stored as described previously[21]. After the initial treatment with proteinase K and SDS described by ref. 22, total RNA from 100 μl of the lysate from the Sterivex cartridges were further purified using the RNeasy tissue kit (Qiagen) and the protocol for lysed cells. To further remove DNA from the RNA preparations, the samples were treated by the DNAfree kit (Ambion) following the manufacturer's protocol. cDNAs were synthesized by reverse transcription using 2 μl of the RNA extracts using random hexamers as primers, using the TaqMan RT kit (Applied Biosystems) according to the manufacturer's protocol. Genomic DNA contamination of cDNA preparations was examined by 5′-nuclease assays comparing gene copies in cDNA preparations and in controls with no reverse transcriptase added. These control assays tested for the presence of both rRNA[21] and protein-encoding genes (M. T. Suzuki et al., unpublished results). In both assays we observed no signal in controls without reverse transcriptase.

The annotated BAC insert sequences are available at the Monterey Bay Coastal Ocean Microbial Observatory site at http://www.tigr.org/tdb/MBMO/.

pufL and pufM amplification

Primers used in this study were pufL, forward (5′-CTKTTCGACTTCTGGGTSGG-3′)[10]; pufM, reverse (5′-CCATSGTCCAGCGCCAGAA-3′) (a modification of the primer reported by ref. 10); and pufM, forward (5′-TACGGSAACCTGTWCTAC-3′).

Phylogenetic analysis

pufM sequences from the current study combined with sequences from public databases were translated and the protein sequences aligned using the pileup program of the Wisconsin package (GCG). DNA sequences and protein alignments were imported into a database using ARB software (http://www.arb-home.de). We aligned DNA sequences based on the protein alignment. Evolutionary distances were calculated with the dnadist program of the PHYLIP package[23], using the Kimura 2-parameter model. Phylogenetic trees were inferred using the neighbour program of the PHYLIP package. To evaluate the reliability of the branching patterns, 100 random bootstrap re-samplings were performed using the program seqboot, with subsequent phylogenetic analyses performed as above. Ribosomal RNA phylogenetic analyses were performed as described above, on alignments encompassing 860 nucleotide sequence positions. For analysis of the shorter pufM cDNA sequences obtained through RT-PCR, a neighbour-joining tree was imported into the ARB database, and the cDNAs were added to tree using the ARB_PARSIMONY program, without local optimization and using a mask that included only those positions encompassing the cDNA sequences.

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Sex differences in emigration and mortality affect optimal management of deer populations

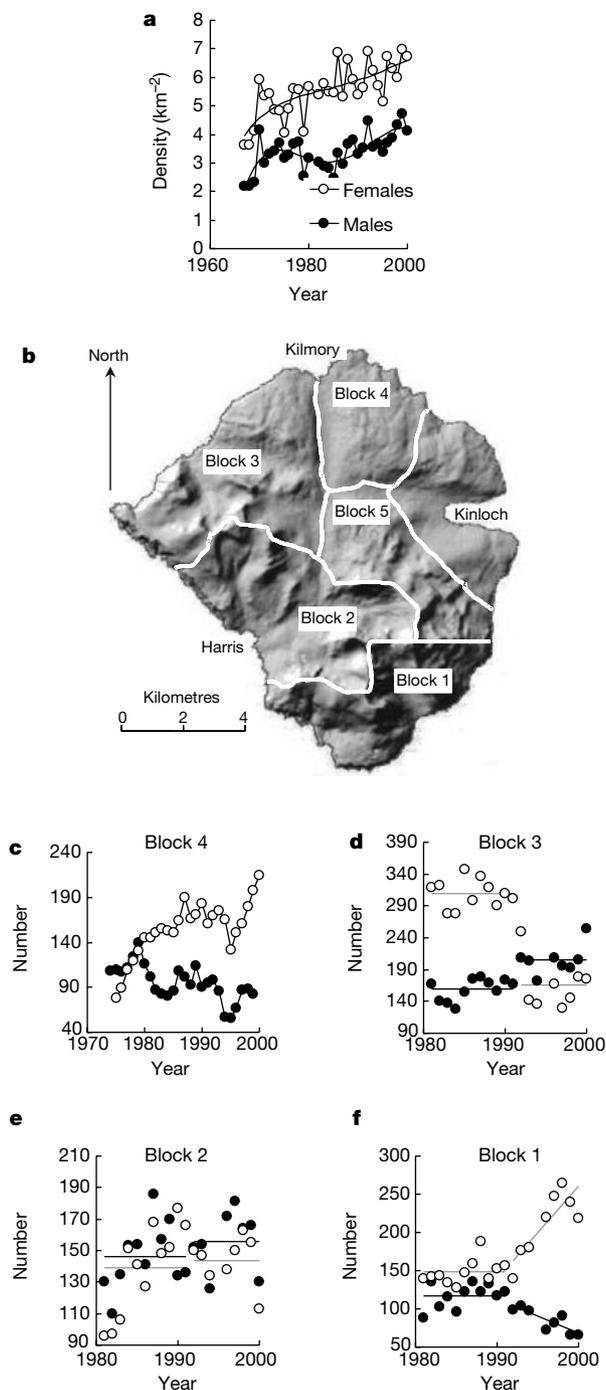T. H. Clutton-Brock*, T. N. Coulson*, E. J. Milner-Gulland†, D. Thomson* & H. M. Armstrong‡

* Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
† TH Huxley, School of Environment, Earth Science, and Engineering Royal School of Mines, Imperial College, London SW7 2BP, UK
‡ Scottish Natural Heritage, 12 Hope Terrace, Edinburgh EH6 5NP, UK

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Populations of red deer that are limited by food, like those of many other ungulates[1–3], commonly include more females than males[4–7]. We assessed the contribution of variation in sex- and age-specific rates of mortality and emigration to density-dependent changes in the adult sex ratio, using long-term observations and demographic experiments involving the red deer population on Rum, Scotland[4,5]. We incorporated these effects in a stochastic model of local populations under different management regimes to show here that, when female numbers are allowed to increase to more than 60% of the ecological carrying capacity, the sustainable annual harvest of males from local deer populations will fall. Because males are typically culled by fee-paying hunters and generate more income than females[5,8,9], income will decrease as the male harvest falls. Because numbers of female deer throughout much of the Highlands probably exceed the threshold at which male density starts to be affected[5], many managers might be able to raise income from local deer populations by reducing female numbers, with potential benefits to the vegetation of Scottish Highland environments[10].

Populations of red deer (Cervus elaphus L.) throughout the Scottish Highlands include roughly twice as many females aged ≥ 1 yr as males (Fig. 1a). To investigate the consequences of increasing population density for males and females, in 1972 we released the red deer population of the 12-km² north block of Rum

(block 4, Fig. 1b) from the annual 14% cull that had been used to control deer density since 1958[5,11,12] (Methods). Subsequently, female numbers in block 4 increased by 100%, whereas male numbers gradually decreased (ref. 6; and Fig. 1c).

Five different density-dependent processes contributed to changes in the adult sex ratio in block 4. As the total number of deer rose, the proportion of males born decreased (ref. 13; and Fig. 2a). Neonatal mortality did not change with density (Fig. 2b), but the mortality of males in their first 2 yr increased relative to females of the same age (ref. 14; and Fig. 2c). Mortality of adults (5–10 yr) increased in both sexes, but was higher in males than in females (Fig. 2d). The proportion of males emigrating to other subpopulations (usually aged 2–4 yr; Methods) rose (Fig. 2e) and the number of males immigrating into the population decreased (Fig. 2f), whereas emigration and immigration by females was rare irrespective of density[15].

By calculating the effects on the adult sex ratio when each of these changes was omitted in turn, we identified changes in male emigration and male survival to be the principal causes of the relative increase in female numbers with rising density (Table 1). The antler size of mature males also showed a progressive decrease after 1972 (refs 4, 5). Increasing emigration probably contributed to this, because better grown males were more likely to emigrate as adolescents than smaller individuals (Table 2), and well-grown adolescents carry relatively large antlers as adults[4,5,15].

If uncontrolled increases in female deer numbers generate biases in the adult sex ratio, then reductions in female density should lead to increases in male numbers. To determine whether this is the case, we selected the west block of Rum (block 3) (which had previously contained more females than males; see Fig. 1d) and increased the annual cull of females from 14% to ∼60% in 1991 and 1992, until female numbers were reduced by 50% (see Fig. 1d). Roughly the same number of adult males (20) continued to be culled each year from the block, while after 1992 the annual 14% cull of females was re-imposed. After the reduction in female density, the number of resident males in block 3 increased by ∼25% and is still increasing (Fig. 1d). Over the same period, no significant increase in male numbers occurred in either of the two neighbouring blocks (2 and 4), where management regimes remained unchanged throughout this period (Fig. 1e, c).

To determine whether reductions in male density had similar effects on female numbers, we reduced male numbers by 50% in the southeast block of Rum (block 1, Fig. 1f), but maintained the same percentage cull on females as before 1991. Low male densities immediately after the cull attracted young males from neighbouring areas and male numbers proved difficult to reduce, despite an annual average cull of 68% of the spring population of males each year between 1991 and 1999. By 1995, however, male numbers in block 1 had decreased by 50% (Fig. 1f) and female numbers in the

Figure 1 Changes in the adult sex ratio. **a**, Average density of male and females per km^2 aged ≥ 1 yr across the Scottish Highlands. **b**, Rum showing the outlines of the five deer blocks. **c**, Numbers of identifiable deer aged ≥ 1 yr using the 12-km^2 north block of Rum (block 4) after the termination of the cull in 1972 (open circles, females; filled circles, males). **d**, Numbers of male and female deer aged ≥ 1 yr during spring counts of the west block of Rum (block 3), before and after high culling rates began to reduce female numbers in 1991–92. Between 1992 and 2000, male numbers were higher than between 1981 and 1991 ($\chi^2 = 21.1$, d.f. = 1, $P < 0.001$). **e**, Numbers of male and female deer using the southwest block of Rum (block 2), where a 14% cull of both sexes was maintained between 1980 and 2000. No significant differences between 1981 and 1992 were present either for males ($\chi^2 = 1.2$, d.f = 1, $P > 0.05$) or females ($\chi^2 = 1.3$, d.f. = 1, $P > 0.05$). **f**, Numbers of male and female deer using the southeast block (block 1) of Rum before and after high culling rates began to reduce male numbers between 1991 and 1995. After 1991, female numbers showed a progressive increase and were significantly higher between 1992 and 2000 than between 1981 and 1991 ($\chi^2 = 22.5$, d.f. = 1, $P < 0.001$). Methods were as in **d**. Few deer were resident in block 5, which comprised higher ground.

Table 1 Effects of demographic changes on adult sex ratios

	Adult sex ratio (% males)	Absolute difference
Observed sex ratio in 1973	55.7	
Observed sex ratio in 1982	34.7	
Predicted sex ratios in 1982 assuming		
no density dependence in % males born	36.2	1.5
no differential effect of density on calf winter survival	38.4	3.7
no differential effect of density on yearling survival	38.1	3.4
no differential effect of density on adult survival	43.2	8.5
no differential effect of density on emigration	44.1	9.4
no differential effect of density on immigration	35.9	1.2

The table shows the contributions of six demographic processes to changes in the adult sex ratio in the north block of Rum between 1973 and 1982. The lower part of column one shows predicted adult sex ratios in 1982, calculated assuming that each demographic change had not occurred. Column two shows the absolute difference between the observed sex ratio in 1982 and the predicted value and provides an index of the relative importance of changes in each demographic variable.

block showed a consistent increase, rising by over 50% by 2000. Because rates of female immigration are usually low (Fig. 1e, f), this change was probably a consequence of increased local recruitment resulting from lower population density. The similar responses of male and female numbers to reduced density of the opposite sex indicate that, despite differences in habitat use between the sexes[16–18], similar resources probably limit male and female numbers.

Differences in density-dependent responses between male and female deer will have local economic consequences. As in many other parts of Europe, most Scottish red deer populations are managed by local landowners or their representatives, and culling regimes commonly differ between neighbouring land units[5,19]. In many parts of the Highlands, female culling rates have been lower than the annual rate of recruitment for several decades[5] though they have recently increased[20]. As a result, female numbers in many areas are probably above the threshold at which they depress male density, contributing (with other factors, including higher culling rates imposed on males[5,21]) to the pervasive female bias in the adult sex ratio[5] (see Fig. 1a).

Income derived from culling males is usually higher than from culling females[9]. Precise figures are unavailable, but a conservative estimate would be a net gain of £200 per adult male culled versus a small net loss per female culled. Female-biased adult sex ratios are consequently likely to be associated with a reduction in potential income relative to deer density. To investigate the implications of density-dependent changes in male and female numbers, we constructed a stochastic model of local red deer populations on Rum under different culling regimes, incorporating the density-dependent changes in sex-specific mortality and emigration shown in Fig. 2 (Methods). Our model investigates the effects of varying culling rates in two neighbouring populations, assuming that no males are culled before they are 5 yr old and that female numbers rise to ecological carrying capacity (k) if no females are culled. In our model, k corresponds to a predicted density of roughly 20 females per km^2 (Fig. 3a), which is similar to observed densities in the north block of Rum; however, the absolute value of k does not have a qualitative effect on our conclusion (Methods).

In our model, female density decreases as the percentage of females culled increases and is higher when neighbouring female populations are not culled (and female emigration rates are consequently low) than when 10% of females in neighbouring areas are culled each year (Fig. 3a). The density of mature males, as well as the potential annual off-take, is higher when few males are culled each year than when a high proportion of males are removed annually (Fig. 3b). For all male culling rates, the highest densities and potential off-takes of males are achieved in populations where

female culling rates are relatively high and female density is relatively low (thus minimizing male emigration and mortality). For any particular culling rate of females, male densities are higher where females in neighbouring areas are not culled or are lightly culled (leading to relatively high female densities and low rates of male immigration) than in areas where neighbouring female populations are subject to higher culling rates and female density is lower (Fig. 3b, c).

Male harvests, in our model, are maximized at relatively low female densities. If neighbouring female populations are not culled, then maximum male densities will be achieved if female populations are reduced to ~50% of the ecological carrying capacity; by contrast, if 10% of females are culled in neighbouring areas (and male emigration rates are higher), then maximum male densities will be achieved if female density is maintained at ~60% of the ecological carrying capacity. These results remain essentially unchanged if male density is replaced by estimated income from management, assuming a return of £200 per male culled and a zero return per female (Fig. 3d, e). Changes in relative income from males and females (ranging from an income of £50 for individuals of each sex to a gain of £250 per male and a loss of £50 per female) have little effect on the optimal density of females.
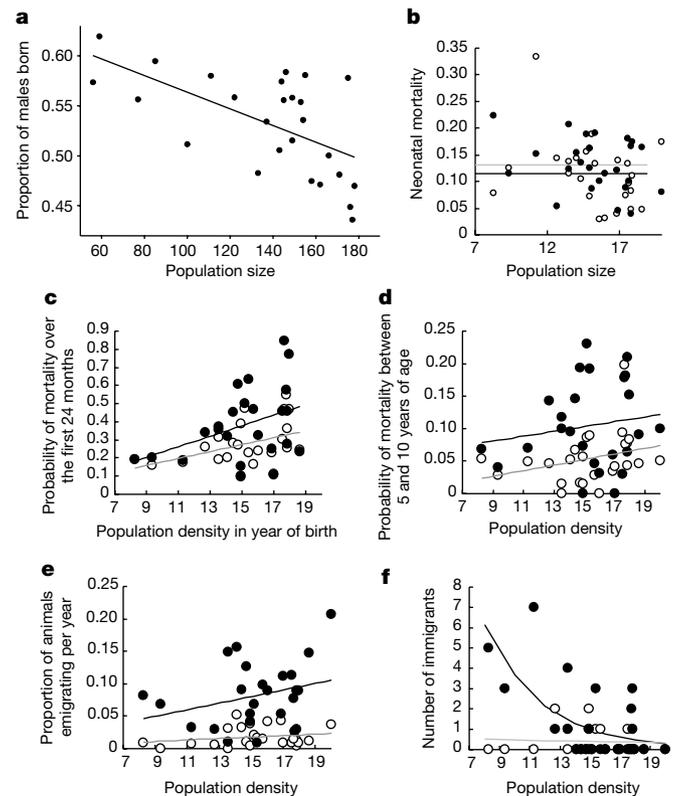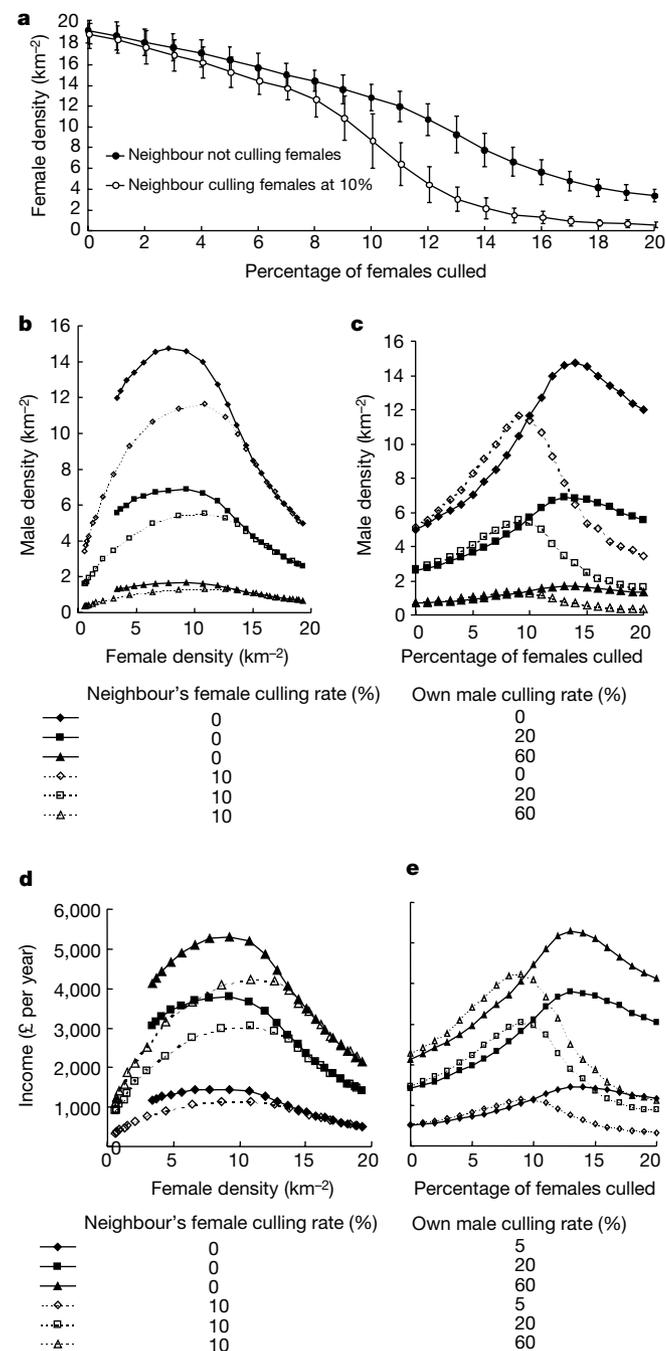

Figure 2 Demographic parameters contributing to the change in adult sex ratio in the deer population of the north block after 1972 (see Fig. 1c). Open circles, females; filled circles, males. **a**, Percentage of calves born each year that were male plotted on population size (males and females), after effects of winter weather were controlled for (from ref. 13). **b**, Probability of mortality of male and female calves in the first three months of life. Mortality over this period was not density-dependent in either sex[4,5]. **c**, Probability of mortality of males and females in the first 24 months of life (males, $\chi^2 = 3.46$. d.f. = 1, $P < 0.1$; females, $\chi^2 = 7.14$, d.f. = 1, $P < 0.05$)[14]. **d**, Probability of mortality of males and females among 5–10-year-olds (males, $\chi^2 = 0.12$, d.f. = 1, $P > 0.05$; females, $\chi^2 = 4.48$, d.f. = 1, $P < 0.05$). **e**, Emigration rates (proportion of residents permanently leaving per year[15]) of males and females (males, $\chi^2 = 4.6$, d.f. = 1, $P < 0.05$; females, $\chi^2 = 0.8$, d.f. = 1, $P > 0.05$). **f**, Immigration of males and females (number of permanent immigrants per year[15]) (males, $\chi^2 = 11.8$, d.f. = 1, $P < 0.01$; females, $\chi^2 = 0.12$, d.f. = 1, $P > 0.05$).

Table 2 Factors affecting male emigration rates

Term	Estimate	χ^2	P
Fitted alone			
Spike length	0.1227	5.7	< 0.05
Birth weight	0.3007	10.5	< 0.001
Population density	0.01227	6.4	< 0.05
NAO	0.2069	18.2	< 0.001
Full model			
Spike length	0.0979	3.1	< 0.1
Birth weight	0.2799	8.2	< 0.01
Population density	0.0139	7.5	< 0.01
NAO	0.2142	18.5	< 0.001
Regression (d.f.)	4	38.8	
Error (d.f.)	331	421.8	

The table shows the estimated regression values of different variables on the probability that males will disperse from the north block of Rum, derived from a logistic regression model. Measures of population density and the NAO were for the year when the animal was a yearling. Yearlings with longer spikes were more likely to emigrate than those with shorter spikes; males with higher birth weights were more likely to emigrate than males that were lighter at birth; and dispersal rates increased with population density as well as in wet stormy winters when values of the North Atlantic Oscillation (NAO) were high. Adult males with longer spikes as yearlings were heavier and had larger antlers as adults[4,5]. Data are for 1974–99.

Relationships between male and female density may be affected by a number of environmental variables not included in our model, including the availability of shelter[22,23], competition for resources with other herbivores[24,25], the size of the management units[5] and the relative rates of culling imposed on the two sexes. In addition, in some parts of Scotland, mature males leave their usual ranges at the start of the rut and travel to other land units where they may be culled before they return[5,26]. If high female densities attract temporary 'rut' immigrants that are likely to be culled, such 'honeypot' effects could reduce the benefits of lowering female density. These effects are unlikely to be important where land units are sufficiently large that temporary 'rut' immigrants constitute a small proportion of males culled or where most males do not travel far to rut[15]. However, where temporary immigrants represent a substantial proportion of males culled, high female densities could be necessary to maintain the harvest of temporary immigrants, although reductions in female density might be expected to raise the number of resident males and to reduce the number of immigrants[15].

If, as we suggest, female deer numbers in many parts of the Scottish Highlands are substantially above 50% of ecological carrying capacity[5], by reducing female numbers, many Scottish deer managers may be able not only to reduce female numbers with little risk of affecting the size of male harvests[27] but also to increase both their annual off-take of mature males and their net income from deer management. Where managers fail to maintain female numbers below ecological carrying capacity, neighbouring estates that cull females at higher rates and attract adolescent males from adjoining areas, are likely to be the principal beneficiaries (see Fig. 3). Because browsing by red deer is implicated in the loss of heather cover and the prevention of tree regeneration[10,22,28], reductions in female numbers are also likely to have benefits for the environment that may, eventually, have further benefits for deer populations. Similar relationships between male and female density probably occur in other sexually dimorphic ungulates where increasing density affects rates of emigration and mortality to a greater extent in males than in females[29–31]. □

Methods

Sex ratios throughout the Highlands

We based estimates of average densities of males and females throughout the Highlands on counts by the Deer Commission (Scotland) at irregular intervals, controlling for the identity of the areas counted[5].

Demographic consequences of increasing density

Until 1972, red deer populations in all five blocks of Rum had been maintained at a density of about 14 deer per km^2 by an annual cull of about 14% of the spring population[5,11,12], but in 1972 the annual cull[4] in block 4 was terminated and numbers were allowed to increase. Records of changes in deer density in the north block after 1972 were based on five censuses of the area each month between January and April, in which the identity and location of each deer seen was recorded[4,5]. Individuals were regarded as resident in the block if they were seen in at least 10% of censuses[15]. Emigrants were individuals previously resident in the block that left the population, whereas immigrants were those that joined the population after being resident in other parts of the island. Emigration and immigration was commonest in males aged between 2 and 5 yr.

To estimate the contributions of different demographic variables to density-dependent changes in the adult sex ratio, we removed the effects of density on each variable in turn while keeping all other vital rates as observed (Table 1), with the population structure in 1973 providing the initial starting values. Values in Table 1 that are closest to the observed sex ratio in 1982 (34.7% male) represent sex-specific density responses that have little effect on the adult sex ratio. Data used in this analysis were restricted to the period 1973–82 because by 1982 the adult sex ratio had stabilized. Estimates of the effects of birth weight, spike length and climate on emigration (Table 2) were derived from a generalized linear model, using data for 1974–99.

Demographic experiments

To investigate the effects of female density on male numbers and of male density on female numbers, we manipulated the relative densities of females in block 3 and of males in block 1 by altering the annual culling regime. Between 1991 and 1992, female numbers in block 3 were reduced by 50%, and between 1991 and 1995 male numbers in block 1 were reduced by a similar proportion. Annual culls of the sex whose density was not altered (males in block 3 and females in block 1) were maintained during the period of the experiment at the same absolute level as over the past decade. Numbers of deer in each block were counted in May each year by an experienced counting team from the Deer Commission (Scotland) using established techniques[5,20].

Population dynamics and density

To assess the likely effects of rising female numbers on the potential harvest of males, we

Figure 3 Results of a stochastic model of two contiguous deer populations subject to different culling regimes, incorporating density-dependent changes in age- and sex-specific rates of fecundity mortality, immigration and emigration, derived from the north block of Rum (see Fig. 2). **a**, Estimated equilibrium density of adult females subjected to different levels of annual cull. **b**, Variation in the density of mature males ($\geq$ 5 yr) at different levels of female density, and different annual culling rates of males (varying from 0 to 60%) where females on neighbouring ground are culled, at 0% per year or 10% per year. **c**, Variation in the density of mature males at different levels of female culling rate (0–20% per year). **d**, Estimated total revenue from culling, with returns set at £200 per male culled and zero pounds per female culled, at different female densities. **e**, Estimated total revenue from culling (as above) at different culling rates for females.

constructed a stochastic population model, parameterized using the density-dependent relationships shown in Fig. 2. Our model simultaneously considered male and female densities and potential harvests in two neighbouring populations that were small enough for differences in the culling regimes imposed on each population to produce local differences in sex-specific emigration and immigration, as well as in mortality. We assumed that both populations were biologically identical and were subject to correlated environmental variability: relaxation of these assumptions was unlikely to affect the direction of predicted trends. Vital rates used were initially calculated deterministically as $R_j = 1/[1 + \exp(-a + bD)]$, where D was the density of mature females (age classes 3 and above), j was the age class and a and b were constants. Sex ratio at birth was calculated as $m = 64.3 - 0.748D$, where m is the percentage of males. Vital rates were subsequently altered to include variability and correlations as follows: for emigration rates, sex ratio at birth and female mortality, $\rho_j = R_j + z\sigma_j$; for fecundity and male mortality, $\rho_j = R_j + \sigma_j z\sqrt{1 - r^2} + r\sigma_j A$, where ρ_j was the stochastic rate, z is a z-value (see below), r was the correlation coefficient between this rate and 3+ female mortality, σ_j^2 is the standard deviation of the vital rate and A was the average value of the z values for 3+ female mortality rates. The values of r were −0.452 for fecundity and 0.522 for male mortality. The z values for population 1 were simple standardized normal deviates. Those for population 2 were calculated as: $z_2 = Z_2\sqrt{1 - r^2} + rz_1$, where Z_2 was the original z value, r was the correlation between populations, and z_1 was the z-value calculated for the equivalent age class and vital rate for population 1. The value of r was 0.7.

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Influence of scene statistics on colour constancy

Jürgen Golz* & **Donald I. A. MacLeod†**

* Department of Psychology, University of Kiel, 24098 Kiel, Germany
† Department of Psychology, University of California at San Diego, La Jolla, California 93093-0109, USA

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The light reflected from an object depends not only on the surface properties of this object but also on the illuminant. The same is true for the excitations of the photoreceptors, which serve as the basis for the perceived colour. However, our visual system has the ability to perceive constant surface colours despite changes in illumination[1]. The average chromaticity of the retinal image of a scene depends on the illumination, and thus might be used by the visual system to estimate the illumination and to modulate the correction that subserves colour constancy[2–4]. But this measure is not sufficient: a reddish scene under white light can produce the same mean stimulation as a neutral scene in red light. Higher order scene statistics—for example, the correlation between redness and luminance within the image—allow these cases to be distinguished. Here we report that the human visual system does exploit such a statistic when estimating the illuminant, and gives it a weight that is statistically appropriate for the natural environment.

A viewed surface reflects towards the observer's eye a characteristic fraction of the light that is cast on it; therefore, the stimulus for vision is the product of an illuminant component and a surface-reflectance component. Colour constancy requires the visual system to disentangle the surface-reflectance component from the product—in some sense discounting the illuminant colour—but the illuminant colour is not generally directly known. Problems like this are common in many aspects of visual perception. They are mathematically underdetermined, and additional constraints must be drawn from the regularities of the physical world to achieve a unique solution.

The mean chromaticity of the retinal image is often proposed to be an indicator of illuminant colour[2–4], because for a given scene this statistic varies systematically with changes in illumination. But in more realistic situations in which the scenes might change as well, this measure is ambiguous (Fig. 1a). To illustrate the ambiguity, consider the problem of distinguishing a predominantly reddish room under white light from a predominantly neutral one under reddish light. The mean chromaticity of the image received by the eye may be the same in these two cases, but human observers can