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Adaptive reproductive strategies

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9.1 Introduction

When in its life should an individual first attempt to reproduce? How often should it breed thereafter? How much effort should it invest in each attempt? And does this vary between individuals in the same population? These questions are central to the many studies investigating adaptive life-history strategies, across the taxonomic spectrum, yet detailed answers are provided by few, particularly in large, free-ranging species. This is because comprehensive data on the costs and benefits of reproduction throughout life are essential for the task, but are difficult to collect in the wild, especially for males in polygynous species. With Soay sheep, however, we have the detailed information with which to investigate the reproductive benefits and costs for both sexes, and the way these vary with the environment and individual phenotype.

In Soays, the costs and benefits of reproduction take on even greater significance given the domestic roots of the population. A brief examination of the Soay life-history reveals unusual patterns that have led many to question whether these are simply the maladaptive legacy of past domestication. Soays certainly bear the hallmarks of artificial selection for high productivity (Chapter 1). Both sexes, but particularly males, mature early (Fig. 9.1) despite incurring high survival costs; and females continue to display fatally high fecundity at peak population densities (Chapter 2). These costs suggest that Soays are too

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fecund for their own good. Yet it remains possible that these are not the result of domestication, but are adaptive responses to their environment. Life-history theory provides a framework within which we can use the observed costs and benefits of reproduction to predict optimal fecundity schedules and to compare these with the patterns we observe.

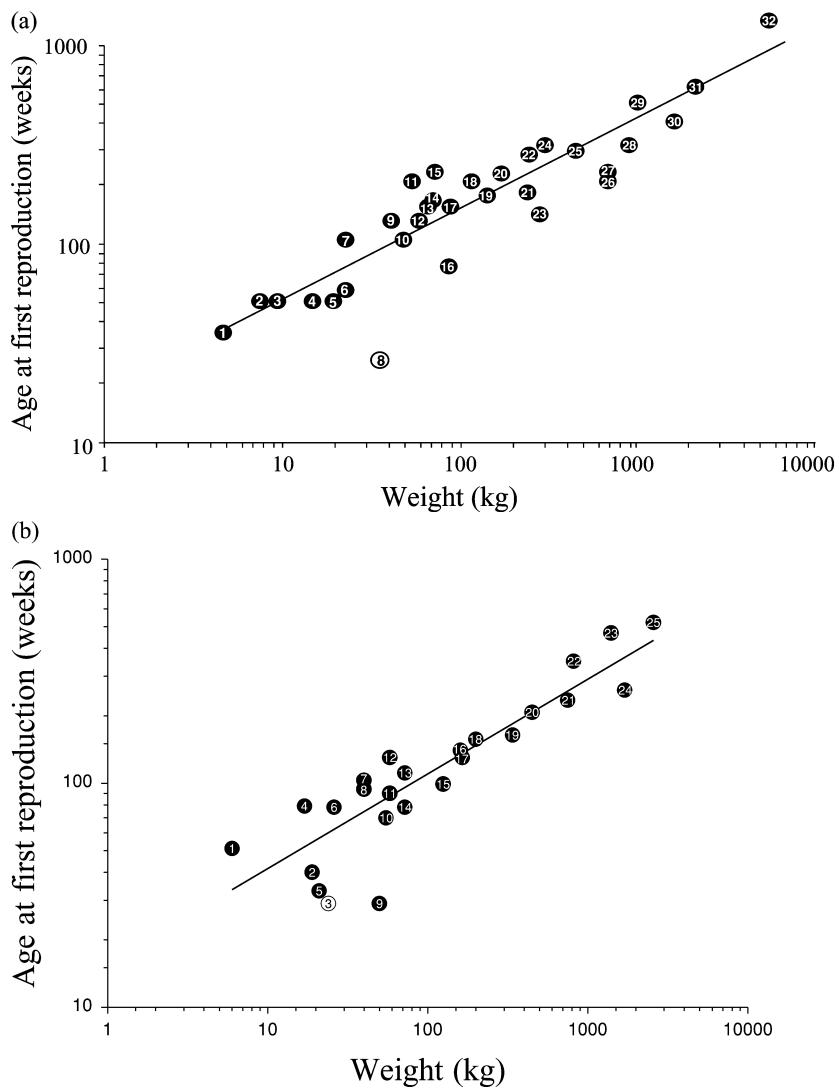


FIG. 9.1. Allometric plots of age at first mating/conception for (a) males and (b) females in the Orders Perissodactyla, Artiodactyla and Proboscidea. Age at maturity is taken as the age at which males are first noted to be actively involved in the breeding season, as distinct from the age at physiological maturity; for females it is taken as age at conception. The equation of the lines are (a) $\log(\text{age}) = 0.46 \cdot \log(\text{weight}) + 1.24$, $r^2 = 0.82$ (b) $\log(\text{age}) = 0.42 \cdot \log(\text{weight}) + 1.17$, $r^2 = 0.76$. The species represented are as follows. Males: 1 *Madoqua kirkii* (Kellas 1954); 2 *Neotragus moschatus* (Kingdon 1979); 3 *Hyemoschus aquaticus* (Kingdon 1979); 4 *Muntiacus reevesi* (Corbett and Harris 1991); 5 *Tayassu tajacu* (Sowls 1966); 6 *Capreolus capreolus* (Corbett and Harris 1991); 7 *Gazella thomsonii* (Robinette and Archer 1971); 8 *Soay sheep*; 9 *Ovis musimon* (Schaller 1977); 10 *Antilocapra americana* (Burt and Grossenheider 1976); 11 *Tragelaphus scriptus* (Kingdon 1979); 12 *Aepyceros melampus* (Jarman 1979); 13 *Gazella granti* (Walther et al. 1983); 14 *Oreamnos americanus* (Geist 1964; et al Houston et al. 1989); 15 *Ovis canadensis* (Blood et al. 1970; Hogg 1987); 16 *Phacochoerus aethiopicus* (Kingdon 1979); 17 *Kobus kob* (Buechner et al. 1966); 18 *Rangifer tarandus* (Leader-Williams 1988); 19 *Damaliscus lunatus* (Estes 1992); 20 *Cervus elaphus* (Clutton-Brock et al. 1982a); 21 *Kobus defassa* (Spinage 1982); 22 *Equus burchelli* (Kingdon 1979); 23 *Hippotragus equinus* (Kingdon 1979); 24 *Camelus dromedarius* (Kingdon 1979); 25 *Alces alces* (Burt and Grossenheider 1976); 26 *Syncerus caffer* (Sinclair 1974); 27 *Taurotragus oryx* (Kingdon 1979); 28 *Bison bison* (Burt and Grossenheider 1976); 29 *Diceros bicornis* (Schenkel and Schenkel-Hulliger 1969); 30 *Hippopotamus amphibius* (Laws and Clough 1966); 31 *Ceratotherium simum* (Owen-Smith 1974); 32 *Loxodonta africana* (Perry 1953; Laws 1966). Females: 1 *Rhynchotragus kirkii* (Kellas 1954); 2 *Sylvicapra grimmia* (Haltenorth and Diller 1977); 3 *Soay sheep*; 4 *Gazella thomsonii* (Robinette and Archer 1971); 5 *Tayassu tajacu* (Sowls 1955; MacDonald 1984); 6 *Ovis musimon* (Bon et al. 1993); 7 *Gazella Grantii* (Walther et al. 1983); 8 *Aepyceros melampus* (Jarman 1979); 9 *Odocoileus hemionus* (Leberg and Smith 1993); 10 *Antilocapra americana* (MacDonald 1984); 11 *Kobus kob* (Buechner et al. 1966); 12 *Cervus elaphus* (Clutton-Brock et al. 1982a); 13 *Kobus leche* (Sayer and van Lavieren 1975); 14 *Ovis canadensis* (Schaller 1977); 15 *Alcelaphus buselaphus* (Kingdon 1979); 16 *Kobus defassa* (Haltenorth and Diller 1977; Spinage 1982); 17 *Conochaetes taurinus* (Millar and Zammuto 1983); 18 *Equus burchelli* (Kingdon 1979); 19 *Taurotragus oryx* (Kingdon 1979); 20 *Syncerus caffer* (Sinclair 1974); 21 *Giraffa camelopardalis* (MacDonald 1984); 22 *Diceros bicornis* (Schenkel and Schenkel-Hulliger 1969); 23 *Hippopotamus amphibius* (Laws and Clough 1966); 24 *Ceratotherium simum* (Owen-Smith 1974); 25 *Loxodonta africana* (Perry 1953; Laws 1966).

Optimal life-history patterns are determined by the fitness costs and benefits resulting from different reproductive strategies. These costs and benefits underlie the trade-offs between different components of fitness that result if resources used for reproduction are diverted from somatic maintenance or future reproduction. For example, high fecundity may allow individuals to produce a large number of offspring, but, if this greatly reduces their future survival, lifetime reproductive output may be reduced. In this case, reduced early fecundity could evolve as an adaptive strategy; but we must be certain that it does not result, instead, from non-adaptive constraints, such as the routing of resources towards growth rather than reproduction (see section 1.4). To understand whether the life-histories of Soay sheep are adaptive we must understand how costs and benefits change with age at first reproduction and investment at each reproductive opportunity.

The benefits of reproduction for young animals are often low, and the costs high, since maturation is an expensive process (Bernardo 1993) and must compete with growth for allocation of resources (Gadgil and Bossert 1970; Stearns 1989). Fecundity is therefore often low for young individuals (Stearns 1992), and any offspring that do result may be smaller or unviable because of poor nutrition before or after birth, or because of parental inexperience in species that care for young (e.g. Røskaft *et al.* 1983; Bell 1984; Festa-Bianchet *et al.* 1995). Young males also tend to be relatively unsuccessful breeders, since access to females is often strongly dependent on body size (studies in Clutton-Brock 1988a; Roff 1992). Moreover, females may actively avoid the attentions of young, inexperienced and unproven males (Cox and Le Boeuf 1977; Owen-Smith 1993; Sabat 1994). In addition to inferior performance, young breeders may experience additional costs such as reduced growth and lower future fecundity (Bercovitch and Berard 1993; Festa-Bianchet *et al.* 1995), greater parasitism (Festa-Bianchet 1989a), or lower survival (Harvey and Zammuto 1985; Reiter and Le Boeuf 1991).

While the 'decision' of when to mature is taken only once, individuals must then choose how much effort to invest at each subsequent breeding attempt. Again, there are costs and benefits to be considered, both for parent and offspring, since there are physical and

physiological limits to how hard an individual can work (Drent and Daan 1980). When these bounds are reached, the per capita investment in each offspring will decline and, with it, the viability of the offspring (Reid 1987). For example, egg quality often declines as clutch size increases in birds (Monaghan *et al.* 1995), while in many taxa the long-term consequences of high fecundity can include reduced future success (Luckinbill and Clare 1985), lower parasite resistance (Ots and Hörak 1996) and poorer survival (Bryant 1979; Seigel *et al.* 1987; Westendorp and Kirkwood 1998). For males, too, reproductive costs can be substantial, particularly in polygynous species (Promislow 1992). Perhaps the most extreme example of costly mating activity is observed in the Australian marsupial mouse *Antechinus* spp., in which every male dies following the first breeding season (Woolley 1966; Lee and McDonald 1985).

Reproductive costs vary widely with both environmental conditions and individual circumstance (section 1.4). Early maturity may be favoured where offspring can make a large contribution to population growth (Fisher 1930; Stearns 1992), or where variable life expectancy reduces the marginal survival costs of heavy reproductive investment. In the latter case, high levels of non-reproductive mortality may mean that the reproductive costs of early breeding are never experienced. When infected by castrating nematodes, for example, water snails massively increase investment in current reproduction at the expense of future survival (Minchella and Loverde 1981), and similarly, parasitic wasps increase reproductive investment when faced with adverse weather likely to increase their mortality (Roitberg *et al.* 1993). In addition, the balance between costs and benefits is strongly influenced by variation in individual condition and quality. Red deer hinds in good condition suffer few costs and give birth to offspring with improved survival chances compared to those of poor-condition hinds, which in turn have higher mortality rates and are also less likely to breed the following year (Mitchell and Lincoln 1973; Clutton-Brock *et al.* 1982a, 1983; Albon *et al.* 1986). Again parasitism can alter the balance between costs and benefits of reproduction as in great tits where a trade-off between offspring quality and number was found only in the presence of ectoparasites (Richner *et al.* 1993) or bighorn

sheep where young ewes only showed a mortality cost of reproduction if also infected by pneumonia (Festa-Bianchet 1989a).

COSTS AND BENEFITS OF REPRODUCTION FOR SOAYS

The costs of early reproduction for Soay sheep on St Kilda are clearly high in some years (Chapter 2). For example, when mortality is high, conception reduces a juvenile female's chance of survival further (section 2.8; Fig. 2.14), and any offspring produced are low quality, around one-third lighter than those of adult females and with lower survival (Clutton-Brock *et al.* 1996). Twinning also has high costs for Soay sheep, resulting in reduced survival rates for both offspring and mother (section 2.6). High fecundity is not always costly, however, and in non-crash years neither juvenile reproduction nor twinning by adults affects mortality risk.

Early maturity of Soay rams also appears to have high costs, but few benefits. Mortality of juvenile males is higher than that of females, following the rut, despite their greater body size (section 2.7). Even though rutting behaviours are costly, juvenile Soays are rarely successful in holding consorts with females and indeed are often actively avoided by females at the peak of oestrus (Grubb and Jewell 1973; I. R. Stevenson, pers. obs.)

Although the costs of reproduction are high for both sexes, they vary widely both with environmental conditions and phenotypic quality. For females, body weight strongly affects reproductive performance: as in many species, heavier individuals have a greater chance of breeding successfully at all ages, and produce heavier offspring, which in turn have superior survival (sections 2.6 and 2.7) (Saether and Heim 1993; Sand and Cederlund 1996; Festa-Bianchet 1998). For males, the benefits of reproductive activity are closely linked to changes in the social environment, which is highly variable due to the frequent periods of high male-biased mortality (Chapter 3) (Clutton-Brock *et al.* 1991; Stevenson 1994). Following population crashes, young males experience a release from competition and may gain considerable reproductive success (Chapter 6) (Bancroft 1993; Stevenson and Bancroft 1995; Pemberton *et al.* 1996). Thus, assessment of the optimal life-history for Soay sheep is not a simple task, and must address variation

in individual quality and the environment. This can only be addressed by modelling the system mathematically.

9.2 Optimal life-histories for female Soay sheep

LIFE-HISTORY MODELLING

Using optimality modelling (Parker and Maynard Smith 1990) it is possible to calculate the reproductive strategies that would maximise individual fitness and then compare these with observed behaviour. In particular, we investigate how the optimal strategy varies with an animal's 'state' (a combination of phenotype and environment) by using state-dependent life-history modelling (McNamara 1991; McNamara and Houston 1992, 1996). This technique uses stochastic dynamic programming (Bellman 1957) to predict the long-term fitness consequences of life-history decisions. The key state variables incorporated in these optimality models are body weight, age and population density. Using empirical data, we parameterised the model with the survival costs and reproductive benefits for females making different reproductive decisions (skip reproduction, produce one offspring or produce two offspring) (Clutton-Brock *et al.* 1996; Marrow *et al.* 1996).

We initially modelled population density by assuming that population crashes occurred on a three-year cycle, and that stages of the cycle succeeded each other regularly. We termed this the 'perfect information model' since, in effect, females could predict population fluctuations. Subsequently, we modified the assumption of a regular cycle to produce a 'random years' model. In this, different levels of population density succeeded each other at random and so females had no information about impending population fluctuations. The random years model is more realistic since we have no evidence of adaptive mechanisms that allow females to make predictions about future population fluctuations. Since the peak of mortality occurs several months after the breeding season (Chapter 3), females make their reproductive decisions when forage is still plentiful and before they have to suffer the consequences of their actions. In addition, this model reflects more accurately the unpredictable population dynamics of recent years rather

than the apparently regular 'cycles' that were observed in the 1980s and early 1990s (Chapter 3).

PREDICTED OPTIMAL STRATEGIES

If females cannot predict population fluctuations (the random years model), then they cannot fine-tune their behaviour but, instead, must follow a strategy that is optimised for average conditions across years. In this case, fecundity cannot respond to population density, but can still be modified according to an individual's weight and age (Fig. 9.2) (Perry 1953; Laws 1966).

The model predicts the optimal strategy for adult females is to breed every year, with the heaviest individuals giving birth to twins. Juvenile females are predicted to conceive single offspring, unless they are relatively heavy, in which case they are expected to avoid reproduction. These predictions do not differ significantly from the

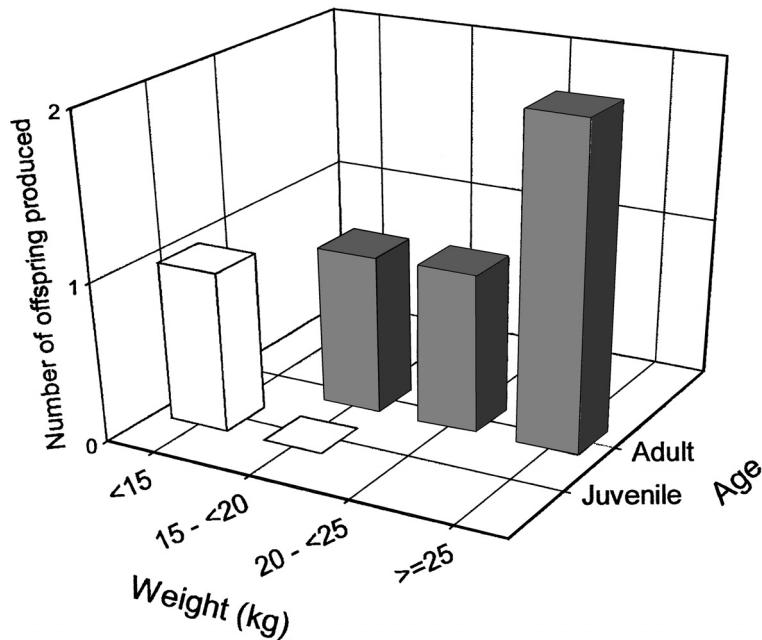


FIG. 9.2. Predicted optimal strategies for females of different ages and weights (random years model). The predicted behaviour is the same across all stages of the population cycle.

reproductive patterns observed in the field across the range of population density (G -test = 1.8, 4 df, $p > 0.5$) (Marrow *et al.* 1996). The agreement is particularly good for adult ewes, suggesting that their reproductive behaviour is close to optimal (Marrow *et al.* 1996). The fit is less good for juveniles, however, with the model over-estimating the fecundity of low-weight individuals and under-estimating that of heavy juveniles. This is likely to reflect its simple nature and, as we show below, these predictions for juveniles are very sensitive to small changes in conditions (see 'Early reproduction and twinning as adaptive strategies for females').

A further test of our model can be gained by comparing the theoretical population dynamics, calculated from optimal strategies, with the dynamics displayed by the real population. The predicted dynamics show a regular cycle (Fig. 9.3), but no long-term changes in population

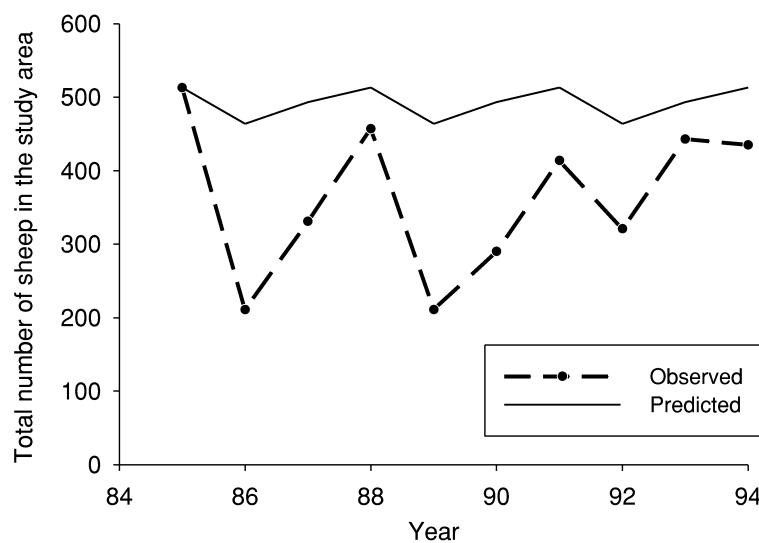


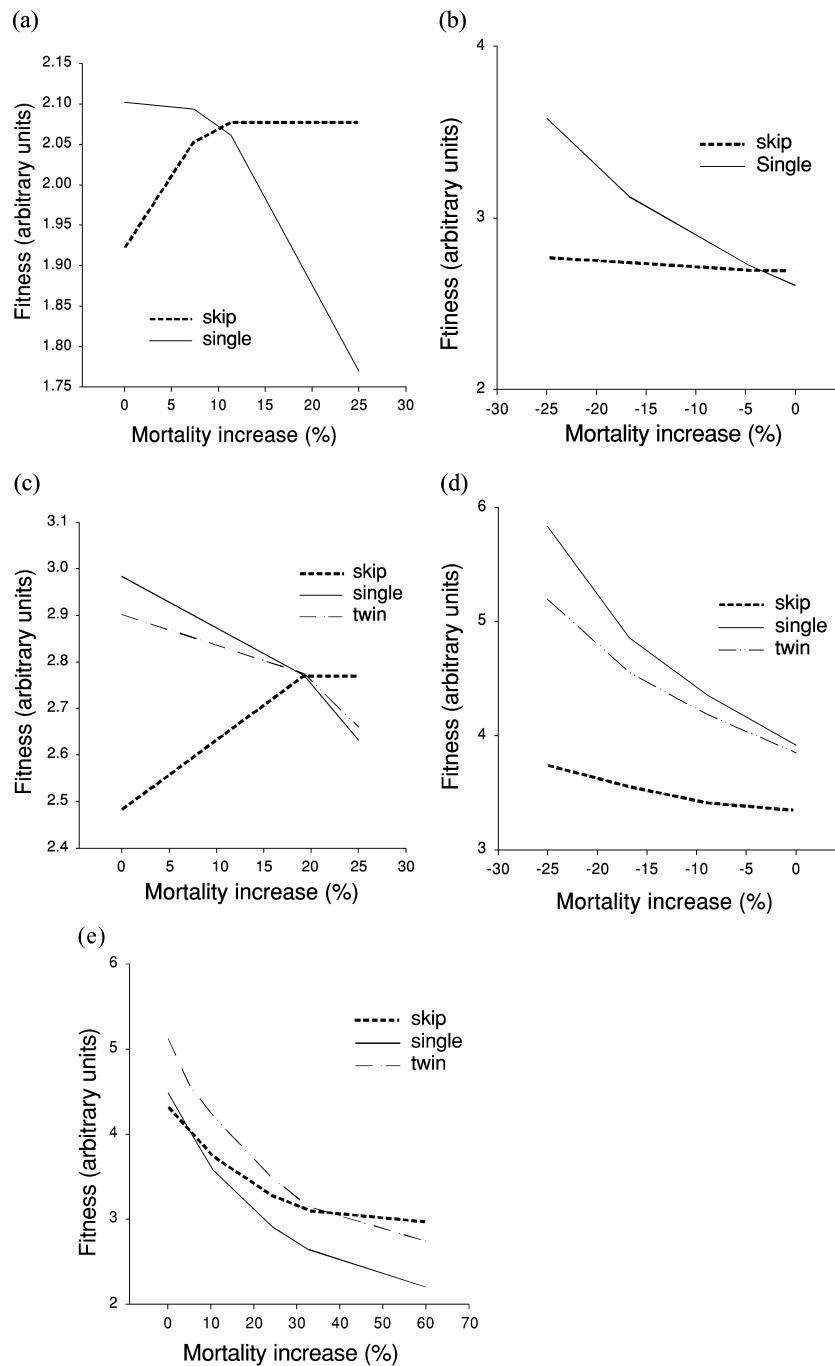
FIG. 9.3. Predicted and observed population dynamics. This shows the predicted population dynamics that result when all females are assumed to follow the random years optimal strategy. The model was started with one animal in each state, and the total population density evaluated over 100 annual decisions. The last nine years are shown scaled so that the population size in 1985 is the same as that observed in the real population. The 'observed' plot is the total number of sheep recorded in the study area between 1985 and 1994.

density. This is similar to the dynamics observed, though the amplitude of fluctuations is less. The fact that the simulation is more regular than observed in the field is likely to be due to the action of the weather (Chapter 3) (Grenfell *et al.* 1998; Coulson *et al.* 2001), which is excluded from our model. Combined with the similarities between the optimal strategy and observed levels of fecundity, and between the levels of fecundity predicted across population fluctuations, this information suggests that female Soays follow a close-to-optimal reproductive strategy based upon their weight and age and limited cues.

EARLY REPRODUCTION AND TWINNING AS ADAPTIVE STRATEGIES FOR FEMALES

We can identify the selective forces that restrict the reproductive tactics of females by examining the sensitivity of the optimality results to changes in the reproductive costs (Clutton-Brock *et al.* 1996; Marrow *et al.* 1996). By changing the mortality costs of different reproductive actions, we can determine the threshold required to alter the optimal strategy for females in a given state. This analysis demonstrates that, although the costs are often high, early breeding probably represents an optimal strategy for female Soays (Fig. 9.4). The mortality risk of breeding for low-weight juveniles must increase by about 12% before delayed reproduction is favoured (Fig. 9.4a). By contrast, a reduction in mortality risk of 4% is needed to make reproduction optimal for heavy juveniles (Fig. 9.4b). Such a small change in mortality costs may explain the discrepancy between the predicted strategy ('don't breed': Fig. 9.2 and Perry 1953; Laws 1966) and observed fecundity (where up to 72% of heavy juveniles are observed to breed: Marrow *et al.* 1996), since environmental variation not included in our model may overcome the mortality costs which make giving birth sub-optimal.

FIG. 9.4. Results of sensitivity analysis of mortality costs of reproduction. Fitness is in arbitrary units. 'Mortality increase' shows the extend to which the mortality costs of reproduction need to change from values predicted from field data, in order to produce the changes in fitness shown. The graphs are drawn for: (a) juveniles of <15 kg; (b) juveniles of 15–20 kg; (c) adult females of 15–20 kg; (d) adult females of 20–25 kg; (e) adult females of >25 kg.



Twinning is only optimal for females in good condition. Lighter females that twin suffer higher mortality than those producing singletons, and also produce poor-quality offspring that are less likely to survive (Chapter 2). For the heaviest females, however, twinning is a good strategy and will persist until mortality is increased to 40% greater than that which has been recorded and a level that is almost certainly never experienced (Fig. 9.4e). Failing to breed is the worst of all options for adult females, and is even worse than twinning by females in poor condition (Fig. 9.4c, d). These results confirm that the predictions of the optimality model are, with the exception of heavy females in their first year (Fig. 9.4b), robust to fluctuations in mortality costs, of a degree plausible in nature.

Our model supports the view that early maturity and high fertility can be optimal strategies for heavy females, but are a poor option for lightweight females, which suffer higher mortality risks. This emphasises that the optimal life-history varies with phenotype and that any concept of a 'species life-history' ignores important substructure within the population. Such structure can pass between generations through maternal effects, producing unexpected results for individual fitness and population dynamics.

9.3 Optimal life-histories for male Soay sheep

ESTIMATING THE SURVIVAL COST OF REPRODUCTION FOR MALES

As we have seen for females, the costs associated with early maturity must be known in order to examine the fitness of the strategy. For males, however, the existence of a trade-off between age at maturity and survival of males has rarely been demonstrated by experimental means in wild ungulates. Two field experiments on St Kilda have demonstrated that rutting activity is indeed associated with reduced survival in this population.

In the late 1970s, Jewell (1997) used physical castration to examine the marked sex difference in survival of Soay sheep. In 1978–80, a number of males ($n = 14, 8, 50$ respectively) were castrated within a few days of birth and their subsequent survival monitored. The

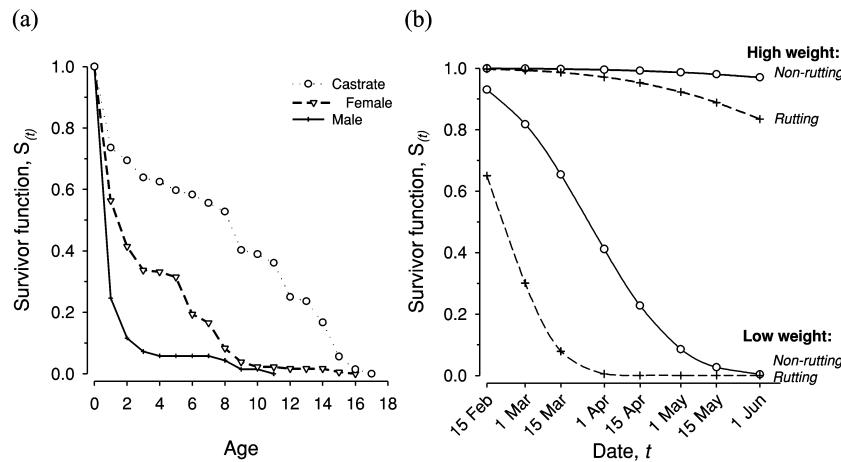


FIG. 9.5. (a) Survival plots for castrates, control males and females from the same cohorts. (Adapted from Jewell 1997.) (b) Survival probabilities for males excluded from rutting by progestogen treatment and control males. Survival plots are shown for 'heavy' and 'light' juveniles (weights in August preceding the rut = 12 kg and 20 kg respectively; mean weight of treated and control males was 15 kg).

results were spectacular, with the survival of castrates outstripping not only their male peers, but also the females of those cohorts and, indeed, several of the following cohorts (Fig. 9.5a). A stark illustration of the cost of being an intact male was observed in March 1989 when, following a particularly severe crash (Chapter 3), there were more castrates alive (the youngest being nine years of age) than there were intact males, of any age, on the entire island (38 castrates, 31 intact males, excluding males *in utero*). Behavioural observations conducted in November 1983 (Jewell 1986) and 1989 (Stevenson 1994) confirmed that the castrates took no part in the rut and fed for around 70% of daylight hours, similar to the feeding level of females, and considerably above the intact males at 30–40%. The last castrate, almost seventeen years of age, died in March 1997; this is the oldest sheep on Hirta since records began. The marked longevity of castrates is in accordance with Fisher (1948) who recorded castrates from the original 1932 introduction (Boyd 1953), which were therefore sixteen years old when spotted in 1948.

Jewell's experiment (1986, 1997) showed that castrates had far better survival than intact males suggesting that it was androgen-dependent. However, it does not specifically connect this male mortality to rutting activity. Androgens control many aspects of development, physiology and behaviour and so a causal link between reproductive activity and mortality cannot be assumed. This link was demonstrated with a refinement of the castration technique, using temporary hormonal castration (Stevenson 1994; Stevenson and Bancroft 1995). Progesterone and its associated steroids (together, 'progestogens') inhibit the production of gonadotrophin-releasing hormone (GnRH) (Knol and Egberink-Alink 1989) which is the start of a 'hormone cascade' (Karsch 1984), stimulating the anterior pituitary to produce luteinising hormone (LH) and follicle-stimulating hormone (FSH) (Knol and Egberink-Alink 1989). Blocking these hormones removes libido, sexual behaviour and aggression (Diamond 1966; Zumpe and Michael 1988; Knol and Egberink-Alink 1989; Zumpe *et al.* 1991), much as physical castration does but with the advantage that the changes are fully reversible (Ericsson and Dutt 1965; Jochle and Schilling 1965). The advantage of this approach is that sexual behaviour can be blocked for the duration of the rut, with minimum effect on 'maleness' either before or after this period. Using this method, in 1991, a group of 18 juvenile males was excluded from the rut in their first year and survival compared with that of controls over the following winter of high population density.

Mortality was some 46% higher amongst the controls than the treated males, though by this stage, plasma testosterone and testicular measurements had returned to normal and were indistinguishable between the groups (Stevenson and Bancroft 1995). Body weight the previous summer strongly influenced mortality and amplified the treatment effect for low weight males (Fig. 9.5b). Rutting activity was thus demonstrated to reduce over-winter survival probability for young males.

As yet, however, there is no examination of how this cost varies with age. Juveniles, together with very old individuals, are the most likely to die during population declines, and reproductive behaviour may therefore be more risky for these groups than for intermediate age classes.

The cost of reproduction demonstrated by this experiment was an immediate one, but future costs may also exist. If, for example, growth is affected by rutting activity in the first year, males may be unable to attain such a large size and so may be less competitive in future; those males that skip reproduction may grow faster, as well as having higher survival, and so may gain greater reproductive success in subsequent years (unfortunately, too few experimental males were recaptured the year after the experiment for this to be examined here). The relative importance of long-term growth costs compared to the immediate over-winter survival costs will vary between years, achieving greater significance at low population density when the survival cost is low. However, alterations of future reproductive success are likely to be relatively unimportant because any benefits of delayed maturity have to be devalued by the risk of not surviving to realise them.

LIFE-HISTORY MODELLING

We used our knowledge of the costs and benefits of reproduction, and their variation with condition, age and density, to predict optimal age at maturity for males. Rather than use stochastic dynamic programming, however, we employed a deterministic, age-structured simulation model (Keen and Spain 1992). The model incorporated a fixed, three-year population cycle (cf. Fig. 9.3), with age- and density-dependent mortality and fecundity rates parameterised from field data. The assumption of a fixed three-year cycle is the same as that in the 'perfect information' model for females, but, as we will see later, the assumptions of the perfect information model are more appropriate for juvenile males. The details of the model are presented in Stevenson and Bancroft (1995), and only a brief summary will be given here.

In order to model the fitness of strategies where first reproduction was delayed, we assumed that the over-winter mortality rate of non-breeders was 0.64 times as great as that of breeders of the same age. This reduction represents the cost of reproduction calculated from the rut exclusion experiment (see above). We varied age at maturity varied from 0.5 to 5.5 years, according to the strategy adopted. Following maturity, the number of male offspring produced by a sheep of a given age was estimated from the density and age-dependent

reproductive success estimates calculated by genetic paternity analysis (Chapter 6). The fitness of an average male, following a given maturation strategy, is estimated by the cumulative number of male descendants that survive to the strategy-dependent age at maturity, produced over 15 years. This measure incorporates the variable ‘discounting’ (Charlesworth 1980) that must be applied to the fitness of successive offspring in growing and declining populations. The overall fitness of a strategy was estimated by the geometric mean of the fitnesses calculated for individuals born at each of the three phases of the population cycle. This model allowed us to examine the basic patterns of fitness for individuals following different maturation strategies, but, in future, it would be interesting to examine the effects of stochasticity, as was done for females.

EARLY REPRODUCTION AS AN ADAPTIVE STRATEGY

In years of low and intermediate population density, early maturity is favoured. In such years, mortality is very low and mainly confined to the very young or very old and so there can be little or no *short-term* cost to reproductive activity for juveniles. Moreover, the benefits gained by young males can be appreciable (Fig. 6.2a; Chapter 6). Juveniles should always take part in these ruts, even though reproductive success declines quickly with population density: in the absence of costs, any success is worthwhile, no matter how small.

At high population density, by contrast, juvenile males should skip reproduction. Mortality for juvenile males is always high in these years (even though adult mortality may be low and the population does not decline) (Chapter 3), reaching 99% in extreme years such as 1986, 1989 and 1999 (Chapter 3). Almost half of this mortality risk is due to reproductive activity (see above) and so those males that skip reproduction can greatly increase their probability of survival and do not trade the higher reproductive success as an adult for the low return of a juvenile at high density. Thus, males should display phenotypic plasticity in their juvenile rutting behaviour, responding to population density as a reliable indicator of mortality risk in the coming winter. Observational evidence supports the model predictions, since

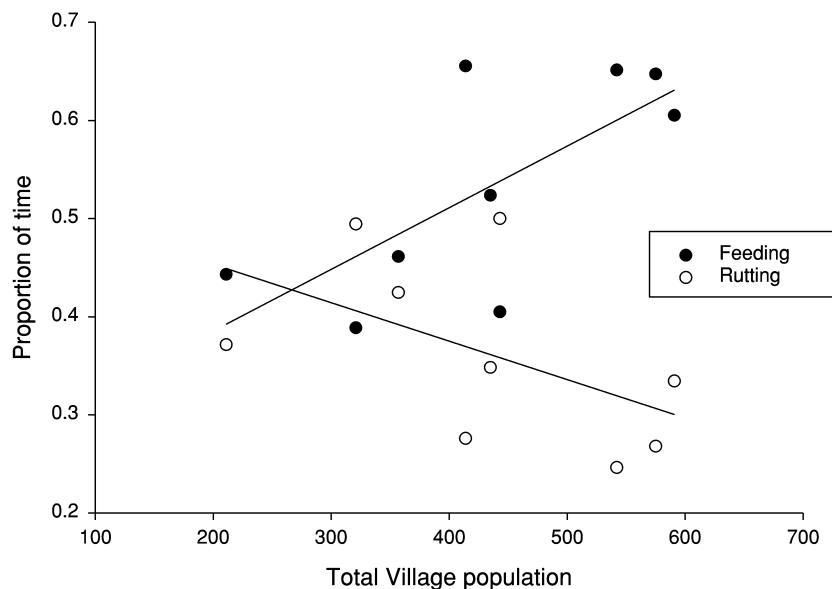


FIG. 9.6. Proportion of time spent feeding and rutting by Juvenile males 1989–98 (excluding 1990).

males do indeed display rutting activity that is negatively correlated with population density (Fig. 9.6).

While the average male should follow this strictly density-dependent strategy, variation may be introduced by differences in condition. When the survival cost of reproduction is reduced for particular categories of males (for instance early-born, heavy males (Chapter 2 and Fig. 9.1) with low parasite burdens (Chapter 7)), early maturity may be favoured, even at high population density; but for those in poor condition, delayed reproduction may increase fitness (Fig. 9.7). Thus, we should not expect to observe a single maturation strategy, but individual, state-dependent variation. This prediction mirrors the findings for females (Marrow *et al.* 1996), and is supported by ongoing work comparing the activity budgets of juvenile males of differing quality (see next section).

In summary, there is no single optimal age at first reproduction for male Soays on St Kilda. Rather, the strategy that maximises individual contribution to future generations is influenced by external

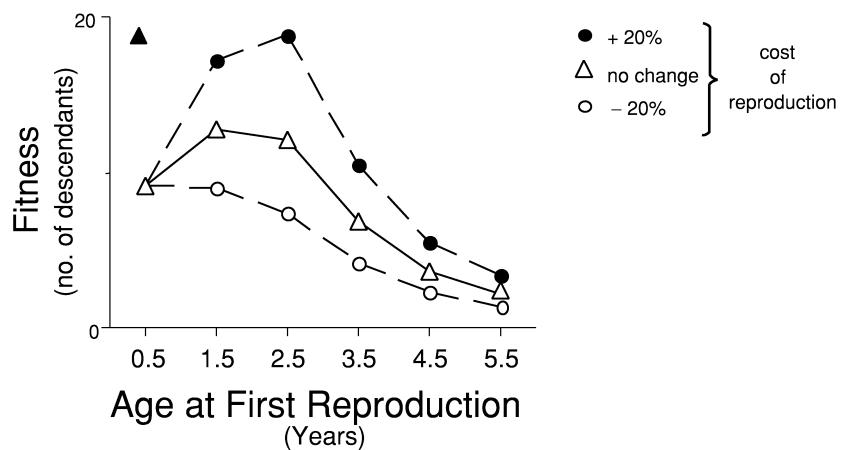


FIG. 9.7. Effect of changing the mortality cost of reproduction on optimal maturation strategy for Soay males. The fitness of maturing in the first year is predicted for the basic model in which males rut as juveniles regardless of population density. This strategy is conservative, and the more realistic plastic strategy that skips precocial reproduction in high-density years has the highest fitness (this is shown by the filled triangle).

factors such as population density, and by individual circumstances like parasite burden, body size, energy stores and date of birth. In the next section, we examine in more detail how variation in phenotype influences the reproductive strategies of males.

PHENOTYPE AND RUTTING BEHAVIOUR

Two broad classes of rutting behaviour can be identified in Soay males. Males either exhibit a 'dominant' or 'subordinate' strategy, determined largely by age, size and horn phenotype, although demography may also play a role. Large, normal-horned adults follow the typical dominant strategy in which the male 'consorts' with individual oestrous females (Grubb 1974b). Small, young and scurred males more often follow an opportunistic 'coursing' strategy, also found in other sheep species (Hogg 1984; Hogg and Forbes 1997). Coursing males rely on hurried matings with undefended females, rather than on direct defence. The subordinate strategy is perhaps better viewed as several convergent strategies rather than a single suite of behaviours. This is

because it encompasses young males, which may in future go on to become dominants, and also scurred adults, which are 'locked' into the subordinate strategy by virtue of their horn type. Many differences between the dominant and subordinate strategies can be readily identified from activity budgets (Fig. 9.8).

Body size and horn size are central to an individual's success at employing the 'dominant' strategy, not only between horn types and age classes, but also within them. For normal-horned males, for example, horn size, skeletal size and body condition are all positively, and independently, associated with the frequency and duration of consorts (Preston *et al.* 2003). This greater time spent in consorts in turn translates into increased success in gaining paternities (Preston *et al.* 2003).

The importance of horn size is even more apparent between the two male horn morphs, which differ hugely in annual reproductive success (Chapter 6), but do not differ in body size. The small horns of scurred males makes them of little use in the defence of oestrous females, and, as a result, they only invest about 5% of their time in consorts at the peak of the rut, compared to about 50% for normal-horned adults (Mann-Whitney U-test $z = 3.18$, $n = 33$, $m = 19$, $p < 0.001$). Instead, they attempt to locate females coming into oestrus before dominant males can sequester them. They then attempt to gain matings, with the minimum of courtship, before continuing their search for the next female. As a result, scurred males are extremely active, especially when the peak number of females are in oestrus, when they spend about 40% of their time moving about the island, and travel twice the distance covered by normal-horned males (695 m/h versus 324 m/h, $t_{14} = 4.9$ $p = 0.0002$). In the absence of unguarded females, scurred males join juvenile males harassing normal-horned adult males and their consorts. If they are successful in separating the female from her consort, a chase frequently results, as the female attempts to escape the attentions of the subordinates. If the defending male cannot fend off the harassing males and regain control, forced copulations are likely to result, often as the female is still running and, when a ewe stops, a succession of males often copulate.

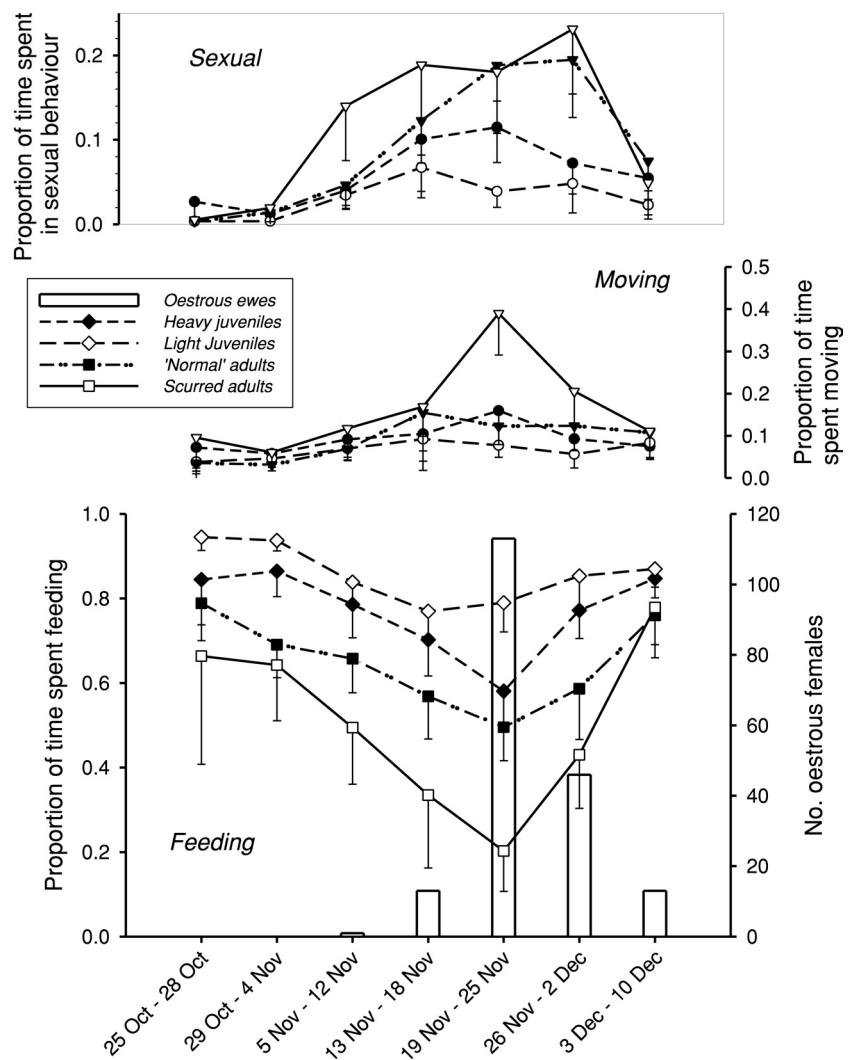


FIG. 9.8. Activity budgets during the rut for scurred and normal horned adult males and heavy and light juvenile males (>1 standard deviation above or below mean August weight). The data are from 1995 and show the proportion of time spent in sexual behaviour, feeding (including rumination) and moving around the island. The shaded bars indicate the number of females in oestrus each week, and the error bars show the 95% confidence intervals. Note that scurred males display peak levels of sexual activity for a greater duration than normal-horned males and are extremely mobile, searching for unguarded females at the peak of the rut. Scurred males consequently feed significantly less than all other groups. Amongst juveniles, rutting activity is positively related to body weight.

Young males show an opportunistic strategy similar to that of scurred adults, attempting to find unguarded females and harassing consorting adults. They invest less time in rutting behaviour, however, are less mobile, and maintain a much higher level of feeding activity than do adults (Fig. 9.8). All forms of rutting activity are depressed in young males in poor condition: throughout the rut, juveniles of below-average weight are involved in fewer agonistic interactions, devote less time to sexual activity and have a higher feeding rate than heavy males (Fig. 9.8). Lightweight males also begin to revert to pre-rut levels of feeding before the peak of ewes in oestrus. This appears to be a facultative difference in behaviour, rather than one imposed by delayed physical maturity. All but one of twenty-nine juvenile males examined in 1991 were physically capable of mating (as judged by the scoring method of Wiggins and Terrill 1953), and all subsequently exhibited a variable level of sexual activity during the rut (I. R. Stevenson, unpublished data). This is confirmed by investigations of captive Soays, which found that hormonal and testicular responses in juvenile males during the rut were reduced by poor nutrition, but that their expression was not delayed (Adam and Findlay 1997).

PHENOTYPE, REPRODUCTIVE SUCCESS AND ADAPTIVE LIFE-HISTORY

Normal-horned males are virtually always attributed more paternities than juvenile or scurred males in a given year (Chapter 6). In the case of juveniles, this is not surprising, but for scurred adults it raises important questions. Scurring is heritable (Chapter 7) (Dolling 1960,a, b; Montgomery *et al.* 1996), yet appears to be highly disadvantageous in males and is uncommon or absent in wild sheep (Geist 1971; Schaller 1977). Having been introduced to Soays by past domestication, why is it still prevalent, at a level apparently unchanged over at least the last 40 years (Chapter 5)? Does it confer benefits, or is it in the process of being lost, slowly, from the population?

One possibility is that scurred males may display an alternative mating strategy, with equal fitness to the normal-horned strategy. Current evidence suggests that the fitness of normal-horned and scurred males may be frequency-dependent (Fig. 9.9a). Although scurred males may gain fewer paternities per breeding season, they may make up for

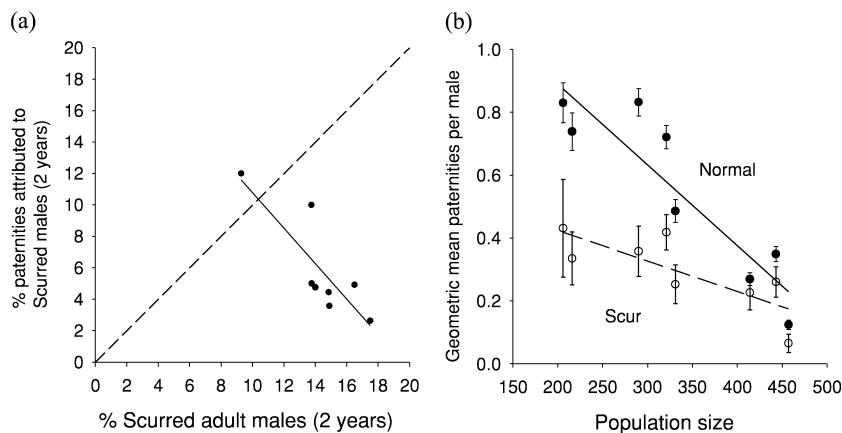


FIG. 9.9. (a) Frequency-dependence of scurred male strategy. As the proportion of scurred males in the population increases, the proportion of paternities gained by them decreases.

(b) Density-dependence of normal/scurred reproductive success. As population density rises, the per capita success of the two strategies converges.

this by greater longevity and so have the opportunity to take part in a greater number of ruts (Chapter 5) (Moorcroft *et al.* 1996). The greater longevity of scurs is paradoxical given their greater mobility, which might be assumed to be costly. We are currently investigating this, but direct measurement of rutting energetics (using the doubly labelled water technique) suggests that appearances may be deceptive and that the expenditure of the two horn types is the same (normal 5544 kJ/day, scurred 5417 kJ/day, $F_{1,37} = 1.08$, ns) (I. R. Stevenson, K. Wilson and D. M. Bryant, unpublished data).

An alternative explanation for the maintenance of scurring in the population is that scurred males may indeed be disadvantaged throughout their life, but this may be opposed by cross-gender balancing selection favouring higher-fecundity scurred females (Chapter 7). At present, it is not possible to say whether male scurring is adaptive, but this is the aim of current research.

SPERM COMPETITION IN SOAY SHEEP

Juvenile and scurred males are heavily dependent on sperm competition for any success they achieve. Since females have prolonged

oestrus and, in contrast to many deer species, will mate repeatedly with many males, subordinates with larger ejaculates will be at an advantage if this allows them to swamp those of other males and fertilise the ovum (Gomendio *et al.* 1998). Dominant males, in turn, might be expected to increase ejaculate investment in each female to minimise the loss of paternities to later-mating males (Hogg 1988). All sheep species display prolonged oestrus, and studies of bighorn sheep suggest that, as in Soays, sperm competition is probably very important. Hogg and Forbes (1997), for example, found that coursing males achieved 40–50% of paternities in two separate populations, a success that must be due largely to sperm competition.

Paradoxically, it appears to be the very success of large males in gaining matings that allows smaller, subordinate males to achieve success through sperm competition. Although high weight and large horns both independently increase the success of a male in gaining copulations and, across the whole rut, increase the number of paternities gained (Preston *et al.* 2001), the relative advantage of large males over subordinates decreases later in the rut (Fig. 9.10b). This appears to be due to sperm depletion of the dominants and a consequent increased success of subordinates in sperm competition (Hogg and Forbes 1997; Preston *et al.* 2001). This effect occurs even though the decline in overt reproductive behaviour over this period is greater for subordinates than dominants (Fig. 9.10). Contrary to the normal pattern, sperm count is negatively correlated with testes size (and body size) late in the rut (Fig. 9.11) and the proportion of abnormal sperm increases (Preston *et al.* 2001).

The importance of sperm competition in Soays is backed by anatomy. Species in which sperm competition is important typically have large testes relative to body mass (Harcourt *et al.* 1981), and Soays have testes that are larger than a wide range of other ungulates (Fig. 9.12) (Lincoln 1989). Though even sheep with large testes suffer depletion late in the rut, testes size is positively related to paternity success across the breeding season as a whole (B.T. Preston, unpublished data). Moreover as the number of oestrous ewes increases, the importance of large testes relative to large horns increases since the

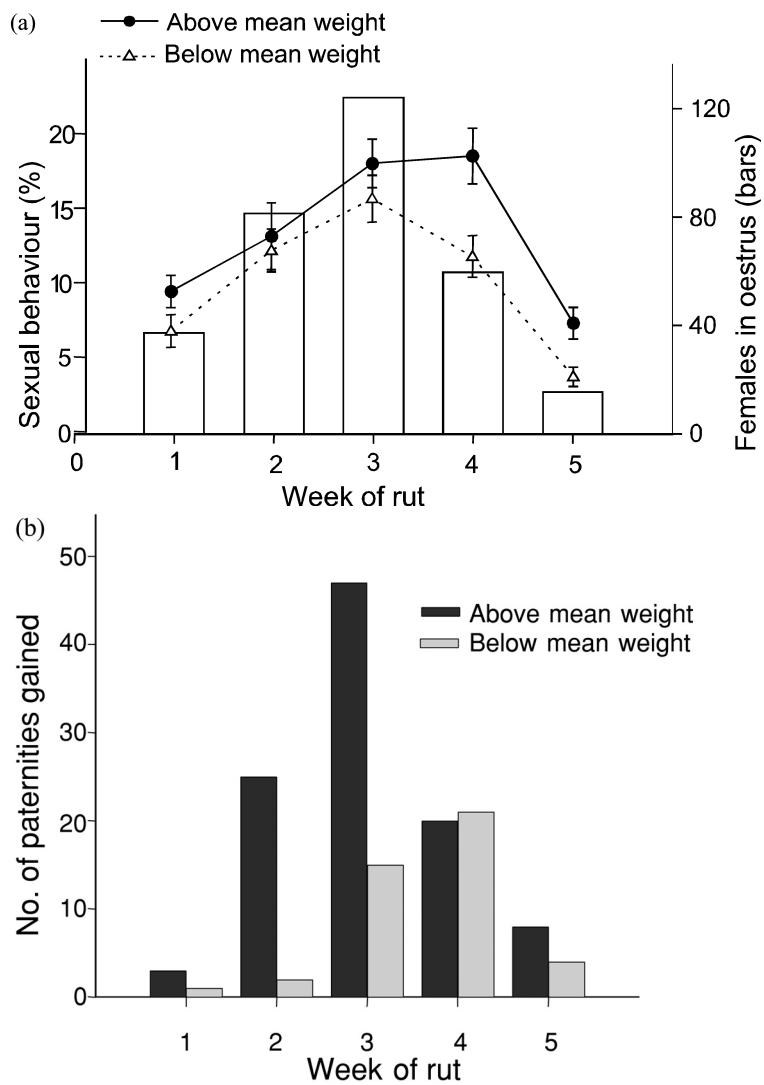


FIG. 9.10. Change in (a) overt sexual activity and (b) resulting reproductive success, over the course of the rut for normal-horned males of above-and below-average weight. Data are from (a) 1996-8 (b) 1986-7; error bars show standard errors. Note that heavier males continue at peak rutting activity for longer than lighter (a), despite the relative increase in success of lighter males later in the rut (b).

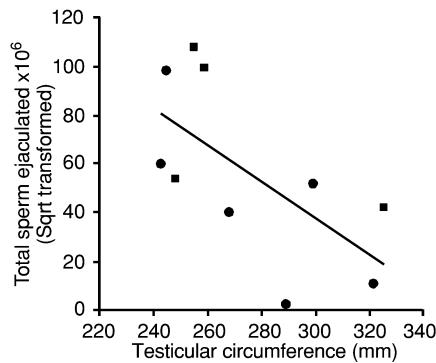


FIG. 9.11. Decline in ejaculated sperm number with scrotal circumference measured at the maximum point. Counts were made in weeks 4 and 5 of 1999 (see Fig. 9.10). (From Preston *et al.* 2001.)

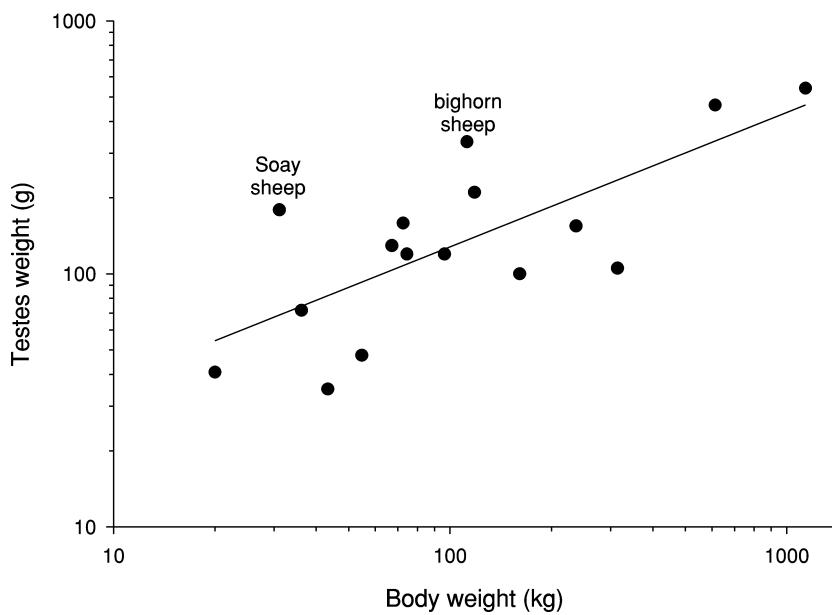


FIG. 9.12. The allometric relationship between body weight and combined testicular weight over fifteen genera of ruminants. Adapted from Hogg (1984). Data for Soays are taken from Lincoln (1989). The equation of the line is $y = 0.5593 + 0.7535x$.

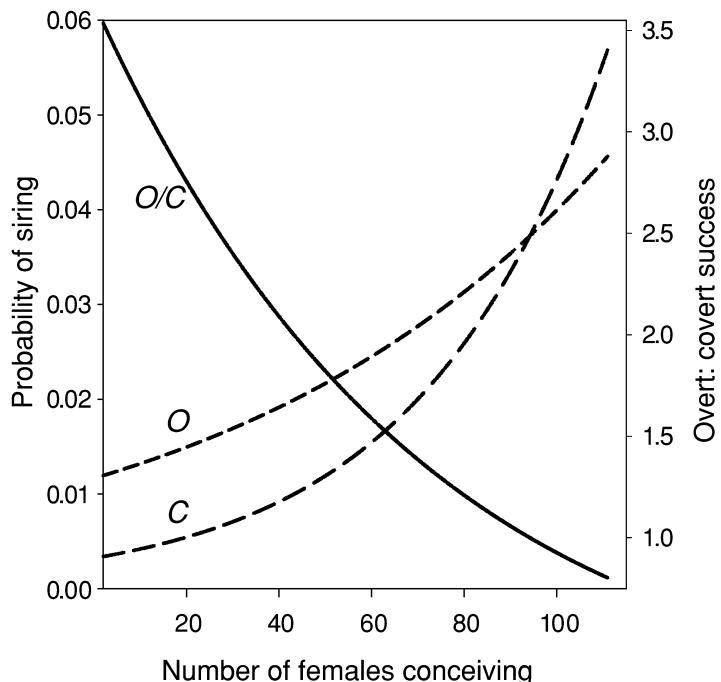


FIG. 9.13. An illustration of the relative influence of overt and covert sperm competition on siring success as the number of females in the population, and hence number of mating opportunities, increases. Predictions of siring success (dashed lines) are for two hypothetical males, one of which makes a greater investment in overt contest competition (O), whilst the second male makes a larger investment in covert sperm competition (C). Predictions for the Overt competitor are calculated using the upper quartile measurement of horn length and the lower quartile measurement of testes size in the adult population; for the Covert competitor the situation is reversed. The relative success of each tactic (O/C) with increasing female availability is also plotted (solid black line). The predictions are based on analysis of factors associated with siring success in the ruts of 1997–9. (From B.T. Preston, unpublished data.)

opportunity for a few big males to monopolise all receptive females declines (Fig. 9.13) (B.T. Preston, unpublished data).

The degree of sperm competition will also vary as population density changes. At high density, females frequently mate with many males: in 1996, for example, a single female was observed to be mounted 160 times by seven different males in the course of

five-and-a-half hours (though it is highly unlikely that intromission was successful in every case; Lindsay (1966) estimated that the success rate varied between 1:5 and 1:10 matings attempts). Consorting males suffer extremely high levels of harassment from subordinates when population density is high and, under these conditions, dominant males are less able to defend females and maintain exclusive mating rights. This is mirrored by the fact that the reproductive success of normal-horned and scurred males converges as density increases (Fig. 9.9b). At high population density, the dominant strategy tends to break down and dominants pursue a more opportunistic strategy, similar to subordinates, relying largely on sperm competition. This is similar to bighorn sheep, where dominant males are more likely to follow the opportunistic coursing strategy in populations where the sex ratio is less female-biased and so competition for mating opportunities is higher (Hogg and Forbes 1997).

FEMALE PREFERENCE

The reproductive success of different male phenotypes is also affected by intersexual selection (Komers *et al.* 1999). Females rarely stand still to allow mating by scurred or young males, except late in oestrus, and often actively avoid them (Grubb and Jewell 1973) as is found in other species (Cox and Le Boeuf 1977; Hogg 1984; Byers *et al.* 1994; Sabat 1994). Females benefit from being in consort with dominant males since they are largely protected from harassment by subordinate males, and oestrus chases are less likely to occur. These chases are both energetically expensive and carry the risk of injury: cases of forced copulation have occasionally resulted in death following accidental rectal rupture. In fallow deer, females may delay oestrus when only young males are present and incur considerable energetic costs avoiding their attentions (Komers *et al.* 1999). Perhaps the most extreme example of the costs of harassment comes from the introduced mouflon population of the Kerguelen archipelago (Réale *et al.* 1996). Unusually for an ungulate, the operational sex ratio is highly male-biased and rams seem unable to form stable hierarchies. It appears that females in oestrus are harassed by many males and in many cases suffer fatal injuries as a result (Réale *et al.* 1996).

If females would prefer to avoid such attention, why do they display prolonged oestrus and accept multiple matings? For elephant seals, bighorn sheep and pronghorn it has been suggested that females may actually be stimulating male intrasexual competition by drawing the attention of dominant males while escaping the attention of subordinates (Cox and Le Boeuf 1977; Byers *et al.* 1994). Certainly, oestrus chases in Soays attract males from the surrounding area and provoke competition. However, dominant males commonly have less stamina and are more likely to give up than the many juveniles that are frequently involved in a chase. Such chases also occur in feral goats, and again dominant males are less agile and often abandon the chase (Pickering 1983). Rather than stimulating competition to select the fittest male, oestrus chases often result in a female being mated by many juvenile, unproven males who may not survive long enough to see a second breeding season. Perhaps a more likely explanation of prolonged oestrus is that female reproductive behaviour reflects phylogenetic history. Wild sheep do not form large family groups, and together with harassment by coursing subordinates, this may render dominant males unable to defend harems. Under such circumstances, it may be difficult for a female to guarantee that she will be first-mated by a high-quality ram; prolonged oestrus and multiple matings may increase the chance that females will be mated by males able to produce large numbers of high-quality sperm.

9.4 Discussion

COMPARISON OF MALE AND FEMALE STRATEGIES IN A FLUCTUATING ENVIRONMENT

Fluctuating population density results in highly variable costs of reproduction for both sexes. At peak density, high fecundity for females and significant rutting activity for males reduces the probability of over-winter survival for an individual (Chapter 2) (Stevenson and Bancroft 1995; Clutton-Brock *et al.* 1996). Conversely, at low and intermediate densities, there appears to be little cost to current reproductive success. There is, however, a fundamental difference between

the sexes in the relative timing of realised reproductive success and the proximate and ultimate costs that are incurred. For females, there appears to be little cost involved in the rut itself. Even in years when the sex ratio is relatively equal, and harassment is common, a female is likely to be the subject of males' attentions for no more than two to four days. This level of disruption seems unlikely to have a major effect on winter survival, since feeding and ruminating still accounts for around 79% of daylight hours during oestrus, compared to around 87% for non-oestrous females (K. Wilson, I.R. Stevenson and B.T. Preston, unpublished data). As a result, females only begin to suffer reproductive costs towards the end of gestation in late winter/early spring (Clutton-Brock *et al.* 1989, 1996; Coulson *et al.* 2001) when their reproductive success is about to be realised. Males, by contrast, contribute no parental care and suffer the costs of reproduction immediately after they have completed their reproductive activities resulting in high mortality earlier in the winter than experienced by females (section 3.5) (Stevenson 1994).

The absence of any form of parental investment by males may, in contrast to females, favour increased investment in the rut at the expense of over-winter survival. Since male mortality rates can be high even when reproductive costs are removed (reaching 44% in the non-rutting juveniles, as described in section 9.3), the low probability of surviving through multiple breeding seasons may tend to favour a semelparous life-history (Promislow and Harvey 1991). In this case, juveniles should invest everything possible in the rut since surviving the winter will not benefit their offspring. By contrast, the minimum 'useful' lifespan for females is almost a year longer since they must survive long enough to rear their offspring to independence. In this respect, Soays bear a certain similarity to *Antechinus* (section 9.1) in which females often have more than one breeding attempt, but males never survive their first year.

Given that females must survive the winter in order to breed successfully, it is strange that they appear unable to respond to population density, while, to some extent, males do (Fig. 9.6). This may be because each sex uses different cues for assessing density, or indeed a reflection of the fact that females require active assessment of the

environment, while males may have an 'assessment' made for them by the simple method of physical exclusion from oestrous females. If males cannot gain access to females then, rather than waste time trying, they may just give up. If the ability to reduce rutting activity (whether by response to density *per se* or through the proxy of competitive exclusion) has a genetic component then this can give rise to the evolution of phenotypic plasticity (Komers *et al.* 1994b, 1997; Komers 1997).

Why do females not tailor their reproductive effort to the costs associated with high population density? Although there is a reduction in the extremes of fecundity (twinning and juvenile conception), there is little response in the proportion of adult females conceiving (Chapter 3, section 3.3). It seems that the main cues that sheep can use to adjust their fecundity – body weight and nutrition – are not good indicators of future conditions on St Kilda. In no year does vegetation availability greatly limit the growth of sheep during the summer (Clutton-Brock *et al.* 1997a) and so body weight is largely independent of population density (Clutton-Brock *et al.* 1996). As a result, body condition in the autumn, which strongly influences fecundity (Gunn *et al.* 1986), is also independent of population density. Furthermore, the increased attention from males at high population density might even increase fecundity through the 'ram effect' (the induction of female puberty, oestrus and ovulation by the presence of males) (Pearce and Oldham 1984), though increased harassment can lower ovulation rates (Raynaud 1972, cited in Thibault 1973).

If the mechanisms that control conception cannot respond to population density, then we might expect the female to display post-conception adjustment of fecundity. Some evidence for the ability of female mammals to perform fine-scale adjustment of embryo sex and number is found in red deer and coypus (Clutton-Brock *et al.* 1986; Gosling 1986; Kruuk *et al.* 1999a). In Soay sheep, however, there is no evidence of a reduced number of embryos being carried late in gestation, suggesting that there is no incidence of either embryo abortion or resorption. This is backed by research in domestic sheep that finds little link between nutrition and embryo wastage after the first month of gestation (Gunn *et al.* 1979; Kelly 1984). Indeed in ungulates

in general, there is little information suggesting that abortion (other than through disease) is common. It seems that although females may have more to gain from a density-dependent fecundity response, they cannot express it, perhaps because of phylogenetic constraints or a relatively recent incidence of large population fluctuations.

To return to the original question, 'Are Soays too fecund for their own good?', the answer appears to be no. Given the constraints of limited information about conditions during the forthcoming winter, and an inability to carry out post-conception adjustment of reproductive investment, our modelling indicates that female Soays exhibit close to optimal behaviour. Males, too, appear to be close to optimal, maturing early when conditions are favourable but tending to delay when the mortality risks are highest. So if Soays are more than just the maladapted flotsam of domestication, what are the broader implications of our study?

SOAYS AS A MODEL SPECIES

It is often tempting to concentrate on the ways in which Soays and their environment are atypical: feral sheep living on a small island that supports only a depauperate range of plant communities, lacking competing grazers and predators, and with no opportunity for immigration or emigration. Yet in many ways Soays are a good model. Their reproductive biology is similar to many wild ungulates, and increasing numbers of these 'wild' populations now live in predator-free environments. In this context a detailed knowledge of reproductive behaviour and the factors affecting fecundity is of growing importance in the management of these populations. Our understanding of these topics is rudimentary, however, and the 'simple' system presented by Soays offers a starting-point for testing many of these ideas.

A good example of the use of Soays as a model is to test the widespread assertion that the rutting behaviour contributes to the male-biased mortality observed in many temperate-zone ungulates (Geist 1971; Clutton-Brock *et al.* 1982a; Pickering 1983; Leader-Williams 1988; Festa-Bianchet 1989b; Miquelle 1990). The suggestion of a link between rutting and differential mortality implies that widely differing reproductive trade-offs are experienced by each sex, yet no other

study has demonstrated this conclusively, let alone examined how the trade-offs vary between individuals. With Soay sheep we can conduct experiments that confirm this link (section 9.3) and can use the wealth of individual-based data to begin an examination of how optimal life-history differs between individuals both within and between the sexes (sections 9.2 and 9.3).

This investigation of individual variation in optimal life-histories is perhaps the most important aspect of our study of Soay reproductive behaviour. It underlines the fact that talk of a ‘species life-history’ refers to that rarest of beasts: the ‘Average Individual’. For real animals, the optimal strategy is a moving target that varies constantly with the state of the animal and its environment (Stearns 1989). Ignoring this ‘substructure’ within the population may, for example, result in the wrong prediction being made about how the dynamics of a population will respond, say, to management or other perturbations (Moorcroft *et al.* 1996; Coulson *et al.* 1999a).

Our studies also demonstrate that the pattern of natural selection is rarely simple, and that even when certain phenotypes appear to be without doubt the fittest, ‘inferior’ individuals may be more successful than we at first imagine. For example, our behavioural observations of rutting males support the typical polygynous model of ‘biggest is best’ (section 9.3), but this does not translate fully into fitness since young or apparently inferior phenotypes may be more successful than simple behavioural data suggest (section 9.3; Chapter 6). This is particularly important in a fluctuating environment, where the periodic relaxation of competition, due to male-biased mortality (Chapter 3), allows these other males to express full reproductive behaviour (Komers *et al.* 1994a) which in turn may bring gain considerable success (Chapter 6). Even at high population density, when *overt* competition is at its strongest, *covert* sperm competition may be busy undermining the behavioural advantage of the ‘classically successful’ large, prime-aged males (section 9.3) (Preston *et al.* 2001). This is an area that deserves further investigation, for although there are many detailed studies of male reproductive behaviour and tactics,

information about the ultimate fitness of these is much less common (e.g. Weatherhead *et al.* 1995; though see Hogg 1984, 1987).

In conclusion, Soay sheep present a model system that is more tractable than many others, but it remains a single example of an unusually simple system. Ultimately, there is a need for similar long-term studies on a wide range of species that can confirm or refute the generality of our findings.