

# Population dynamics and resource use of red deer after release from harvesting in New Zealand

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**Abstract:** Despite periods of extensive government-funded control, fluctuating commercial exploitation and ongoing recreational hunting, little is known about how red deer (*Cervus elaphus scoticus* Lönnberg) in New Zealand respond to the cessation of harvesting in terms of population growth rate and resource use. We describe the population dynamics and resource use of red deer in a montane catchment over 5 years (1962–67) following cessation of intensive government-funded control in 1961. Locations and sex–age classes of deer were observed monthly along a fixed route in the Harper-Avoca catchment, inland Canterbury. A total of 2036 red deer groups were observed. The number of groups observed annually increased during the study but no trends in median (2 or 3) or modal (1 or 2) group sizes were found. Population growth rates ( $r$ ) of deer were extraordinarily high in the first two years (e.g.  $2.33 \pm 0.22$  for adult females and  $1.61 \pm 0.23$  for adult males), but decreased in subsequent years and were not biologically possible without substantial immigration and/or changes in detectability of deer. Sexual segregation and selection of vegetation types (alpine grassland, montane grassland, and forest) and 10 topographic landforms showed stronger intra-annual than inter-annual patterns. Segregation was greatest in spring and summer, least in the rut, and variable in winter. In all seasons, sexual segregation was greatest at 25- and 50-ha scales, moderate at 100-ha, and absent at the 500- and 1000-ha scales. Selection of vegetation types also varied seasonally, with deer of both sexes preferring montane grasslands in spring and summer and alpine grasslands in the rut. Backslopes were preferred landforms in spring and summer, spurs during spring and the rut, and hollows during the rut. Our results highlight the need to consider spatial scale, immigration, and detectability in the design of red deer culling and harvesting programmes. Studies of home-range size and use, migration patterns, dispersal rates and distances are required to better understand the impacts of red deer on New Zealand ecosystems and the effects of management on red deer populations.

**Keywords:** *Cervus elaphus*; control; exotic; habitat; immigration; invasive species; maximum population growth rate; maximum rate of increase; sexual segregation; vegetation

## Introduction

Introduced red deer (*Cervus elaphus scoticus* Lönnberg) have broad distributions in the North, South and Stewart islands of New Zealand (Fraser et al. 2000) and are popular with recreational and commercial harvesters (Nugent 1992). There has been ongoing concern about the impacts of red deer on some New Zealand ecosystems (review in Forsyth et al. 2010) and the species is considered a pest in the New Zealand Biodiversity Strategy<sup>1</sup>. Government-funded eradication/control programmes also have a long history at a variety of temporal and spatial scales (reviews in Caughley 1983; Harris 2002). Despite much interest in the management of red deer as both a resource and pest, there is limited information on their population dynamics or resource use in New Zealand.

A key parameter in population dynamics is the rate of population growth ( $r$ ; Caughley 1977; Sibly & Hone 2002), i.e. the instantaneous rate of annual population change. The greatest possible rate at which a population can increase is termed the maximum population growth rate ( $r_m$ ), and both  $r$  and  $r_m$  are usually presented as annual rates for long-lived mammals such as deer (Caughley 1977).  $r_m$  can be estimated from log-transformed temporal changes in estimates of abundance ( $\ln[N_{t+1}/N_t]$ ) when resources are not limiting (i.e. the population is colonising or is growing after being reduced to low densities) and the population is not subject to predation or disease (Caughley 1977).

Seven published studies, all conducted outside New Zealand, have estimated  $r_m$  using that approach (Table 1). Nugent and Fraser (2005) described two studies in which the maximum rates of increase of red deer following aerial 1080 possum control in New Zealand were estimated at 0.33 and 0.56; however, these unpublished studies were based on faecal pellet counts, which can be subject to substantial measurement error (Forsyth et al. 2007) and are not considered further here. Changes in detectability can also influence estimates of population growth rate (MacKenzie & Kendall 2002), and none of the studies listed in Table 1 accounted for that possibility.

Many deer species exhibit sexual differences in spatial organisation and resource use (i.e. sexual segregation; Main 2008). Adult male red deer in Europe aggregate with, or as close as possible to, adult females during the rut, but otherwise are spatially segregated (Clutton-Brock et al. 1982, 1987; Bonenfant et al. 2004). A wide variety of ecological and social explanations exist for sexual segregation in ungulates, but a recent review suggested that it is an evolutionary response to different reproductive strategies: males select resources to maximise energy gains in preparation for the rut, whereas females select habitats with combinations of resources that contribute to offspring survival (Main 2008). On the Isle of Rum (Scotland), sexual segregation increased as the abundance of red deer increased following release from culling (Clutton-Brock et al. 1987, 2002). There were also substantial changes to the demographic and spatial structure of the population (Coulson et al. 2004).

<sup>1</sup> <http://www.doc.govt.nz/templates/MultipageDocumentPage.aspx?id=39969>

**Table 1.** Published estimates of  $r_m$  for red deer (*Cervus elaphus*). The mean of these estimates (0.30) was used as either a moderately or strongly informed prior in our analyses.

Estimated $r_m$	Source
0.38	Houston (1982)
0.37	Burris & McKnight (1973, cited in Gogan & Barrett 1987)
0.31	Gogan & Barrett (1987)
0.30	McCorquodale et al. (1988)
0.29	Gogan & Barrett (1987)
0.27	Murphy (1963) and Caughley (1977)
0.191	Eberhardt (1987)

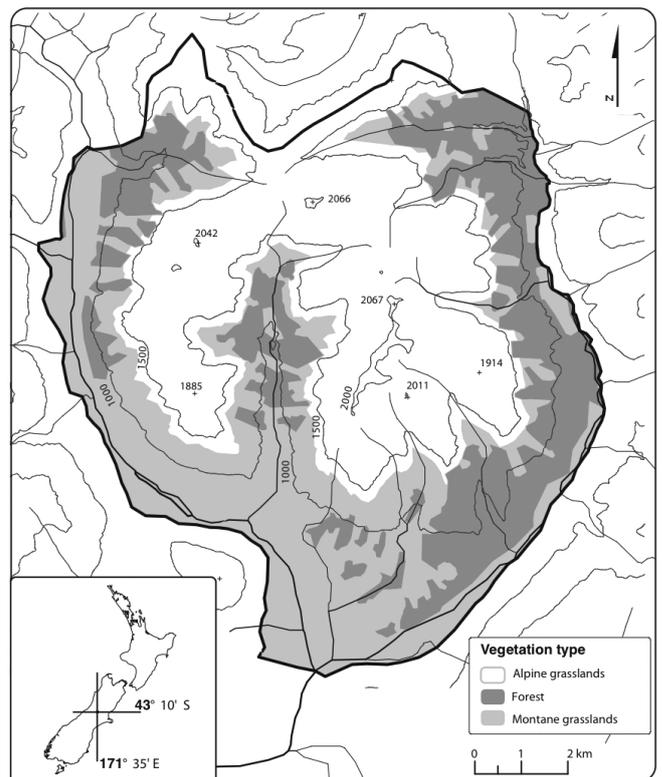
Seasonal patterns of vegetation and topographic landform use by deer are likely to be driven, at least partly, by food quality and quantity (Albon & Langvatn 1992; Main 2008). The Southern Alps of New Zealand are a highly seasonal environment, dominated by short growing seasons (Wardle 1991) and strong changes in forage availability through snow cover (e.g. Forsyth 2000). Casual observations suggest that both male and female red deer tend to utilise forest in winter, lowland grasslands in spring, and higher-altitude grasslands in summer and autumn (Nugent & Fraser 2005). Lavers et al. (1983) showed seasonal differences in the diets of 455 red deer shot in the Murchison Mountains (eastern Fiordland) during 1976–80, with trees and shrubs eaten more in winter than in other seasons, and grasses and some small herbs (e.g. *Ranunculus* and *Senecio*) eaten most in summer. Plant community composition in the Southern Alps also reflects topographic landform as an important determinant of soil fertility and drainage (e.g. Wiser et al. 1998). Red deer in the Southern Alps are thought to prefer fertile sites because these contain the highest diversity and biomass of preferred food plants (e.g. the grasses *Chionochloa pallens* and *C. flavescens* in alpine grasslands; Lavers 1978; Rose & Platt 1987). Sika deer (*Cervus nippon*) in the central North Island made intensive use of valley floors in spring, apparently because of the flush in growth of highly palatable grasses and herbs (Davidson 1973).

Here we use 5 years of red deer observations to test four key predictions about population dynamics and resource use in a New Zealand population of red deer following the cessation of government-funded hunting that had substantially reduced population density (Batcheler & Logan 1963). First, although maximum population growth rate is theoretically specific to a location (Caughley 1977), constraints on survival and reproductive rates within *Cervus* suggest that  $r_m$  for the red deer population in our study area would be unlikely to greatly exceed the rates observed elsewhere (Table 1). Second, that male and female red deer would be spatially segregated except during the rut. Third, that sexual segregation would increase with increasing abundance of deer. Fourth, that resource use would vary seasonally, with all sex–age classes preferring valley bottoms in spring (following ‘green up’) and higher elevation grasslands in summer and autumn.

## Methods

### Study area

The study area (43°10' S, 171°40' E) is c. 10 974 ha of mountainous terrain with peaks c. 2000 m a.s.l. and valley bottoms at 600 m a.s.l. (Fig. 1). The terrain is topographically diverse through erosional and fluvial modification of glacially steepened slopes. A weather station at 914 m a.s.l. and 5 km east of the study area recorded a mean annual temperature of 8.0°C, precipitation of 1447 mm year<sup>-1</sup>, and irradiance of 4745 MJ m<sup>-2</sup> year<sup>-1</sup> (based on 13 years of data; McCracken 1980). Monthly mean daily temperature is greatest in February (13.9°C) and lowest in July (2.0°C). Air temperature decreases by 0.7°C, and rainfall increases by 21.9 mm year<sup>-1</sup> for every 100-m rise in altitude (McCracken 1980). Annual rainfall

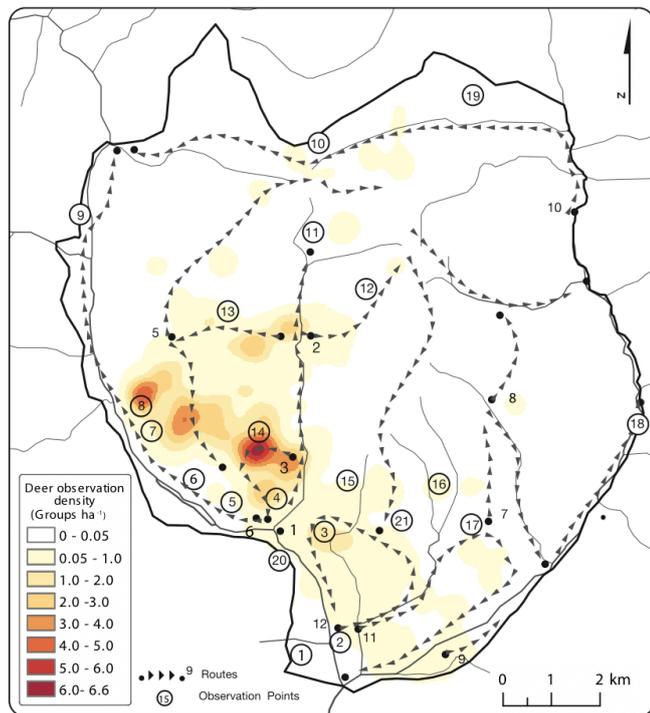


**Figure 1.** Location of the study area (bounded by the bold solid line) centred on the Harper (east) and Avoca (west) catchments. Numbers are contours (1000, 1500 and 2000 m) and spot heights.

increases from about 1200 mm in the east to 2000 mm in western parts of the study area (Griffiths & McSaveney 1983). Soils are predominantly Allophanic Brown Soils (Hewitt 1992) derived from greywacke, loess and colluvium. Mineral forest soils in the study area have high amounts of exchangeable Al and very low base saturation (Davis 1990).

Mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest, montane grasslands, and alpine grasslands cover 23%, 34% and 43% of the study area, respectively (see below). Mountain beech forms virtually monotypic stands between valley bottom and treeline (1400 m a.s.l.). The simple, open-understoreyed forest had a relatively intact canopy during the study (Wardle & Allen 1983; Allen et al. 1999). Where fire has removed forest (predominantly in the south-eastern part of the study area; Fig. 1) montane grasslands extend from valley bottom to treeline (Packard 1947). These grasslands, which have been subjected to burning, are susceptible to exotic plant invasions, and between 1960 and 1965 there was an increase in cover by exotic *Hieracium* species and sweet vernal (*Anthoxanthum odoratum*), and a decline in native fescue-tussock (*Festuca novae-zelandiae*) and bare ground (Rose 1983). The alpine grasslands, dominated by *Chionochloa* snow tussocks, extend up to 1800 m a.s.l. and were typically increasing in tiller length and abundance during the study period (C.L. Newell and A.B. Rose, unpubl. data). Variation in each of the three major vegetation types reflects topographically related gradients in soil fertility and moisture availability (e.g. Rose et al. 1995; Wiser et al. 1998), as well as forest development (Allen et al. 1997; Coomes & Allen 2007).

Red deer colonised the catchments of the study area in about 1910 (Logan 1956) and apparently underwent the eruptive dynamic that typifies populations of large herbivores establishing in non-native ranges (Forsyth & Caley 2006). Due to concerns about the impacts of deer and Alpine chamois (*Rupicapra rupicapra*) on erosion, five animal control operations were conducted from 1936 to 1953 (Batcheler & Logan 1963). However, it is not known how these operations affected the abundance of deer (Hickling 1986). Another



**Figure 2.** Observation routes and points searched monthly during the study and the density (groups  $\text{ha}^{-1}$ ) of red deer (*Cervus elaphus*) observations in the Harper-Avooca catchment (1962–67).

control programme, beginning in 1955, covered the entire Harper-Avooca catchment (see Batcheler & Logan 1963). Hunting ceased in November 1961 to enable the present study to be conducted. Counts of red deer faecal pellets in plots along 17 transects indicated a steady temporal decline in the percentage of plots with faeces, from about 52 in 1955 to about 27 in 1961 (Hickling 1986). The greatest decline in the percentage of defecations was in alpine grassland, with smaller declines in montane grassland and forest (Hickling 1986). Other exotic mammalian herbivores common in the study area were brown hare (*Lepus europaeus*) and brushtail possum (*Trichosurus vulpecula*). Domestic sheep (*Ovis aries*), domestic cattle (*Bos taurus*) and an occasional European rabbit (*Oryctolagus cuniculus*) were present on the valley floors during the study.

### Field observations

From November 1962 to April 1963, monthly searches of the study area were undertaken by M.J.W. Douglas to refine routes and observation points and to train observers. From December 1962 to March 1967, the same route (Fig. 2) was walked over a 10-day period in the same sequence and, as far as possible, at the same time of day in each month. Some parts of the route were not walked when snow conditions were considered dangerous. The same view was searched at each observation point using 8–12 $\times$  binoculars and 12–30 $\times$  spotting scopes. The following data were recorded for each group (defined as one or more individuals) of deer observed: date, time, six-figure grid reference (New Zealand Map Series 1, 1:63 360) and number of individuals per sex–age class (see below). Six sex–age classes were used: ‘calf’ (<12 months), ‘juvenile male’ (12–24 months), ‘juvenile female’ (12–24 months), ‘adult male’ ( $\geq 24$  months), ‘adult female’ ( $\geq 24$  months), and ‘unknown’.

Observations were pooled into the following four periods: summer (January–February), rut (March–May), winter (June–September), and spring (October–December). Our definition of the rut was based on observations of deer behaviour during the study (M.J.W. Douglas, pers. obs.). Definitions of the other seasons reflected plant phenology within the study area, with summer the period of greatest forage quantity and winter the least (R.B. Allen, pers. obs.). The numbers of deer counted in each sex–age class in each season and year were corrected for the numbers of hours spent searching.

## Population dynamics

### Group sizes

We describe the range of group sizes and the mean ( $\pm$  SE), median, and modal group sizes for each sex–age class during each study year. Work elsewhere had shown that the only stable association was between a female and her unweaned calf (Clutton-Brock et al. 1982, p. 182), although large temporary herds could also form (e.g. 150 deer; Challies 1990). We therefore expected little variation in median and modal group sizes throughout the study, but we did expect that the maximum group size would increase as the population grew.

### Population growth rates

Following Eberhardt and Simmons (1992), the basic model we used was

$$\ln(y_{ijt}) = a_{ij} + \sum_{t=1}^T r_{it} + \varepsilon_{ijt}, \quad (1)$$

where  $y_{ijt}$  is the index of population size of sex–age class  $i$  in season  $j$  and year  $t$ ,  $a_{ij}$  is the effect on the index in season  $j$  for the  $i$ th sex–age class,  $r_{it}$  is the annual population growth rate of sex–age class  $i$  between years  $t-1$  and  $t$  (with  $r_{i1} = 0$ ) and  $\varepsilon_{ijt}$  is a random error term associated with each observation. If  $\varepsilon_{ijt}$  is assumed to have a normal distribution with mean 0 and standard deviation  $\sigma$ , then  $y_{ijt}$  can be assumed to be log-normally distributed. Note that if the annual growth rate is assumed to be constant over time, then eqn 1 reduces to:

$$\ln(y_{ijt}) = a_{ij} + r + \varepsilon_{ijt}, \quad (2)$$

which, if it is assumed  $y$  is a good index of population size, will be equivalent to

$$\ln(N_{ijt}) = \ln(N_{ij}) + r + \varepsilon_{ijt}, \quad (3)$$

with  $r$  being the maximum annual growth rate ( $r_m$ ) when the conditions outlined above (see Introduction) are met.

As there are a range of published estimates of  $r_m$  for *Cervus elaphus* (including subspecies that hybridise freely with *C. elaphus scoticus*; Table 1) it was decided to incorporate this information by fitting each model with three different prior distributions: (1) a vague prior parameterised as a normal distribution with mean 0 and standard deviation 100; (2) a moderately informed prior parameterised as a normal distribution with mean 0.3 and standard deviation 0.32; and (3) a strongly informed prior parameterised as a normal distribution with mean 0.3 and standard deviation 0.1. The mean values for the moderately and strongly informed priors were estimated from Table 1, and their standard deviations are approximately 5 and 1.6 times the observed standard deviation, respectively.

A range of models with particular constraints placed upon  $r$  were considered. First, a model denoted  $r(\cdot)$  in which  $r$  is constant in time and does not vary between sex–age classes (‘adult females’, ‘adult males’ and ‘others’). Second, a model denoted  $r(\text{Classes})$  in which  $r$  is constant in time but varies between sex–age classes. Third, a model denoted  $r(\text{Year})$  in which  $r$  varies annually, but is the same value for all three classes. Fourth, a model denoted  $r(\text{Year}+\text{Classes})$  in which  $r$  varies annually but with a consistent difference among the three classes across time (so one class will always have the highest population growth rate and another class the lowest). Fifth, a model denoted  $r(\text{Year}\times\text{Classes})$  in which  $r$  varies annually and varies between classes with no additional constraints. Note that models  $r(\cdot)$  and  $r(\text{Classes})$  are equivalent to the constant annual growth rate model in eqn 2.

The models were fitted to the data using OpenBUGS version 2.2.0 software (Thomas et al. 2006). Two Markov chains of 110 000 iterations were run for each model–prior combination, the first 10 000 iterations being discarded (i.e. burn-in period) and the remainder used for inference (Brooks & Gelman 1998). Convergence was assessed by visual inspection of the chain-histories, which appeared to occur within the first 1000 iterations. The relative parsimony of each model was evaluated with the Deviance Information Criterion

(DIC; Spiegelhalter et al. 2002). Models with small DIC values are considered more parsimonious descriptions of the data. Data for calves, juvenile males and juvenile females were not analysed separately because sample sizes were very low in the first two years of the study and there were concerns about misclassification among these sex-age classes.

**Sexual segregation and resource use**

The degree of sexual segregation was quantified in two ways: the proportion of groups that contained adult deer of both sexes ('mixed groups') and the spatial distribution of male and female groups. We used logistic regression to model the proportion of mixed groups as a function of season, year, and their combinations using the glm function in the statistical freeware R version 2.9.0 (R Development Core Team 2009). We compared the models using Akaike's Information Criterion (AIC), with number of groups the sample size. As for DIC, models with small AIC values are considered more parsimonious descriptions of the data (Burnham & Anderson 2002).

Analysis of the spatial distributions of sexually segregated and aggregated groups was challenging. The data may best be described as a repeatedly observed spatial point pattern, but methods for analysing such data are underdeveloped (Bell & Grunwald 2004). Despite their having well-known drawbacks (e.g. Fortin & Dale 2005) we used quadrat-based analyses, an approach that was appropriate for two reasons. First, due to the low resolution of the locations ( $\pm 100$  m) many observations shared grid coordinates. Second, strong knowledge gains have been made using quadrat-based analyses of the spatial distributions of wildlife, including deer (e.g. Kie & Bowyer 1999). Quadrat analyses were conducted at five spatial scales: 25, 50, 100, 500, and 1000 ha. At each scale, we used Syrjala's modification of the Cramér-von Mises test (Syrjala 1996) to compare the distributions of male and female groups by season and year. The Syrjala (1996) test compares spatial distributions in a way that is insensitive to differences in sample size, appropriate here as we could not divide the irregularly shaped study area into quadrats of equal area. Constraining the analyses to only those quadrats that fitted entirely within the study area would have excluded many observations clustered near the southern edges. We therefore calculated the area of each quadrat that fell within the study area and normalised the number of observations by the area sampled. We represented the location of each quadrat as the centre of the largest circle that could be inscribed within it. Quadrat group counts and locations were calculated using the R package spatstat (Baddeley & Turner 2005); Syrjala's test was performed with the R package ecespa (de la Cruz 2008).

Resource use was determined by overlaying the grid reference of each observation onto three data layers in a geographic information system (GIS): elevation, vegetation type, and topographic landform. Because the original grid references were to the nearest 100 m we used a 100-m buffer around each point and calculated the average value (elevation) or majority type (vegetation and landform) within the buffer. The elevation (m a.s.l.) of each observation was extracted from Landcare Research's 25-m-resolution digital elevation model (DEM; Barringer et al. 2002). 'Vegetation type' was a combination of Newsome's (1987) vegetation types and elevation. Non-forested areas < 1350 m a.s.l. were classified as 'montane grasslands' and those > 1350 m a.s.l. were classified as 'alpine grasslands'. 'Forest' was aggregated from the forest types in Newsome (1987).

Topographic landform elements were identified from the DEM by combining a classification of 15 'form elements' based on slope and curvature (e.g. peak, saddle, hollow, ridge, shoulder) within a  $7 \times 7$  moving window into a coarser scale classification of three landscape contexts, valley, hill, and hillslope (Schmidt & Hewitt 2004). Using the landscape context allowed for aggregation of pixels into contiguous features (e.g. classifying a ridge line as 'ridge' rather than a collection of peaks, ridges, spurs, pits, plains and saddles). The complete 45-member classification was deemed too complex for practical use, so similar categories were combined to yield 10 classes (Barringer et al. 2008): backslope, channel, footslope, hollow, plateau, ridge, shoulder, spur, terrace, and valley.

We used a chi-squared test of independence to determine whether resources were utilised in proportion to their availability (Manly et al. 1993). Overall chi-square statistics were calculated for deer groups by vegetation type and topographic landform, and for each of these resources by season and year.

**Results**

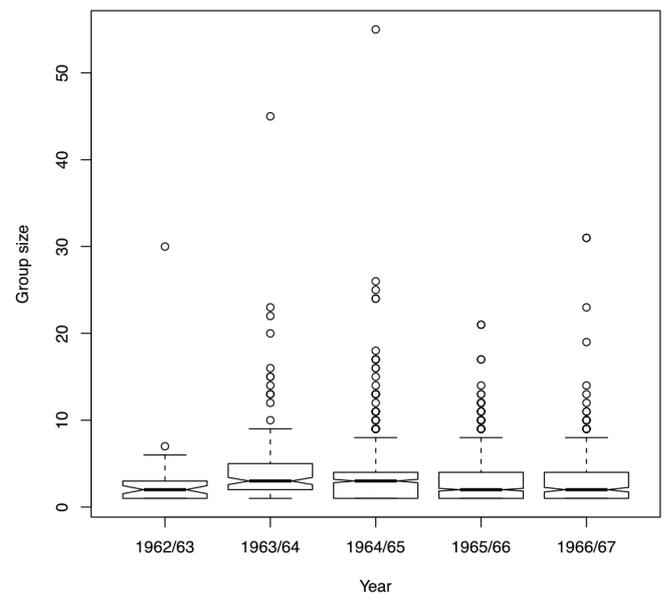
**Population dynamics**

*Group sizes*

A total of 2036 red deer groups, consisting of 31% male, 42% female, 11% mixed, and 16% calves, were observed during the study. Most deer groups were observed in the south-west of the study area (Fig. 2). The number of groups observed annually increased during the study (Table 2). However, the median and modal group sizes did not change during the study and the mean group size did not increase greatly (Table 2; Fig. 3). The largest group observed was 55 (November 1964); groups larger than 20 were rare (Fig. 3).

**Table 2.** Red deer (*Cervus elaphus*) group sizes during the four complete years of the study in the Harper-Avoca catchment (1962–66). The totals row shows aggregate values for the four complete years.

Year	Number of groups	Mean (SE)	Median	Mode	Range
1	46	2.7 (4.4)	2	1	1–30
2	131	4.6 (5.5)	3	2	1–45
3	561	3.6 (4.0)	3	1	1–55
4	974	3.0 (2.5)	2	2	1–21
Total	1712	3.3 (3.4)	2	1	1–55



**Figure 3.** Distribution of red deer (*Cervus elaphus*) group sizes in the Harper-Avoca catchment (1962–67) by year. The median group size for each year is shown as a heavy black line; the inter-quartile range (IQR) is enclosed by the box. The whiskers extend to the most extreme datum that is <1.5 times the length of the box; more extreme values are shown as open circles. The notches extend to  $\pm 1.58 \times \text{IQR} / \sqrt{n}$  and are approximate 95% confidence intervals for the difference between two medians (R Development Core Team 2009).

Population growth rates

With a vague or moderately informative prior, the model  $r(\text{Year}+\text{Class})$  was ranked as the most parsimonious by a substantial margin (Table 3). With a strongly informative prior, the  $r(\text{Year}+\text{Class})$  model was ranked second, slightly behind the simplest model  $r(\cdot)$ . The most parsimonious model (i.e.  $r(\text{Year}+\text{Class})$  with vague priors) had no discernable pattern in the residual plots to indicate a systematic lack of fit. The residual plots for models based upon eqn 2, with both vague and strong priors, showed undesirable systematic patterns (not shown). With a vague prior, residuals tended to be negative at the beginning and end of the time series and positive near the middle. With a strong prior on the annual population growth rate, residuals tended to be negative at the beginning of the time series, and positive at the end of the series. These systematic patterns indicated that a constant annual growth rate model was a poor fit to the data. This conclusion was supported by considering the more general models and ranking all models in terms of DIC (Table 3). The resulting posterior distributions for  $r$  ( $r(\text{Year}+\text{Class})$  model, vague prior) are summarised in Table 4.

Annual population growth rates were highest in the first year of the study, decreased in the following years, and were lowest for all three classes in the penultimate year of the study (Table 4). The estimates of  $r$  for all sex–age classes from the most parsimonious model greatly exceeded published overseas estimates of  $r_m$  in the first year of the study, but were variable thereafter (Table 4 cf. Table 1). Estimates of  $r$  were within the range of overseas estimates (i.e. 0.19 – 0.38) for adult females in year 4 and adult males in years 3 and 5. However, the adult male population declined substantially from year 3 to year 4 and did not change from year 4 to 5. The other age-sex classes did not change from year 3 to 4. The mean for the posterior distribution of the difference between adult male and adult female growth rate was  $-0.72$  (i.e. males were lower) with a standard deviation of 0.13. The mean for the posterior distribution of the difference between all other deer and adult females was  $-0.18$  with a standard deviation of 0.13.

**Table 3.** Differences in Deviance Information Criterion (DIC) values between each model and the most parsimonious model for the 15 models explaining the population growth rate of red deer (*Cervus elaphus*). The DIC of the best model for each of the three prior distributions is highlighted in bold.

Model	Prior distribution		
	Vague	Moderate	Strong
$r(\cdot)$	64.54	71.54	<b>64.74</b>
$r(\text{Class})$	52.14	53.24	73.74
$r(\text{Year})$	27.37	42.54	74.34
$r(\text{Year}+\text{Class})$	<b>0.00</b>	<b>20.53</b>	65.64
$r(\text{Year}\times\text{Class})$	12.43	46.04	77.84

**Table 4.** Mean and standard deviation (SD) of the posterior distribution for  $r$  from the model  $r(\text{Year}+\text{Class})$  with a vague prior (normal distribution with 0 mean and SD = 100).

Year	Adult females		Adult males		All others	
	Mean	SD	Mean	SD	Mean	SD
2	2.33	0.22	1.61	0.23	2.15	0.23
3	1.02	0.23	0.30	0.23	0.84	0.23
4	0.23	0.21	-0.50	0.22	0.05	0.22
5	0.87	0.27	0.14	0.27	0.69	0.27

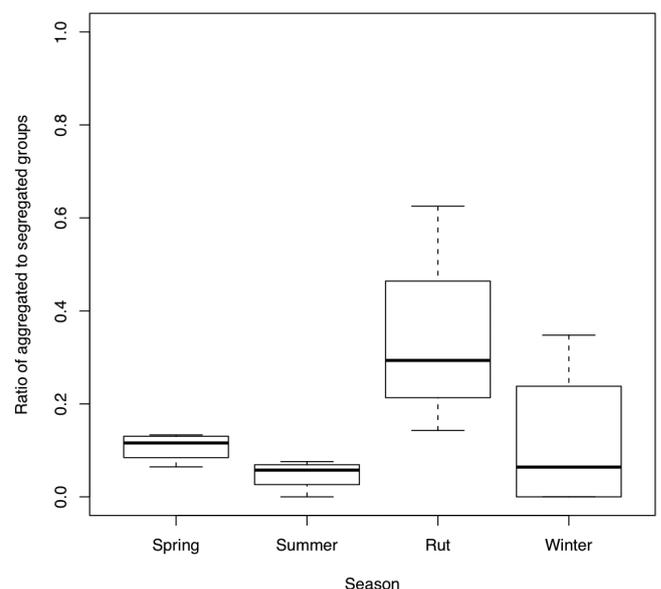
Sexual segregation and resource use

The proportion of mixed groups was lowest in summer and greatest, as expected, in the rut (Table 5; Fig. 4). Sexual segregation among groups was least variable in spring and summer (Fig. 4).

There was a shared distribution of male and female groups during the rut but strong evidence for sexual segregation in summer at all spatial scales (Table 6). Patterns were more scale-dependent in spring and winter. In spring, there was strong evidence of segregation at small scales (25 and 50 ha), moderate evidence at the 100-ha scale, but little evidence of segregation at larger scales (Table 6). Conversely, in winter there was weak evidence for segregation at the smallest scale and strong evidence for spatial segregation at the 1000-ha scale. However, there was no indication of spatial segregation at the intervening scales. Patterns of sexual segregation at the 50-ha scale are shown for the most (spring) and least (rut) segregated seasons in Fig. 5. Consistent with our prediction, there was a shared distribution of male and female groups early on in the study and increased segregation at the end of the study (Table 7).

**Table 5.** Akaike’s Information Criterion (AIC) and residual deviance from logistic regression: candidate models that predict the proportion of sexually segregated red deer (*Cervus elaphus*) groups as a function of season and year. Only the four complete study years in the Harper-Avoca catchment (1962–66) were included in the analysis.  $K$  is the number of parameters and  $w_i$  is the Akaike weight. Models are listed in descending order of parsimony.

Model	$K$	AIC	$w_i$	Residual deviance
Season	3	68	0.72	10.8/12 = 0.90
Year + Season	4	70	0.26	10.8/11 = 0.98
Year $\times$ Season	5	75	0.02	15.7/11 = 1.43
Year	3	125	0.00	72.2/14 = 5.16
Intercept only	2	123	0.00	72.2/15 = 4.81



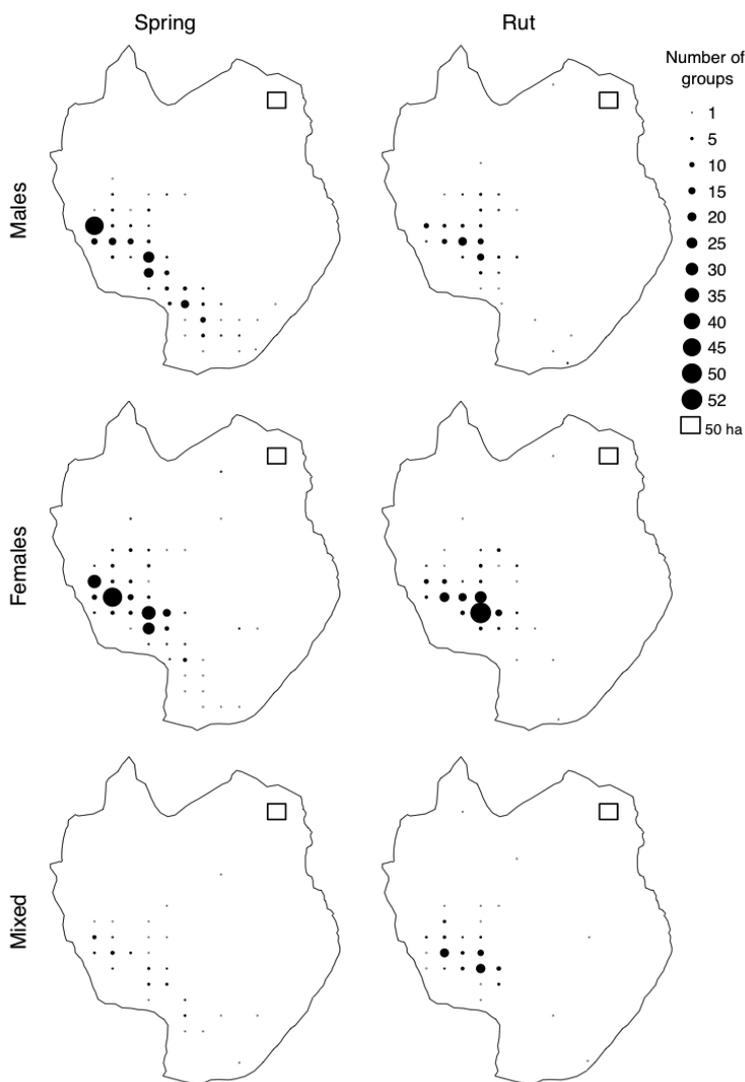
**Figure 4.** Ratio of sexually aggregated to segregated groups of red deer (*Cervus elaphus*) in the Harper-Avoca catchment (1962–66) by season. Symbols are as for Fig. 3 except that notches are not shown on this figure.

**Table 6.** Syrjala's (1996) test statistic (and associated *P*-value) comparing the spatial distribution of male and female red deer (*Cervus elaphus*) groups in four seasons for different-sized quadrats in the Harper-Avooca catchment (1962–66). Significant test statistics and *P*-values (i.e. <0.05) are highlighted in bold.

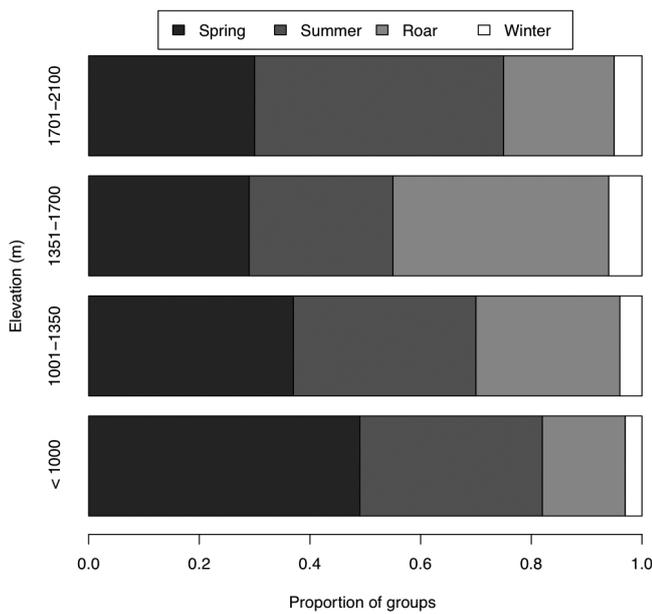
Quadrat area (ha)	Spring	Summer	Rut	Winter
25	<b>2.58 (0.007)</b>	<b>3.40 (0.002)</b>	0.67 (0.217)	5.86 (0.073)
50	<b>1.44 (0.008)</b>	<b>1.86 (0.001)</b>	0.44 (0.264)	3.59 (0.100)
100	<b>0.80 (0.046)</b>	<b>0.87 (0.007)</b>	0.14 (0.529)	1.35 (0.172)
500	0.14 (0.117)	0.21 (0.080)	0.04 (0.553)	0.37 (0.345)
1000	0.18 (0.131)	0.23 (0.069)	<0.01 (0.969)	<b>0.33 (0.026)</b>

**Table 7.** Syrjala's (1996) test statistic (and associated *P*-value) comparing the spatial distribution of male and female red deer (*Cervus elaphus*) groups in each of the four study years for different-sized quadrats in the Harper-Avooca catchment (1962–66). Significant test statistics and *P*-values (i.e. <0.05) are highlighted in bold.

Quadrat area (ha)	Spring 1962 – winter 1963	Spring 1963 – winter 1964	Spring 1964 – winter 1965	Spring 1965 – winter 1966
25	4.11 (0.780)	<b>11.25 (0.005)</b>	<b>1.98 (0.003)</b>	<b>1.96 (0.014)</b>
50	3.09 (0.807)	<b>5.10 (0.031)</b>	1.07 (0.080)	0.19 (0.068)
100	1.33 (0.715)	2.41 (0.053)	<b>0.56 (0.019)</b>	0.60 (0.056)
500	0.40 (0.929)	0.41 (0.264)	0.12 (0.297)	0.12 (0.061)
1000	0.37 (0.589)	0.93 (0.074)	<b>0.16 (0.023)</b>	0.10 (0.118)



**Figure 5.** Patterns of spatial segregation during spring (most segregated) and the rut (least segregated) for male groups, female groups and mixed groups of red deer (*Cervus elaphus*) at the 50-ha scale in the Harper-Avooca catchment (1962–67).



**Figure 6.** Proportions of red deer (*Cervus elaphus*) groups observed in the Harper-Avooca catchment (1962–67) in four elevation bands by season.

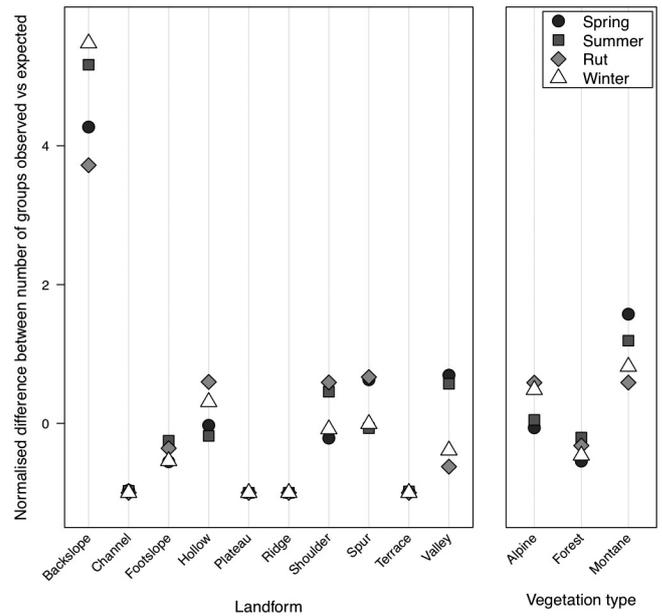
Use of the study area by red deer varied seasonally according to elevation, landform, and vegetation type. Deer groups were observed at high elevations in all seasons, but proportionately more in summer and winter than in spring and the rut (Fig. 6). Low elevations were used most in spring and least in winter (Fig. 6). Across all years the use of topographic landforms ( $\chi^2 = 322.2437$ , d.f. = 9,  $P < 0.001$ ) and vegetation types ( $\chi^2 = 466$ , d.f. = 2,  $P < 0.0001$ ) were non-random (Fig. 7). We predicted that deer would preferentially use valley bottoms in spring. Although deer did use the valley bottoms more in winter and spring than in summer and the rut ( $\chi^2 = 29$ , d.f. = 3,  $P < 0.0001$ ), many fewer groups across all seasons were observed in valley bottoms than expected (Fig. 7). Deer intensively used backslopes and spurs in spring ( $\chi^2 = 160$ , d.f. = 9,  $P < 0.001$ ), backslopes in summer ( $\chi^2 = 72$ , d.f. = 9,  $P < 0.001$ ), and hollows and spurs during the rut ( $\chi^2 = 171$ , d.f. = 9,  $P < 0.001$ ). In spring and summer red deer groups favoured montane grasslands ( $\chi^2 = 42$ , d.f. = 3,  $P < 0.001$ ), but in the rut they used alpine grasslands more than expected ( $\chi^2 = 50$ , d.f. = 3,  $P < 0.001$ ) (Fig. 7). Across all seasons, the use of vegetation type and topographic landform was not influenced by year (not shown).

## Discussion

Our results show that the red deer population in the Harper-Avooca catchment increased more rapidly than was expected based on published maximum rates of population growth estimated overseas, that males and females were sexually segregated outside the rut, and that both sexes made substantial use of montane and alpine grasslands.

### Population dynamics

In contrast to our prediction, the maximum annual population growth rates for all three classes of red deer were far greater ( $r = 1.61 - 2.33$ ) than both the mean (0.30) and maximum (0.38) previously reported for *Cervus elaphus* (Table 1). Although estimated population growth rates varied between adult males, adult females, and others, each had a similar temporal pattern with highest rates observed between years 1 and 2, and lower rates in the last three years of the study (Table 4).



**Figure 7.** Seasonal differences between observed and expected numbers of red deer (*Cervus elaphus*) groups in the Harper-Avooca catchment (1962–67) by landform and vegetation type. ‘Alpine’ and ‘Montane’ are both grasslands. Differences were normalised by expected values (i.e. (observed–expected)/expected).

The published estimates of  $r_m$  in Table 1 represent the maximum plausible rates of annual in situ population growth that could be expected for the Harper-Avooca population following release from culling. The very high population growth rates early in the study may have been due in part to younger female age at first reproduction in New Zealand (Daniel 1963), but the decline in population growth rates with time suggests that other processes also operated. The detectability of deer may have changed during the course of the study, increasing immediately after the cessation of hunting in November 1961 and then declining (Douglas 1971). Indices of abundance can be corrected for detectability (MacKenzie & Kendall 2002) but we could not do so here, given the data collection protocols used during the 1960s. We emphasise that our analyses were made using an index of abundance and it was assumed that any changes in the value of the index (after correcting for seasonal differences in behaviour) were relative to changes in absolute abundance. Therefore, monthly and seasonal counts are not estimates of absolute abundance. There is considerable anecdotal information documenting how ungulates change their behaviour in response to human activities such as hunting (e.g. Nugent & Fraser 2005) and it is possible that at least some of the observed population growth rate was a consequence of surviving deer spending more time in grassland than forest (Douglas 1971; Hickling 1986). However, we found no evidence that the use of vegetation types by deer changed during our study.

Another possible explanation for the high observed population growth rate is immigration of deer into the study area from adjacent catchments. Our study area was surrounded by Crown and leasehold land that, although subject to government and recreational hunting, contained higher densities of deer than our study area when hunting ceased in 1961 (Batcheler & Logan 1963; Davidson 1965). There are few data on the home ranges and movements of red deer in New Zealand, but hinds fitted with individually unique collars that were captured in pens in the Harper-Avooca catchment during the 1970s had a mean ( $\pm$  SE) range size (based on resightings) of 552 ha ( $\pm$  64 ha,  $n = 48$ ; R.J. Henderson, unpubl. data). Of the eight marked deer that were subsequently shot outside the Harper-Avooca catchment, two young stags and one adult hind had travelled 20 km from their capture pens (R.J. Henderson, unpubl. data). Male red deer in the Bavarian Alps largely used the home ranges of their mothers for the first two

years of their lives, but then dispersed up to 15 km to establish new home ranges (Georgii & Schroder 1983). In a Norwegian population of red deer, young males were more likely to disperse (up to 37 km) at high population densities, and were likely to settle in areas with a lower deer density; female dispersal rates were lower and independent of density (Loe et al. 2009). Given the small size of our study area relative to the surrounding landscape matrix that contained moderate to high densities of deer (Davidson 1965), substantial immigration almost certainly would have occurred throughout the study period. For example, 30 adult males seen at the south-western edge of the study area on 12 January 1963 (i.e. during the first year of the study) were considered to be immigrants because they had previously been observed on lease-hold land south-east (i.e. outside) of the study area (M.J.W. Douglas, pers. obs.).

Although groups of up to 150 red deer have been observed in New Zealand (Challies 1990), the modal group size during our study was 1 or 2 and did not increase during the study (Table 2; Fig. 3). Hence, the increasing population was characterised by more small groups of deer rather than by larger groups of deer. These results are in agreement with overseas work showing that the only stable social association is a female and her unweaned calf (Clutton-Brock et al. 1982).

Lastly, a recent major advance in the study of animal movement is the availability of relatively cheap global positioning system (GPS) technology that can be attached to ungulates (e.g. Johnson et al. 2002). A GPS-collar can record thousands of animal locations over a variety of time frames and can provide insight into animal movements and resource selection at a range of spatial and temporal scales (e.g. Forester et al. 2007). We recommend the use of GPS technology for future studies of movements and resource selection by deer in New Zealand.

#### Sexual segregation and resource use

Our prediction that male and female red deer would be spatially segregated except during the rut was supported by the data. Interestingly, segregation was highly variable during winter, a result that we attribute to the variable extent of snow cover during June–September; when snow was deep and extensive, the sexes aggregated where there was least snow cover (M.J.W. Douglas, pers. obs.), as also observed for Himalayan tahr (*Hemitragus jemlahicus*; Tustin & Parkes 1988; Forsyth 1999, 2000) and Alpine chamois (Clarke 1986) in the eastern Southern Alps of New Zealand.

Our results were consistent with the findings of Clutton-Brock et al. (1987, 2002) on the Isle of Rum (Scotland), where sexual segregation increased as the abundance of red deer increased following release from culling. Clutton-Brock et al. (1987) suggested that increasing densities of females decreased the quantity of forage such that males moved to other areas (see also Main (2008) for other explanations). However, this is unlikely to explain our findings because the dominant tussocks (*Chionochloa* spp.) in our study area continued to increase in abundance and tiller length during the 1960s even though red deer were immediately and consistently (1962–67) observed more frequently in montane than alpine grasslands, particularly in spring and summer. Trends in faecal pellet frequency (Hickling 1986) suggested that deer were less abundant in forests than grasslands; hence, forage availability in forest was unlikely to have been a driver of sexual segregation.

Grasslands at all elevations in our study area were used less in winter than in the other three seasons (Fig. 7), a pattern consistent with that shown by sika deer in the central North Island (Davidson 1973) and red deer in Norway (Albon & Langvatn 1992). Reduced accessibility of grasses and forbs due to snow cover, along with increased locomotory and thermal costs for deer, likely explain the reduced use of grasslands by deer in winter. It has been widely recognised that red deer prefer, and hence have greater impacts in, some topographic landforms than others (e.g. Wardle 1984). Local-scale studies in alpine grasslands and beech forest have concluded that red deer utilise landforms that relate to compositional variation in vegetation driven by nutrient availability (e.g. Rose & Platt 1987; Stewart & Harrison 1987; Forsyth et al. 2005). Other factors may also

drive the topographic preferences of deer. Sika deer in the central North Island utilised valley bottoms in spring because of early plant growth there (Davidson 1973), but this was not the case for red deer in our study area. Depending upon season, red deer utilised backslopes and spurs disproportionately in the Harper-Avoca catchment. That finding was unexpected because those areas had relatively infertile soils (Rose et al. 1995; Wiser et al. 1998).

#### Management implications

Extensive commercial and state-funded harvesting has, at times, dramatically reduced the abundance of deer at a variety of spatial scales in New Zealand (e.g. Nugent & Fraser 1993; Tanentzap et al. 2009). However, population processes after harvesting have not been adequately studied to ensure effective deer management. Thus, our results suggest that immigration is a major driver of rapid population recovery following intensive harvesting at the scale (c. 11 000 ha) of the Harper-Avoca catchment. If immigration was indeed the cause of the high population growth rate, then control methods would need to be applied more often and/or more intensively, or the area subject to control would need to be made larger. Immigration has apparently bedevilled small-scale deer control operations by allowing rapid recovery of populations (e.g. red deer on Secretary Island (Sanson & Von Tunzelman 1985) and white-tailed deer (*Odocoileus virginianus*) on Stewart Island (Challies & Burrows 1984)).

There are at least two ways in which demographic studies of deer populations could assist deer-harvesting programmes in New Zealand. First, further estimates of population growth rates are needed for a variety of landscapes to help determine appropriate harvest rates. Second, estimates of emigration/immigration rates are needed to help us understand the influence of context (e.g. size and spatial location of management) on population dynamics (e.g. Clutton-Brock et al. 2002).

Although our study showed an increase in the abundance of a red deer population in 5 years following cessation of control, there was little change in resource use. Hence, any impact of the increasing red deer population in the Harper-Avoca catchment would have been manifested through higher densities in the same vegetation types and landforms rather than through deer using a wider range of vegetation types and landforms. In contrast, we observed marked changes in resource use among seasons. This could have important consequences for red deer impacts as the recovery of vegetation from defoliation is sometimes strongly controlled by season (Maschinski & Whitham 1989; Obeso & Grubb 1994). We suggest that patterns of resource use can be used, in part, as a basis for determining the extent and timing of control operations. Such operations may directly reduce deer abundance, or alter resource use. Red deer control in spring might be used to reduce impacts on certain sites at sensitive times in the growing season. When red deer in grasslands were subjected to harvesting they made greater use of forest (Hickling 1986), so a relaxation of hunting in grasslands might be used to reduce forest impacts. During our study, however, the forest canopy appeared to be too dense for deer to reduce the growth of seedlings (Wardle 1984; Coomes et al. 2003). Our resource-use examples highlight how further research on plant–herbivore interactions might lead to more effective management.

The three introduced large herbivores in the Southern Alps are red deer, Alpine chamois and Himalayan tahr and there is interest in their interactions within a multi-pest management context (Forsyth et al. 2000; Parkes & Forsyth 2008). The present study has shown that red deer utilise montane and alpine grasslands, seasonally, and work in the Avoca catchment during the 1970s showed that chamois also used these vegetation types (Clarke 1986; Clarke & Frampton 1991). Tahr have been infrequently observed in the Harper-Avoca catchment, but in Carneys Creek, about 80 km south of our study area, tahr also used alpine grasslands, seasonally (Forsyth 2000). Although red deer were virtually eliminated by helicopters from the open grasslands of the eastern Southern Alps during the 1980s (see appendix 1 in Forsyth 1997), relaxation of red deer harvesting could lead to greater sympatry with chamois and tahr. In the eastern Southern Alps chamois and tahr are predominantly browsers and grazers, respectively (Parkes & Forsyth

2008), but understanding the relative impacts of deer, chamois and tahr now requires that red deer diet be studied in that area.

## Conclusions

Our study showed that the observed population growth rate of red deer in a 11 000-ha area of the Southern Alps after the cessation of intensive hunting was far greater than biologically possible without substantial immigration and/or changes in detectability. Ancillary information on movements of deer subsequently captured in the Harper-Avoca catchment suggests that immigration played an important role. Although the abundance of deer increased during the study, there was strong segregation of male and female groups in spring and summer; sexes were most aggregated during the rut. Both sexes made intensive use of montane and alpine grasslands, particularly in spring and summer. Our results highlight the need to consider the size and spatial context of deer management areas. There is little information on the home ranges, migration patterns, use of resources, and dispersal rates and distances of red deer in New Zealand, but these data are required for the design of more effective deer management programmes.

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## References

- Albon SD, Langvatn R 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65: 502–513.
- Allen RB, Clinton PW, Davis MR 1997. Cation storage and availability along a *Nothofagus* forest development sequence in New Zealand. *Canadian Journal of Forest Research* 27: 323–330.
- Allen RB, Bellingham PJ, Wiser SK 1999. Immediate damage by an earthquake to a temperate montane forest. *Ecology* 80: 708–714.
- Baddeley A, Turner R 2005. spatstat: An R package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1–42.
- Barringer JRF, McNeill S, Pairman D 2002. Progress on assessing the accuracy of a high resolution digital elevation model for New Zealand. Proceedings of the 5<sup>th</sup> International Symposium on Spatial Accuracy Assessment in Natural Resources and Environmental Data, 10–12 July, (2002), Melbourne. Pp. 187–195.
- Barringer JRF, Hewitt AE, Lynn IH, Schmidt J 2008. National mapping of landform elements in support of S-Map, a New Zealand soils database. In: Zhou Q, Lees B, Tang G eds *Advances in digital terrain analysis. Lecture Notes in Geoinformation and Cartography*. Berlin, Springer. Pp. 443–458.
- Batcheler CL, Logan PC 1963. Assessment of an animal-campaign in the Harper-Avoca catchment. *New Zealand Forest Research Notes* 27: 1–27.
- Bell ML, Grunwald GK 2004. Mixed models for the analysis of replicated spatial point patterns. *Biostatistics* 5: 633–648.
- Bonenfant C, Gaillard J-M, Klein F, Maillard D 2004. Variation in harem size of red deer (*Cervus elaphus* L.): the effects of adult sex ratio and age-structure. *Journal of Zoology (London)* 264: 77–85.
- Brooks SP, Gelman A 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7: 434–455.
- Burnham KP, Anderson DR 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York, Springer. 488 p.
- Caughley G 1977. *Analysis of vertebrate populations*. London, John Wiley. 234 p.
- Caughley G 1983. *The deer wars: the story of deer in New Zealand*. Auckland, Heinemann. 187 p.
- Challies CN 1990. Red deer. In: King CM ed. *The handbook of New Zealand mammals*. Auckland, Oxford University Press in association with the Mammal Society, New Zealand Branch. Pp. 436–458.
- Challies CN, Burrows L 1984. Deer control and vegetation response on Stewart Island. *What's New in Forest Research* 126. Rotorua, Forest Research Institute. 4 p.
- Clarke CMH 1986. Chamois movements and habitat use in the Avoca River area, Canterbury, New Zealand. *New Zealand Journal of Zoology* 13: 175–198.
- Clarke CMH, Frampton CM 1991. Structural changes in an apparently stable chamois population in Basin Creek, Canterbury, New Zealand. *New Zealand Journal of Zoology* 18: 233–241.
- Clutton-Brock TH, Guinness FE, Albon SD 1982. Red deer: behavior and ecology of two sexes. Chicago, University of Chicago Press. 378 p.
- Clutton-Brock TH, Iason GR, Guinness FE 1987. Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). *Journal of Zoology (London)* 211: 275–289.
- Clutton-Brock TH, Coulson TN, Milner-Gulland EJ, Thomson D, Armstrong HM 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415: 633–637.
- Coomes DA, Allen RB 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology* 95: 27–40.
- Coomes DA, Allen RB, Forsyth DM, Lee WG 2003. How reversible are the impacts of introduced deer in New Zealand forests? *Conservation Biology* 17: 450–459.
- Coulson T, Guinness F, Pemberton J, Clutton-Brock T 2004. The demographic consequences of releasing a population of red deer from culling. *Ecology* 85: 411–422.
- Daniel MJ 1963. Early fertility of red deer hinds in New Zealand. *Nature* 200: 380.
- Davidson MM 1965. Changes in wild mammal populations in Canterbury. *New Zealand Forest Service Information Series* 52. Wellington, NZ Forest Service. 51 p.
- Davidson MM 1973. Use of habitat by sika deer. In: Orwin J ed. *Assessment and management of introduced mammals in New Zealand forests*. FRI Symposium 14. Rotorua, New Zealand Forest Service, Forest Research Institute. Pp. 55–67.
- Davis MR 1990. Chemical composition of soil solutions extracted from New Zealand beech forests and West German beech and spruce forests. *Plant and Soil* 126: 237–246.
- De la Cruz M 2008. Métodos para analizar datos puntuales. In: Maestre FT, Escudero AY, y Bonet A eds *Introducción al análisis espacial de datos en ecología y ciencias ambientales: Métodos y aplicaciones*. Madrid, Asociación Española de Ecología Terrestre, Universidad Rey Juan Carlos y Caja de Ahorros del Mediterráneo. Pp. 76–127.
- Douglas MJW 1971. Behaviour responses of red deer and chamois to cessation of hunting. *New Zealand Journal of Science* 14: 507–518.
- Eberhardt LL 1987. Population projections from simple models. *Journal of Applied Ecology* 24: 103–118.
- Eberhardt LL, Simmons MA 1992. Assessing rates of increase from trend data. *Journal of Wildlife Management* 56: 603–610.
- Forester JD, Ives AR, Turner MG, Anderson DP, Fortin D, Beyer

- HL, Smith DW, Boyce MS 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs* 77: 285–299.
- Forsyth DM 1997. Ecology and management of Himalayan thar and sympatric chamois in the Southern Alps, New Zealand. Unpublished PhD thesis, Lincoln University, Canterbury, New Zealand. 140 p.
- Forsyth DM 1999. Long-term harvesting and male migration in a New Zealand population of Himalayan tahr *Hemitragus jemlahicus*. *Journal of Applied Ecology* 36: 351–362.
- Forsyth DM 2000. Habitat selection and coexistence of the Alpine chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. *Journal of Zoology (London)* 252: 215–225.
- Forsyth DM, Caley P 2006. Testing the irruptive paradigm of large-herbivore dynamics. *Ecology* 87: 297–303.
- Forsyth DM, Parkes JP, Hickling GJ 2000. A case for multi-species management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand. *New Zealand Journal of Ecology* 24: 97–103.
- Forsyth DM, Richardson SJ, Menchenton K 2005. Foliar fibre predicts diet selection by invasive red deer *Cervus elaphus scoticus* in a temperate New Zealand forest. *Functional Ecology* 19: 495–504.
- Forsyth DM, Barker RJ, Morriss G, Scroggie MP 2007. Modeling the relationship between fecal pellet indices and deer density. *Journal of Wildlife Management* 71: 964–970.
- Forsyth DM, Wilmshurst JM, Allen RB, Coomes DA 2010. Impacts of introduced deer and extinct moa on New Zealand ecosystems. *New Zealand Journal of Ecology* 34: 48–65.
- Fortin M-J, Dale MRT 2005. *Spatial analysis: A guide for ecologists*. Cambridge, NY, Cambridge University Press. 365 p.
- Fraser KW, Cone JM, Whitford EJ 2000. A revision of the established ranges and new populations of 11 introduced ungulate species in New Zealand. *Journal of the Royal Society of New Zealand* 30: 419–437.
- Georgii B, Schröder W 1983. Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the Alps. *Oecologia* 58: 238–248.
- Gogan PJP, Barrett RH 1987. Comparative dynamics of introduced tule elk populations. *Journal of Wildlife Management* 51: 20–27.
- Griffiths GA, McSaveney MJ 1983. Distribution of mean annual precipitation across some steepland regions of New Zealand. *New Zealand Journal of Science* 26: 197–209.
- Harris LH 2002. The deer menace. A history of government pest control operations, 1930–1987. L. H. Harris, Post Box 2276, Wellington 6015, New Zealand.
- Hewitt AE 1992. New Zealand soil classification. DSIR Land Resources Scientific Report 19. Lower Hutt, DSIR. 133 p.
- Hickling GJ 1986. Red deer population surveys in the Harper-Avooca catchment (1956–1983). FRI Bulletin 107. Christchurch, Forest Research Institute. 10 p.
- Houston DB 1982. The northern Yellowstone elk: ecology and management. New York, Macmillan. 474 p.
- Johnson CJ, Heard DC, Parker KL 2002. Expectations and realities of GPS animal location collars: results of three years in the field. *Wildlife Biology* 8: 153–159.
- Kie JG, Bowyer RT 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80: 1004–1020.
- Lavers RB 1978. The diet of red deer (*Cervus elaphus*) in the Murchison Mountains: A preliminary report. In: Seminar on the takahe and its habitat 1978. Invercargill, Fiordland National Park Board. Pp. 187–198.
- Lavers RB, Lee WG, Wilson JB, Mills JA 1983. Foods of red deer in the Murchison Mountains, Fiordland, New Zealand. *New Zealand Journal of Ecology* 6: 151–152.
- Loe LE, Mysterud A, Veiberg V, Langvatn R 2009. Negative density-dependent emigration of males in an increasing deer population. *Proceedings of the Royal Society of London B* 276: 2581–2587.
- Logan PC 1956. Some problems in the control of wild and domestic animals in a critical hydro-electric catchment. *New Zealand Journal of Forestry* 7: 68–75.
- MacKenzie DI, Kendall WL 2002. How should detection probability be incorporated into estimates of relative abundance? *Ecology* 83: 2387–2393.
- Main MB 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology* 89: 693–704.
- Manly BFJ, McDonald LL, Thomas DL 1993. *Resource selection by animals: statistical design and analysis for field studies*. 1<sup>st</sup> edn. London, Chapman & Hall. 177 p.
- Maschinski J, Whitham TG 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134: 1–19.
- McCorquodale SM, Eberhardt LL, Eberhardt LE 1988. Dynamics of a colonizing elk population. *Journal of Wildlife Management* 52: 309–313.
- McCracken IJ 1980. Mountain climate in the Craigieburn Range, New Zealand. In: Benecke U, Davis MR eds *Mountain environments and subalpine tree growth*. Technical Paper 70. Wellington, New Zealand Forest Service Forest, Forest Research Institute. Pp. 41–59.
- Murphy DA 1963. A captive elk herd in Missouri. *Journal of Wildlife Management* 27: 411–414.
- Newsome PFJ 1987. The vegetative cover of New Zealand. *Water & Soil Miscellaneous Publication* 112. 153 p + 2 map sheets.
- Nugent G 1992. Big-game, small-game, and gamebird hunting in New Zealand: hunting effort, harvest, and expenditure in 1988. *New Zealand Journal of Zoology* 19: 75–90.
- Nugent G, Fraser KW 1993. Pests or valued resources? Conflicts in management of deer. *New Zealand Journal of Zoology* 20: 361–366.
- Nugent G, Fraser W 2005. Red deer. In: King CM ed. *The handbook of New Zealand mammals*. 2nd edn. Melbourne, Oxford University Press. Pp. 401–420.
- Obeso JR, Grubb PJ 1994. Interactive effects of extent and timing of defoliation, and nutrient supply on reproduction in a chemically protected annual *Senecio vulgaris*. *Oikos* 71: 506–514.
- Packard WP 1947. Lake Coleridge catchment: a geographic survey of its problems. *New Zealand Geographer* 3: 19–40.
- Parkes JP, Forsyth DM 2008. Interspecific and seasonal dietary differences of Himalayan thar, chamois and brushtail possums in the central Southern Alps, New Zealand. *New Zealand Journal of Ecology* 32: 46–56.
- R Development Core Team 2009. *R: A language and environment for statistical computing*. Vienna, R Foundation for Statistical Computing.
- Rose AB 1983. Succession in fescue (*Festuca novae-zelandiae*) grasslands of the Harper-Avooca catchment, Canterbury, New Zealand. FRI Bulletin 16. Christchurch, Protection Forestry Division, Forest Research Institute. 35 p.
- Rose AB, Platt KH 1987. Recovery of northern Fiordland alpine grasslands after reduction in the deer population. *New Zealand Journal of Ecology* 10: 23–33.
- Rose AB, Platt KH, Frampton CM 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: Effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* 19: 163–174.
- Sanson LV, Von Tunzelman JR 1985. Wild animal control plan for Secretary Island, Fiordland National Park, 30 June 1985–1 July 1988. Invercargill, New Zealand Forest Service.
- Schmidt J, Hewitt A 2004. Fuzzy land element classification from DTMs based on geometry and terrain position. *Geoderma* 121: 243–256.
- Sibly RM, Hone J 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society, London B* 357: 1153–1170.
- Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A 2002. Bayesian measures of model complexity and fit (with discussion). *Journal*

- of the Royal Statistical Society B 64: 583–640.
- Stewart GH, Harrison JBJ 1987. Physical influences on forest types as deer habitat, northern Fiordland, New Zealand. *New Zealand Journal of Ecology* 10: 1–10.
- Syrjala SE 1996. A statistical test for a difference between the spatial distributions of two populations. *Ecology* 77: 75–80.
- Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. *Journal of Applied Ecology* 46: 1064–1072.
- Thomas A, O'Hara B, Ligges U, Sturtz S 2006. Making BUGS open. *R News* 6: 12–17.
- Tustin KG, Parkes JP 1988. Daily movement and activity of female and juvenile Himalayan thar (*Hemitragus jemlahicus*) in the eastern Southern Alps, New Zealand. *New Zealand Journal of Ecology* 11: 51–59.
- Wardle JA 1984. The New Zealand beeches: ecology, utilisation and management. Wellington, New Zealand Forest Service. 447 p.
- Wardle JA, Allen RB 1983. Dieback in New Zealand *Nothofagus* forests. *Pacific Science* 37: 397–404.
- Wardle P 1991. *Vegetation of New Zealand*. Cambridge University Press. 672 p.
- Wiser SK, Allen RB, Clinton PW, Platt KH 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79: 2071–2081.

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