The Maintenance of Genetic Polymorphism in Small Island Populations: Large Mammals in the Hebrides [and Discussion]

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The maintenance of genetic polymorphism in small island populations: large mammals in the Hebrides

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SUMMARY

Conventionally, small populations living on islands are expected to lose genetic variation by drift. Fluctuations in population size, combined with polygynous mating systems, are expected to contribute to the process by increasing sampling effects on genetic variation. However, in individually monitored populations of Red deer on Rum and Soay sheep on St. Kilda, which experience fluctuations in population size, two processes have been identified which mitigate loss of genetic variation. First, in a number of examples, population reductions are associated with selection. Selection may be in favour of heterozygotes, or, as we have documented in several cases, it may fluctuate in direction temporally. Second, in Soay sheep, in which mortality over population crashes is male-biased, ostensibly leading to low effective numbers of males, molecular studies show that there are systematic changes in the reproductive success of young males, and in variance in male success, that broaden genetic representation compared with expectation.

1. INTRODUCTION

In this paper we seek to emphasise a particular virtue of island populations: they can be used to evaluate the population genetic processes responsible for changing allele and genotype frequencies, and hence levels of genetic variation. This virtue is distinct from the more commonly discussed merits of island populations for investigating speciation, which occupy most of the other contributions to this symposium, and for investigating loss of genetic variaton in island-hopping founder events, exemplified by Gilbert *et al.*'s (1990) investigation of California Channel Island fox (*Urocyon littoralis*) populations.

Island populations have numerous practical advantages for investigating certain population genetic processes. First, immigration and emigration are often minimal or absent for practical purposes, leaving selection and genetic drift as the only processes likely to affect levels of genetic variation. Second, the finite population size and often single management authority responsible for whole islands makes island populations exceptionally tractable for detailed studies. It is no coincidence that many of the classic long-term, individual-based studies which have contributed to our knowledge of population dynamics, behavioural ecology and natural selection are based on islands (e.g. Red deer (*Cervus elaphus*; see Jewell *et al.* 1974; Clutton-Brock *et al.* 1982), Soay sheep (*Ovis aries*; see Clutton-Brock *et al.* 1991), Darwin's finches (*Geospiza* spp; see Grant 1986), Song sparrows (*Melospiza melodia*; see Smith & Dhondt 1980), collared flycatchers (*Ficedula albicollis*; see Gustafsson 1986)). Finally and perhaps most importantly, island populations are frequently subject to changes in population size, either due to external factors (e.g. weather: Darwin's finches (Grant 1986) and Song sparrows (Keller *et al.* 1994)) or due to intrinsic instability (e.g. Soay sheep; see Grenfell *et al.* 1992), offering unusual opportunities to investigate the relation between population dynamics and genetic variation.

It is the conventional wisdom of population genetics theory that fluctuations in population size, and specifically reductions in population size, will result in loss of genetic variation. This is because, after a population decline, the individuals that survive to breed are a random but small sample of the preceding population. Two assumptions underpin this wisdom. First, it assumes that selection is weak or absent during population reduction. Whereas this is likely to be true in deliberately designed laboratory experiments or in some natural catastrophes, it is not necessarily so for all kinds of population reduction. For example, any population reduction which includes intraspecific competition for scarce resources might involve selection, and there are at least two processes through which this could retard loss of genetic variation, namely through selection for heterozygotes or through selection for alternative alleles during periods of population decline and recovery. In general theoretical studies have predicted that selection that fluctuates in direction, though perhaps slowing loss of genetic variation, cannot maintain it. Recently, however, Ellner & Hairston (1995) have shown that with overlapping generations, genetic variation can be maintained by selection that fluctuates in direction. The second common assumption is that distribution of male mating success remains constant despite changing population size and demography. There have been few investigations of this point from the population genetic viewpoint, even though we know that in some vertebrates mating systems can vary dramatically with population demography (e.g. fallow deer; see Langbein & Thirgood 1989)

Here, we investigate these issues in two individually monitored island populations of ruminants, Red deer living on the Isle of Rum, Inner Hebrides, and Soay sheep living on Hirta in the St. Kilda archipelago, Outer Hebrides. In the course of each study, the population has experienced marked changes in population size, allowing us to investigate whether there are systematic associations between fitness measures and genetic factors through population fluctuations, and whether there are systematic changes in the distribution of male mating success associated with population fluctuations.

2. THE STUDY POPULATIONS

(*a*) *Red deer*

The Isle of Rum (10600 ha) is one of the Inner Hebrides, lying about 20 km west of the Scottish mainland. After extirpation in the 18th century, Red deer were reintroduced to Rum from 1845 onwards, from at least four source populations elsewhere in the U.K. In recent years, the whole island deer population has ranged between 1200 and 1700.

Red deer living in the North Block of the Isle of Rum have been the subject of intense, individual-based monitoring since 1971 (Clutton-Brock *et al.* 1982; Clutton-Brock & Albon 1989). Over this time approximately 1700 individuals have been monitored from birth, through all reproductive attempts, to death. In general, females adopt a home range similar to their mother's, whereas males emigrate from their natal area at about 2 years of age. There are no physical barriers between the study area and the rest of the island, and through male emigration and immigration, the study population is panmictic with that of the rest of the island. At any time the study population constitutes about one quarter of the total island population.

Culling ceased in the study area at the start of the study, and this has led to changes in the density and demography of the population. Over the first 8 years the female population rose to about four times its original number and it now fluctuates around the apparent carrying capacity of the study area (figure 1*a*). In the same period, the male population has fluctuated and, if anything, declined slightly (figure 1*a*) with the consequence that what was initially an area with a male-biased population now holds a strongly female-biased population. Rising deer density has been accompanied by density-dependent responses in fitness components, especially in juvenile survival and female fecundity (Clutton-Brock *et al.* 1985, 1987). In common with other sexually dimorphic vertebrates, juvenile survival is strongly female biased, accounting for much of the female bias in the current adult population (Clutton-Brock *et al.* 1985).

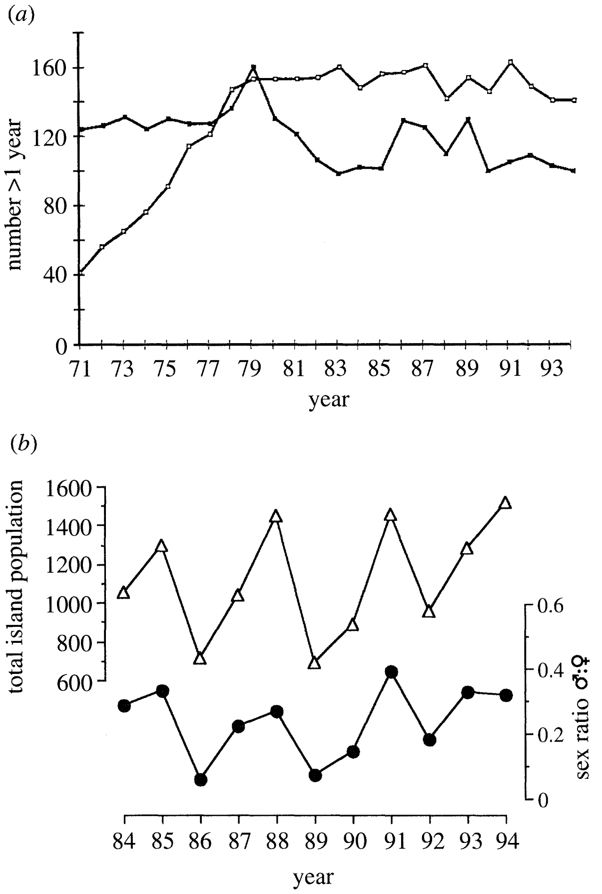

Figure 1. (*a*) Number of male and female Red deer (older than one year) regularly using the Isle of Rum study area (open squares: females; filled squares: males). Since cessation of culling in 1971 female numbers (and hence overall density) have quadrupled, whereas male numbers have declined slightly. (*b*) Population size on the whole island of Hirta since 1984, and sex ratio of individuals > 1 year, showing correlated fluctuations of these two measures.

(*b*) *Soay sheep*

The St. Kilda archipelago lies some 200 km west of the Scottish mainland. Soay sheep are primitive domestic sheep which have existed unmanaged on the St. Kildan island of Soay (99 ha) for centuries if not millenia. In 1932, 107 sheep were introduced to the neighbouring island of Hirta (638 ha).

Soay sheep have been intensively monitored within the Village Bay area of Hirta (ca. 175 ha) since 1985 (Clutton-Brock *et al.* 1991, 1992), and again about 1700 individuals have been followed over this time. The monitored population constitutes about one third of the whole island populaton, with which it is panmictic. The study was initiated because annual censuses of the whole island and a previous period of intensive study (Jewell *et al.* 1974) indicated unusual, unstable population dynamics. At intervals of 3–5 years, the population experiences overwinter population crashes in which up to 70% of the population may die (Clutton-Brock *et al.* 1991, 1992; Grenfell *et al.* 1992) (figure 1*b*). The sheep population dynamics are a consequence of the generally high level of fecundity in Soay sheep, which allows them, in a single summer, to increase to well above the overwinter carrying capacity of the herbage (Clutton-Brock *et al.* 1997). Parasitism by gastrointestinal nematodes appears to contribute to the severity of the crashes (Gulland 1992; Gulland & Fox 1992; Gulland *et al.* 1993).

Over population crashes, survival is again female biased, probably because males go into the winter in poor condition following the November rut (Stevenson & Bancroft 1995). In addition, mature animals survive crashes better than yearlings, and particularly, lambs (Clutton-Brock *et al.* 1992). In consequence, both the sex ratio (figure 1*b*) and the age structure (not illustrated) fluctuate systematically with population size, offering the opportunity to study their effects on the distribution of male mating success.

A striking feature of Soay sheep, which precipitated some of the investigations reported here, is that they show two obvious phenotypic polymorphisms. First, there is polymorphism for pelage colour and pattern, with the principle morphs controlled by two loci each having two alleles (Doney *et al.* 1974). Second, Soays have variable horn phenotype, ranging from no horns (polled), through small, mis-shapen horns knowns as scurs, to normal horns. This variation is heritable (I. R. Stevenson, unpublished data), but complicated by different expression in the sexes: a greater proportion of males have normal horns.

(*c*) *Molecular investigations*

Since 1982 and 1985 respectively, samples have been collected from all study area deer and sheep when they were handled or found dead. The samples have been subjected to various molecular techniques, including protein electrophoresis, DNA fingerprinting and more recently microsatellite DNA profiling (Pemberton *et al.* 1988, 1991, 1992; Gulland *et al.* 1993; Bancroft *et al.* 1995*a*, *b*). These studies have confirmed that despite their history, Soay sheep retain substantial heterozygosity; for example, across 34 protein loci average heterozygosity is 7.78%, high for a mammal (Bancroft *et al.* 1995*a*). The molecular data for known individuals in both populations has been used to investigate whether associations exist between alleles or genotypes and fitness (Pemberton *et al.* 1988, 1991; Gulland *et al.* 1993; Bancroft *et al.* 1995*b*; Illius *et al.* 1995) and to identify paternity (Pemberton *et al.* 1992). The results reported in this paper constitute a mix of previously reported and new results derived from this work. We now address the two issues raised in the Introduction in turn.

(i) *Where population fluctuations involve varying intraspecific competition, there may be systematic selective effects which act to retard loss of genetic variation*

The rising density of deer in the Rum study area, and the population crashes and recoveries seen on St. Kilda, involve individuals facing changing levels of competition for food. In each case, this leads to increased mortality, particularly affecting younger age classes and males, and in the case of deer, there are also marked changes in fecundity. In a series of previous investigations, we have shown that for some polymorphic systems, mortality and/or fecundity is not random with respect to phenotype, genotype or alleles (Pemberton *et al.* 1988, 1991; Gulland *et al.* 1993; Bancroft *et al.* 1995*b*; Illius *et al.* 1995; Moorcroft *et al.*). Here, we review patterns which suggest to us that these associations, combined with fluctuating population dynamics, could slow the rate of loss of genetic variation or maintain it.

Isocitrate dehydrogenase (*Idh-2*) *in deer*

At the protein level, two alleles are detectable at Idh-2. Remarkably, across all genotyped individuals ($N = 993$) the two allele frequencies are 0.502 and 0.498. Among calves born into the study population, heterozygotes are significantly more likely to survive to two years of age than homozygotes (Pemberton *et al.* 1988). This association is particularly strong in females (Pemberton *et al.* 1988, 1991). In common with other associations discussed below, no mechanism for this association is known and it is possible that Idh-2 is marking the effects of a linked locus.

This example serves to illustrate the possibility that one consequence of intraspecific competition may be selection for heterozygous individuals. The idea of selection for heterozygotes has a long history (see review by Allendorf & Leary 1986), and various mechanisms could be responsible for heterozygote advantage. One possibility is that selection favours outbred individuals, as has been documented for a weather-driven population crash in Song sparrows on Mandarte Island, British Columbia (Keller *et al.* 1994). However, another possible explanation is that there could be a selective advantage to having more than one version of an enzyme molecule, perhaps due to greater kinetic adaptability. Either way, a consequence of such selection will be to maintain genetic variation in the population at the locus concerned.

The other examples we cite below illustrate an alternative mechanism which may prevent loss of genetic variation in fluctuating populations, namely that fluctuating levels of intraspecific competition may result in temporal variation in the direction of selection.

Mannose Phosphate Isomerase (*Mpi*) *in deer*

At the protein level, two alleles are detectable at Mpi. In the total study population sample, allele *s* is at approximate frequency 0.85 and allele *f* at 0.15. Among calves born into the study population, individuals with an *f* allele are significantly more likely to die before reaching 2 years of age (Pemberton *et al.* 1988, 1991).

Conversely, in adult female fertility (pregnancy) and fecundity (production of calves), there appear to be significant advantages to having an Mpi *f* allele. Study area females with an *f* allele breed at an earlier age and tend to be more fecund over their lifespan (Pemberton *et al.* 1991), and in shot females from non-study area parts of Rum, Mpi *f*-carriers are more likely to be pregnant (Pemberton *et al.* 1991).

Set in the context of changing population density, these observations would have the following consequences. At low density, when juvenile mortality is negligible, the Mpi *f* allele should increase through its association with higher fertility and fecundity in females. At high density, when juvenile mortality becomes a more important component of fitness variation (Clutton-Brock *et al.* 1985, 1987), the Mpi *s* allele will be favoured and its frequency will increase, as illustrated in the study area deer (Pemberton *et al.* 1988). It seems likely that fluctuating density would retain both alleles in the population.

Changes in the study area population density on Rum were dictated by a change in human management strategy and occured relatively slowly, but conceptually similar examples are apparent within the Soay sheep population on St. Kilda, in which relatively short-term population fluctuations occur without human intervention (figure 1*b*).

Horn morphs in Soay sheep

As outlined above, there is heritable horn variation in the Soay population, with frequencies for normal, scurred and polled individuals being 87, 11 and 2% respectively in rams and 36, 21 and 35% respectively in ewes. Male sheep with normal horns are behaviourally dominant to polled and scurred individuals, and almost certainly have a mating advantage, because they are able to sequester females in exclusive mating consorts (I. R. Stevenson, personal communication). One might therefore predict that sexual selection would have fixed normal horns in the population, or at least in males (in many ruminant species, weapons are confined to males and all females are polled). However, individuals of both sexes with scurred horns consistently survive population crashes better than individuals that are polled or have normal horns (Moorcroft *et al.* 1996). The mechanism for this superior survival is unknown and is currently being investigated. Whatever the mechanism, this superior survival helps to explain why horn polymorphism persists in the population.

Adenosine deaminase (Ada) in Soay sheep

At the protein level, two alleles are detectable at Ada. In the total study population sample, allele *s* is at approximate frequency 0.75 and allele *f* at 0.25. Over three successive population crashes, *ff* individuals consistently survived worst, and in the most extreme crash, heterozygotes survived the best (Gulland *et al.* 1993). Ada *ff* sheep also have the highest gastrointenstinal nematode burdens at certain times of year, suggesting the survival effect is mediated through parasite resistance (Gulland *et al.* 1993).

Recent investigations of variation in female fecundity on St. Kilda have revealed an interaction between Ada genotype, population size and fecundity (Ada + Ada.population size $X^2 = 14$, d.f. = 4, $p < 0.05$; figure 2). The fecundity of Ada *ff* females is the least responsive to rising density. It is possible that both the higher worm burdens and greater crash mortality observed are a consequence of these individuals conceiving at high density. Though it may appear from these observations that the *f* allele should decline, this does not take into account the value of lambs produced at different population sizes. As we will show below, lambs born immediately following a population crash are particularly valuable, broadly because they have a clear 2–4 years in which to breed before another crash occurs. Ada *f*-carrying individuals, by not responding to rising population size, have a greater probability of producing one of these high-value lambs than *ss* individuals. It therefore seems possible that the maintenance of the Ada polymorphism in the Soay population is again connected with the different responses of the genotypes to changing population density.

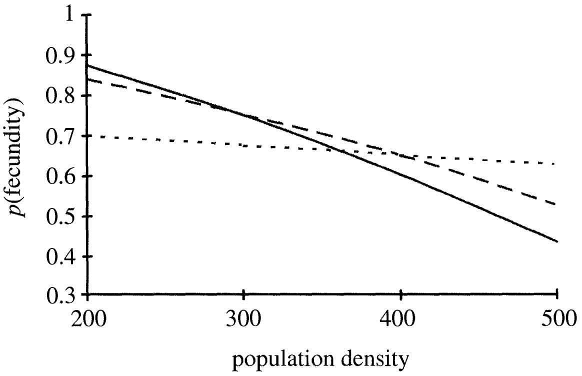

Figure 2. Interaction between the probability that a female Soay sheep has a lamb (*p*(fecundity)), Ada genotype (*ss*: solid line; *sf*: long-dashed line; *ff*: short-dashed line) and population density on Hirta (Ada + Ada.population size, $X^2 = 14$, d.f. = 4, $p < 0.05$). The fitted ordinal logistic model also included the effects of female age and breeding experience and interactions between these terms and population density.

(ii) *Where population fluctuations alter the demography of populations, there may be systematic changes in the distribution of male mating success which retard loss of genetic variation*

Calculations of effective population size for polygynous populations often assume that matings are divided between the mature males present in the population regardless of the population's size or demography. Thus, after a population decline leaving a female-biased population, it is assumed that surviving adult males obtain large numbers of the available matings. However, in Soays, behavioural observations show that ram lambs (aged 7 months) participate in the rut to an extent which varies from year to year (Stevenson & Bancroft 1995). They participate most in post-crash ruts, when the older ram population is small and the population is strongly female-biased. In this section, we use paternity data attributed by molecular techniques to investigate the genetic consequences of this and related aspects of the mating system. We concentrate on the population in the years 1986–1993. As shown in figure 1*b*, over this period, the study population varied substantially in size and sex ratio.

The Soay sheep mating system has been described by Grubb (1974). Soay sheep are highly seasonal and mate in November. Both sexes are promiscuous. Ewes come into oestrus for 24–36 h, and mate repeatedly during this time. Oestrous ewes are often detected by small, young or scurred rams and chased and mated by several of them. More frequently, an exclusive consort is formed with a single mature ram for hours at a time, resulting in repeated mating by the same pair. For most of the years indicated, rut consort information was collected by censusing, but in tests using DNA fingerprinting or single locus profiling, consort information was found to be a poor predictor of paternity (Bancroft *et al.* submitted). This is probably because the census-based approach misses many chases and changes in consort partnerships. To pursue the identification of paternity and the success of ram lambs in gaining paternities, we employed an entirely genetical approach to identifying paternity.

We used locus-specific protein and microsatellite markers to investigate paternity for 921 lambs with sampled mothers born into the study area in the years following the ruts 1986–1993. Most individuals have been genotyped at 15 to 17 loci (for identity of loci see Bancroft *et al.* 1995*a*; Smith 1995), and the candidate fathers for each lamb consisted of all the tagged rams known to be alive in the preceding rut, which varied from 68 to 227 males in different years. We used a computer program (T. C. Marshall, unpublished data) written in dBASE IV to conduct all comparisons, and log-likelihood ratios, which can often discriminate two or more candidate males even though they both match a putative offspring and have low exclusion probabilities. The analyses described below are based on 663 paternities (of 921 cases investigated) attributed to the most likely male with a log-likelihood ratio over 2.0. A simulation which incorporated appropropriate biological and genetic parameters for the population was used to derive log-likelihood ratio thresholds giving 95% confidence in a paternity identification being correct. Three-hundred-and-twenty-one of the 663 cases (48%) fell into this category. The remaining paternity identifications are less secure but, importantly, allow us to estimate the number of males which obtained no paternities in each year. Most lambs with no assigned father were probably sired by immigrant, unsampled rams.

Mating success of young rams

As anticipated from rut census data (Stevenson & Bancroft 1995), ram lambs (7 months old at the rut) obtain more paternities in those years when the older rams are few in number (figure 3*a*). Similarly, yearling rams obtain more paternities when older rams are few in number (figure 3*b*) with the exception that in those ruts when the yearling class has been decimated by a population crash (ruts 1986 and 1989), there are few yearlings around to obtain paternities. Thus, in precisely those years (following a crash) when the effective number of males in the population might be expected to be low, young males, which were *in utero* during the crash, are particularly successful in obtaining paternities.

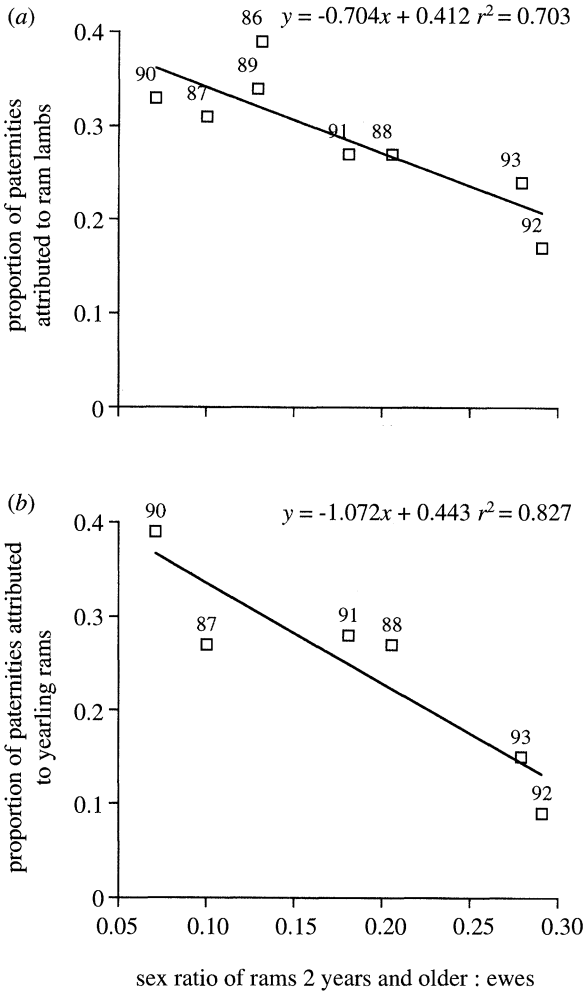

Figure 3. Proportion of paternities attributed to young rams in relation to (on horizontal axes) sex ratio of rams 2 years and older to ewes. The latter attempts to measure the extent to which older rams can gain exclusive access to oestrous ewes. (*a*) Ram lambs (aged 7 months at the rut). (*b*) Yearling rams (aged 19 months at the rut). Note that the ruts for 1986 and 1989 are missing from this graph since in each case only three rams survived the relevant crash to become yearlings, and as a result their cohort had very low paternity success.

As a consequence of their success when young, and continued absence of older age classes as they grow older, one might predict that cohorts of rams born following a population crash would have greater mean individual lifetime reproductive success (LRS) than other cohorts. Preliminary data (some relevant animals are still alive at the time of writing) confirm that the two ram cohorts studied which were born after a crash (1986 and 1989) have been more successful than the cohorts that succeeded them.

Variation in sibship size

The distribution of the number of rams obtaining different numbers of paternities in each year varies systematically with population demography. The

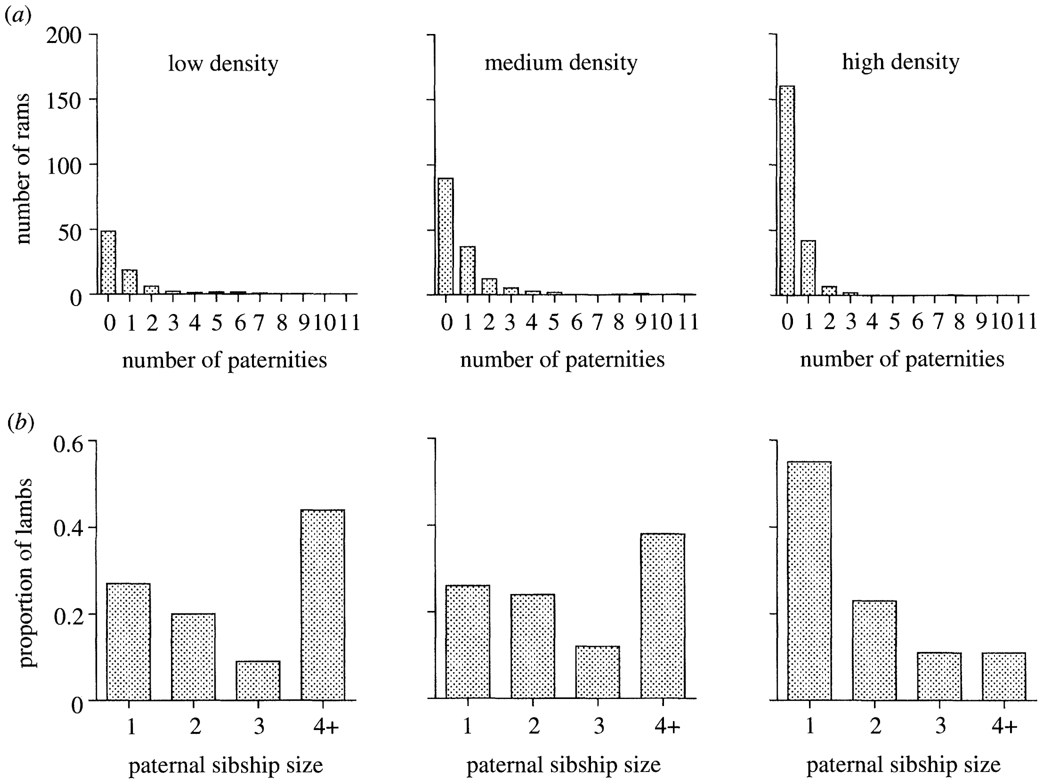

Figure 4. Population size-related variation in the rut in Soay sheep. Figures are mean values for ruts that occurred at low (1986 and 1989), medium (1987, 1990 and 1992) and high (1988, 1991, 1993) population density. (*a*) Distribution of the number of rams with different numbers of paternities. In a multinomial regression model applied to the whole dataset 1986–1993, the probability of a male siring multiple offspring is significantly associated with population size ($X^2 = 37.92$, d.f. = 1, $P < 0.001$). In low density ruts, individual older rams are able to obtain multiple paternities, despite the efforts of young rams (figure 3), which account for about half the cases in the 1- and 2- lamb categories. (*b*) Distribution of paternal half sibship size. Note that in ruts occurring at high density (immediately before a crash) most lambs conceived are the only offspring of their father in their cohort. By contrast, in ruts occurring at low density, most lambs have paternal half sibs in their cohort.

pattern is that in ruts that occur at high density, paternity is relatively evenly spread, with most rams getting zero, one or two paternities. Using a multinomial regression model, the probability of a ram siring multiple offspring is significantly associated with population size ($X^2 = 37.92$, d.f. = 1, $P < 0.001$; figure 4*a*). Thus, despite the depredations of young rams (above), the low density ruts which follow population crashes do allow surviving older rams to get multiple paternities. Nevertheless, young rams have an important impact on these ruts, obtaining about half the paternities in the one- and two-lamb categories.

Variation in the distribution of male success between years has an important effect on the size of the paternal half sibships subsequently born. Thus, most lambs conceived in high density ruts are the sole representative of their father in their cohort. By contrast, most lambs conceived in low density ruts have paternal half sibs in the same cohort (figure 4*b*). Interestingly, therefore, the lambs which are *in utero* during a population crash, which, if they survive, go on to enjoy high LRS, are a particularly representative sample of the pre-crash male population.

4. DISCUSSION

The purpose of this paper has been to outline two general processes, selection and variation in the distribution of male mating success, which may buffer loss of genetic variation by genetic drift during population fluctuations in nature. In this section we discuss how widespread these processes are likely to be, and some practical implications.

Many documented population reductions have undoubtedly resulted in loss of genetic variation. One of the best examples, among large mammals, is the Northern elephant seal (*Mirounga angustirostris*) (Bonnell & Selander 1974; Hoelzel *et al.* 1993). In this case, in which the decline was caused by hunting, it seems likely that mortality was random with respect to genotype and thus adhered to neutral population genetic expectations. However, the overwhelming number of vertebrate population size changes, including declines, are probably caused by habitat change, and, depending on their severity, may involve selection. Few field studies have the data resolution to investigate selection in relation to population change, but all those that do have shown selective processes likely to retain variation. Apart from the Red deer and Soay sheep studies reported here, these include

Darwin's finches in the Galapagos (Grant 1986) and Song sparrows on Mandarte Island (Keller *et al.* 1994). More studies are required to confirm the generality of selection during population size change.

Fluctuations in the distrubution of male mating success, with changes in population size, density or demography have not been extensively documented. Again it should be no surprise that individuals have variable their involvement in mate competition according to ambient levels of competition. Again, there are few studies which have explicitly addressed this topic. However, in a recent analysis of 20 years of male rut behaviour in Red deer, which is strongly correlated with true success as measured by DNA fingerprinting (Pemberton *et al.* 1992), T. H. Clutton-Brock *et al.* (unpublished data) have shown that in this species also, young males have variable mating success. A major task for the future is to assess the strength of these processes in retaining genetic variation. In particular, estimating effective population size in populations with overlapping generations, fluctuating population size and varying distribution of male mating success is an urgent requirement.

Population genetic investigations in island populations form important practical models for species conservation. It is axiomatic to modern conservation biology that genetic variation must be preserved in endangered species, to avoid inbreeding depression and to allow future genetic adaptation, but at present the models employed make relatively simple assumptions about the process of genetic drift during population size fluctuations. The studies reported here suggest processes which should be investigated further and taken into account in species conservation studies.

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Discussion

P. H. A. Sneath (*Department of Microbiology and Immunology, Leicester University, Leicester LE*1 7*RH, U.K.*) We know that island forms of mammals commonly evolve into dwarf forms. Is anything known about the energy requirement for growing horns, and could this explain the observed tendency of Soay sheep to have small horns? Is it possible that, in times of food scarcity, small-horned individuals could have a selective advantage?

J. M. Pemberton To clarify the facts first: normal-horned Soay sheep, particularly males, have relatively large horns for their size, but there is a polymorphism in which some individuals of both sexes have small (scurred) horns or no horns at all. We have demonstrated that in times of scarcity scurred animals do have a selective advantage, because they survive better. It is quite possible that this is due to differences in energy requirement associated with growing horns, but we have not determined this: it is a topic we plan to investigate in the future.