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THE DEMOGRAPHIC CONSEQUENCES OF RELEASING A POPULATION OF RED DEER FROM CULLING

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Abstract. A change in population density can generate spatial and demographic effects that can have an impact on fluctuations in population size for many years. Although the demographic effects of time lags have been incorporated into analyses of time series data, there are few detailed descriptions of the long-term demographic consequences of a change in density. We use detailed, individual-based data from a population of red deer (*Cervus elaphus*) from the North Block of the Isle of Rum, Scotland, to describe long-term demographic and spatial effects of a change in density. The population was released from hunting pressure in 1972. Over the following 10 years population density doubled and, since the early 1980s, has fluctuated around ecological carrying capacity. The cessation of culling led to long-term transient spatial and demographic effects that have persisted for 30 years. Different vital rates responded to the increase in density at different rates, causing long-term changes to the demographic and spatial structure of the population. These changes altered the impact of different age- and sex-specific vital rates on annual changes in population size. These changes are still ongoing, 30 years after cessation of the cull, suggesting that a change in density may generate transient dynamics that persist for several generations.

Key words: *age structure;* Cervus elaphus; *cohort effects; culling release; density dependence; Isle of Rum; population increase; red deer; Scotland; transient dynamics; vital rates.*

INTRODUCTION

The causes and consequences of changes in population density have been the focus of much research, with density dependence considered to be a ubiquitous feature of the dynamics of most populations. Much work has focused on time-lagged effects of a change in density (May 1973, 1981, Fryxell et al. 1991, Royama 1992, Berryman and Turchin 1997, Kaitala et al. 1997, Leirs et al. 1997, Nisbet 1997, Post et al. 1997, Coulson et al. 2001, Lande et al. 2002). Such time lag effects can be caused by variation in individual life histories that can generate cohort effects, or by autocorrelated environmental noise, and can persist for many years. This understanding of the causes and importance of lagged density-dependent effects on population dynamics recently led Lande et al. (2002) to devise an elegant method for combining time series data with a simple description of the life history to estimate total density dependence across the life cycle. This method undoubtedly will have a major impact on research identifying the strength of density-dependent processes, especially in iteroparous species. Despite the methodological advance of Lande et al. (2002) in estimating total density dependence from relatively common forms of ecological data, there are surprisingly few detailed descriptions of the long-term consequences of a change in population density. In this paper we provide a detailed description of the long-term consequences of an increase in density from a population of red deer living in the North Block of the Isle of Rum, Scotland (Clutton-Brock et al. 1982).

Why should a current change in density in age-structured populations generate effects that persist for many years? Different vital rates respond to an increase in density at different rates (Eberhardt 1977, Albon et al. 2000, 2002): the age at first reproduction responds to density dependence before fecundity and juvenile survival, which in turn respond to density dependence before adult survival (Eberhardt 2002). These differences in the onset of density dependence may have consequences for the demographic structure of the population that continue for some years after density has stabilized (Lande et al. 2003). For example, if animals born at higher density differ phenotypically from those born at lower density, and if these phenotypic differences affect survival and fecundity throughout life (Metcalfe and Monaghan 2001), the demography and dynamics of the population may change as more individuals that were born at high density permeate the population. Our objectives in this paper are to explore patterns of temporal variation in vital rates and the impact of these vital rates on the rate of population increase for three decades following the cessation of culling.

The red deer (*Cervus elaphus*) population living in the North Block of Rum increased in density as a result of the cessation of culling in 1972 (Clutton-Brock et

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al. 1982). Prior to 1972 the population was predominantly limited by hunting, with an unselected ~14% of females and males removed annually (Clutton-Brock et al. 1985, 2002, Milner-Gulland et al. 2000). Following the cessation of culling, the population doubled in size from ~150 animals during the 1960s to ~300 animals in the 1980s and 1990s (Clutton-Brock et al. 1982). Prior to 1972 the population was limited by culling; during the period of population increase, the predominant limiting factor was the birth rate; but since the population reached ecological carrying capacity, the population has been food limited (Clutton-Brock et al. 1985, Albon et al. 2000, Coulson and Hudson 2003), with starvation being the predominant cause of death (Clutton-Brock et al. 1997*a*). The effects of the increase in density in depressing first-winter survival (Guinness et al. 1978*b*, Clutton-Brock et al. 1987*a*, *b*), yearling survival (Clutton-Brock et al. 1982, 1985), adult survival (Albon et al. 2000), fecundity (Guinness et al. 1978*a*, Kruuk et al. 1999), and antler size (Kruuk et al. 2002), and in increasing age at first breeding have previously been reported (Langvatn et al. 1996). The long-term effects of an increase in density on the spatial and demographic composition of the population have not, until now, been reported in detail.

In this paper we describe the long-term demographic and spatial consequences of releasing a population of red deer from culling, and report 27-year time series of age- and sex-specific vital rates and the impact of these vital rates on population growth. Our results show that the release from culling is still influencing the demographic structure of the population and that these ongoing structural changes affect the dynamics by altering the association between different vital rates and population growth. We conclude that the lagged demographic and spatial effects of an increase in density can persist for up to three decades.

Methods

Study area

All data were collected between 1974 and 2001 in the North Block, Isle of Rum, Scotland (57°01′ N, 06°17′ W; NM-402996), where the red deer population is the subject of a long-term individual-based study (Clutton-Brock et al. 1982, Pemberton et al. 1996). Since 1971, animals born into the population have been caught within hours of birth, tagged, and weighed. They subsequently have been followed throughout life, with breeding attempts and death date recorded. The recapture rate within winter censuses is 1.0 (Fan et al. 2003), and generally the whereabouts of animals that have emigrated from the study area to other parts of the island are known (Clutton-Brock et al. 1982). Furthermore, routine mortality searches result in the finding of carcasses of animals that have died within the study area. Pregnant females are visually identifiable in the weeks before birth, and the calves of these females are caught and marked. Consequently, we have accurate measures of age- and sex-specific vital rates and population size and structure. We do not consider uncertainty in estimates, as this is negligible. Full details of the data collection methodology are given in Clutton-Brock et al. (1982).

Census data have been collected since January 1974, providing grid references accurate to 100 m for each animal seen on each census day (Coulson et al. 1997). Censuses are conducted by one person walking a set route (routes differ slightly in summer and winter) and recording the identity and position of each animal seen (Clutton-Brock et al. 1982). The median number of censuses conducted each year was 40, with a range of 25 (in 1985) to 61 (in 1974 and 1975). Incomplete censuses that were abandoned due to adverse weather were removed from the database and repeat sightings of the same animal on the same census were also removed.

Temporal and spatial variation in population size

For the purpose of this paper, the population size is defined as the number of animals that were alive on 15 May (just before the onset of calving and after the majority of mortality) that had been seen in $\geq$10% of winter censuses in each year. We chose a 10% cutoff to distinguish between residents and transients. Our definition of density is slightly different than those previously used, which do not stipulate that animals have to be alive on 15 May. We chose this cutoff point because the transition matrices (see *Population dynamics*) that we use to examine changes in population size are pre-breeding matrices and run from 15 May in year j to 14 May in year $j + 1$. Deer years are labeled with j; most winter mortality in year t actually occurs in the first four months of calendar year $j + 1$.

Age-specific survival, fecundity, and dispersal rates were calculated for each year. The parsimonious age structure for survival and emigration rates were estimated using mark–recapture–recovery methods. We classified adult males as yearlings, 2–8 year-olds, and >8-year-olds, and classified adult females as yearlings, 2–10 year-olds, and >10 year-olds. Recruitment rates were the products of fecundity and offspring survival rates to one year of age. We split survival to one year of age into summer survival (from birth to 1 October) and winter survival (from 1 October to 14 May) (Clutton-Brock et al. 1982). Using time series of vital rates, we estimated how many years of data were required before estimates of the mean and the variance in each vital rate had stabilized. For each year, j, we constructed a time series of n years between 1974 and j. We used these data to estimate the arithmetic mean and variance as a function of the length of the study. We assumed that a mean or variance had stabilized if its estimates showed no significant temporal trend over five consecutive years or more. In cases in which apparent stabilization was reversed by a subsequent extreme value

of a vital rate, we assumed that the mean or variation of a vital rate had, in fact, not stabilized by the first five-year period of apparent stability.

Small-scale spatial heterogeneity can have important dynamical influences on vertebrate population dynamics (Coulson et al. 1997, 1999). We examined how the sex structure of the population varied spatially following the release from culling. We calculated the distance between all animals that were seen in each census. For each year, the mean distance between each dyad of animals was calculated. Hierarchical cluster analysis with average link clustering was used to construct a measure termed ''local population density.'' By altering the distance threshold at which individuals are considered to be clustered, a range of local population densities can be calculated, ranging from the population consisting of N clusters each of a single individual through to one cluster of N individuals. Full details of the method are given in Coulson et al. (1997). To show how local population density has changed over time throughout the study area, we plotted the mean position of each cluster and shaded the plot as a function of the size of each cluster, using the degree of clustering that has been shown to be associated with variation in survival rates (Coulson et al. 1997).

Population dynamics

To explore the impact of each vital rate on the proportional change in population size from one year to the next, λ, we constructed annual transition matrices for each year of the study. For each year, we constructed a partitioned Leslie matrix of age- and sex-specific recruitment rates and age- and sex-specific rates of remaining within the population (survival rate $\times$ nonemigration rate). The first subdiagonal represents the probability that females and males of known age will remain in the population until the following year. Like recruitment rates, these rates also consist of more than one vital rate: the probability of survival and the probability of not emigrating. Because the probability of sighting animals living within the population is 1.0 (Fan et al. 2003) we do not need to model survival in a mark–recapture framework to estimate survival rates. We do not consider immigration because it is negligible in this population (Clutton-Brock et al. 2002), with most dispersal being from the high-density study area to other parts of the island (Clutton-Brock et al. 1997*b*). We did not group ages into classes within the matrices because this would not have allowed us to explore cohort effects.

Each annual transition matrix, $\mathbf{T}_j$, can be multiplied by a vector ($\mathbf{n}_j$) containing the number of animals of each age and sex in the population in that year. The sum of the vector $\mathbf{n}_j$ gives N_j, the population size in year j; $\mathbf{n}_{J+1}$ is the vector product of $\mathbf{T}_j\mathbf{n}_j$ and the sum of $\mathbf{n}_{j+1}$ is equal to N_{J+1}, the population size in year $j + 1$. We can calculate λ between year j and year $j + 1$ as N_{J+1}/N_j or estimate it as the dominant eigenvalue of $\mathbf{T}_i$.

For each annual transition matrix we calculated sensitivities and elasticities of λ_j (Caswell 2001). Sensitivities ($\delta\lambda/\delta a_{rc}$) of a matrix element a_{rc} (where r and c index the matrix row and column, respectively) are the change in λ resulting from a small change in that matrix element. Elasticities ($\delta\log\lambda/\delta\log a_{rc}$) are the proportional change in λ resulting from a proportional change in a matrix element; consequently, elasticities sum to one. Elasticities and sensitivities of λ are often estimated analytically assuming the stable age structure (Caswell 2001). However, because the age and sex structure of vertebrate populations can fluctuate independently of current total population size (Coulson et al. 2001), we estimated sensitivities and elasticities numerically using the observed population age and sex structure. We did this by independently altering the value of each matrix element by 1% and recalculating N_{j+1}. We calculated $\delta\lambda$ and $\delta\log\lambda$ using observed values of $\mathbf{n}_j$. Identical results could have been obtained analytically using methods developed by Fox and Gurrevich (2000).

Because the matrix element describing the probability of remaining in the population is the product of more than one vital rate, the sensitivities and elasticities of the constituent vital rates are the same as the elasticities and sensitivities of the matrix element (Caswell 2001). Consequently, we only report sensitivities and elasticities of the matrix elements and not of the vital rates comprising them. So, although we report annual values for each vital rate, we only report sensitivities and elasticities of matrix elements.

By summing sensitivities or elasticities (Caswell 2001) within each annual transition matrix, we estimated changes in the impact of vital rates for different demographic classes on the population dynamics of the total population. By summing sensitivities and elasticities across different transition matrices (e.g., $e_{21(t)} + e_{32(t+1)} + \ldots$ where e_{rc} is the elasticity of matrix element a_{rc} and t is year), we were able to approximate the contribution of a cohort to the population dynamics.

RESULTS

Temporal variation in numbers

Prior to culling, the population in the North Block consisted of ~80 adult males and 90 adult females (Clutton-Brock et al. 1982). These estimates were made by the Red Deer Commission (now the Deer Commission for Scotland, DCS). Annual counts are still made by the DCS and they typically estimate the study area population as being 10–20% larger than the known population because they count over a larger area and because the counting procedure causes disturbance to the deer, with some temporarily entering the study area.

Since the cessation of culling in 1972, the study area population increased throughout the 1970s before

reaching ecological carrying capacity in the early 1980s (Fig. 1a). The maximum population size recorded was in 1986, when the population contained 317 adults (116 males > 12 months of age and 201 females > 12 months of age). Although total population size has been relatively constant since the early 1980s (Fig. 1a), there has been a marked increase in the number of females (Fig. 1b) and a marked decrease in the number of males (Fig. 1c). These trends, although noisy, may be continuing (Clutton-Brock and Coulson 2002). The changes in the population sizes of males and females have led to a continuing bias in the proportion of adult females in the population (Clutton-Brock et al. 2002). The fluctuations in population size correspond to a percentage annual change of $+4.28 \pm 0.125\%$ (values are mean $\pm$ 1 SD) for adult females, $-1.13 \pm 0.192\%$ for adult males, and $+1.10 \pm 0.128\%$ increase for the total adult population.

Spatial variation

Changes in density have been accompanied by changes in the small-scale spatial structure of the population. The increase in female density has not occurred uniformly throughout the study area (Fig. 2); the greatest increase has been in the north and northeast of the study area where the most productive grasslands occur (Iason et al. 1986). In parts of the study area where local female density has increased, the density of males has declined, although this was a slow process occurring over several years. By the late 1990s, there were very few males living permanently in the areas of highest female density, and resident males are now effectively absent from the areas of highest adult female density.

Age structure

The age structure of the population took ≥20 years to stabilize after the cessation of culling. Albon et al. (2000) and Milner-Gulland et al. (2000) have previously reported that as the population increased and then fluctuated around ecological carrying capacity, the proportion of older animals in the population increased. This is reflected by temporal fluctuations in the average age of the population aged ≥12 months (Fig. 3a). The female population aged from having a mean age of ~5 years old in the early 1970s, to a mean age of ~6.5 years in the 1980s. Since the mid-1990s, the mean age may have stabilized at <6 years. The average age of the male population has changed less, but has shown greater variation; as with the female component of the population, the mean age has remained relatively constant over the past five years, but at 4.0 years.

As well as displaying the total size of the population, Fig. 1a–c also shows the composition of the population in terms of cohorts. During the early years of the study, each cohort of the male population constituted a similar proportion of the population. However, over time some cohorts began to constitute a greater proportion of the

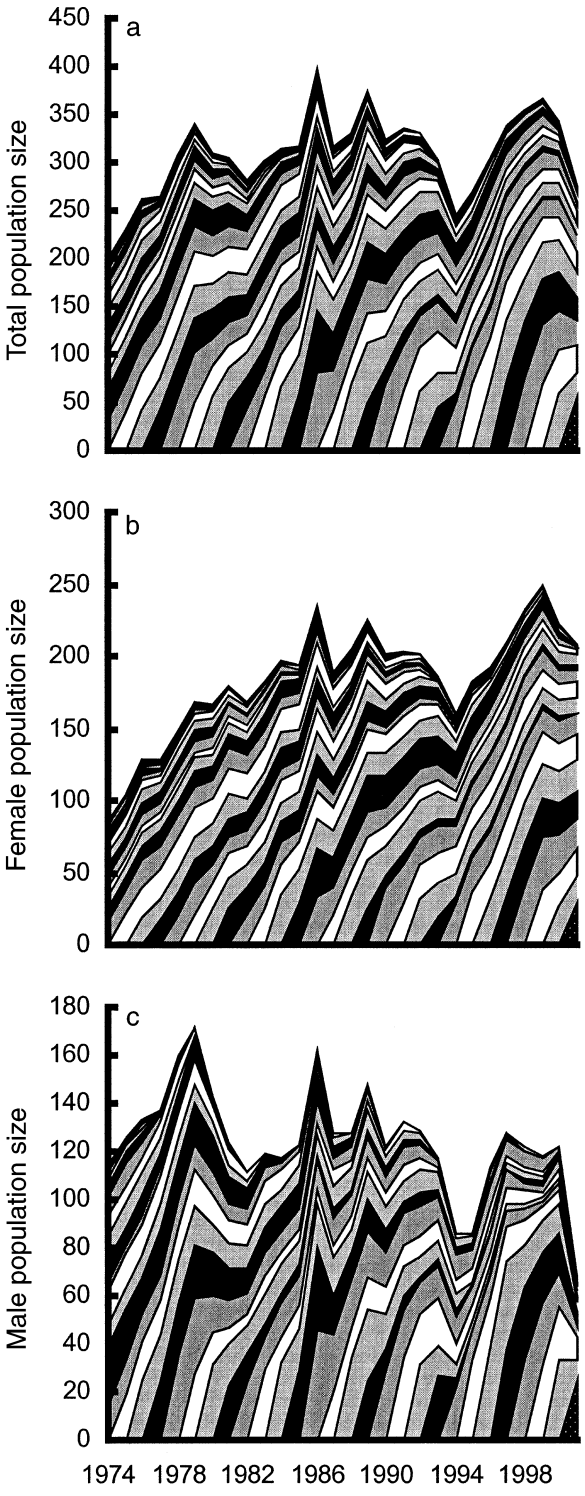

FIG. 1. Dynamics of (a) the red deer population, (b) the female component of the population, and (c) the male component of the population from 1974 to 2000. The black, gray, and white areas represent the demographic structure of the population. Each diagonal stripe represents a cohort. Wide stripes represent cohorts that constitute a large component of the population and narrower stripes represent cohorts that constitute a smaller component.

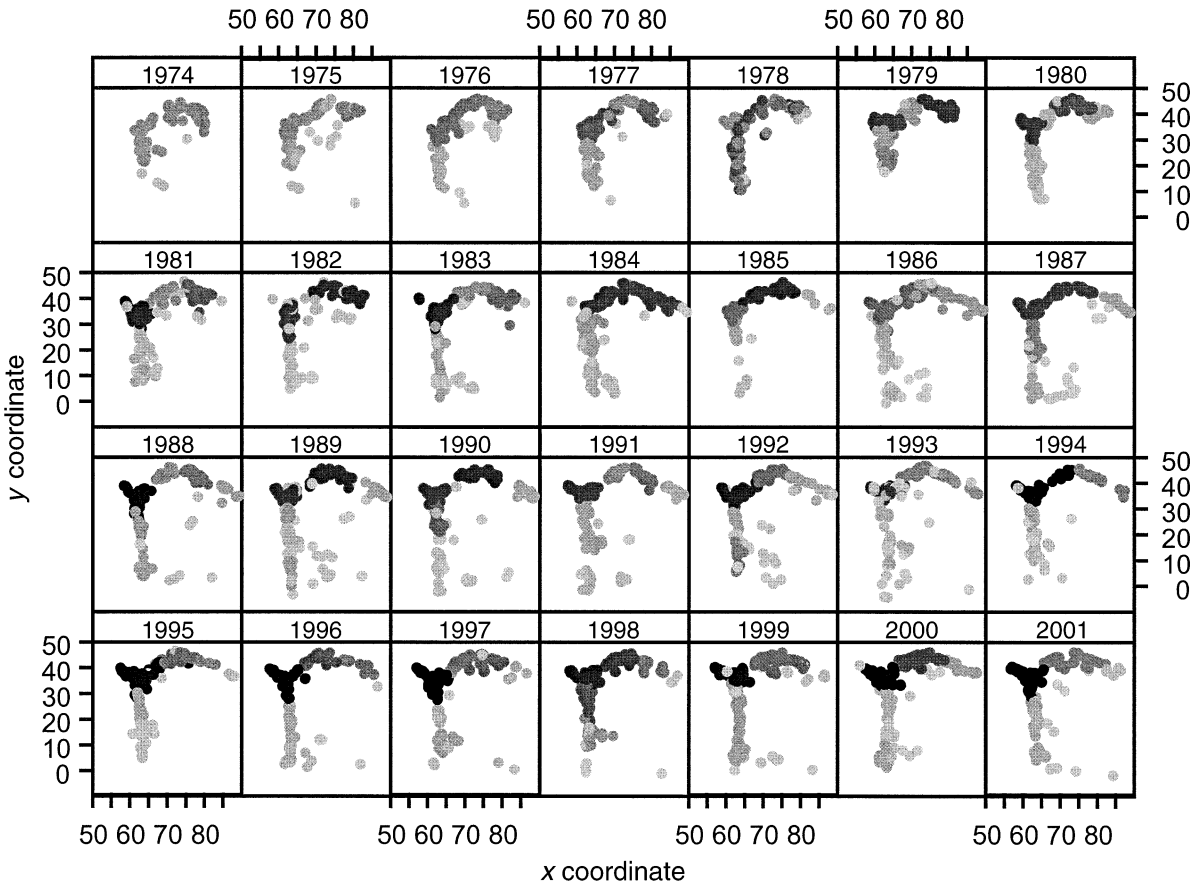

FIG. 2. The local population density of adult females (>12 months old) between 1974 and 2001. The darker the shading, the higher is the local population density.

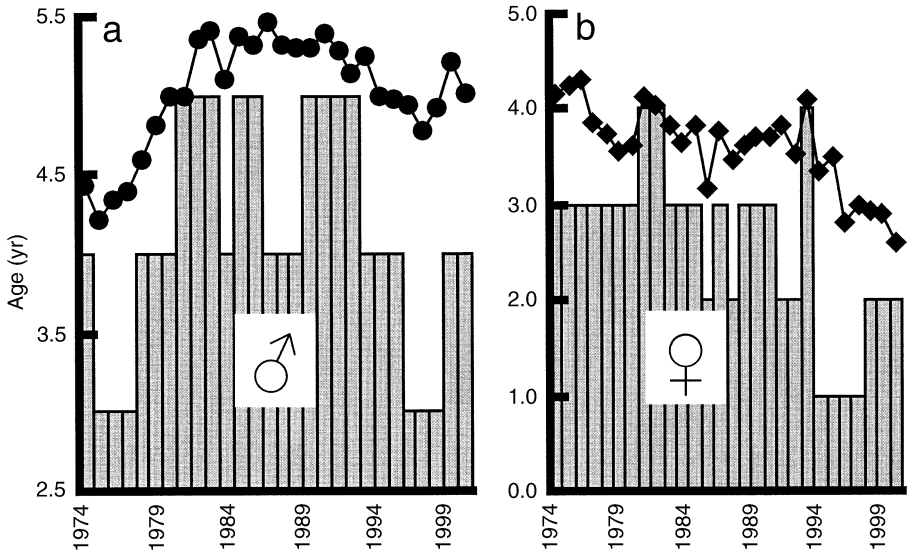

FIG. 3. Changes in red deer age structure over the course of the study: the mean (line) and median (bars) age of adult (>12 months old) male (a) and female (b) components of the population over the years from 1974 to 2001.

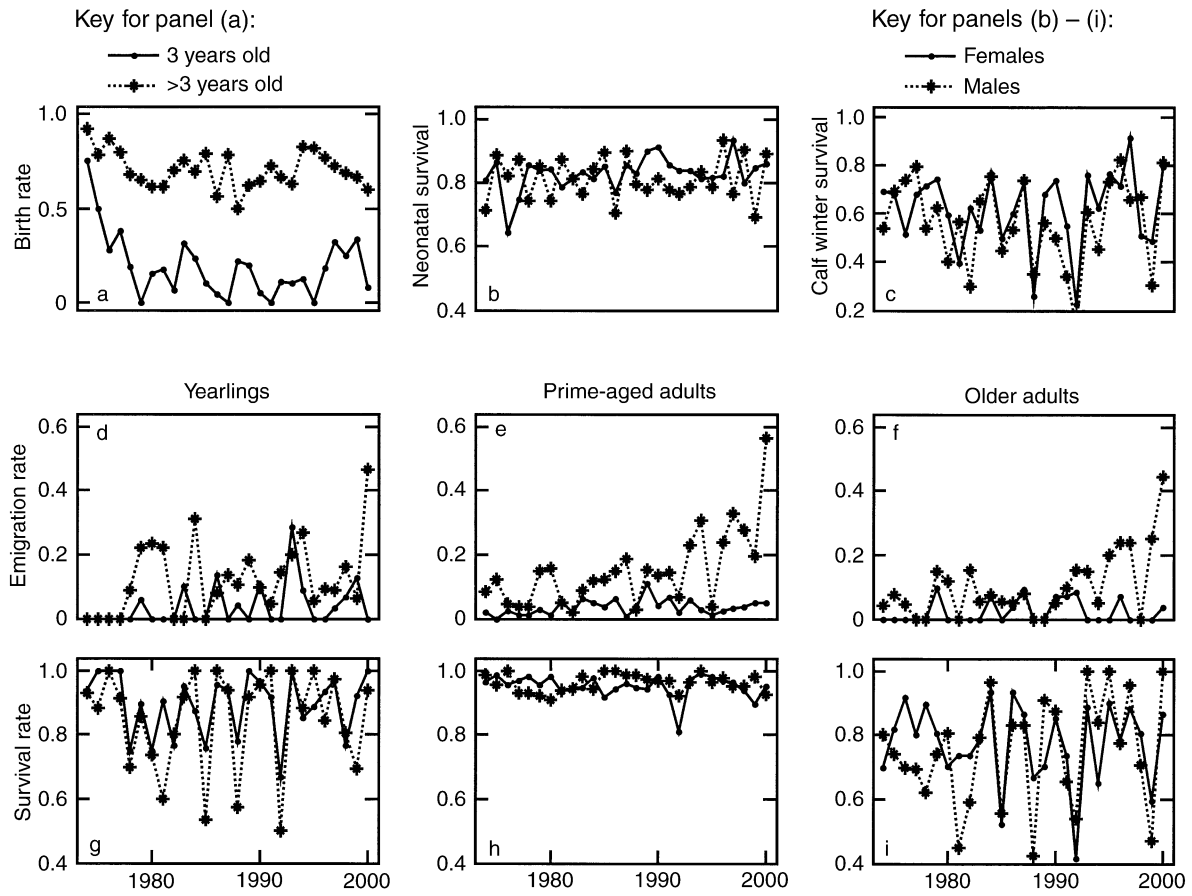

FIG. 4. Time series of class-specific vital rates from 1974 to 2000: (a) birth rates of 3-year-old hinds and those >3 years old; (b) male and female summer survival (from birth to 1 October); (c) male and female calf overwinter survival (1 October–15 May); emigration rates of (d) yearlings, (e) prime adults, and (f) older adults; and survival rates of (g) yearlings, (h) prime adults, and (i) older adults.

population than others. In contrast, in the female component of the population, the variance in the proportion of each cohort within the population has remained approximately constant over time.

Temporal variation in birth rates and survival

Vital rates have fluctuated to different extents over the course of the study (Fig. 4), although none has shown persistent temporal trends. Survival of juveniles over their first winter of life and survival of yearlings and older adults tended to fluctuate most, as is typical of ungulate species (Gaillard et al. 1998, 2000). With the exception of prime-aged adult survival, male vital rates had greater variances than their female equivalents. With the exception of neonatal survival, survival rates tended to be more strongly correlated between the sexes than were emigration rates (Fig. 4).

By 2001, 13 out of 18 estimates of the mean values of vital rates had stabilized (Table 1). There was no apparent pattern in the number of years required before estimates of the mean had stabilized across vital rates; for example, male summer survival stabilized within 5 years, whereas female summer survival took 21 years. Variation in vital rates required more years of data to stabilize than did the mean values: variation in eight of the 18 vital rates that we examined are yet to stabilize (Table 1).

Population dynamics

An examination of the elasticities and sensitivities of the annual transition matrices suggests that the increase in density has led to continuing changes in the association between matrix elements and λ, suggesting that the demography and dynamics of the population have not yet reached equilibrium following release from culling. Elasticities and sensitivities of several of the matrix elements show continuing directional changes and are displayed for each annual transition matrix in Fig. 5. Adult survival has the highest elasticities, whereas recruitment has the lowest, as has been shown previously for other populations of large mammals (Eberhardt 1977, 2002, Gaillard et al. 2000). Elasticities of yearling and older adult survival are similar in size, although there has been an increase in the size of

TABLE 1. Estimates of the number of years of data required until the mean and variance in vital rates of red deer stabilized; minus signs represent those vital rates for which the parameters are yet to stabilize.

	Time to stabilization (years)			
	Females		Males	
Vital rates	Mean	Variance	Mean	Variance
Summer survival	21	20	5	21
Calf winter survival	17	25	12	25
Yearling emigration	25	23	···	···
Prime adult emigration	20	15	···	···
Older adult emigration	22	10	···	···
Yearling survival	12	10	11	···
Prime adult survival	···	···	18	···
Older adult survival	25	···	···	23

Note: Birth rate (sexes pooled) for 3-year-olds has mean of 25 years for stabilization, with no stabilization yet in variance; for red deer >3 years old, birth rate stabilizes after 17 years, and variance after 12 years.

the older adult elasticities that is not observed for yearlings.

As the study has progressed, variation in some sensitivities and elasticities has stabilized while others continue to increase (Fig. 6). For example, variance in recruitment elasticities and sensitivities of males and females continues to increase, as does variance in elasticities and sensitivities of yearling survival (Fig. 6).

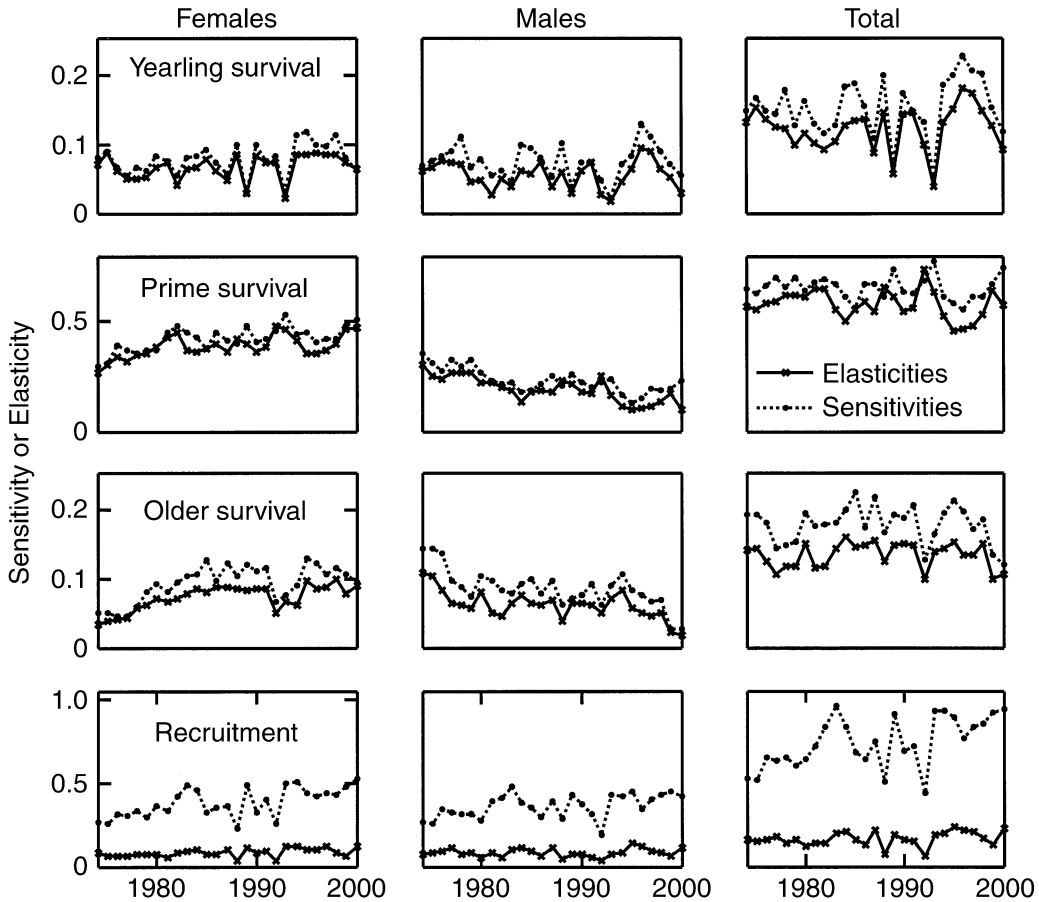

FIG. 5. Sensitivities (dashed lines) and elasticities (solid lines) of the λ for all model parameters, 1974–2000. The temporal patterns of changes in elasticities and sensitivities are qualitatively similar. Those differences in the patterns that do exist arise due to differences in scaling in the calculation of each (see Link and Doherty 2002).

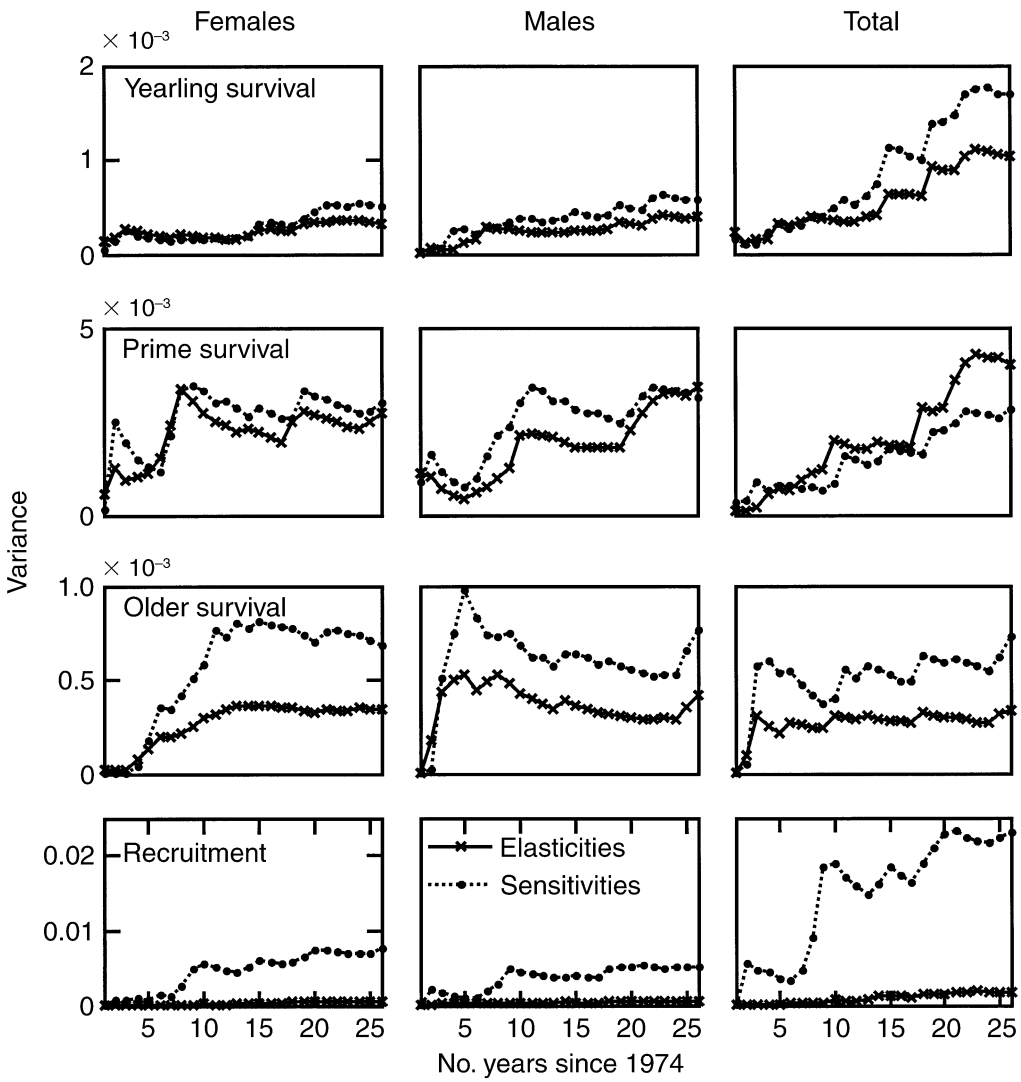

FIG. 6. Plots of estimates of the variation in elasticities and sensitivities and the length of the study. The label "$\times 10^{-3}$" above some *y*-axes indicates that the actual variance is 1000 times smaller than the axis scale numbers indicate.

In contrast, female prime-adult survival and variance in elasticities and sensitivities of older adult survival appear to have stabilized.

Cohort effects

Because the annual transition matrices consisted of animals of all ages represented in the population, we could sum both the sensitivities and elasticities longitudinally across matrices to estimate the potential impact of cohort variation on the population dynamics (Fig. 7). We could only consider cohorts born between 1974 and 1985 because animals were still alive from later cohorts. There was a twofold difference in the contribution of different cohorts to the population dynamics: the 1975 cohort had over twice the elasticity, and nearly twice the sensitivity, of the 1982 cohort. The contributions of the female and male components of each cohort to the population dynamics were correlated if sensitivities were considered ($F_{1,10} = 13.21$, $P = 0.005$), but were not correlated if elasticities were considered ($F_{1,10} = 0.445$, $P = 0.52$).

Successful cohorts were successful throughout life. The elasticities and sensitivities of the recruitment of the focal cohort in their year of birth on the population dynamics were not strongly correlated with the total elasticity or sensitivity for males and females, but the elasticities and sensitivities of recruit production were correlated with the total cohort elasticities and sensitivities (Table 2). Similarly, elasticities of yearling survival, prime-adult survival, and older adult survival tended to be correlated with total elasticities and sensitivities of the cohort (Table 2).

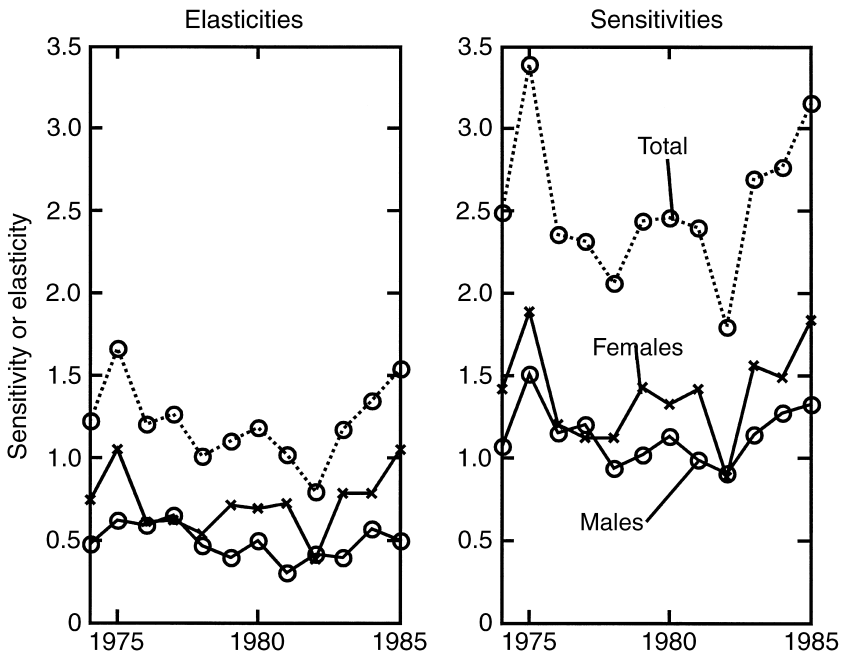

FIG. 7. Cohort elasticities and sensitivities for the female (solid lines and ×'s) and male (solid line and open circles) components of the population, and for both sexes combined (broken line and circles).

DISCUSSION

Fluctuations in population density can have delayed consequences for population growth. Although lagged effects have been the focus of much theoretical and some empirical work (May 1973, Fryxell et al. 1991, Nisbet 1997, Post and Stenseth 1998, Bjornstad et al. 1999), and now can be incorporated into the empirical analysis of time series of population size (Lande et al. 2002), detailed data that allow description of these time-lagged consequences on the demographic and spatial structure of populations and on the association between vital rates and changes in population size are unusual. We have used the individual-based data collected on red deer living in the North Block of Rum, Scotland (Clutton-Brock et al. 1982) to provide a detailed description of the demographic and dynamical consequences of an increase in density that followed the cessation of culling. Our results suggest that an increase in density can generate lagged demographic and spatial effects that persist for up to 30 years and possibly longer. The generation length of red deer on Rum, estimated as the average age of breeding females within the population over the course of the study, is 7.98 years (Coulson et al., *in press*); the demographic and dynamical consequences of releasing the population from culling has therefore persisted for 3.76 generations.

Lagged effects of an increase in density can occur, in part, because different vital rates respond to density at different rates. Eberhardt (1977) initially proposed and then supported (Eberhardt 2002) a general rule in long-lived, age-structured populations, that an increase in density generates ''an apparent sequence of changes in vital rates'' (Eberhardt 2002). An increase in density leads first to an increase in mortality rates of juveniles, followed by an increase in the age at first reproduction, followed by a reduction in reproductive rates of adult females, with adult mortality rates being the last vital rate to be affected. Previous research on our study population has demonstrated that juvenile survival (Clut-

TABLE 2. Associations between the sensitivities and elasticities of a cohort and the sensitivities and elasticities of vital rates for that cohort, shown by r^2 values from a linear regression.

Vital rate	Sensitivities		Elasticities	
	Males	Females	Males	Females
Recruitment in year of birth	0.1	0.02	0.21	0.001
Recruit production	**0.59**	**0.889**	0.14	**0.87**
Yearling survival	0.03	**0.69**	**0.76**	**0.79**
Prime adult survival	0.17	**0.93**	**0.84**	**0.96**
Older adult survival	**0.49**	**0.75**	**0.49**	**0.68**

Note: Boldface r^2 values are significant at $P < 0.05$.

ton-Brock et al. 1982, 1987*b*) and age at first reproduction (Langvatn et al. 1996) both responded almost immediately to an increase in population density, followed by fecundity rates (Guinness et al. 1978*b*, Clutton-Brock et al. 1985, Kruuk et al. 1999). It is only recently that a density-dependent effect on adult survival has been observed (Albon et al. 2000, Fan et al. 2003). Our previous results consequently support Eberhardt's sequence. The detailed nature of our data allowed us to examine more fully how this sequence has affected the demographic and spatial structure of the population and how changes in structure have influenced the contribution of different vital rates to changes in population size.

The probable order of events that generate long-term effects of the increase in density in our study population starts with a reduction in available food resources when the population becomes progressively more food limited as ecological carrying capacity is approached. This reduces juvenile growth rates, increasing juvenile mortality and increasing the age at which individuals reach sexual maturity, thus increasing age at first reproduction. Within adults, an increase in density and reduction in food resources may depress the amount of energy available for reproduction in each year, thus lowering reproductive rates. Finally, as individuals that are born at high density and that suffered the developmental costs of a harsh environment during early development (Metcalfe and Monaghan 2001) permeate the population, adult survival rates may become depressed. Because each of these processes occurs at different rates following the initial increase in density (Eberhardt 1977, 2002), the demographic structure of the population changes slowly over time, generating a long-term transient in the demography of the population. This long-term transient affects the numbers of individuals in each age class, which in turn alters the association between vital rates and population growth. This chain of events produces differences in the rates at which estimates of the mean and variance in vital rates and their impact on population growth stabilize.

The demographic structure of our population continued to change for many years after the cessation of culling and may not have stabilized yet. The average age of the population and the proportion of animals in different age classes may not have stabilized yet (Albon et al. 2000, Milner-Gulland et al. 2000). The average age of the female component of the population initially increased, stabilized, and then decreased, whereas the average age of the male component did not exhibit an initial increase and has shown no period of persistent temporal trend. However, over the last five years of the study, the average age dropped by about one year and has remained relatively constant. These sex differences presumably have resulted because male emigration rates have increased since the population has been at ecological carrying capacity. In contrast, female emigration rates have remained approximately constant (Fig. 4; see Rose et al. 1998, Clutton-Brock et al. 2002). The continuing change in the adult sex ratio has occurred to the largest extent in those parts of the study area where local female density is highest. As local female density has increased, local male density has decreased, such that some parts of the study area, especially the herb-rich *Agrostis–Festuca* greens that are preferred grazing sites (Iason et al. 1986), are now nearly devoid of resident males. Female red deer are smaller than males and are better able to utilize the short-cropped vegetation on the greens (Conradt et al. 1999). It is presumably this grazing pressure that has led to the exclusion of males from these greens and the observed increasing sexual segregation over the course of the study (Conradt et al. 1999). These small-scale changes in the spatial structure of the population are reflected by the population sex ratio, which has become progressively more female biased as the study has progressed.

The change in the demographic structure of the population and the different times at which different vital rates have responded to the increase in density have affected the impact of different vital rates on the annual changes in population growth (λ). Many previous studies using elasticities and sensitivities have applied retrospective analyses (Gaillard et al. 2000, Sæther and Bakke 2000) in which the elasticities are calculated from an average transition matrix spanning multiple years and then are multiplied by estimates of variation of the respective matrix element (Caswell 2001). This approach, and similar approaches that have been applied to the red deer data (Clutton-Brock et al. 1985, Brown et al. 1993, Albon et al. 2000) that are the focus of this paper, to estimate the association between variation in vital rates and variation in λ. In this paper we are interested in the association between each vital rate and the changes in population size from one year to the next; thus we use the prospective approach. We do not attempt to decompose the variation in population growth.

Different vital rates are associated with the annual λ values to different extents in different years. Although survival of prime-aged adult females had large sensitivities and elasticities in all years, as expected for large ungulates (Gaillard et al. 2000, Eberhardt 2002), the importance of its elasticity varied nearly twofold, from 0.2653 in 1974 to 0.4699 in 1992. Similar temporal variation in the importance of elasticities and sensitivities was observed for other traits. For example, the relative importance of survival and emigration of older females has increased because of increases in the proportion of the population made up of older females. Most applications of retrospective and prospective matrix methods to large-herbivore populations have considered only the female component of the population (Gaillard et al. 1998, 2000). Another novelty of our work is that we consider both sexes (also see Bonenfant et al. 2002). The most striking result from

doing this is the ongoing downward trends in elasticities and sensitivities of male vital rates, which have resulted from the ongoing change in the population sex ratio.

The consequences of the cessation of culling and the subsequent increase in density still have an impact on the population. It is too early to categorically say that the age structure and average age of the population have stabilized. The mean and variance in many vital rates are still increasing (Table 1), temporal trends in elasticities are also still occurring, and variation in elasticities of recruitment and survival of some age and sex classes has still not stabilized. This evidence suggests that a change in density can generate long-term lagged effects that persist for multiple generations. These results indicate that if perturbations to a population caused by biotic or abiotic catastrophic processes occur every few generations, it is probable that the population may never attain equilibrium.

We have also estimated the impact of different cohorts on the dynamics of the population by summing elasticities and sensitivities of matrix elements across multiple annual matrices. The method has demonstrated large differences between cohorts that are likely to be a consequence of variation across years in early development. Our results (Table 2) add further support to the idea that differences early in life persist throughout life and can generate consequences for population dynamics (Lindstrom and Kokko 2002). It should, however, be noted that these methods are only approximate. An elasticity or sensitivity is specific to an individual matrix with its own growth rate, λ (Caswell 2001). Because different years have different λ values, sensitivities and elasticities summed across different matrices cannot be interpreted in the standard way. However, in ergodic systems, such as long-lived, iteroparous vertebrates, where λs are comparatively similar over time, it is likely (but mathematically unproven) that our approach will provide a good approximation to the impact of a cohort on the dynamics of a population.

Our results have demonstrated that a change in density can have time-lagged consequences that persist over multiple generations. These long-term transient dynamics arise because of changes in the spatial and demographic structure of the population, which themselves can persist for multiple generations because different vital rates respond to density at different rates. Although time-lagged, density-dependent effects have long been acknowledged, it is unusual for lags of more than two years to be incorporated in empirical analyses. However, recent work by Lande et al. (2002) has demonstrated the importance of including longer term lagged effects generated by life history effects. Our results provide one of the first detailed descriptions of long-term effects that a change in density can generate in a population of a long-lived vertebrate.

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Literature Cited

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, T. H. Clutton-Brock, and J. M. Pemberton. 2000. Temporal changes in the key factors influencing the population dynamics of red deer. Journal of Animal Ecology **69**:1096–1109.

Berryman, A., and P. Turchin. 1997. Detection of delayed density dependence: comment. Ecology **78**:318–320.

Bjornstad, O. N., J. M. Fromentin, N. C. Stenseth, and J. Gjosaeter. 1999. Cycles and trends in cod populations. Proceedings of the National Academy of Sciences (USA) **96**: 5066–5071.

Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer (*Cervus elaphus*) in a temperate forest. Ecography **25**:446–458.

Brown, D., N. D. E. Alexander, R. W. Marrs, and S. Albon. 1993. Structured accounting of the variance of demographic change. Journal of Animal Ecology **62**:490–502.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987*a*. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. Journal of Animal Ecology **56**:857–871.

Clutton-Brock, T. H., and T. N. Coulson. 2002. Ungulate population dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London B **357**: 1299–1306.

Clutton-Brock, T. H., T. Coulson, E. J. Milner-Gulland, H. M. Armstrong, and D. Thomson. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature **415**:633–637.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997*a*. Stability and instability in ungulate populations: an empirical analysis. American Naturalist **149**:195–219.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987*b*. Early development and population dynamics in red deer. 1. Density dependent effects on juvenile survival. Journal of Animal Ecology **56**:53–67.

Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. Journal of Animal Ecology **54**:831–846.

Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997*b*. Density related changes in sexual selection in red deer. Proceedings of the Royal Society of London B **264**:1509–1516.

Conradt, L., T. H. Clutton-Brock, and D. Thomson. 1999. Habitat segregation in ungulates: are males forced into suboptimal foraging habitats through indirect competition by females? Oecologia **119**:367–377.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology **78**:852–863.

Coulson, T., S. Albon, J. Pilkington, and T. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. Journal of Animal Ecology **68**:658–671.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay Sheep. Science **292**:1528–1531.

Coulson, T., and E. Hudson. 2003. When is the birth rate the key factor associated with population dynamics? Pages 114–130 *in* W. Holt, A. Pickhard, J. Rodger, and D. Wildt, editors. Reproductive science and integrated conservation. Cambridge University Press, Cambridge, UK.

Coulson, T. N., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock. *In press*. Estimating selection on neonatal traits in red deer using elasticity path analysis. Evolution.

Eberhardt, L. L. 1977. Optimal policies for the conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation **4**:205–212.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology **83**:2841–2854.

Fan, Y., B. J. T. Morgan, E. A. Catchpole, and T. N. Coulson. 2003. Modelling the survival and dispersal of red deer using mark–recapture–recovery data. Report UKC/IMS/03/19, IMS University of Kent, Canterbury, UK.

Fox, G. A., and J. Gurevitch. 2000. Population numbers count: tools for near-term demographic analysis. American Naturalist **156**:242–256.

Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management **55**:377–385.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution **13**:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yocooz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367–393.

Guinness, F. E., S. D. Albon, and T. H. Clutton-Brock. 1978*a*. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. Journal of Reproduction and Fertility **54**: 325–334.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978*b*. Factors affecting calf mortality in red deer (*Cervus elaphus*). Journal of Animal Ecology **47**:817–832.

Iason, G. R., C. D. Duck, and T. H. Clutton-Brock. 1986. Grazing and reproductive success of red deer. The effect of local enrichment by gull colonies. Journal of Animal Ecology **55**:507–515.

Kaitala, V., J. Ylikarjula, E. Ranta, and P. Lundberg. 1997. Population dynamics and the colour of environmental noise. Proceedings of the Royal Society of London B **264**: 943–948.

Kruuk, L. E. B., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and F. E. Guinness. 1999. Population density affects sex ratio variation in red deer. Nature **399**:459–461.

Kruuk, L. E. B., J. Slate, J. P. Pemberton, S. Brotherstone, F. E. Guinness, and T. H. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution **56**:1683–1695.

Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford, UK.

Lande, R., S. Engen, B.-E. Sæther, F. Filli, E. Matthysen, and H. Weimerskirch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. American Naturalist **159**:321–337.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology **65**:653–670.

Leirs, H., N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, and W. Verheyen. 1997. Stochastic seasonality and nonlinear density dependent factors regulate population size in an African rodent. Nature **389**:176–180.

Lindstrom, J., and H. Kokko. 2002. Cohort effects and population dynamics. Ecology Letters **5**:338–344.

Link, W. A., and P. F. Doherty. 2002. Scaling in sensitivity analysis. Ecology **83**:3299–3305.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1981. Models for single populations. Pages 5–30 *in* R. M. May, editor. Theoretical ecology: principles and applications. Blackwell Scientific, Oxford, UK.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution **16**:254–260.

Milner-Gulland, E. J., T. N. Coulson, and T. H. Clutton-Brock. 2000. On harvesting a structured ungulate population. Oikos **88**:592–602.

Nisbet, R. M. 1997. Delay-differential equations for structured populations. Pages 89–118 *in* S. Tuljiapurkar and H. Caswell, editors. Structured population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York, USA.

Pemberton, J. M., J. A. Smith, T. N. Coulson, T. C. Marshall, J. Slate, S. Paterson, S. D. Albon, and T. H. Clutton-Brock. 1996. The maintenance of genetic polymorphism in small island populations: large mammals in the Hebrides. Philosophical Transactions of the Royal Society of London B **351**:745–752.

Post, E., and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology **67**:537–543.

Post, E., N. C. Stenseth, R. Langvatn, and J. M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society of London B **264**:1317–1324.

Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. Journal of Animal Ecology **67**:979–986.

Royama, T. 1992. Analytical population dynamics. Chapman and Hall, New York, New York, USA.

Sæther, B., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**:642–653.