Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*

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When hunting species in which the sexes differ substantially in value, sex-selective harvesting can increase income dramatically. In some hunted species, for example the red deer *Cervus elaphus* in Scotland, there are also marked ecological differences between the sexes. In red deer, stag mortality and dispersal rates are substantially higher when hind densities are high. Hence, there is a trade-off between having enough hinds to produce valuable stags, but keeping densities low enough to minimise losses from dispersal and stag mortality. We develop a model, parameterised for red deer on Rum, to explore these trade-offs. This stochastic, age and sex-structured model includes two neighbouring estates with differing harvesting policies. Due to stag dispersal, estates with low hunting levels act as sources of stags for neighbouring estates that harvest more heavily. The optimal harvesting strategy depends on the actions of neighbours, but keeps hinds below 50% of carrying capacity and imposes heavy hunting pressure on stags. Scottish deer estates aim to harvest fewer stags and more hinds than the model suggests as optimal, which could lead to substantially reduced incomes. We explore the reasons for this mismatch between predicted optimal behaviour and actual harvesting strategies by incorporating realistic levels of uncertainty, bias and infrequent population counts into our model. We show that the estates' harvesting strategies lead to approximately optimal hind harvesting, because hind numbers are generally underestimated in counts, whereas the uncertainty surrounding population sizes leads to a lower than optimal stag harvest. The most effective method of improving incomes is to increase count frequency. This modelling approach is broadly applicable, both for the management of hunted species under uncertainty and for spatially explicit conservation policies such as no-take areas.

Key words: Cervus elaphus, hunting, dispersal, red deer, Rum, sex differences, stags, uncertainty

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In recent years there has been a move away from considering harvested populations as homogeneous towards recognising that sustainability and profitability are strongly affected by exploitation that varies in intensity between different components of the population. Both theoretically and in practice, it has been shown that offtake can be improved by selectively hunting different age and sex classes, hunting differentially by location and hunting at particular points in the species' life history. For example Tuck & Possingham (1994) and Lundberg & Jonzén (1999) explore the effects of spatially differentiated hunting in model source-sink populations, while Skonkoft, Yoccoz, Stenseth, Gaillard & Loison (2002) look at optimal hunting strategies for chamois *Rupicapra rupicapra* moving between a protected and a hunted area. Based on large-scale data from moose *Alces alces* harvests, Solberg, Loison, Sæther & Strand (2000) and Solberg, Loison, Ringsby, Sæther & Heim (2002) show how changes in hunter selectivity for age and sex classes impact population productivity through changes in age and sex ratios. Kokko (2001) demonstrates how the timing of hunting with respect to life history affects yields.

Changes in population age and sex structure and in relative densities in adjacent regions, whether caused by hunting or other factors, have both direct and indirect effects on yields from hunting. Direct effects include the increase in population productivity when the population is female-biassed (e.g. Catto 1976). Indirect effects, for example through changes in behaviour, are increasingly being recognised as potentially just as important for the long-term sustainability of hunting (e.g. Sutherland & Gill 2001, Sainte-Marie, Sevigny & Carpentier 2002, Milner-Gulland, Bukreeva, Coulson, Lushchekina, Kholodova, Bekenov & Grachev 2003). Direct and indirect effects occur together, so for example changes in sex ratio caused by selective hunting for males have a range of more or less subtle effects on population dynamics, which need to be taken into account when planning sustainable hunting strategies (Mysterud, Coulson & Stenseth 2002).

A common difficulty encountered when attempting to manage hunting is the effect of uncertainty on our ability to manage both for sustainability and profit. The theory of optimal harvesting under uncertainty is well-developed and advancing rapidly (Quinn & Deriso 1999, Lande, Engen & Sæther 2003). Uncertainty can be divided into observation uncertainty (the effect of poor monitoring), process variance due to the effects of demographic and environmental stochasticity and model bias (models that do not adequately capture reality; Shea & the NCEAS Working Group on Population Management 1998). Observation uncertainty is often the dominant problem in harvested populations, and can be reduced by improved monitoring. Whether this occurs in practice depends on the ratio of the indirect cost of uncertainty through reduced yields and the direct cost of improved monitoring (Clark & Kirkwood 1986).

Red deer as a case study

The red deer *Cervus elaphus* is a species in which males are commercially hunted both for meat and for antlers. Hence, the two sexes have very different monetary values. Its population dynamics are complex, with major ecological differences between the sexes, age classes and neighbouring areas, both in terms of demographic rates and dispersal behaviour (Clutton-Brock, Guinness & Albon 1982, Milner-Gulland, Coulson & Clutton-Brock 2000). A long-term individually-based data set from the island of Rum allows us to tease out these complexities. Hence, the red deer on Rum are a particularly good system for examining the trade-offs involved in managing a species to maximise profits from hunting, when the two sexes differ substantially both ecologically and in their economic value.

Red deer are hunted both for trophies and meat, but while shooting a mature stag for its antlers can be very profitable, estates barely break even from harvesting hinds for their meat. Red deer population dynamics are primarily driven by hind density, rather than total population density (Clutton-Brock et al. 1982). The two sexes vary in their dispersal behaviour; hinds and juveniles are highly philopatric, whereas stags are much more mobile (Clutton-Brock & Albon 1989). Scottish deer estates are not fenced, so animals can move freely between them. Selective hunting experiments have shown that reductions in hind density lead to increases in stag numbers; this is due to reductions in both mortality and emigration rates (Clutton-Brock, Coulson, Milner-Gulland, Thompson & Armstrong 2002). Given

that neighbouring estates may be following different harvesting strategies, an estate's profits may be dependent not only on their harvesting strategy, but also on the strategies followed by neighbouring estates. For example, if an estate harvests hinds at a very low level, and thus has high hind densities, valuable stags may disperse away into neighbouring estates that do harvest heavily, and so have lower hind densities. Another issue facing managers is that estates tend to count their deer infrequently, and counts may be prone to high levels of error and bias. This adds a further layer of difficulty when attempting to optimise hunting strategies.

Here we develop a population model that considers the two factors affecting deer management: the demographics of red deer populations, particularly their age and sex-specific dispersal behaviour, and the quality of data available to managers when they decide on a hunting strategy. We relate these two factors to the management objective of maximising profits from hunting. Our model is a stochastic age and sex-structured two-population model, in which the focal estate and neighbouring estate can harvest their deer populations at different rates. It is the first simple demographic model for red deer that uses realistic levels of stochasticity in combination with age and sex structures, and considers the effects of harvesting strategies on dispersal behaviour. Previous deterministic models of red deer harvesting strategies that do not include dispersal include Clutton-Brock & Lonergan (1994) and Buckland, Ahmadi, Staines, Gordon & Youngson (1996). Trenkel (2001) includes uncertainty in estimates of population parameters but again without dispersal. Milner-Gulland et al. (2000) use a similar model to that presented here, including dispersal, but at a smaller spatial scale (the hind group) and considering only hinds.

In this paper, we first demonstrate the effects of dispersal on profits, and describe the optimal strategy for the focal estate under various scenarios. We then relate estates' harvesting strategies to the quality of information that they obtain on the status of their herds, and show how improvements in the information available to managers could lead to substantial improvements in income.

Methods

The model describes the dynamics of two red deer populations, which are linked through dispersal and shared environmental conditions, and which have the same underlying relationships between density and vital rates. These two populations are assumed to inhabit two separate neighbouring estates. We base the model at the estate level, as this is the level at which management decisions are ultimately made. Previous studies have shown that deer population dynamics can vary markedly between adjacent hind groups within an estate (Milner-Gulland et al. 2000). Hence, by looking at dispersal between estates and survival and fecundity within estates, we are examining the problem at the scale which best captures the dynamics of the system.

The data used to parameterise the model were collected from regular censuses of individually recognisable animals over a period of 25 years in the North Block of Rum (see Clutton-Brock et al. 1982). The functional forms and parameter values used in the model were estimated by analysis of the proportions of each age group dying, reproducing and dispersing, using general linear models. Each demographic group was analysed independently. Proportion data were analysed with a binomial error structure, and count data were analysed with a Poisson error structure. If data were over-dispersed, a scale parameter was estimated to allow for a more accurate calculation of standard errors around regression estimates and estimates of significance. These data show that vital rates are strongly related to the density of adult hinds (in their third year or older), rather than to the overall population density, but with substantial variability around the relationship. Hence, in all cases adult hind density was used as the independent variable in the model. We first describe the deterministic model, and then discuss our methods for adding stochasticity to the model.

In the deterministic model, the following logistic functional form best describes the data for fecundity and mortality rates:

$$R_{i,j} = \frac{1}{1+e^{-a+bD}} \qquad (1),$$

where R is the vital rate for sex i and age j, a and b are constants, and D is the density of adult hinds. The values of the constants are given in Table 1, and the fits are shown in Figure 2 in Clutton-Brock et al. (2002). Sex ratio at birth is assumed to vary linearly with hind density, following Kruuk, Clutton-Brock, Albon, Pemberton & Guinness (1999; see Table 1).

Dispersal is a key component of red deer population dynamics. Individual-based data on immigration and emigration rates are available for the North Block of Rum. For the rest of the island, data on immigration rates by sex are available. There are no data on where emigrants from the North Block go to, or where immigrants into the other populations have come from. Hence,

Table 1. Constants for vital rates used in the deer population model, shown for the proportion of the population dying (Mortality), the number of offspring (Fecundity) and the percentage of births that are male (Birth SR) in a given year at a particular hind density. Age is given as the year of life, e.g. age 3 is the third year of life. Hinds give birth for the first time in their third year of life. For mortality rates, two values for the standard deviation are given; σ_1 for densities below 14 hinds/km² and σ_2 for higher densities. Fecundity rates and the birth sex ratio have the same standard deviation at all hind densities. Fecundity and mortality rates are related to density as per Equation 1, birth sex ratio by a linear regression ($y = a + bx$). Fits of these functions to the Rum data are shown in Figure 2 of Clutton-Brock et al. (2002).

Rate	Sex	Age	a	b	σ_1	σ_2
Mortality	♀	1	-3.76	0.1487	0.06794	0.1835
	♂	1	-2.77	0.1126	0.08275	0.2338
	♀	2	-4.24	0.1387	0.08703	0.08111
	♂	2	-3.28	0.1011	0.09453	0.1653
	♀	3-5	-4.468	0.0685	0.01235	0.03069
	♂	3-5	-3.92	0.0426	0.03101	0.03652
	♀	6-8	-4.45	0.1014	0.0339	0.05448
	♂	6-8	-3.092	0	0.05279	0.03807
	♀	9-13	-4.853	0.1642	0.03083	0.05612
	♂	9-13	-1.607	0.0269	0.05398	0.1726
	♀	14+	-1.2	0.0184	0.1377	0.1832
	♂	14+	0.18	0.031	0.4923	0.4501
Fecundity	♀	3-5	-0.608	0.0537	0.0625	
	♀	6-8	0.515	-0.0288	0.1217	
	♀	9-13	0.619	-0.0237	0.2506	
	♀	14+	0.1	-0.0351	0.2383	
Birth SR			64.38	0.748	5.219	

both immigration and emigration rates can only be related to the absolute density of the focal population, rather than to the relative density. The North Block data are difficult to interpret because the area was released from hunting at the beginning of the data collection period, while surrounding areas continued to be hunted, and thus were generally at lower population densities.

We estimated emigration rates from the North Block data, which were best fitted by a linear regression of the proportion of an age and sex group leaving the population against hind density (Table 2A; Clutton-Brock et al. 2002). But because it is important to account for immigration events into low density populations, we used the poorer data for the entire island to calculate immigra-

tion rates. Data were poor both because immigration is a comparatively rare event, so that the number of observations on which to base our model was small, and because observations for the whole island are made by sex only, not by age class. However, these data are markedly better than any other data available on red deer dispersal in Scotland. The best fitting function was (see Table 2B, Clutton-Brock et al. 2002):

$$I_{i,x} = k_1 + \frac{k_2}{(1+k_3 e^{-k_4(D-k_5)})^{\frac{1}{k_5}}} \qquad (2),$$

where I is the number of individuals of sex i immigrating

Table 2. Constants for A) the linear regression ($y = a + bx$) relating the proportion of an age and sex group leaving the population in a given year to hind density, and B) the logistic function relating the number of immigrants of each sex entering a population to the hind density of the population that they enter (Equation 2). Considering A): in the two-population model, the regressions are constrained so that the proportion leaving is ≥ 0. In the single population model, these equations represent both emigration and immigration, so that the proportion leaving becomes negative (individuals enter the population) at low hind densities. The standard deviation of the regression follows a step function, changing from σ_1 at densities < 14 hinds/km² to σ_2 at higher densities. Animals do not emigrate in their first year, so values are given only for those in their second year or older. Considering B): the hind density is constrained to be ≤ 50 hinds/km². The fit of the functions to the Rum data is shown in Figure 2 of Clutton-Brock et al. (2002).

A)	Sex	Age	a	b	σ_1	σ_2	
	♀	2	0.0295	0	0.01989	0.07255	
	♂	2	-0.0352	0.0082	0.06744	0.102	
	♀	3-5	-0.0542	0.00552	0.02264	0.03025	
	♂	3-5	-0.066	0.01499	0.1116	0.1174	
	♀	6-8	-0.036	0.00314	0.007093	0.01789	
	♂	6-8	-0.0733	0.0088	0.05797	0.1009	
	♀	9-13	-0.0105	0	0.01836	0.01905	
	♂	9-13	-0.0232	0.00376	0.04229	0.07962	
	♀	14+	-0.0396	0	0.05988	0.02706	
	♂	14+	0.0152	0	0.1424	0.09939	
B)		k1	k2	k3	k4	k5	σ
	♀	3.406	4.782	0.01112	0.3193	17.17	2.0
	♂	-0.187	18.453	6.53	1.532	12.621	3.0

into population x (x = 1, 2) in a given year at a hind density of D, and k_{1-5} are constants. These individuals were randomly divided into age classes, but in such a manner that the probability of an individual immigrating into population 2 being of age class j was dependent on the proportion of the emigrants from population 1 that belonged to age class j. The number of immigrants of each sex into one population was constrained not to exceed the number of emigrants of that sex from the other population. Hence, the immigration rate depended weakly on hind density in the other population, through that population's emigration rate. However, the number of immigrants into one population was generally less than the number of emigrants from the other population. This reflects the situation observed on Rum, and is attributable partly to dispersal-related mortality. Although we model a two-estate system for simplicity, deer estates actually form an open system, with more distant estates receiving and providing occasional dispersers. Hence, by using empirical data to parameterise our dispersal model rather than constraining it to be a closed system, we improve the realism of the model. As expected, immigration rates calculated from Equation 2 were much higher for stags than for hinds at low hind densities, and were highly variable for both sexes.

Our model does not include temporary immigration of stags into areas with high hind densities during the rut. In some parts of Scotland, stags leave their usual ranges at the time of the rut, and may be hunted before they return. However, our model represents the situation in which estates are so large that the temporary immigrants only constitute a small proportion of the animals hunted, or in which stags do not travel far to rut, as is the case on Rum (Clutton-Brock, Rose & Guinness 1997).

Variability in vital rates was high in the data, and hence was an important component of the model. Residuals around the density-dependent relationships given above were normally distributed, with standard deviations shown in Table 1. However, in the case of mortality and emigration rates, residuals increased with increasing hind density; the best fit to this was a step change in standard deviation at a hind density of 14 individuals/km^2.

Sex ratio at birth and emigration rates were assumed to be responding to density changes rather than to climate, while adult hind mortality in population 1 was taken as the base vital rate with which other rates were correlated. Hence, these rates are modelled as uncorrelated with other vital rates:

$$\rho_{i,j} = R_{i,j} + z\, \sigma_{\iota,\varphi} \qquad (3),$$

where $\rho_{i,j}$ is the stochastic rate for sex i and age class j, $R_{i,j}$ is the deterministic rate, z is a z-value (see below), and $\sigma_{\iota i,j}$ is the standard deviation (see Table 1).

Within a population, variation in stag mortality rates and fecundity rates was correlated with the mean deviation of adult hind mortality rates from the deterministic rates calculated in Equation 1:

$$\rho_j = R_j + \sigma_j\, z\, \sqrt{1 - r^2} + r\, \sigma_j A \qquad (4),$$

where r is the correlation coefficient between the rate and adult hind mortality, and A is the average of the z-values for adult hind mortality rates. The values of r used are shown in Table 3, and are the means of the significant correlations found in the data between fecundity, stag mortality and adult hind mortality rates.

Equation 4 represents the fact that if adult hind mortality happens to be higher or lower than average in a given year, for example due to bad weather, other vital rates are likely to be similarly affected. Hence, this is a simple way of representing the effects of climate on the deer population. A more complex, though realistic, model would include environmental factors explicitly,

Table 3. Other parameter values used in the model.

Parameter	Value	Source
Correlation between adult hind mortality and fecundity rates	-0.452	Data from Rum North Block
Correlation between adult hind mortality and stag mortality	+0.522	Data from Rum North Block
Correlation between z-values of the two populations	+0.7	Average correlation between two island populations of Soay sheep (Grenfell et al. 1998)
Hind age at first hunting	2	
Stag age at first hunting	5	
Profit/individual hunted, hinds	£0	Deer Commission for Scotland, pers. comm.
Profit/individual hunted, stags	£200	Deer Commission for Scotland, pers. comm.
Number of loops per simulation	50	
Number of years per loop	20	
If data are poor:		
Frequency of counts (every X years)	7	Deer Commission annual reports
Bias (proportion of population counted)	0.8	Deer Commission annual reports
Observation error in counts (CV)	0.2	Deer Commission annual reports

for example the North Atlantic Oscillation (Forchhammer, Stenseth, Post & Langvatn 1998, Coulson, Catchpole, Albon, Morgan, Pemberton, Clutton-Brock, Crawley & Grenfell 2001), and would separate the effects of demographic and environmental variation on vital rates (Lande et al. 2003).

We also modelled the linkage between the vital rates of the two populations; through correlation between the z-values used in Equations 3 and 4. The z-values for population 1 are simple standardised normal deviates. Those for population 2 are calculated as:

$$z_2 = Z_2 \sqrt{1-r^2} + rz_1 \qquad (5),$$

where Z_2 is the original z-value, r is the correlation between the populations, and z_1 is the z-value calculated for the equivalent age class and vital rate for population 1. The r-value is based on data from Soay sheep *Ovis aries* and the North Block of Rum (see Table 3). Equation 5 links the two populations through shared climatic conditions; if it is a good or bad year for one population, neighbouring populations are likely to be similarly affected.

In the model, vital rates depend on hind density at the end of the winter; this is the point at which annual density estimates are made for the North Block population. The sequence of events broadly followed reality; count, births (spring), dispersal (summer), hunting (autumn) and mortality (winter). Fecundity rates were assumed to be independent of stag numbers so long as at least one adult stag was present in either population during the spring (otherwise fecundity was set to zero). Integer numbers were used for the number of individuals in age and sex classes. Because the numbers involved were small, removals from and additions to the population through births, deaths and dispersal were carried out using random numbers rather than rounding. Removals by hunting were calculated by multiplying the hunting mortality rate by the total number of stags or hinds available for hunting rounded to the nearest integer and randomly removing this number from the age classes but in proportion to the size of the age classes. This meant that the number hunted was as planned, but that the age classes from which the individuals were removed were not pre-determined. This is realistic as it is not possible to age live red deer accurately once they have reached adulthood. Given the lack of data on the economics of deer hunting, the income obtained from hunting an animal was assumed to be constant (i.e. both the unit cost and price received were independent of market dynamics or population density). No fixed costs were considered; hence the income per animal
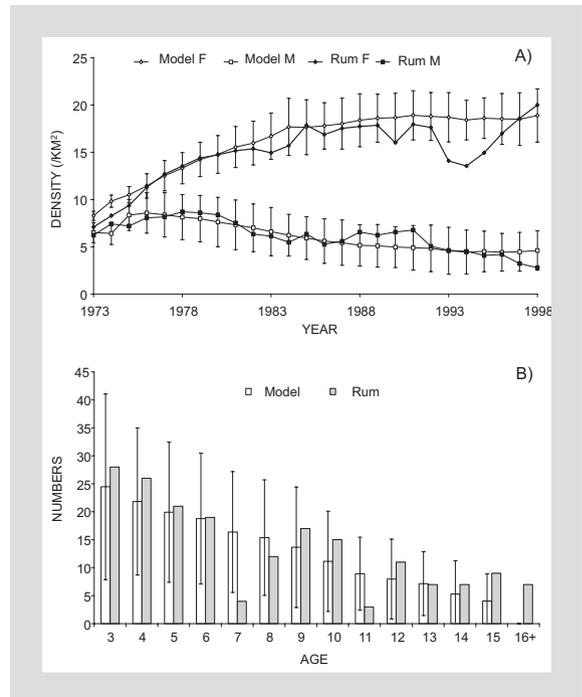

Figure 1. Fit of the population model to the data from which it was derived. The model was run starting from the observed population structure in 1973 when hunting stopped in the North Block of Rum. The mean and confidence interval over 50 simulations are shown (A) for the density of mature stags (Model M, age > 5 years) and hinds (Model F, age > 2 years), together with the equivalent actual densities in the North Block (Rum M, Rum F). In B) the mean adult hind population structure (with 95% confidence intervals) for the model in 1998 is shown compared to the actual population structure (Rum).

killed was assumed net of all costs involved in the management of the population. Killing a stag led to a good income, while killing a hind was assumed to be financially neutral (see Table 3).

We ran the model for a range of proportional hunting mortalities, reflecting the fact that deer management advice in Scotland is given in terms of a proportional hunting strategy. This allows us to relate our results directly to current management advice. The populations started at the age and sex-structure of an unhunted population and the model was run for 40 years to remove transitional effects before results were generated for the following 20 years. For each hunting mortality rate 50 simulations were run. The model was also used to represent a single population, perhaps on an isolated estate. In this case, emigration and immigration were modelled together, and depended only on hind density in the population itself (see Table 2A). This model was checked for consistency with the data used to parameterise it by running it for the North Block of Rum, starting from the population structure observed when
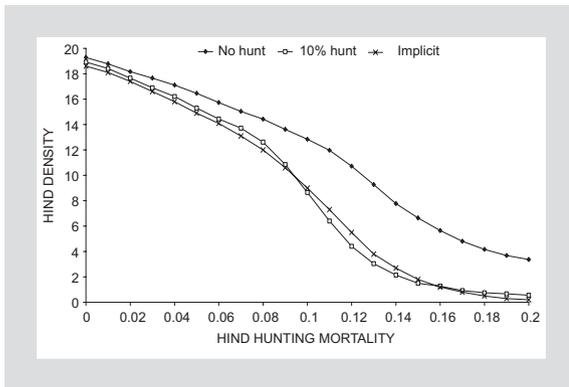
Figure 2. Hind density (in individuals/km²) plotted against the proportion of hinds (≥2 years of age) killed each year. The relationship holds for all stag hunting mortalities less than 100%, because vital rates depend on hind rather than on stag densities. The results are shown for the case where the neighbouring population is not hunted (No hunt) and where both sexes of the neighbouring population are hunted at a rate of 10% a year (10% hunt). They are also shown for the case in which only one population is modelled, hence the neighbour's strategy is implicit in the dispersal function used (Implicit).

hunting stopped in 1973. The predicted numbers of hinds and stags over time and the hind age structure predicted for 1998 are shown in Figure 1; despite the expected variability, the model fitted well to the data set. This suggested that it adequately represented the dynamics of the Rum population.

Results

Effects of neighbours

The effect of hunting on the deer population of the focal estate depends strongly on the level of hunting on neighbouring estates (Fig. 2). Hind density is non-linearly related to hunting mortality, with a rapid decline in density at intermediate hunting mortalities, and a long tail where density declines slowly as hunting mortality increases. This long tail is caused by immigration into the depleted population. If neighbouring estates do not hunt, their high hind densities lead to high migration into the hunted focal population; hence, density declines more slowly with hunting mortality, and the focal population can thus be hunted more heavily. The results when neighbours are not explicitly modelled are very similar to those obtained when neighbours kill 10% of both sexes. Hence, the single population model approximates the situation where there is a population of relatively low density in the surrounding area.

The optimal hunting strategy for the focal population (the strategy which maximises the expected income) also depends on the actions of neighbours (Table 4). If the neighbour hunts both sexes at 10% (or if no neighbour is present) then it is optimal to hunt hinds at 9-10%. If the neighbour does not hunt, the optimal hunting mortality on hinds increases to 13%. This is because there is a trade-off operating for estate owners. No income is obtained from killing hinds, but only from stags. However, the number of stags available to hunt depends on hind density in two opposing ways; hinds are required in order to produce stags, but stag survival and immigration are negatively related to hind density. The maximum number of huntable stags, and hence the maximum income, is obtained at an intermediate hind density (Fig. 3A). If the neighbours do not harvest, their hind population density is high and large numbers of stags

Table 4. Optimal hunting mortality rates shown for eight (1-8) different scenarios for hinds (Fhm) and stags (Mhm). Hinds and stags show densities at the optimum, Income shows the annual income from hunting at the optimum in £, and Change shows the percentage change in income, relative to scenario 1, from adopting a different strategy. The first option with both sexes of both populations being hunted at 10% represents the current situation. The density of hinds in the population (#/km²; Hinds) is shown as those aged three years or older, as these are the age classes that affect vital rates. The density of stags (#/km²; Stags) is shown for the huntable age classes, aged five years or older. The values are mean population sizes in spring (before migration and births have occurred) over 20 years after transients have finished, taken over 50 simulations. The coefficient of variation (CV) is shown in brackets.

Scenario	Neighbour		Focal		Optimum density				Income	Change
	Fhm	Mhm	Fhm	Mhm	Hinds		Stags			
1	0.1	0.1	0.1	0.1	8.85	(14.64)	7.89	(8.32)	1983 (8.32)	100
2	0.1	0.1	0.09	1	10.87	(9.45)	0	(0)	4512 (7.01)	228
3	0.09	0.9	0.09	0.9	11.54	(8.51)	0.23	(7.96)	4400 (6.07)	222
4	0	0	0.13	1	9.29	(8.43)	0	(0)	5569 (5.22)	281
5	0	0	0.1	0.1	12.99	(4.22)	7.91	(7.74)	1985 (7.71)	100
6	0.08	0.9	0.1	0.1	12.58	(7.49)	0.22	(10.84)	2124 (6.7)	107
7	0.08	0	0.1	0.1	12.72	(6.96)	10.85	(7.86)	2290 (6.4)	115
8	-	-	0.1	0.75	9.2	(9.95)	0.5	(8.99)	3100 (8.94)	156

Scenarios:
1: Status quo - both estates hunt 10% of both sexes each year;
2: Neighbour status quo, focal population optimises income;
3: Focal population optimises income, neighbour copies them;
4: Focal population optimises, neighbour does not hunt;
5: Focal population status quo, neighbour does not hunt;
6: Focal population status quo, neighbour optimises their income;
7: Focal population status quo, Neighbour optimises focal's income;
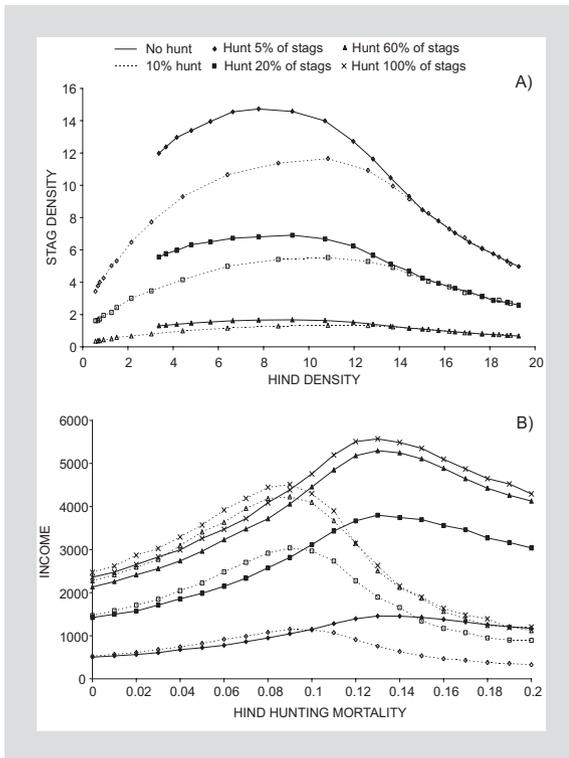8: Only one population modelled, income optimised.

Figure 3. Effect of hind density (in individuals/km²) on stag density (in individuals/km²; A) and the relationship between hind hunting mortality rate and income (in £/year; B). In both cases, the results are shown for the case when the neighbour does not hunt (—; No hunt) and when the neighbour hunts both sexes at 10% (⋯; 10% hunt). Results are shown for a range (0.0 - 0.2) of hind hunting mortalities on the focal population, and for focal population stag hunting mortalities of 0.05, 0.2, 0.6 and 1.0. Hind hunting mortality and hind density are non-linearly related as shown in Figure 2.

migrate into the focal population. In this situation there is less requirement for hinds to be available in the focal population to produce stags, so it is optimal to reduce the hind density further and maximise the stag immigration and survival rates (Fig. 3B).

The optimal hunting mortality for stags is the highest rate at which there is no risk of losing all mature stags; in the model at least one mature stag is required in the population for breeding. However, immigrating stags can fulfil this requirement, so if there is an unhunted neighbouring population, it is possible to kill all the stags in the focal population. If the neighbouring population is also hunted, a few mature stags must be left, reducing the optimal hunting mortality. As income is directly related to the number of stags killed, the highest income is obtained when the neighbour does not hunt (see Table 4). This leads to high immigration to the focal population, allowing hinds to be kept at low density to maximise immigration and survival rates, and allowing all mature stags to be killed each year. This gives a yield 2.8 times that obtained under the current hunting regime. Even if the neighbour continues to hunt according to status quo, the focal estate's income can still be increased 2.3 times by slightly reducing the hunting mortality of hinds and killing all mature stags.

Looking at the effects of the neighbour's actions on the focal population's income when the focal population is hunted at 10%, we again see the trade-off between births and migrations. If the neighbour stops harvesting and the focal population harvests at the status quo, the focal population's income is unchanged. This is because hind immigration into the focal population reduces births and male survival, cancelling the benefits of stag immigration that would have occurred if hinds in the focal population could have been hunted at a higher rate. The focal population's profits can be maximised (given that it continues to harvest at 10%) if the neighbour harvests its females at 8% and harvests no stags; this ensures the maximum number of immigrant stags while reducing hind immigration to the focal population.

Because the population model is empirically derived from detailed data on the Rum deer population, we

Table 5. Effects of changes in the revenue per animal hunted on the model results. The results are shown for two scenarios; when the neighbouring population is not hunted, and when it is hunted at 10% for both sexes. Column headings are as for Table 4. The revenues shown cover a range of plausible scenarios (assuming that the reasonable ranges are +£ 20 - -£ 50 for hinds and +£ 150 - +£ 200 for stags). The first row (A) shows the baseline assumption, the second (B) is when hinds are relatively valuable, the third (C) when hinds are costly to hunt, and the fourth (D) (which is not plausible) shows the extreme case when both sexes yield the same revenue.

Scenario	Revenue per		Focal		Optimum density		Income	Change
	Hind	Stag	Fhm	Mhm	Hinds	Stags		
Neighbour does not hunt								
1A	0	200	0.13	1	9.29 (8.43)	0 (0)	5569 (5.22)	100
1B	20	150	0.13	0.95	9.32 (7.37)	0.13 (9.01)	4502 (4.19)	81
1C	-50	150	0.14	1	8.03 (8.77)	0 (0)	3316 (5.33)	60
1D	50	50	0.12	1	10.98 (6.08)	0 (0)	2268 (3.27)	41
Neighbour hunts at 10%								
2A	0	200	0.09	1	10.87 (9.45)	0 (0)	4512 (7.01)	100
2B	20	150	0.09	0.9	11.39 (8.26)	0.23 (7.3)	3753 (5.15)	83
2C	-50	150	0.09	1	11.44 (7.98)	0 (0)	2809 (7.86)	62
2D	50	50	0.09	1	11.45 (7.73)	0 (0)	1856 (4.79)	41

restrict our sensitivity analyses to our assumptions concerning the revenues obtained per individual harvested. Within plausible ranges changes in the revenue per hind or stag have no effect on the manager's optimal strategy (Table 5), and generally the income curves remain similar in shape to Figure 3B. However, if the revenue per hind is negative (scenario C), then incomes begin to increase again at low hind hunting mortalities. If the income per hind was negative then another optimal strategy would emerge in which all stags and no hinds were hunted (because the cost of hunting hinds would be so high that the benefits of low hind density from improved stag dispersal and survival rates would be cancelled). However, this only occurs at unrealistic values. For example, with no harvesting by neighbours and all mature stags being killed at a revenue of £150/stag, revenues per hind would have to be -£155 in order for the optimum to switch from a high hind harvest to no hind harvest. Scenario D, where both sexes produce the same revenue, leads to income curves that are similar in shape to those shown in Figure 3, although, as expected, they are flatter, with less marked differences between the strategies. This suggests that the results are not sensitive to the assumptions made about revenues, but rather reflect the underlying biology of the system.

Dispersal is a key component of the model, and one that is likely to vary between red deer populations. Our results are based on the dispersal behaviour of the Rum population. In order to investigate the effects of our assumptions about dispersal on the model results, we also ran the model without any dispersal taking place. Without dispersal, the trade-off when deciding on a hunting strategy lies between the absolute number of stag calves produced and those calves' survival to maturity. Despite reductions in fecundity and an increasingly female-biassed sex ratio, the absolute number of stag calves born increases with hind density. Calf production and survival to maturity balance, so that when dispersal does not occur, there is very little difference in income over a range of hunting mortalities from 0 to 8% of hinds per year (Fig. 4). This contrasts markedly with the situation when dispersal occurs, when not hunting hinds hard enough leads to a significant loss of income.

Effects of data quality on harvesting strategies
The majority of Scottish deer estates aim to follow the recommendation by the Deer Commission for Scotland (DCS); that 14-16% of both sexes should be harvested each year. This policy appears very much at odds with the results found above. A hunting mortality of 14% for
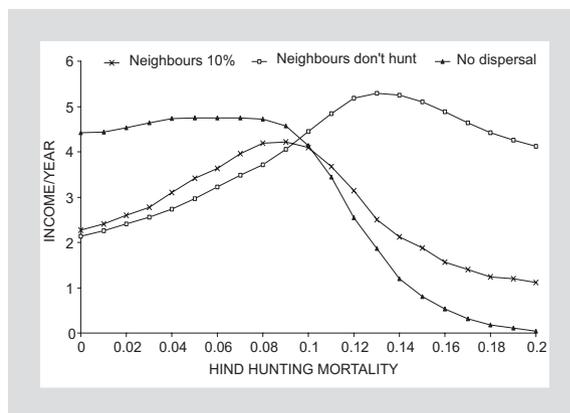

Figure 4. Effects of assumptions about dispersal on the model results shown as the income (in 1000s of £/year) obtained per year against hind hunting mortality assuming that 60% of mature stags are shot annually. The results are shown when the neighbour hunts 10% of both sexes or does not hunt at all (as in Fig. 3), and when there is no dispersal between estates (hence the neighbour's actions are irrelevant).

hinds is only optimal if the surrounding deer population is at a very high density, allowing immigrants to restock the population. Conversely, killing only 14% of stags does not maximise the income for the estate (see Fig. 3B). As the estates have been harvesting deer for many years, and thus should have a good idea of their optimal strategy, this raises doubts about the model results. However, estates do not always have good information on which to base their harvesting decisions. Estates count their deer infrequently, and their counts are usually underestimates. DCS counts occur about every seven years, while confidential data suggest that some estates may underestimate numbers by at least 20% and perhaps by up to 50%. Counts are also likely to have a high level of variability surrounding them; our data suggest that a coefficient of variation of 20% is common. Counts are carried out in spring, just before births take place, rather than directly before the hunting season starts. All these factors lead to discrepancies between stated and actual hunting mortalities imposed on a population. The results presented above are for situations when the population size is known exactly at the time of hunting.

We used the simplified model in which only the focal population is explicitly considered to investigate the effects of poor data on an estate's optimal hunting strategy. This model produces results that are similar to the two-estate model when the neighbouring estate is harvesting both sexes at 10% each year (see Fig. 2). We assumed that the number of individuals to be hunted was calculated on the basis of a spring count with observation error and bias, and that this same number was killed each year until the next count took place. Table
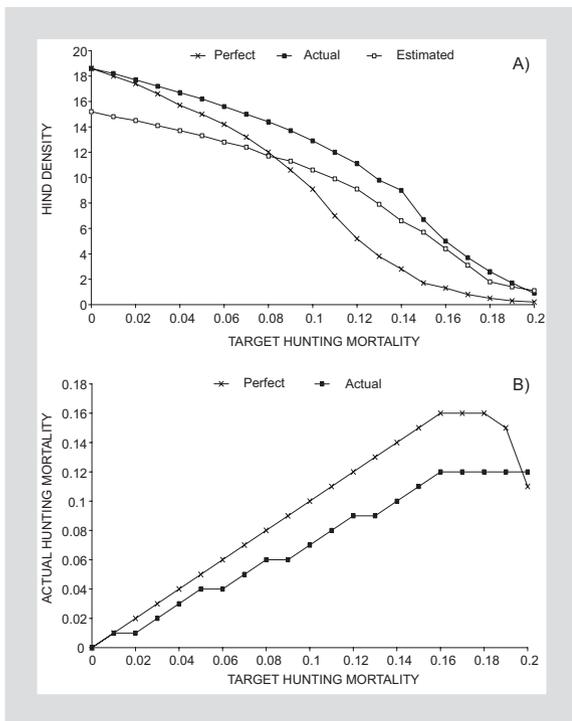
Figure 5. Relationship between hunting mortality and hind density (in individuals/km²; A). With perfect data ('Perfect') the relationship is as shown for the 'Implicit' situation in Figure 2. The actual data available to deer estates leads to a less steep relationship between the target hunting mortality (i.e. the proportion of the hinds that they think they are hunting) and the actual hind density ('Actual'), hence the target hunting mortality is higher when data are poor. The relationship that would be observed by the deer estates (hence on which they would base their hunting strategy) is less steep than with perfect information, but the density appears lower than it actually is ('Estimated'). B) shows the relationship between the target hunting mortality and the actual hunting mortality when the data are perfect and with the data quality actually available. As expected, with perfect data the target hunting mortality is the same as the actual hunting mortality except at high hunting mortalities. At these high levels, the number of animals is so low that killing an integer number leads to a lower proportion killed than expected. With the actual data quality, the actual hunting mortality is consistently lower than the target level.
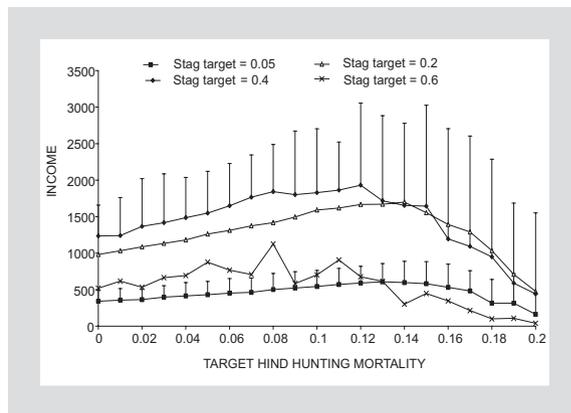

Figure 6. Relationship between the expected annual income (in £/year) and hunting mortality for a range (0 - 0.2) of target hind hunting mortalities and target stag mortalities of 0.05 - 0.6, shown for the situation when the manager has access only to poor data (uncertain, biassed and irregular counts). Confidence intervals around the expected incomes increase with stag hunting mortality, here shown using the upper confidence intervals for stag hunting mortalities of 0.05 and 0.4. All results are 20-year means over 50 simulations, taken after transients.

3 shows the parameter values used in the simulations, which are taken from expert assessments of the quality of counts undertaken by Scottish deer estates. The quality of data available means that deer estates are underestimating the size of their hind populations; hence the hunting mortalities that they are actually imposing are lower than they perceive (Fig. 5).

Poor data has a profound effect on both the optimal strategy and the income obtained from hunting (Table 6). The optimal strategy changes from killing 10% of hinds and 75% of stags to killing 13% of hinds and 35% of stags. However, this increase in hunting mortality on hinds is perceived rather than actual; a target of 13% leads to an actual hunting mortality on hinds of 10%, the true optimal level. The large reduction in the proportion of stags killed is a response to uncertainty;

Table 6. Effects of poor data on the model results expressed as the percentage change in the expected annual monetary income from the income obtained with a perfect survey (Income %). Results are means over 20 years for 50 simulations. The income under a perfect survey is £ 3,107. The optimal target hunting mortality (Thm) is shown for hinds and stags under each scenario, as well as the expected actual hunting mortality (Ahm) that this target leads to (CV in brackets). Scenarios shown are: a perfect survey (results equivalent to scenario 8 in Table 4), a poor survey (parameter values typical of many deer estates, given in Table 3), a poor survey but with no observation error (CV = 0), a poor survey but carried out annually (Annual), a poor but unbiased survey (Bias = 1), a poor survey carried out just before the hunt rather than in the preceding spring (Autumn).

		Thm		Ahm	
	Income (%)	Hind	Stag	Hind	Stag
Perfect	100	0.1	0.75	0.1 (0.59)	0.76 (0.44)
Poor	67	0.13	0.35	0.1 (24.68)	0.22 (22.39)
CV = 0	72	0.14	0.35	0.1 (4.15)	0.21 (10.35)
Annual	93	0.14	1	0.1 (5.78)	0.43 (3.84)
Bias = 1	67	0.11	0.25	0.1 (13.42)	0.2 (16.78)
Autumn	73	0.11	0.3	0.09 (17.32)	0.29 (24.65)

because at least one mature stag is required in the population, and because the number of mature stags present is low and highly variable between years, the target hunting mortality can not be so high as to risk killing all stags in one year. This uncertainty can be seen in Figure 6, where the confidence interval around the income obtained is strongly related to stag hunting mortality, and the income curve is relatively flat. Thus at a target stag hunting mortality of 0.2, for example, any target hind hunting mortality between 0.1 and 0.15 gives an expected income more than 90% of the maximum. Similarly, a doubling of the target stag hunting mortality from 0.2 to 0.4 only gives a 14% increase in expected income. Income drops off much more rapidly if a manager harvests too many hinds than if s/he harvests too few, which may give a further incentive to harvest hinds at lower than optimal rates in conditions of uncertainty.

Hence, it is not surprising that, given the data available, deer estates stick to relatively simple strategies such as the target of harvesting about 15% of both sexes each year as suggested by the DCS. Using this target leads to an expected actual hunting mortality of 10% on each sex. This is the hunting mortality we use as status quo in the two-population model above. Under our model assumptions, the target of harvesting 15% of both sexes gives an expected income of £1,309 ± 493 per year, which is 63% of the maximum that could be obtained by increasing the target stag hunting mortality to 0.35. Although it reduces the mean income, a target hunting mortality of 15% of the stags does not improve the variability around the mean; the coefficient of variation (CV) at the optimum hunting mortality is 17%, compared to 19% for the 15% target. Hence, increasing the perceived stag harvest to 35% would have clear benefits for estates.

There are several components to poor data quality. Moving from spring to autumn surveys or eliminating the uncertainty in the count data would lead to a slight improvement in the expected income, and removing the bias in the count has a minimal effect. However, a major increase in income would be obtained by carrying out annual rather than infrequent counts (see Table 6). This is because basing numbers to be killed on outdated information about population sizes means that hunting levels must be lower than otherwise optimal in order to ensure that all stags are not harvested by mistake. As the frequency of counts increases, the optimal target stag hunting mortality also increases dramatically, causing an increase in income (Fig. 7). Income is also improved by reducing the CV and bias, but the effect is much less marked. Target hunting mortality on both
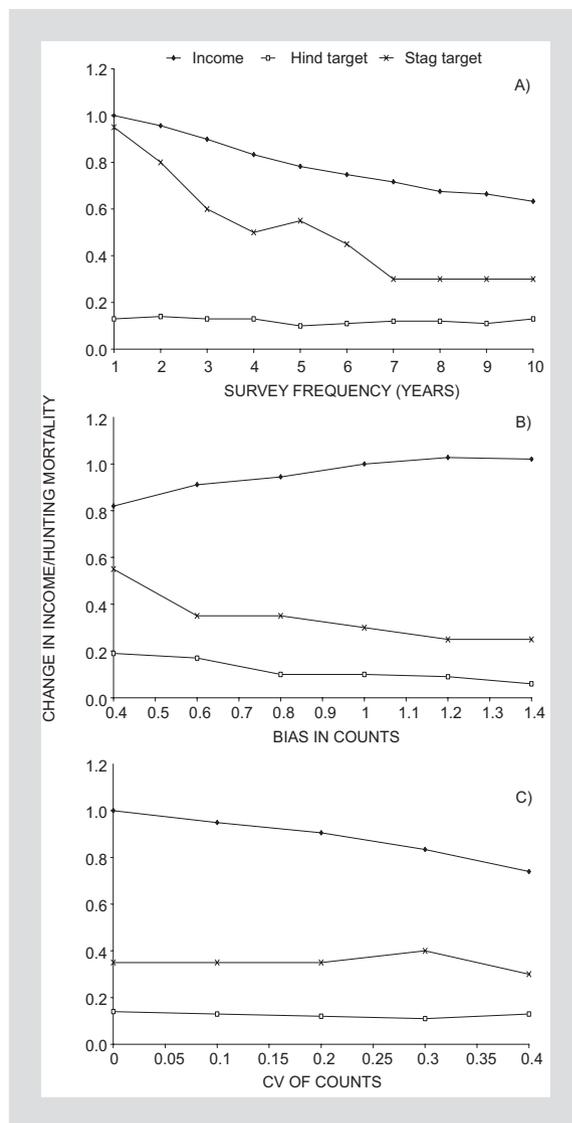

Figure 7. Effect of changes in data quality on income and hunting mortalities. Income is shown as the maximum obtainable (at the optimal hunting mortality) for a given data quality, normalised to that obtained under a perfect survey ('Change'). Target hunting mortalities are shown for both hinds and stags. In each case, one parameter is changed while the others are held constant at the values for a poor survey (see Table 3). The ranges tested encompass likely variation in data quality for Scottish estates. In A) the survey frequency varies between annual and once every 10 years; in B) the bias in the counts varies from 0.4 (on average the count is 40% lower than the actual population size) to 1.4 (40% higher than the actual population size) and in C) the coefficient of variation (CV) of the counts varies from 0 (no variability) to 0.4 (standard deviation is 40% of the mean).

sexes increases as the bias towards underestimation of the population size increases, compensating for the bias, but otherwise changes in data quality are not reflected in trends in hunting mortality rates (see Fig. 7).

Discussion

In this paper we have considered optimal strategies for a deer estate wishing to maximise expected income using a population model parameterised for the North Block of Rum. We have shown that the harvesting policy of neighbouring estates is an important determinant of an estate's optimal strategy due to density dependent dispersal, particularly by mature stags. Given that neighbouring estates are harvesting hinds at around 10% annually, the optimal strategy for an estate is to harvest hinds at similar rates, but to harvest stags (which generate income) at very high rates. If neighbouring estates do not harvest, the focal estate can harvest their hinds harder. These results are due to a trade-off between the requirement for reproductive females to produce offspring and the strong effect of hind density on survival and dispersal rates, particularly among stags.

We have also shown that the poor quality of the data on which estates base their harvesting decisions is a major factor determining both their harvesting policies and their incomes. Under the current circumstances, the differences between perceived and actual harvesting rates in any given year are likely to be large. This is not conducive to good management. The model suggests in particular that an improvement in the regularity of counts would allow a higher stag harvest, and hence increase an estate's income substantially. However, it is likely that increasing the regularity of counts regularity would be costly. We have not included the costs of improved data quality in this analysis. Only when these costs are weighed against the resultant improvements in income, can an integrated strategy for management be devised, which maximises profits in the face of uncertainty.

Comparing our results to the situation on Rum illustrates the way in which our predictions relate to data. Until 1973, the policy was to harvest hinds throughout the island at 14%. Our model predicts that this perceived harvesting rate was indeed near optimal, given the poor quality of the data. The poor data meant that the actual harvesting rate was only around 10%. Since 1973, count quality has improved throughout the island, and the North Block has ceased to be hunted. Our model predicts that the hind harvesting rate of about 14% in the rest of the island is still near optimal. This is no longer because the population size is being underestimated, but because the populations are sustained by emigration from the neighbouring high density North Block population.

This illustration is qualitative and anecdotal. The next step is to test the model using quantitative data, and particularly to test its general applicability to deer populations in other parts of Scotland where environmental conditions are very different. Rum is a poor habitat for red deer with low productivity and small body size compared to other Scottish populations (Clutton-Brock & Albon 1989). Hence, vital rates and dispersal behaviour might be very different in other populations. Equation 2 is a particular functional form for the relationship between dispersal number and hind density, representing the best fit to the Rum data. Similarly, our equations for the dependence of vital rates on hind density are empirically derived best fits. Although this gives us some confidence in the results for the particular population under study, a different functional form of density dependence would produce slightly different results. However, sensitivity analyses suggest that the general patterns that we report are robust, so long as density-dependent stag mortality and dispersal occur. Milner-Gulland et al. (2000) explored the effects of assuming density dependent or density independent hind dispersal on optimal hind hunting strategies for the Rum population, and found relatively minor effects as hinds are philopatric.

Here we have considered only permanent dispersal. In some cases stags may immigrate into areas of high hind densities temporarily at the time of the rut (I. Gordon, pers. comm.). If temporary immigrants are an important component of an area's stag population, then hunting hinds might be positively disadvantageous to an estate's income. However, on Rum temporary immigrants are not significant, and there are no data for other Scottish red deer populations that are sufficiently detailed to explore this possibility further.

One aspect of red deer biology that can not be captured by this model is stag quality; given the lack of data on the influence of stag quality on estate owners' harvesting decisions, we assume that all mature stags are identical in quality, and hence in income-generating power. Differences in quality between adult males can be important and are related to dispersal propensity. For example, Clutton-Brock et al. (2002) show that well-grown males with good antler development are more likely to emigrate. Antler size is heritable, increases with age and varies with climate and population density (Kruuk, Slate, Pemberton, Brotherstone, Guinness & Clutton-Brock 2002). These relationships could lead to complex interactions between stag quality and hind density. Taking stag quality into consideration is likely to reduce the optimal stag harvesting rates that we predict, so as to allow stags to mature, and may also increase hind harvesting rates as a way of reducing stag emigration rates. It would also lead to more complex har-

vesting strategies that take stag quality into account in the selection of individuals to be hunted.

The issue of stag quality, the high level of variability that exists in the Rum population, linked to climatic features (Coulson, Albon, Guinness, Pemberton & Clutton-Brock 1997, Kruuk et al. 1999, Coulson, Milner-Gulland & Clutton-Brock 2000) and the presence of strong cohort effects (Rose, Clutton-Brock & Guinness 1998, Coulson, Guinness, Pemberton & Clutton-Brock 2004) all suggest that an individually-based model may well be more informative than the age and sex structured model presented here. However, this increase in detail parameterised specifically for the Rum population would lead to a loss of generality.

We used simulations to investigate optimal strategies assuming that the neighbour's hunting strategy is either constant or identical to the focal estate's strategy. However, it would also be possible to look at optimal strategies in a system where the two estates both can vary their strategies using a game theoretical framework. This has been used for natural resource management in the past, particularly for trans-boundary fisheries (Kaitala & Pohjola 1988, Munro 1990). Bhat, Huffaker & Lenhart (1996) developed theoretical models for a similar situation, but involving a wildlife pest (hence immigration is unwelcome), and showed that the optimal harvesting rate is where the marginal cost of hunting equals the marginal cost of the damage inflicted by the wildlife. However, when the landowners assume that their neighbour will hunt in such a way as to maximise the damage inflicted on their land, a non-cooperative solution may develop so that neither landowner hunts at all, and damage is maximised. There are obvious parallels with the situation for deer estate owners (except that they wish to encourage rather than discourage immigration). We chose not to use game theory in this paper because of the complexity of our model, which was necessary to capture the age and sex-specific characteristics of red deer migration; nevertheless our results highlight the importance of considering the actions of neighbours in managing mobile natural resources.

Although we concentrated on Rum's red deer population, the issues that we have highlighted are very broadly applicable. Uncertainty, particularly with respect to data quality, is a major issue for the sustainable management of natural resources (Ludwig, Hilborn & Walters 1993). Previous studies have shown that inaccurate and biassed population estimates make the successful use of sophisticated hunting strategies extremely difficult (Ludwig & Walters 1985, Milner-Gulland, Shea, Possingham, Coulson & Wilcox 2001), and suggest that threshold harvesting policies are better (Engen,

Lande & Sæther 1997). Spatially explicit management strategies, such as marine reserves or no-take areas, are now being investigated as potentially valuable tools for combatting uncertainty (Lauck, Clark, Mangel & Munro 1998, Sladek Nowlis & Roberts 1999, Tuck & Possingham 2000). In no-take areas, one part of the area is protected from hunting with the intention that individuals will disperse into neighbouring hunted zones. However, the effects of spatially varying hunting strategies depend crucially on the dispersal behaviour of the target species (Apostolaki, Milner-Gulland, McAllister & Kirkwood 2002). In particular, as we have shown here, it depends on the interaction between hunter preferences for particular age and sex classes, and the age and sex classes which actually disperse.

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