	25.17	4.9	< 0.001
Mother's weight	1	46.73	7.1	< 0.001
Pop cycle, mother's age	2	4.31	1.1	< 0.05
Residual	342			
Total	350			

6. Analysis of deviance for factors affecting survival of juveniles to 1 year of age.

Terms	d.f.	Deviance	% deviance	<i>P</i>
Sex	1	7.9	0.8	< 0.001
Pop-cycle				
(pre, crash, post)	2	46.5	4.7	< 0.001
Mother's age (0, > 0)	1	9.0	0.9	< 0.005
Birthweight	1	37.2	3.8	< 0.001
Pop-cycle, birthweight	2	18.6	1.9	< 0.001
Residual	702	706.5		
Total	709	983.7		
Terms excluded				
No-lambs (1, 2)	1	0.8	NS	
No-lambs, Pop-cycle	2	1.3	NS	

Juveniles produce offspring that are lighter than those of adult ewes (Fig. 2b; Table 4, Model 5). Partly as a result of the lighter birth weights of their offspring, juveniles are less likely to raise their progeny to weaning (6 weeks) or maturity (12 months) than older mothers (Table 5; Table 4, Model 6). This difference occurs in pre- as well as post-crash years but is greatest in crash years, when less than 10% offspring born to juveniles survive to maturity. The lower birth weights of the offspring of juvenile mothers are not responsible for the whole of this effect, for they show lower sur-

Table 5. Predictions from generalized linear regression models: effects of mother's age on (a) birthweight (kg) (Table 4, model 3), and (b) survival of juveniles to 12 months (Table 4, model 4). Values shown are for single offspring of a ewe of average weight for her age class at conception (juvenile, 14.2 kg; > 1 year, 23.1 kg) (\pm SE)

Year category	Age of mother at conception	
	≤ 1 year	≥ 1 year
Pre-crash	1.51 \pm 0.126	2.34 \pm 0.048
Crash	1.71 \pm 0.103	2.22 \pm 0.050
Post-crash	1.37 \pm 0.188	1.63 \pm 0.044

(a)

Year category	Effect of mother's age on survival offspring	
	≤ 1 year	≥ 1 year
Pre-crash	0.59 \pm 0.062	0.78 \pm 0.029
Crash	0.06 \pm 0.02	0.14 \pm 0.03
Post-crash	0.38 \pm 0.084	0.60 \pm 0.043

(b)

vival than the offspring of older females when differences in birth weight are controlled (Fig. 2c; Table 5, Model 6).

The (individual) birth weights of twins are lower than those of singletons (Table 6a; Table 4, Model 5) and their survival is lower in crash and post-crash years (Table 6b; for offspring of mothers 1–6, $t_{344} = 15.7$, $P < 0.001$). The lower survival of twins is apparently attributable to their reduced birth weight for it disappears when birth weight is controlled (Table 4, Model 6).

As in many other dimorphic mammals (Clutton-Brock *et al.* 1991), males are born heavier than females (Table 4, Model 5). Despite this, juvenile males suffer higher mortality rates than juvenile females, both absolutely and relative to their birth weight (Table 6c; Table 3, Model 6), especially in post-crash and crash years.

ARE REPRODUCTIVE TACTICS OPTIMAL?

The results of our state-dependent life-history model (see above) suggest that the number of offspring produced should vary with the mother's weight as well as with the year of the cycle (Fig. 3a–c). In pre-crash years, all lambs should produce singletons but only the heaviest ewes should produce twins (Fig. 3a). In contrast, in crash years, all juveniles as well as ewes of less than 20 kg should avoid breeding, while even heavier ewes should avoid twinning (Fig. 3b). The highest fecundity should occur in post-crash years: here, all juveniles should produce singletons while all older females should produce twins (Fig. 3c).

While there is a consistent tendency for fecundity to increase with body weight in all categories of

Table 6. (a) Average birth weights (weights are averaged across all stages of the cycle and are corrected for capture age) of single and twins born to mothers of different ages (\pm SE).

Mother's age (years)	Single	Twin
< 1	1.33 \pm 0.038 ($n = 140$)	– ($n = 0$)
1–6	2.02 \pm 0.029 ($n = 434$)	1.55 \pm 0.048 ($n = 79$)
> 6	2.18 \pm 0.060 ($n = 79$)	1.44 \pm 0.054 ($n = 32$)

(b) Average survival (across post-crash and crash years) of singletons and twins born to mothers of different ages (\pm SE).

Mother's age (years)	Single	Twin
< 1	0.04 \pm 0.021 ($n = 93$)	– ($n = 0$)
1–6	0.37 \pm 0.027 ($n = 304$)	0.29 \pm 0.071 ($n = 42$)
> 6	0.49 \pm 0.066 ($n = 59$)	0.14 \pm 0.078 ($n = 21$)

(c) Average survival (across the years) of male and female offspring born to mothers of different ages (\pm SE).

Mother's age (years)	Male	Female
< 1	0.28 \pm 0.057 ($n = 64$)	0.24 \pm 0.053 ($n = 66$)
1–6	0.47 \pm 0.033 ($n = 219$)	0.59 \pm 0.031 ($n = 249$)
> 6	0.53 \pm 0.072 ($n = 49$)	0.55 \pm 0.064 ($n = 62$)

animals, it does not vary with population size in the predicted manner (Table 1, Fig. 3b). In crash years, fecundity is substantially higher than expected: a substantial proportion of juveniles produce singletons (< 15 kg, 50%; < 20 kg, 72%); most animals of < 20 kg produce singletons; and a substantial proportion of prime ewes produce twins (< 20 kg, 4%; < 25 kg, 8%; > 25 kg, 23%). In contrast, in pre- and post-crash years, fecundity levels are lower than expected. Though all juveniles are predicted to breed, a substantial number fail to do so while twinning rates in the heavier categories of ewes are consistently lower than values predicted by our model (see Table 1, Fig. 3a, c).

ARE REPRODUCTIVE TACTICS OPTIMAL WITHIN CONSTRAINTS?

The results described above suggest that the sheep are able to adjust their fecundity to their body weight but not to fluctuations in population size and associated changes in the costs of breeding. This raises a subsidiary question: if they are unable to respond appropriately to changes in population size, do their

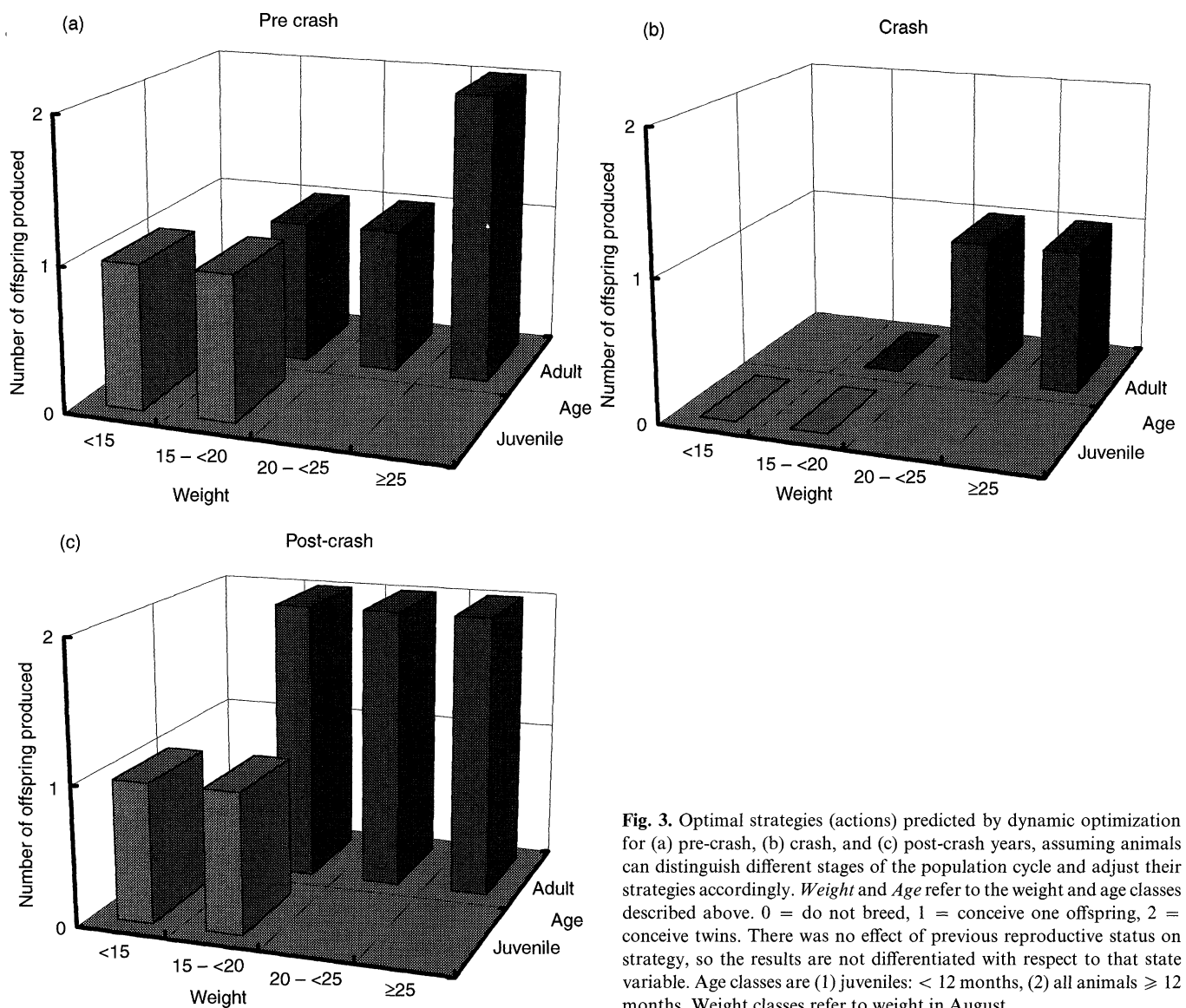


Fig. 3. Optimal strategies (actions) predicted by dynamic optimization for (a) pre-crash, (b) crash, and (c) post-crash years, assuming animals can distinguish different stages of the population cycle and adjust their strategies accordingly. *Weight* and *Age* refer to the weight and age classes described above. 0 = do not breed, 1 = conceive one offspring, 2 = conceive twins. There was no effect of previous reproductive status on strategy, so the results are not differentiated with respect to that state variable. Age classes are (1) juveniles: < 12 months, (2) all animals ≥ 12 months. Weight classes refer to weight in August.

observed, weight-specific levels of fecundity correspond to an 'average' optimum calculated across years of varying density?

To model this situation, we allowed any stage of the cycle to succeed the present one with equal probability, preventing the animals from predicting the status of the following year. The predicted actions for this case are given in Fig. 4. The model predicts that juveniles of < 15 kg should produce single offspring while those of 15–20 kg should avoid breeding. Ewes under 25 kg would be predicted to produce a single offspring while ewes over 25 kg would be expected to twin.

In most cases, this model predicts observed patterns of fecundity. The most obvious discrepancy between the predictions of the model and our empirical results was the predicted avoidance of breeding by heavier juveniles (see Fig. 4). This result probably occurs because heavy juveniles that avoid breeding are substantially more likely to survive than light juveniles that do so (Fig. 1a). As a result, breeding leads to a

greater decline in the survival probability of heavy juveniles than in the survival probability of light ones, raising the marginal costs of breeding. However, only a small reduction in the costs of breeding is necessary for reproduction to be favoured among heavier juveniles (Fig. 5b). Twinning is rather more common among ewes of 20–25 kg than our model predicts, ranging from 8 to 20%, depending on the year of the cycle (see Table 1). In contrast, it is less common than predicted among ewes of over 25 kg, ranging from 23 to 35% in relation to the year (Table 1). In addition, ewes over 6 years old showed a persistent tendency to produce more twins than younger animals (Table 1).

SENSITIVITY ANALYSIS

In assessing the results from optimization models, it is important to test the sensitivity of the results to changes in model parameters and assumptions (Gladstein, Carlin & Austad 1991; Houston, McNamara & Thompson 1992). We perform sensitivity

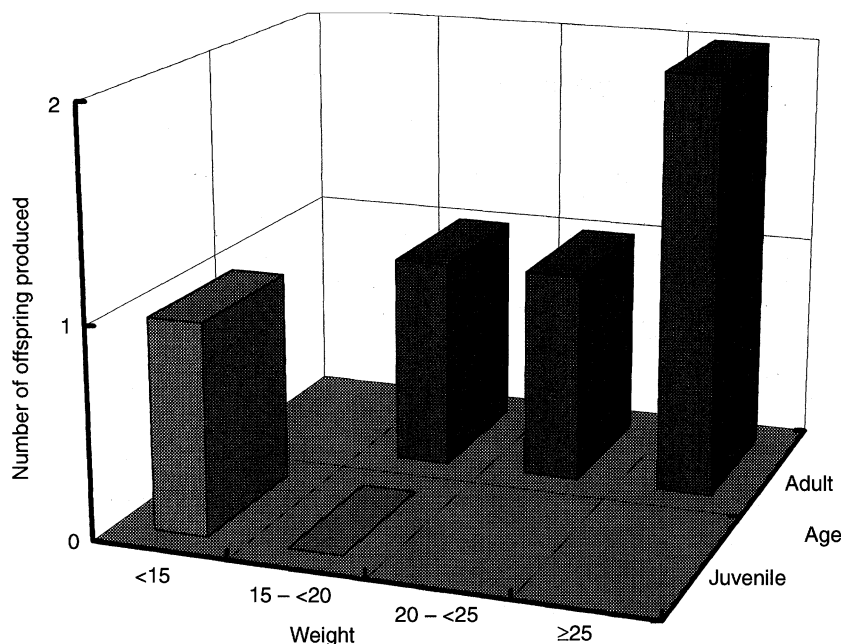


Fig. 4. Optimal actions predicted by dynamic optimization, when animals experience any stage of the population cycle with equal probability in the following year. Under these conditions, mothers have imperfect information about population density in the following year though they can adjust their fecundity to their body weight in August.

analysis of model results in two ways. First, we check the sensitivity of the optimal strategy results as we modify controls on effects of quality other than through the state variables included in the model. Secondly, we test the robustness of the optimal strategy as assumptions about the mortality costs of reproduction are varied.

A separate issue is whether animals following the optimal strategy have a substantial selective advantage over animals following alternative strategies for, if they do not, small changes in environmental conditions could remove the advantage of the optimal strategy in nature. McNamara & Houston (1986) have developed the notion of 'canonical cost' to measure this selective advantage. The canonical cost of a decision in a given state, is the difference between the fitness of an animal following the optimal decision and the fitness of an animal following that decision, assuming all subsequent behaviour is optimal.

Elsewhere (Marrow *et al.* 1996) we measure the canonical costs of alternative actions for the two optimization models we consider here. There we show that, for the majority of values of state variables, the canonical costs of suboptimal actions are substantial, and animals that follow the optimal strategies have a real selective advantage. As a consequence we do not repeat the analysis here, and readers are referred to that paper for more discussion of the issues involved.

Robustness of predictions as effects of quality differences varied

In all the results shown above the effects of quality on ewe survivorship, other than through the main state variables (Fig. 1d), were controlled for by making the consequences of producing no offspring identical to

those of producing one offspring, in non-crash years. This removed the expected higher survivorship of reproducing ewes. We checked the robustness of predictions to this deviation from the statistical models by first restoring the parameters to their predicted values, so including quality differences not accounted for by the state variables, and secondly, setting the survivorship of reproducing ewes to be identical to that of non-reproducing ewes. This controlled for effects of phenotypic quality in the opposite way to the model results above.

Whether or not animals could use information about the population cycle, the different combinations of parameters that we tested gave the same optimal strategies (Figs 3 and 4). We conclude from the results of this sensitivity test that, although there are phenotypic effects acting in the population that we cannot take into account in the models through lack of data, our models based upon weight, age, and stage of the population cycle give a robust estimate of the optimal strategy, even when the effects of unknown phenotypic variation on survival are taken into account.

Robustness of predictions to changes in mortality costs

Another possible source of error in the model is through errors in the estimated cost of reproduction. We attempted to reduce these errors by choosing model parameters that corresponded to the minimal statistical models required to explain trends in survival. To test the robustness of our results with errors in estimation of costs, we repeated the dynamic optimization while changing the predicted mortality probability for certain classes of animal (Fig. 5). By recording the fitness values we could assess changes

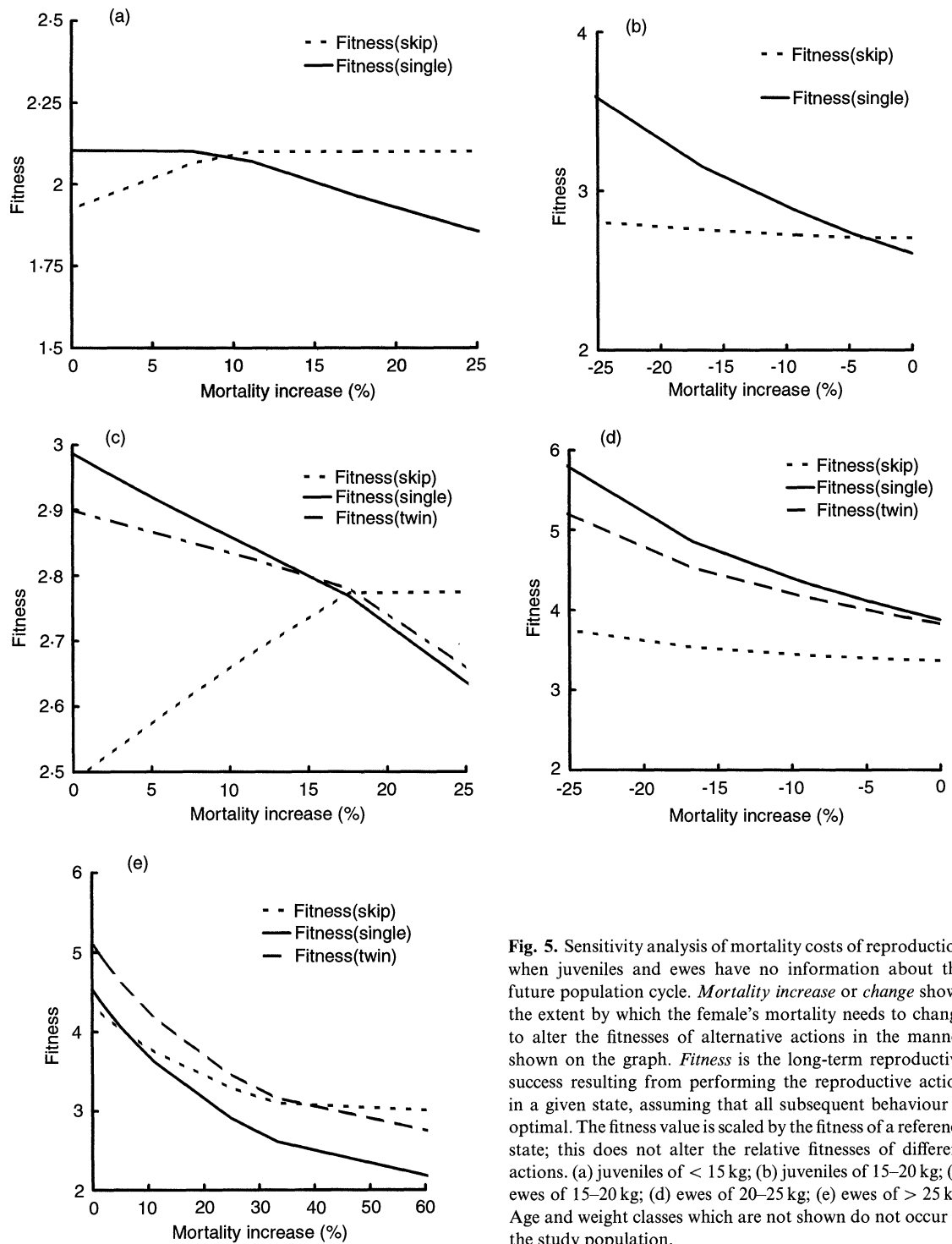


Fig. 5. Sensitivity analysis of mortality costs of reproduction when juveniles and ewes have no information about the future population cycle. *Mortality increase* or *change* shows the extent by which the female's mortality needs to change to alter the fitnesses of alternative actions in the manner shown on the graph. *Fitness* is the long-term reproductive success resulting from performing the reproductive action in a given state, assuming that all subsequent behaviour is optimal. The fitness value is scaled by the fitness of a reference state; this does not alter the relative fitnesses of different actions. (a) juveniles of < 15 kg; (b) juveniles of 15–20 kg; (c) ewes of 15–20 kg; (d) ewes of 20–25 kg; (e) ewes of > 25 kg. Age and weight classes which are not shown do not occur in the study population.

to the optimal strategy, as the decision which gave the highest fitness changed.

We investigated successively how great a change in the mortality costs of breeding would be necessary to cause juveniles of < 15 kg to avoid breeding; juveniles of 15–20 kg to breed; ewes of 15–20 kg to avoid breeding and ewes of 20–25 kg to avoid twinning. Figure 6a shows that a 10% increase in mortality costs would be necessary for juveniles of < 15 kg to avoid breeding. Only a 4% reduction in the mortality costs of breeding would be necessary to favour breeding by heavier

juveniles (Fig. 5b) suggesting that, in better years, avoiding breeding would not be the optimal action for heavier juveniles. For ewes in the lightest weight category (15–20 kg), a substantial (20%) increase in mortality would be necessary to favour avoiding breeding altogether (Fig. 5c) while, for those in the 20–25 kg range, producing a single offspring remains the optimal action at all mortality levels that we investigated (Fig. 5d). For ewes over 25 kg, twinning remains the optimal action unless observed mortality costs rise by more than 40% (Fig. 5e).

We conclude that for the exception of juveniles under 15 kg, the predicted optimal strategy is robust to errors of reasonable magnitude in the estimation of mortality costs of reproduction.

Discussion

Our results emphasize the extent to which the costs of breeding vary between categories of females as well as between years. As might be expected, the effects of breeding on the mother's survival were most pronounced among lighter mothers and were small among heavier ones (Fig. 1c). These effects varied between years: in non-crash years, there were no discernible costs of producing or rearing offspring to the mother's survival or subsequent breeding success in any category of mothers.

In crash years, by contrast, pregnant juveniles were less likely to survive than those that failed to conceive or lost their foetus at an early stage of pregnancy, while ewes were most likely to die if they produced twins and least likely to do so if they were not pregnant. The costs of breeding again varied between categories of mothers.

The benefits of breeding also varied between years of the cycle as well as between different age and weight categories of mothers. Both in post-crash years (when neonatal mortality was high) and in crash years (when many juveniles died in winter), the survival of offspring was related to their birth weight, which varied with their mother's age and weight (Fig. 2b). The offspring of heavier mothers were born heavier and had an improved chance of survival. In addition, the mother's age had an independent effect: when birth weight and mothers' weight were controlled, the offspring of juveniles still showed lower survival than those of older females. As a result of these effects, the benefits of breeding to juveniles and light ewes declined in crash and post-crash years.

The costs of gestation and lactation in the sheep show a pronounced contrast with similar costs in red deer (Clutton-Brock *et al.* 1983). In red deer, females that are pregnant are apparently no more likely to die in winter than non-pregnant females while there are substantial costs associated with rearing calves: mothers that successfully raise offspring are more likely to die the following winter and, if they survive, are less likely to breed again than mothers that have not raised calves (Clutton-Brock, Albon & Guinness 1989; Clutton-Brock, Guinness & Albon 1982; F. E. Guinness, unpublished data). This is apparently a result of the costs of lactation rather than gestation, for mothers that bear calves but lose them in their first month of life do not show lower survival the following winter than those that fail to bear calves altogether (Clutton-Brock *et al.* 1989). The contrast between sheep and deer is probably related to the timing of reproduction. The principal energetic costs of gestation in ungulates occur during the last 1–2 months

before parturition (Robbins 1983; Sadleir 1969). In Soay sheep, this occurs in February and March, when food availability is at its lowest and the energetic costs of thermoregulation can be substantial. In contrast, in red deer, the greatest costs of gestation occur in April and May, when food availability and weather conditions have improved.

The higher costs of lactation in red deer are probably also partly attributable to differences in breeding timing. The sheep produce their lambs in April and suckling has fallen to low levels by the end of May (Robertson *et al.* 1992). As a result, ewes have much of the summer to regain condition lost during lactation and, by August, (live) body weight does not differ between females that have failed to breed, raised one offspring or raised two offspring (Table 2b). In contrast, female red deer continue to suckle their young until the early winter and mothers that have raised calves successfully are lighter and have lower fat reserves at the onset of winter (Mitchell, McCowan & Nicholson 1976). As a result, they are less likely to conceive again and less likely to survive the winter (Clutton-Brock *et al.* 1983). These comparisons emphasize the extent to which relatively minor differences in the timing of breeding can affect demographic processes and the selection pressures associated with them.

Optimal reproductive decisions clearly vary with phenotype as well as with population density. While younger and lighter ewes should breed in non-crash years when density is low, they would raise their fitness by avoiding breeding altogether in crash years when density is high (Fig. 4). Similarly, while older and heavier ewes should conceive twins in non-crash years, they should avoid doing so in crash years. However, there is no evidence that the sheep track these changing optima (Table 1): instead, their decisions appear to depend on their body weight alone. If we assume that ewes adjust their reproduction to their body weight but cannot vary this relationship with the stage in the population cycle, our model suggests that ewes in the lighter two weight classes should conceive single offspring and only the heaviest ewes should produce twins (Fig. 4). The optimal strategy for lighter juveniles is to bear a single offspring while, counter-intuitively, our model predicts that heavier juveniles of 15–20 kg should avoid breeding though only a small reduction in the costs of breeding is necessary for reproduction to be favoured among heavier juveniles (Fig. 5b). This probably occurs because the marginal costs of breeding in crash years are higher for heavier juveniles (see above).

The reproductive patterns of ewes resemble the predictions of the model though their responses are, in general, rather more conservative than expected. The substantial majority of ewes breed each year and twinning is only common among the heavier animals, where it still falls short of the levels predicted by the model (see Table 1). Between 50% and 73% of lighter

juveniles breed each year while, contrary to prediction, most heavier animals do so. However, sensitivity analyses for this prediction show that only a small reduction in breeding costs is necessary for reproduction to be favoured in this category (Fig. 5b). Elsewhere (Marrow *et al.* 1996) we follow a population which performs the optimal strategy and compare the proportions performing each reproductive action with those observed. The results are consistent with those presented here.

These results are relevant to interpretations of the unstable dynamics of Soay sheep (Clutton-Brock *et al.* 1991). Soay sheep show higher fecundity and lower ages at first breeding than most wild sheep (Geist 1971; Jorgenson *et al.* 1993; Festa-Bianchet *et al.* 1995). One explanation of the persistent tendency for the St Kilda population to peak and crash is that ancient human selection has been responsible for maladaptively high fecundity which, in turn, generates high breeding costs, intermittently high mortality and population instability. A contrary argument is that, as Soay sheep were introduced to the St Kilda archipelago over 1000 years ago and their numbers have probably been naturally regulated for much of this time (Boyd & Jewell 1974), natural selection might be expected to have eliminated suboptimal reproductive tactics from the population. As we describe above, the unusually high costs of early breeding in crash years are offset by substantial benefits in non-crash years and there is little evidence that the high fecundity of Soay sheep is maladaptive if we assume that they are unable to adjust their fecundity directly to changes in population density. This carries the implication that intermittently high reproductive costs and fluctuations in population size are unlikely to be restricted to feral ungulates and may occur in other species characterized by high fecundity and weak or delayed density dependence in reproductive parameters.

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