On harvesting a structured ungulate population

E. J. Milner-Gulland, T. N. Coulson and T. H. Clutton-Brock


Variation in demographic rates within a spatially structured population could have important consequences for management decisions, harvesting strategies and offset rates. Although there is a growing body of evidence suggesting that demographic rates vary within populations over a range of spatial scales, there has been little research investigating the consequences of this variation for population management. In this paper, data on the dynamics of two female red deer sub-populations on Rum are analysed, and evidence is presented for differences between the fecundity and mortality rates of the two sub-populations. A simple harvesting model is developed to represent the dynamics of the two sub-populations, including density-independent migration between sub-populations and spatially correlated environmental variability. The highest monetary yield in the model is obtained by harvesting the more resilient sub-population at a higher rate. Surprisingly the losses involved in harvesting both sub-populations at the same rate are insignificant. However, if migration were density-dependent, the size of one sub-population would be more relevant to harvesting policy for the other sub-population. The results of this empirical study are compared to theoretical work on spatially structured populations; it is shown that when a species has complex age- and sex-structured population dynamics, previous theoretical results may not hold.

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Life history rates and population dynamics can vary over a wide range of spatial scales, both within and among populations. Although there is a growing awareness that this spatial variability is ecologically important (Hastings 1993, Lewis 1994, Pinelalloul 1995, Coulson et al. 1997), there has been little research exploring the consequences of spatial variation in life-history rates on the dynamics of harvesting a population. The underlying spatial structure of a harvested stock is a potentially important determinant of the sustainability and profitability of harvesting that stock. Managers usually treat the individuals within an area as a homogeneous population, ignoring this spatial structure.

Some theoretical work has been done on harvesting populations connected by diffusion of individuals (Clark 1990). Clayton et al. (1997) and Keeling et al. (1999) modelled the harvesting of a spatially structured stock made up of two pig species, when harvest costs increase with distance from the end-market. Tuck and Possingham (1994) modelled two sub-populations connected in a source-sink structure. If the optimal harvesting strategy were modelled for each sub-population independently, it would suggest that the more produc-
tive stock should be more heavily harvested. However, Tuck and Possingham showed that it can be optimal to harvest the less productive stock heavily, and the more productive stock lightly, because the more productive stock is a net exporter of propagules to the other stock. This makes it more valuable as a source of colonising individuals than through direct harvest. This result depends on the relative magnitudes of the migration rate between populations and the growth rates of the individual populations; Lundberg and Jonzén (in press) explore the relative influence of these rates on the outcome of harvesting in a model source-sink population.

In this paper we develop a simple model of the interaction between spatial structure and harvesting strategy. We model two sub-populations with different fecundity and mortality rates, which are linked by the migration of individuals. The model is applied to red deer (*Cervus elaphus L.*) females on the island of Rum. The red deer population of Rum has been studied in detail since 1971 (Clutton-Brock et al. 1982, 1997a, b). The data on the population dynamics of the deer are unusually detailed and comprehensive, but are representative of red deer in other parts of Scotland (Clutton-Brock and Albon 1989). Red deer are generally managed on an estate-level basis, with all female sub-populations being hunted at the same rate. If there are biological differences between female sub-populations, as we show, these may need to be taken into account by estate managers wishing to maximise profits from female culls.

It would not be illuminating to use a meta-population model for this system, because there is no dynamic of sub-population extinction and recolonisation, the sub-populations can spend a significant proportion of their time at densities below carrying capacity, and migration rates are low (Gilpin and Hanski 1991). Clutton-Brock and Lonergan (1994) used a deterministic age-sex structured model to examine the trade-offs between female and male culls. However, here we use a simplified population model, and ignore males because their population dynamics are not spatially structured in the same way as are females (Clutton-Brock et al. 1982). We also consider the economics of harvesting more explicitly.

Study area and animals

All data were collected in the North Block of the Isle of Rum, Scotland (57°01′N, 06°17′W, NM-402996) where the red deer are the subject of a long-term individual-based study (Clutton-Brock et al. 1982, Pemberton et al. 1996). The total study area covers approximately 5 km² and consists of areas of high quality herb-rich *Agrostis-Festuca* grassland and poorer quality *Calluna, Trichophorum, Molinia* heath and *Molinia* grasslands. The high density of deer has led to little, if any, succession in the plant community (Clutton-Brock et al. 1982).

Culling stopped in the study area in 1972 and since then, detailed life-history data have been collected for approximately 90% of animals living within the study area. Calves are born in late May and June and are caught within a fortnight of birth and marked with a unique combination of collar and ear tags. Individuals are followed throughout their lives with all breeding attempts and death date recorded. Mortality mostly occurs between October and May (Guinness et al. 1978, Albon et al. 1987, Clutton-Brock et al. 1987b). The deer year is defined as running from 15 May, when winter mortality has occurred and before calving has begun, to 14 May in the following year. Life history parameters are calculated for deer years with the year reference corresponding to the start of the time period; for example the adult mortality rate for 1982 is the proportion of adults that died between 15 May 1982 and 14 May 1983. Regular census data consisting of ordnance survey grid positions have been collected since 1974 allowing the spatial dynamics of the population to be investigated. Since 1974 there have been an average of 47 censuses yr⁻¹ (i.e. ± 2.6) (Coulson et al. 1997). In this study we use life-history and census data from 1974 to 1995.

The study area consists of vegetation communities of different nutritional quality, largely associated with topographical and biotic factors, and fitness varies spatially across these communities (Guinness et al. 1978, Iason et al. 1986). Guinness et al. (1978) defined four discrete areas (Upper Kilnory Glen, Lower Kilnory Glen, Intermediate, Shambhnan Insir) and showed that fitness varies between these areas. Coulson et al. (1997) demonstrated that calf survival in the first winter, a key factor influencing the dynamics of the population (Brown et al. 1993) varies within the study area. An examination of the census data since 1974 shows that the four divisions of Guinness et al. (1978) are now best considered as two separate sub-populations, Kilnory Glen (KG) and Shambhnan Insir (SI; Fig. 1). In this study we treat the study population as these two sub-populations and classify animals as belonging to a sub-population in each year by their mean proximity over all censuses in which they were seen during that year.

Adult males and females have very different behaviour patterns in their use of space (Clutton-Brock et al. 1982); females are typically loyal to their maternal home range throughout their lives, while males disperse. Males occupy different areas to the females throughout most of the year. Because of these differences, we consider only females in this analysis.
Population dynamics and life history parameters

After culling ceased in 1972, the population increased until it reached carrying capacity in the mid 1980s (Fig. 2). The SI sub-population reached carrying capacity sooner than the KG sub-population. Although the mean densities of the two sub-populations since 1984 are rather similar (Table 1), the KG sub-population contains more individuals due to its larger area.

Fecundity and mortality rates vary greatly from year to year. Fecundity rates (number of calves per female) show no evidence of density dependence, while mortality rates are significantly density dependent, both in juveniles and adults (Fig. 3a, b). Although the slopes of the regressions of mortality rate on sub-population size are very different for the two sub-populations (Fig. 3c), the large variability in the data mean that they are not significantly different. Neither are the mean values of any parameter at carrying capacity significantly different ($t$-tests, $P > 0.1$, df = 17). The variances in juvenile mortality rate and fecundity rate at carrying capacity are near-significantly different between the two populations, with SI being the more variable population ($F$-tests, d.f. = 12. Juvenile mortality $P = 0.059$, Fecundity $P = 0.088$, Adult mortality $P = 0.19$; Fig. 4).

Since the population has been at carrying capacity, the sizes of the two sub-populations have been significantly positively correlated ($F_{10} = 5.98$, $P = 0.035$). This is due to the sub-populations being exposed to similar climatic conditions (Grenfell et al. 1991). Within a sub-population, climatic variability may cause temporal autocorrelation, which can be modelled as coloured noise (Steele and Henderson 1994, Halley 1996). An analysis of demographic rates on the Rum sub-popula-

![Fig. 1. (a) The distribution of herb-rich Agrostis-Festuca grassland through the study area (darkest shading), based on a vegetation survey by Ball (1974). Because of the high deer density, this survey is still accurate (T. N. Coulson pers. obs.). (b) black grid squares contain 95% of all deer sightings for census data 1971 to 1993. Grid squares are 100 m by 100 m.](image1)

![Fig. 2. Changes in the density of the Sharnham Insir and Kilnory female sub-populations on Rum, 1974–1995. Culling stopped in the area in 1972. Carrying capacity is assumed to have been reached by 1984. The area used by the Kilnory sub-population is around 3 km$^2$, by the Sharnham Insir sub-population 2 km$^2$. Note that the two sub-populations reached carrying capacity at different times.](image2)
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept, density dependent adult mortality function, KG</td>
<td>$i_1$</td>
<td>$-0.0739$</td>
<td>See Fig. 3c</td>
</tr>
<tr>
<td>Slope, density dependent adult mortality function, KG</td>
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<td>See Fig. 3c</td>
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<tr>
<td>Standard deviation, adult mortality, SI</td>
<td>$\sigma_2$</td>
<td>$0.093$</td>
<td>See Fig. 3b</td>
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<tr>
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</tr>
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<td>Data to 1990 in Clutton-Brock et al. (1997a); 1990-5 unpublished</td>
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<td>$0.74$</td>
<td>Calculated from data for 1984-95</td>
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<tr>
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<td>Mean number of individuals dispersing from a sub-population each year</td>
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<td>$0.727$</td>
<td>See Fig. 5, Calculated separately for each sub-population and summmed</td>
</tr>
<tr>
<td>Price received per carcass (£)</td>
<td>$P$</td>
<td>$55$</td>
<td>Data from Red Deer Commission, Inverness (pers. comm.)</td>
</tr>
<tr>
<td>Cost of killing a single individual in a 1-km² area at carrying capacity (£)</td>
<td>$c$</td>
<td>$20$</td>
<td>Data from H. Rose (pers. comm.)</td>
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<tr>
<td>Size of area inhabited, KG (km²)</td>
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<td>$3$</td>
<td>Estimated, T.N. Coulson, Fig. 1</td>
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<tr>
<td>Size of area inhabited, SI (km²)</td>
<td>$A_2$</td>
<td>$2$</td>
<td>Estimated, T.N. Coulson, Fig. 1</td>
</tr>
</tbody>
</table>

The table shows parameter values used in the model, KG = Kilmory Glen sub-population, SI = Shammad Inisir population.

Tions since 1984 (when the confounding influence of population growth had ceased) shows no evidence of significant temporal autocorrelation in either sub-population, but a strong correlation between the juvenile mortality rates in a particular year in the two sub-populations ($R = 0.74$, $P = 0.006$). The correlation between adult mortality rates is non-significant ($R = 0.44$, $P = 0.14$), and there is no significant correlation between fecundity rates. This suggests that juvenile mortality is strongly affected by the weather, and that both sub-populations are similarly affected.

Although the sub-population sizes are correlated, this correlation only explains 31% of the variance, suggesting that the rates of dispersal between sub-populations are not sufficient to allow close entrainment of the dynamics. The unexplained 69% of the variation could be caused by differences in the age structure and vital rates between the sub-populations. Brown et al. (1993) and Albon et al. (unpubl.) have demonstrated variation in juvenile survival rates of calves born to females in different age classes and in fecundity rates between age groups. A break-down of the age structure in each sub-population shows that the age structure is more stable in KG than in SI (Fig. 4).

There are various reasons why two geographically proximate sub-populations of individuals of the same species might show different dynamics. Clutton-Brock et al. (1982) assign the differences in fecundity and mortality rates to differences in density, rather than differences in the density-dependent processes themselves. However, the analysis above suggests that this explanation is not adequate in itself once the sub-populations have reached carrying capacity. A more likely explanation in this case may be differences in the quality of the forage available to each sub-population. For example, SI has a lower proportion of herb-rich Agrostis-Festuca grassland, which is favoured by the females (Clutton-Brock et al. 1987a; Fig. 1).

There is little migration between the two sub-populations, despite their geographical proximity. Red deer females do not move readily between sub-populations, because of the cohesive nature of sub-population social
structure. Over the 22 yr during which the deer have been studied, only 32 individuals have been observed moving between the sub-populations, with an average dispersal rate from one sub-population to the other of 0.73 females/year. Most studies of dispersal among vertebrates, both theoretical and empirical, suggest that density-dependent dispersal is likely to be the norm (McPeek and Holt 1992, Doncaster et al. 1997). However, in red deer, dispersal rate is not density-dependent.

Fig. 4. The age structure of sub-populations over time in Kilmoor Glen (KG) and Shamhnan Insir (SI). The age structure is more stable in KG than in SI.

(KG: $F = 1.56, P = 0.23$; SI: $F = 1.10, P = 0.31$) and does not vary significantly between the two sub-populations ($t$-test; $P = 0.48, 39$ d.f.). The number of individuals dispersing from a sub-population each year is well described by a Poisson distribution (Fig. 5).

Fig. 5. The observed number of individuals moving from one female sub-population to the other in a year, plotted against a Poisson distribution, with the mean number moving taken as 0.727 per year. There is no significant difference between the observed frequency of migrations and the expected frequency under a Poisson distribution ($\chi^2 = 1.52, NS$). Data are aggregated for both sub-populations, and for the years 1974–1995.
A model of female population dynamics

All the parameter values used in the population model are listed in Table 1, and are estimated using data from the two Rum female sub-populations. The model assumes that juvenile and adult mortality rates are linearly dependent on sub-population size (see Fig. 3c), but that fecundity is independent of sub-population size. Fecundity varies from year to year according to a normal distribution, with the mean and variance observed in the Rum sub-populations. Mortality rates are also assumed to be normally distributed, but are correlated between sub-populations (Brown and Rothery 1993). The variance distributions around the linear survivorship functions are not correlated between juveniles and adults. Fecundity and mortality rates are not correlated and are not permitted to take negative values.

For sub-population 1:

\[ M_1 = \max(M_{1i} + \sigma_{1i}, 0) \]  

(1)

For sub-population 2:

\[ M_2 = \max(M_{2i} + \rho \sigma_{2i} \sqrt{1 - \rho^2}, 0) \]  

(2)

where \( M_{xi} \) = mortality rate (either juvenile or adult) in sub-population \( x \) in year \( t \) (\( x = 1, 2 \)), \( M_{Nxi} \) = deterministic density-dependent mortality rate in sub-population \( x \) (of size \( N \) in year \( t - 1 \)), \( \sigma_z \) = standard deviation of mortality rate in sub-population \( x \), \( z \) = independent standardised normal random variables, and \( \rho \) = correlation coefficient between mortality rates in the two sub-populations.

The deterministic density-dependent mortality rates, \( M_{Nxi} \), are calculated separately for juveniles and adults for each sub-population from the curves in Fig. 3c, as \( M_{Nxi} = b_i + s_i N_x \), where \( b_i \) is the intercept of the curve, \( s_i \) is the slope of the curve, and \( N_x \) is the size of the sub-population (Table 1).

The fecundity and mortality rates are used to calculate the new sub-population size:

\[ N_x = a_x N_x (1 + f_x) \]  

(3)

where \( N_x \) = new size of sub-population \( x \), \( a_x \) = adult survivorship in sub-population \( x \) \( (1 - M_x) \), \( N_x \) = size of sub-population \( x \) in year \( t - 1 \), \( f_x \) = juvenile survivorship in sub-population \( x \) \( (1 - M_x) \), and \( f_x \) = fecundity rate in sub-population \( x \).

\( N_x \) is rounded to an integer value, and then dispersal between the two sub-populations is assumed to occur, with the probability of an individual dispersing from one sub-population to the other being described by a Poisson distribution (Fig. 5). This model describes the dynamics of the Rum deer sub-populations well, as would be expected given that the model parameter values are derived from these data (Fig. 6).

Manager decision-making

Deer managers are assumed to aim to maximise their profits from culling females. They are assumed to have a strategy of culling a certain proportion of each sub-population each year, and are assumed to be able to cull different proportions of the two female sub-populations. In calculating the monetary yield from a particular culling strategy, we consider the variable costs of deer culling only, ignoring the fixed costs of management. These fixed costs are not relevant to the decision-making of a manager when deciding how many of each sub-population to cull, rather than whether to cull at all. We assume that the variable costs of culling are predominately related to search time, with the costs of searching inversely proportional to population size. The profits from culling a particular sub-population are calculated as:

\[ \Pi_x = H_x \left( \frac{p - c_x}{N_x} \right) \]  

(4)

where \( \Pi_x \) = profit from culling sub-population \( x \), \( H_x \) = number of individuals culled from sub-population \( x \), \( p \) = price obtained per female carcass, \( c_x \) = cost of killing a single individual alone in a 1-km² area, \( A_x \) = area inhabited by sub-population \( x \), and \( N_x \) = size of sub-population \( x \) when culling begins.

Because the manager has long-term control of the deer resource, the optimal strategy would maximise profits in the long run, rather than just in the current year. Thus we take the profit obtained by the manager as the steady profit obtained in the long term; this implicitly assumes a zero discount rate.

The size of a sub-population after culling affects the number of individuals available for harvesting in the future, and thus future profits. In order to calculate the manager's optimal strategy, a technique such as Stochastic Dynamic Programming (SDP) would need to
be used (Mangel and Clark 1988, Possingham 1996,
Milner-Gulland 1997). This would allow the interaction
between the sub-populations to be taken into account
when deciding on the harvesting strategy. The dynamics
of the sub-populations are correlated because of their
geographical proximity, but the only modelled linkage
between them is through migration. Thus the use of
SDP would allow both sub-population size and migration
between sub-populations to be taken into account
by harvesters. This might be important if a sub-popula-
tion became very small, although the fact that migra-
tion on Rum is density independent lessens the impact
of the size of one sub-population on the optimal strat-
egy for the other. In practical terms, in a managed
population such as that of Rum, sub-population sizes
would not be allowed to drop to dangerously low
levels, and thus calculating the optimal strategy is un-
likely to add much to our understanding of the inter-
action between spatial structure and harvesting. SDP is
prone to serious computational limitations (Shoemaker
and Johnson 1987); modelling the Rum sub-popula-
tions would stretch the limits of computational feasi-
Nity. For these reasons, we model the effects of
harvesting strategies that consider each sub-population
separately, while acknowledging that the best option
among the modelled strategies cannot be considered
optimal.

Results
The annual harvesting mortality rate for each sub-popu-
lation was varied systematically between zero and 20% of
the sub-population, in combination with each har-
vesting mortality rate for the other sub-population. The
model was run for 50 yr, 100 times for each combina-
tion of harvesting mortalities, with the sub-population
sizes and yields recorded for the last 20 yr of each
simulation, after transitional effects have finished.

Fig. 7 shows the results of these simulations. The
mean total population size (of the two sub-populations
together) declines as each harvesting mortality rate
increases, as expected (Fig. 7a). However, the total
population size declines at a slower rate as harvesting
mortality on the SI sub-population increases, than on
the KG sub-population. This is not just because the SI
sub-population represents a smaller proportion of the
total population than KG, but is because the SI sub-
population has a steeper density-dependent response,
and so is more productive under harvesting. This can
be seen by plotting the monetary (Fig. 7b) and physical
(Fig. 7c) yields from harvesting. The monetary yield is
maximised by harvesting the KG sub-population at
about 10% per annum, and the SI sub-population at
about 14% per annum. The physical yield (number
killed each year) is maximised by harvesting at a rate of

Fig. 7. The effects of different sub-population harvesting mor-
tality rates on the mean total population size and yield of the
Rum red deer population. Means are calculated as the mean of
20 yr (after transitional effects have finished) for 100 simul-
ations. KG = Kilnmore Glen, SI = Shannan Insir. a) Total
population size, b) Monetary yield, c) Number of deer killed
per annum.
The yields obtainable from the population significantly; in the absence of variability the monetary yield is maximised at a hunting mortality rate of 12% (KG) and 16% (SI) and the physical yield at 14% (KG) and 18% (SI).

Currently, deer managers ignore the biological differences between sub-populations in deciding on a culling strategy. We have shown that there are observable biological differences between two Rum red deer sub-populations. By examining the effect of harvesting both sub-populations at the same rate, the losses incurred by managers following this strategy can be estimated, compared to the yields obtainable by harvesting the sub-populations at different rates (Fig. 8b, c). The maximum total monetary yield from harvesting at only one rate is lower than the maximum obtainable if the harvest rates are different in each sub-population, because the different responses to harvesting are ignored. However, in this case, the losses incurred from harvesting at only one rate are relatively low, with a maximum yield (at a harvesting mortality of 10%) of 96% of the yield obtainable when the two populations are hunted at different rates. A similar result is obtained for the physical yield from the population. The monetary yield becomes negative at high harvesting mortalities because of the increasing cost of harvesting at low densities. However, as the harvesting mortality rate gets higher, the equilibrium population size becomes very low, so that in most years there is no harvesting (because the number killed is rounded to the nearest integer), and thus the costs of harvesting tend to zero.

Although the two female sub-populations are different biologically, they are linked through density-independent female migration (Fig. 5). The effects of harvesting will interact with this migration. For example if migration were density dependent, then a sub-population would be more able to withstand harvesting pressure if there were a neighbouring sub-population at higher density. If migration rates were higher, this would tend to even out the density differences between the two sub-populations (though not the biological differences). These effects are shown in Fig. 9. The effects on number killed are shown, with the same harvesting mortality rate on each sub-population, but the results are similar for population size and monetary yield. The results are shown for a mean migration rate of two individuals per year moving from one sub-population to the other, either irrespective of sub-population size (density independent), or with the mean number moving increasing linearly from zero to two as density increases (density dependent). This rate is more than double the rate estimated for the Rum population (0.727), and is shown to demonstrate the effects of increasing the migration rate on the results. The results at a mean migration rate of 0.727 are in between the results for a rate of 2 and no migration.
The effects of changing the migration rate differ between sub-populations. For the SI sub-population, the highest harvests can be obtained when there is no migration, and the lowest when migration between sub-populations is density-dependent. For KG, on the other hand, the highest harvests are obtained when there is density-dependent migration, and the lowest when it is density independent. This is because the SI sub-population will tend to lose individuals with density-dependent migration, because its size remains relatively high under harvesting pressure. Thus the KG sub-population will tend to benefit from inward migration from SI. However the SI sub-population is most resilient to hunting when there is no drain on sub-population size from migration. The results with density-independent migration are very similar to those for no migration at lower hunting mortalities. At higher hunting mortalities, the fact that individuals migrate away from very small populations means that density-independent migration leads to a higher chance of population extinction than no migration.

![Diagram](image)

**Discussion**

We have shown here that differences may exist between the density-dependent mortality and fecundity rates of adjacent female sub-populations, using the example of the Kilmory Glen and Shamman Inisr sub-populations of females on Rum. These differences are particularly marked among juveniles, and are likely to stem from differences in habitat quality and population structure rather than differences in female density. Using a simple harvesting model, we have demonstrated that these biological differences lead to differences in the harvesting mortality producing the maximum yield, so that the maximum monetary yield from the Shamman Inisr sub-population is obtained at a harvest rate 40% higher than that producing the maximum yield in Kilmory. This might suggest that the harvesters could be losing a substantial proportion of their potential profits by harvesting the two populations at the same rate, rather than considering the two populations separately. However, because the yields are relatively similar over the range of harvesting mortalities in question (10–14%), the actual losses incurred are small; managers harvesting the sub-populations at the same rate still receive 96% of the yield obtainable under differential harvesting.

This study uses long-run data on the population dynamics of a particular red deer population, so that its detailed predictions are specific to that population. Ideally, these predictions should be experimentally tested. However, they do give some more general lessons for harvesting structured populations. The model highlights the importance of a detailed understanding of the dynamics of harvested populations, and in particular that there may be sub-populations within a population that have sufficiently different dynamics for this to have a significant effect on optimal harvest rates. An added complication is that the dynamics of neighbouring sub-populations may be correlated through exposure to similar climatic variation, and may be linked through migration. Both of these were shown to be the case for the Rum sub-populations.

We have shown that the effect of migration depends on whether it is density dependent or density independent. At low hunting mortalities, density-independent migration is very similar in effect to no migration, and so the linkage between the sub-populations is not likely to be significant in determining optimal hunting strategies. This is the case for the Rum population. However, if the sub-populations were linked by density-dependent migration, as is thought to be more usual among vertebrates, then the effect would be to even out the density-related differences between the sub-populations.

Dispersal is frequently assumed to be density dependent (McPeek and Holt 1992, Doncaster et al. 1997), yet our results show that for female red deer dispersal is density independent. If dispersal is a response to differ-
ences in the densities of the starting population and the destination population, dispersal could appear density independent if the two populations were at similar densities. At carrying capacity the two sub-populations SI and KG do have similar densities, but because the two sub-populations reached carrying capacity in different years there are years when their densities differed substantially. There was no significant difference between these years and years when the populations were similar in density; both had density-independent dispersal (Fig. 5).

The ideal model for finding the optimal harvest strategy in this situation would be a state dynamic model. In the case of the Rum population, the relatively weak linkage between the two sub-populations means that an adequate approximation to the optimal strategy can be found using a simple simulation model. However, in situations where the sub-populations are more closely linked, for example through large-scale density-dependent migration, a state dynamic model would be needed, because the optimal strategy for one sub-population could be strongly dependent on the size of the other sub-population.

The ecological literature on spatially structured populations has so far concentrated on populations that have relatively simple internal dynamics and a source-sink structure or density-dependent dispersal (Pulliam 1988, Dias 1996, Doncaster et al. 1997). Few people have considered the issue of harvesting spatially structured populations, but they too have concentrated on the same relatively simple population structures (Clark 1990, Tuck and Possingham 1994), or ignored sub-population dynamics (McCullough 1996). McPeek and Holt (1992) showed theoretically that when ecological conditions in patches fluctuate in time and space, but with broadly similar ranges in each patch, selection should favour generalist adaptations to this range of ecological conditions, and a high dispersal propensity. Thus sub-population differentiation is not likely in these conditions. In this paper we have examined a population in an area where ecological conditions fluctuate in space and time over a broadly similar range. However, this population has a rather complex, sex-differentiated social structure, in which life-history parameters are strongly age-determined. We have shown that female dispersal is rare and density independent, and the dynamics of the two sub-populations are not as closely coupled as might have been expected from their geographical proximity. This study thus provides an empirical example suggesting that further theoretical work is required on the spatial dynamics of populations in cases where population structure is complex.

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