Farmed red deer home range, habitat use and daily movement patterns in a Southland, New Zealand, tussock grassland over calving and lactation

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Abstract. Considerable expansion of red deer farming has occurred in the South Island high country of New Zealand. On these farms, breeding hinds are usually continuously grazed (set-stocked) at low population densities in large highly modified native-tussock grassland paddocks during their calving and lactation seasons. The present study determined how these hinds use the tussock grassland over this critical period, identifying the most essential resources for them and also some potential long-term consequences of their behaviour on the grassland ecosystem. This was achieved by tracking nine GPS-collared hinds over 2 years on a high-country deer farm in Te Anau, Southland, New Zealand. The home ranges of the GPS-tracked hinds varied widely, occupying between 15% and 52% of the total paddock area. Vegetation dominated by naturalised exotic pasture species covered the greatest proportion (>60%) of eight of nine hind home ranges. In contrast, tussock-dominant vegetation coverage was far more variable (0.4–46%), with several indicators suggesting that this vegetation type was used as a substitute for pasture areas under high intra-specific competition among the deer. Both pasture- and tussock-dominant vegetation was used in proportion to its availability. In contrast, shrub-dominated vegetation was used less than its proportional availability, indicating that it was not being put under as much foraging or grazing pressure. This has implications for the further ingestion of this vegetation type over time. There was also clear evidence that certain paddock topography was being favoured by the hinds, namely steeper and higher-altitude areas of a paddock. On the basis of these findings, some potential methods for aiding in the management of these extensive tussock grassland paddocks under deer grazing are suggested.

Additional keywords: Cervus elaphus, diurnal rhythms, remote sensing, resource selection.

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Introduction

The South Island high country pastoral zone of New Zealand stretches east of the main divide of the Southern Alps, occupying ~5 million ha of inland mountain ranges and open plains >500 m above sea level (asl; Douglas and Allan 1992). For New Zealand, this landscape represents an iconic cultural heritage of expansive pastoralism and unique biodiversity (Swaffield and Hughie 2001) and it has also been an important part of New Zealand livestock farming since the first pioneering ‘run HOLDERS’ settled the land in the early to mid-1800s (Daly 1990). Early pastoral development involved repeated regimes of burning the indigenous vegetation, followed by grazing the young palatable regrowth, which changed many high-country ecosystems from once being tall tussock (Chionochloa sp.)-dominated grasslands and shrublands to a variable mosaic of exotic grasses and herbs, indigenous short and tall tussocks, and woody shrubs (O’Connor 1982). Compared with intensive farming in New Zealand lowland regions, South Island high-country stations (farms) are characterised by their large size (often >1500 ha), low livestock densities (<4 ewes/ha), energy and labour inputs, and highly seasonal constraints to management, especially in terms of climatic factors and in situ forage-biomass production (Matthews et al. 1999).

In New Zealand over the past 30 years, red deer (Cervus elaphus) farming has mainly been based on intensively managed lowland systems, using highly developed paddocks of improved exotic pasture grasses and herbs and specialised forage crops. These pasture-based systems normally produce 10–17 t DM/ha year (Radcliffe 1974) and carry 8–12 deer/ha (Asher and Pearse 2002). However, over the past decade, there has been a large increase in the number of red deer breeding hinds being farmed in the South Island high country (Peoples and Asher 2009). Much of
this expansion has stemmed from the recognition that deer farming has a high level of compatibility with the natural resources of high-country ecosystems and can generate more favourable economic returns than do traditionally run sheep and beef-cattle enterprises. It is also recognised that red deer, which are not yet highly genetically selected for domestication traits, may exhibit better reproductive productivity in tussock grasslands that mimic a more ‘natural’ environment, particularly over calving. Many advocates of extensive deer-farming systems in New Zealand provide anecdotal evidence of improved reproductive performance of red deer hinds, argued to be a result of reduced stress due to a better calving habitat (e.g. natural vegetative cover for new born calves) and lower deer-stocking rates, as individual breeding hinds usually seek isolation from the rest of the herd at parturition (Asher and Pearse 2002).

While capable of supporting pastoral grazing, these tussock grasslands produce much less annual biomass than do other more intensive New Zealand farming systems, with typical forage-production yields of 2–3 t DM/ha.year (Cossens and Brash 1981) necessitating grazing stocking rates as low as one or two deer per hectare. To accommodate economically viable-sized deer herds, specialised permanent deer-proof fencing is established around large tracts of land, often covering highly variable topography, soil types and vegetation. A common farm-management practice is to continuously graze (set-stock) red deer breeding hinds in these paddocks from just before parturition (November–December) through until calf-weaning (February–May), and also over the winter season (June–August).

Although wild red deer have existed through much of the South Island high country for well over 100 years, their population densities have probably never exceeded 0.1–0.3 deer/ha (Forsyth et al. 2010). In contrast, extensively farmed red deer are stocked at densities of 1–4 deer/ha, which is almost an order of magnitude greater density than that for wild deer (Peoples and Asher 2009). Thus, the potential impacts on high-country ecosystems could be unprecedented unless managed appropriately. With little known about how red deer use and affect these high-country ecosystems, it was the objective of the present study to remotely track adult breeding hinds with GPS collars over the late-spring–summer calving and lactation season to gain an understanding of the main habitats that they use, and also their daily movement and activity patterns. This information is not only essential for developing the knowledge required for managing the impacts of red deer hinds on the high-country environment, but will also give a greater understanding of adult hind requirements over this critical time of the year for deer breeding farms.

Materials and methods

Study site

The study was conducted at Haycocks Station (45°30′40″S, 168°01′20″E), located 30 km east of the township of Te Anau, Southland, New Zealand, in the following three adjoining tussock grassland paddocks: ‘Rough Gully’ (251 ha), ‘Beehive Gully’ (160 ha) and ‘Big Basin’ (185 ha; Fig. 1a). These paddocks were deer-fenced in 2003, but, before this, their indigenous tussock and shrubland vegetation had already undergone significant modification through being aerially broadcast-sown with exotic pasture plant species, aerially top-dressed with fertiliser, and regularly grazed with sheep and beef cattle. The elevation of the paddocks ranged between 400 and 700 m asl and they had hill slopes of 12–28° (Fig. 1b). Both Rough Gully and Big Basin had predominantly south-west-facing aspects whereas Beehive Gully was south facing (Fig. 1b). The main exotic grass and legume species in the paddocks were crested dogtail (Cynosurus cristatus), cocksfoot (Dactylis glomerata), browntop (Agrostis capillaries) and white clover (Trifolium repens). Red tussock (Chionochloa rubra subsp. cuprea) was the dominant indigenous tufted grass, with silver tussock (Poa cita) and blue tussock (Poa colensoi) being the next-most prominent. Matagouri (Discaria toumatou) was the main woody shrub species present (Clarke 2011). Red deer breeding hinds were set-stocked each year in the paddocks at a population density of 2.5 hinds/ha from late spring (October) through to late autumn (April–May), and the paddocks were also grazed for a short 21-day period in winter with breeding cows at 2.4 cows/ha.

The annual rainfall at the study site is 1076 mm and is distributed evenly throughout the year, with February being the driest month (84 mm) and October the wettest month (106 mm). The mean annual air temperature is 9.4°C, ranging from 14.7°C in January to 3.8°C in July (NIWA 2012).

Global positioning system (GPS) tracking of red deer hinds

Over the late spring through to late autumn seasons of 2006–2007 (Year 1) and 2007–2008 (Year 2), a small subsample of adult (>3-year-old) red deer hinds, of a larger breeding herd of 600 animals, was remotely tracked by fitting them with GPS neck collars (Blue Sky Telemetry Inc., Edinburgh, Scotland). The collars were fitted in October of each year, just before the herd was set-stocked in the Rough Gully study paddock for calving, and were not retrieved until 7 months later in April–May when the herd was mustered for calf weaning. In total, seven randomly selected hinds were fitted with collars in Year 1 and another eight hinds were fitted with collars in Year 2 (Table 1), using protocols approved by the AgResearch Invermay Animal Ethics Committee under the New Zealand Animal Welfare Act (1999). All of the GPS-tracked hinds were diagnosed as being pregnant by rectal ultrasonography (White et al. 1989) and the herd had an expected mean calving date in the third week of November.

In Year 1, the GPS collars were programmed to take positional fixes every 60 min, whereas, in Year 2, extra batteries were added to the units to allow this interval to be reduced to 30 min. The modified GPS collars each weighed 590 g, which is equivalent to ~0.5% of a hind’s bodyweight.

All of the GPS units deployed on the hinds in Year 1 suffered major physical damage, with only two units being fitted to Hind Y116 and Y121 regularly recording positional data for >4 weeks (Table 1). In contrast, after redesigning the collars, seven of the eight collars deployed in Year 2 functioned for the entire duration of the planned study (16 weeks) and successfully logged between 88% and 98% of all possible fixes over this period (Table 1). Given the very limited datasets available for Hinds Y119, Y120, Y117, Y122 and Y130 in Year 1 and YB02737 in Year 2, these hinds were omitted from any further statistical analyses (Table 1). The study period analysed for Year 1 and Year 2 were from 2 November 2006 to 6 December 2006 and from 8
November 2007 to 29 February 2008 respectively. These intervals were the maximum period that all the GPS units commonly function for in each study year and also covered the expected calving dates of the hinds.

The GPS data from the neck collars were downloaded into the geographical information system (GIS) computer software package ArcGIS 9.1 (ESRI, Redlands, California, USA). None of the GPS fixes were differentially corrected. However, stationary testing, conducted across a range of locations at Haycocks Station, indicated that the GPS units had a measurement error of between 1 and 7 m. The GPS fixes for each hind were overlaid onto detailed vegetation and topographical maps of the study paddocks, so as to determine their home range, daily movement patterns and habitat use.

**Vegetation and topography mapping of the study site**

The dominant vegetation types in the study paddocks were mapped from a high-resolution aerial photograph taken of the site in February 2002 (NZ Aerial Mapping Ltd, Hastings, New...
This photograph was a multispectral digital image that included red, green and blue (RGB) wavebands and had a spatial resolution of 0.8 m per pixel. The image scene was geo-referenced to a series of ground control points in ArcGIS, resulting in it having a geo-location root mean square error of 1 m. eCognition Version 3.0 (Definiens AG, München, Germany) object-oriented image-analysis computer software was used to subdivide (segment) the study paddocks into a range of discrete land-cover objects (polygons) consisting of clusters of pixels with similar spectral characteristics. In eCognition, the extent that smaller image objects are merged into larger ones is controlled by a scale factor and homogeneity criterion. The former specifies the maximum allowable increase in object heterogeneity after merging two objects, thus indirectly governing their overall size, whereas the latter controls the actual merging decision process, and includes two mutually exclusive properties, namely, spectral heterogeneity and geometrical shape (Laliberte et al. 2004). The values for these parameters were selected using a systematic trial and error approach, through visually comparing the outlines of the segmented objects to the vegetation types that were able to be clearly identified in the original digital image. These vegetation cover types included shrubland-, tussock-, high-quality pasture-, and low-quality pasture-dominated vegetation, and also bare ground. High-quality pasture consisted predominantly of pasture plant species that were in a vegetative state. In contrast, low-quality pasture areas had more senescent (dead) material and inflorescences (flower and seed head).

The spectral properties (signatures) of land-cover objects that most widely represented each of the five main vegetation types were used as reference samples (training sites) for automatically classifying all of the remaining objects segregated in the study paddocks, through using a nearest-neighbour algorithm. Afterwards, the newly classified thematic image was visually checked against the original image and any clearly misclassified land-cover objects were manually reclassified into their correct class (Mathieu et al. 2007).

Field-surveying (ground-truthing) was conducted in 2007 to validate the vegetation map. This involved walking transects across the study paddocks, and with a hand-held GPS receiver recording the locations of ground cover representative of each vegetation type classified on the vegetation map. At each sample location, a 4-m² survey plot was marked out and the dominant vegetation type covering its area was recorded. In total, 167 plots were sampled. In ArcGIS, the GPS ground-truthed locations were overlaid onto the vegetation map and the accuracy of the nearest-neighbour algorithm-classified vegetation types was assessed using an error (confusion) matrix (Congalton 1991). On the basis of the error matrix, the vegetation map had an overall accuracy statistic of 89% and a Kappa statistic of 84%. The overall accuracy statistic is the percentage of ground-truthed sample plots correctly classified in the vegetation map (Foody 2002), whereas Kappa statistic is a more conservative accuracy statistic, as it adjusts for possible agreement that could have occurred simply by random chance alone (Stehman 1997).

A 15-m spatial-resolution digital elevation model of the site, obtained from Land Information New Zealand, was used in ArcGIS to create three-dimensional models (layers) of the aspect, slope and elevation in each study paddock. Each of these topographic variables were split into discrete categories (classes) and their respective total paddock areas were calculated using ArcGIS Spatial Analyst software (ESRI, Redlands, CA, USA). Aspect was subdivided into eight cardinal directions, each representing 45°, while slope and elevation were split into the following respective categories: arable (0–11°), hill (12–28°), and steepland (>28°) slopes; and low (401–500 m), mid- (501–600 m), and high (601–700 m) paddock elevations.
Statistics

Estimation of hind home range (HR) and core area (CA)

The HRs of the GPS-tracked hinds, and more intensively used CAs within these HRs, were calculated from the GPS fixes by using the fixed-kernel method (Worton 1989) in the software package ‘Home Range Tools for ArcGIS’ Version 1.1 (Rodgers et al. 2007). Contour lines (isopleths) encompassing 95% of each hind’s utilisation distribution were used to represent their HR for performing ‘normal’ daily activities such as feeding, resting and ruminating, and nurturing their calves, and to exclude any occasional exploratory forays into outlying areas (Bertrand et al. 1996). In contrast, 50% isopleths were used as an indicator of CAs receiving the most consistent or intensive use by a hind. A single temporal scale was used covering breeding-hind parturition and lactation.

Topographical relief and vegetation within each HR and CA were calculated on an area basis using the ‘zonal – tabulate area’ function of the ArcGIS Spatial Analyst software (ESRI). For these analyses, both the high- and low-quality pasture types were combined into a single ‘Pasture’ class, given the vegetation map was based on a 2002 digital image taken when their relative abundances could have been strongly influenced by sheep and cattle grazing occurring in the paddocks at the time, as opposed to the effects of deer grazing, which did not commence until a year later in 2003.

Hind paddock-scale habitat-selection ratios

For each GPS-tracked hind, a selection ratio of its use of a vegetation class relative to the paddock abundance (availability) of the same class was calculated (Manly et al. 2002). Owing to some of the hinds changing paddocks during the monitoring period, daily usage and availability were first calculated and then summed across all days to calculate the selection ratios. To determine whether a vegetation class was used in proportion to its availability, a one-sample Student’s t-test was used to test the difference of the selection ratio from 1 (Hobbs and Bowden 1982) and also a simple sign test was used to test whether the proportion of GPS-tracked hinds with selection ratios of >1 was significantly different from 50%. A selection ratio of 1 indicates that the vegetation class is used exactly in proportion to its availability, whereas that of >1 indicates that it is favoured and <1 that it is avoided. The GPS-tracked hinds were treated as the primary sampling units and it was assumed that they had complete unrestricted access to the entire paddock that they were in for each GPS fix. Similar selection ratios were also calculated for discrete hill-slope, elevation and aspect categories.

Hind daily (24-h) cyclical movement patterns

The movement velocity (m/h) that collared hinds travelled at between successive GPS fixes was used as an indicator of their activity levels over the course of a day. An average daily (24-h) cycle was calculated by breaking up each day into either 60-min (Year 1) or 30-min (Year 2) subintervals, and averaging the distance travelled in each subinterval for the entire calving and lactation study period. These values were then smoothed using a ‘LOESS smoother’ (locally weighted scatterplot smoothing) to produce graphical displays showing each GPS-tracked hind’s average daily (24-h) cyclical movement pattern (Pépin et al. 2009). Several other parameters were used to describe the spatial movement patterns of the hinds within the study paddocks and also the habitat characteristics that were occupied by the hinds for each 24-h subinterval. These parameters included hind hill-slope (degrees) and elevation (m asl) positions, measured as absolute values, and hind hill-slope aspect and vegetation usage, measured as a percentage of the GPS fixes recorded for each subinterval.

Results

Hind HR and CA

In both Year 1 and Year 2, just before parturition, all of the GPS-tracked hinds were initially set-stocked along with the main 600-hind herd in the Rough Gully study paddock, and they were meant to remain in this paddock through until calf-weaning in autumn (April–May). However, three hinds (Y116, Y121 and Y130) in Year 1 and two hinds (Y6 and Y1184) in Year 2 escaped into the adjoining Beehive Gully and Big basin paddocks for varying durations over the study period. The lower incidence of hind paddock-migration in Year 2 is likely to have reflected preventative measures taken by the farm manager in the Rough Gully paddock to block identified routes of escape from the previous year.

The biophysical characteristics of each GPS-tracked hind’s HR, and also the size of their 50% CA, are presented in Table 2. Individual hind HR size varied widely between 38 ha and 130 ha, equating to 15% and 52% of the total Rough Gully paddock land area respectively (Table 2, Fig. 2). In Year 1, Hind Y116 and Hind Y121 inhabited markedly different HRs, with the HR of Hind Y116 in Beehive Gully being much smaller in area, centred at a higher altitude, and containing a more even mixture of the different vegetation types than did the HR of Hind Y121 that co-inhabited both Rough Gully and Big Basin (Table 2, Fig. 2a).

In Year 2, two distinct groups were present among the GPS-tracked hinds, with Or146, Or385, Y81, and Y22 (Group 1) sharing strongly overlapping HRs and, similarly, the HRs of Hind Y6 and Y85 (Group 2) also overlapped (Fig. 2b). The HRs of Or146, Or385, Y81 and Y22 (Group 1) were centred above Rough Gully’s mid-elevation of 530 m asl and pasture was the dominant vegetation type within them, accounting for, on average, 71% ± 7% (mean ± coefficient of variation) of the land area (Table 2). This group of hinds also consistently had a small proportion of shrubland within their HR (9% ± 3%). However, the tussock content of their HR was more variable, with the HRs of Hind OR385, Y81, and Y22 containing 18% tussock, while the HR of Hind OR146 had only 5% tussock (Table 2). The HRs of Hind Y6 and Y85 (Group 2) were centred around Rough Gully’s mid-elevation, and contained mainly pasture (83% ± 1%), with a small proportion of shrubland (16% ± 5%), and very little tussock (0.5% ± 12%) (Table 2, Fig. 2b). The HR of Hind Y1184 also contained vegetation similar to this second group of hinds, and it was located even further downslope in the catchment (Table 2, Fig. 2c).

The 50% CAs within the HRs varied in size from 9.6 ha to 28.5 ha, corresponding to 6.7% and 13.9% of the total paddock area respectively (Table 2). Thus, the hinds concentrated ~50%
of their space use in 14–25% of their total HR, indicating marked heterogeneity in space use.

**Habitat usage relative to paddock-scale availability**

Pasture-dominant vegetation was used 5–20% more than its availability by six of nine GPS-tracked hinds (Table 3). However, at the herd population level, there was no statistical evidence that this vegetation type was being used any more than in proportion to its availability (Table 3). All of the GPS-tracked hinds using pasture more than in proportion to its availability had >70% of this vegetation type within their HR and were located at mid- to low paddock elevations (Table 2). In contrast, the hinds that used pasture less than in proportion to its availability had a HR located further up-slope (Table 2) and instead mainly used tussock-dominant vegetation to a greater extent (Table 3). Only Hinds Y116 and Y1184 used shrubland and exposed bare ground respectively, more than their availability, indicating that the red deer hinds generally under-utilised these two vegetation cover types (Table 3).

All nine GPS-tracked hinds used the hill slope class ranging between 12° and 28° marginally more than in proportion to its availability by, on average, 10%, indicating positive selection (Table 4). Conversely, seven of nine tracked hinds used the arable slope class of between 0° and 11° less than in proportion to its availability, with usage among all of the tracked hinds being, on average, 32% less than what was available (Table 4). The usage of steepland slopes (>28°), relative to their availability, was much more variable, with no clearly consistent pattern among the individual hinds or previously identified groups (Table 4).

Only one of nine GPS-tracked hinds (Hind Y1184) used the lowest paddock-elevation class (401–500 m) slightly more than in proportion to its availability, with the average usage of this elevation class by all of the GPS-tracked hinds being 55% less than available (Table 4). The use of mid-paddock-elevation (501–600 m) and upper paddock-elevation (601–700 m) classes, relative to their availability, was much less consistent among the GPS-tracked hinds, with no clear trends. The only exception was all hinds with HRs centred above the Rough Gully paddock’s mid-elevation (Hinds Y116, Or385, Y22, Y81, and Or146) used the upper-elevation class (601–700 m) 35–273% more than in proportion to its availability, indicating they were actively selecting this elevation class (Table 4).

Only one GPS tracked hind (Y1184) of nine used north-east- and east-facing aspects more than in proportion to their availability, with the average usage of these aspects being 45% and 24% less than available respectively (Table 5), indicating that the herd was generally avoiding these aspects. The majority of hinds also used north-facing aspects less than in proportion to their availability, but the statistical evidence of this effect at the herd-population level was weak (Table 5). All of the other aspects were generally used in proportion to their availability, with no consistent pattern in usage among the GPS-tracked hinds (Table 5).

**Hind daily (24-h) cyclical movement patterns**

All of the GPS-tracked hinds expressed well defined patterns of daily behaviour in terms of their movement velocities, altitude, hill slope and aspect position and vegetation usage. Hind movement velocities generally peaked at dawn (0600 hours to 0700 hours) and dusk (2000 hours to 2100 hours), with the hinds travelling greater distances between GPS fixes during the day than at night (Fig. 3a, b). This bimodal (double-peaked) daily rhythm was very consistent among eight of nine GPS-tracked hinds (Fig. 3a). Minimum hind movement occurred particularly just before midnight (2330 hours) and remained relatively low until the early hours of the morning (0300 hours). During daylight hours, there was also generally a lull in hind movement about mid-afternoon (1500 hours; Fig. 3a, b).

Most of GPS-tracked hinds with HRs above the mid-elevation of Rough Gully study paddock (Hinds Or146, Or385, Y81 and Y22) progressively travelled downhill by ~40 m from sunrise through until a couple of hours after midday (Fig. 3c). Thereafter, they proceeded to ascend uphill again, reaching a maximum elevation by about midnight, and remaining there through until the early hours of the next morning. The rate of change in elevation position was particularly marked during the morning and late-afternoon through until late-evening bouts of increased
hind spatial movement (Fig. 3a, c). In contrast, GPS-tracked hinds with a HR at mid- to low paddock elevations either did not markedly change their elevation position over the course of a day (Hinds Y1184 and Y85) or they showed the opposite trend (Hinds Y121 and Y6), instead moving up hill in the morning and back down again in the afternoon and evening (Fig. 3c).

Most of the GPS-tracked hinds also moved into a slightly steeper terrain from about midnight through until about dawn, although, on average, the increase in hill slope was only 2.2° ± 0.71 (mean ± s.e.; Fig. 3e, f). Throughout the day, all of the GPS-tracked hinds generally remained within the hill-slope class of between 12° and 28° (Fig. 3e). West-facing hillsides were the predominant aspect used by the GPS-tracked hinds.
However, the usage of this aspect decreased sharply, particularly during the early hours of the morning through until just after sunrise, compensated instead mainly with increasing north-west-facing hillside usage over this same period of time (Fig. 4).

The use of pasture-dominant vegetation remained above 65% for the majority of GPS-tracked hinds (7 of 9) throughout the day (Fig. 5a, b). In contrast, for all of the hinds that had an appreciable content (>18%) of tussock-dominated vegetation within their HR (Hinds 116, Or385, Y81 and Y22), the use of this vegetation type decreased by 10–25 percentage points during the daytime, with minimum usage occurring particularly about noon (Fig. 5c, d). Conversely, all of the GPS-tracked hinds increased their usage of shrub-dominated vegetation by 6–10 percentage points during the daytime, generally peaking about, or just after, noon (Fig. 5e, f).

### Discussion

**Hind HR size**

Home-range size for farmed deer is constrained by paddock size. However, all hinds within this study exhibited HRs that were considerably smaller than the total area (251 ha) available to them, ranging between 38 and 130 ha. Many factors affect a deer’s HR size, including the size and dispersion of productive feeding areas, favourable resting and refuge areas available to each deer (Said et al. 2005), access to water sources (Hervert and Krausman 1986), local climatic conditions (Rivrud et al. 2010), degree of disturbance by human activities (Lovari et al. 2007), and the particular sampling and estimation methods used for calculating the HR size (Börger et al. 2006a).

Even within the farmed population, there was considerable variation in the HR size for individual hinds. Generally, animals

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### Table 3. Hind vegetation-selection ratios (usage as a fraction of paddock availability)

See Table 1 for explanation of hind IDs. Natural log-transformed mean and s.e. are given in parentheses. Selection ratios: 1, habitat usage is exactly in proportion to its availability; >1, habitat is favoured; and <1, habitat is avoided.

<table>
<thead>
<tr>
<th>Hind ID</th>
<th>Year</th>
<th>Pasture</th>
<th>Dominant vegetation type</th>
<th>Bare ground</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y116</td>
<td>1</td>
<td>0.88</td>
<td>1.05</td>
<td>2.41</td>
</tr>
<tr>
<td>Y121</td>
<td>1</td>
<td>1.18</td>
<td>0.05</td>
<td>0.47</td>
</tr>
<tr>
<td>Or385</td>
<td>2</td>
<td>0.60</td>
<td>5.50</td>
<td>0.89</td>
</tr>
<tr>
<td>Y6</td>
<td>2</td>
<td>1.05</td>
<td>0.17</td>
<td>1.00</td>
</tr>
<tr>
<td>Y22</td>
<td>2</td>
<td>0.97</td>
<td>2.88</td>
<td>0.25</td>
</tr>
<tr>
<td>Y81</td>
<td>2</td>
<td>1.10</td>
<td>1.53</td>
<td>0.28</td>
</tr>
<tr>
<td>Or146</td>
<td>2</td>
<td>1.18</td>
<td>0.31</td>
<td>0.46</td>
</tr>
<tr>
<td>Y1184</td>
<td>2</td>
<td>1.20</td>
<td>0.12</td>
<td>0.56</td>
</tr>
<tr>
<td>Y16</td>
<td>2</td>
<td>1.16</td>
<td>0.10</td>
<td>0.64</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>1.04 (0.01)</td>
<td>1.30 (-0.81)</td>
<td>0.77 (-0.49)</td>
</tr>
<tr>
<td>s.e.</td>
<td></td>
<td>(0.07)</td>
<td>(0.56)</td>
<td>(0.23)</td>
</tr>
<tr>
<td>P-value mean ≠ 1</td>
<td>0.847</td>
<td>0.185</td>
<td>0.065</td>
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</tr>
<tr>
<td>Number of hinds &gt; 1</td>
<td>6</td>
<td>4</td>
<td>1</td>
<td>1</td>
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<tr>
<td>Sign test</td>
<td>0.508</td>
<td>1.000</td>
<td>0.039</td>
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</tbody>
</table>

### Table 4. Hind hill-slope- and altitude-selection ratios (usage as a fraction of paddock availability)

See Table 1 for explanation of hind IDs. Natural log-transformed mean and s.e. are given in parentheses. Selection ratios: 1, habitat usage is exactly in proportion to its availability; >1, habitat is favoured; and <1, habitat is avoided.

<table>
<thead>
<tr>
<th>Hind ID</th>
<th>Year</th>
<th>Arable (0–11°)</th>
<th>Hill slope (12–28°)</th>
<th>Steepland (&gt;28°)</th>
<th>Lower (401–500 m)</th>
<th>Middle (501–600 m)</th>
<th>Upper (601–700 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y116</td>
<td>1</td>
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<td>0.45 (-2.05)</td>
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<td>(0.13)</td>
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<td>(0.16)</td>
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with a larger body mass need a larger HR to meet their greater metabolic requirements (Harestad and Bunnell 1979). However, this relationship is not always evident where essential resources are plentiful (Dussault et al. 2005) and the hierarchical social structure of the herd could counter this relationship by more dominant, heavier hinds securing the most resource-rich and easily accessible areas of the paddock, thus reducing the overall area they require (Tufto et al. 1996). Older hinds may also have been able to move more efficiently among favoured areas in the paddock on the basis of previous experiences (Sáld et al. 2009).

How essential resources required by the hinds are spatially distributed can have a marked effect on the HR size. Several researchers have shown that cervids have smaller HRs when the patch and edge density of the landscape is high (Kie et al. 2002; Anderson et al. 2005; Börger et al. 2006b). This is attributed to the deer needing multiple habitat types for foraging and finding refuge, with their closer proximities enabling easier and quicker access among them (Anderson et al. 2005). However, if the resource dispersion at Haycocks Station was a large contributing factor to the HR size, then the percentage of HR area covered by each hind’s 50% CA should have also varied widely, which clearly did not occur (Table 2). For it to be a major factor, the HR and 50% CA would be expected to be closer in size for smaller HRs. No such relationship was found for the limited number of deer tracked in the present study (linear relationship for 50% CA as a percentage of HR, 2 = 0.21, root mean square error = 2.8, P = 0.216).

The reproductive state of the GPS-collared hinds would have influenced the total size of their HR (Bertrand et al. 1996; van Beest et al. 2011) as this affects both their nutritional requirements and social behavioural patterns (Clutton-Brock et al. 1982; Asher et al. 2014). The feed intake requirement of a hind increases markedly over the last trimester of gestation and during lactation, and if resource competition is high, this would be likely to force them to forage much more widely. Also, immediately after calving, the spatial movement of a hind can be constrained by the hiding strategy and limited mobility of their new-born calves (Asher et al. 2014).

**Hind HR location in the landscape**

Home-range locations spanned the full range of altitudinal gradients present in the main Rough Gully study paddock and all of the HRs contained a mixture of pasture-, shrubland- and tussock-dominant vegetation to varying extents (Table 2, Fig. 2). The use of a broad range of altitudinal and vegetation gradients is in accordance with other studies, which have shown that red deer can inhabit and thrive in a wide variety of environments, ranging from low-altitude meadows and forests, up into alpine grasslands (Staines 1974; Georgii 1980; Lovari et al. 2007; Bee et al. 2010). This high level of environmental adaptability is aided by their strong seasonality in feed-intake requirements and ability to switch between forage and browse plants as an opportunistic mixed or intermediate feeder-type ruminant (Milne et al. 1978; Hofmann 1989).

However, while red deer are capable of feeding on a variety of vegetation types, when given the opportunity, they will normally concentrate their feeding activities on areas with the most easily digestable plant biomass, enabling them to maximise their daily average energy-intake rate (Clarke et al. 1995; Fraser and Gordon 1997). Diet-selection studies conducted in Scotland have shown that red deer prefer to eat vegetative pasture plants over tussocks and shrubs, when they are given equal access to all three vegetation types (Fraser and Gordon 1997). This is likely to be the major reason why pasture-dominant vegetation covered >60% of the HR for eight of nine GPS-tracked hinds, with the percentage of the total HR area covered by this vegetation type being the most consistent of all of the vegetation types present in the study paddocks (Table 2).

Despite the dominance by pasture, all HRs contained a moderate level of shrubland-dominant vegetation (ranging from 8.5% to 17%) and, similarly to pasture, the variability in shrubland coverage was low (CV of 9%), indicating that it was consistently used among the GPS-tracked hinds. Hinds with
more pasture instead of tussock in their HR also tended to have more shrubland than on average (Table 2). The more consistent coverage of shrubland vegetation in each hind’s HR, than of other vegetation types such as tussock (Table 2), indicated that it is still ‘valued’ by the hinds for some other reason(s), possibly shelter or protective cover (Mysterud and Østbye 1999). In the wild, red deer are known to be ‘edge dwellers’, selecting scrub or forest and open-grassland habitats. Therefore, the availability of a variety of habitats within their HR is likely to be important for red deer. During the calving period, pregnant hinds are also known to seek isolation and cover for parturition (Clutton-Brock et al. 1982).

The percentage of tussock-dominant vegetation in each HR was far more variable among the GPS-tracked hinds (ranging from 0.4% to 46%; CV 39%) and was used instead of both pasture and, to a lesser degree, shrubland (Table 2). Clarke (2011) observed that the inter-tussock spaces at Haycocks Station contained a high proportion of exotic pasture species and, on

![Graphs showing daily (24-h) cyclical movement patterns for individual hinds and mean value ± standard error. Hinds: OR146 (---), OR385 (----), Y1184 (---), Y22 (---), Y6 (---), Y81 (---), Y85 (---), Y116 (---), Y121 (---). Timing of sunrise and sunset over study period was 0550 hours to 0720 hours and 2040 hours to 2140 hours respectively.](image-url)
the basis of the botanical species present, Netzer (2008) estimated that this vegetation type had an intermediate feed value between the pasture and shrubland vegetation. Thus, the tussock-dominant vegetation would still provide the breeding hinds with the duel benefits of moderately nutritious forage and low cover. In the face of potentially strong intra-specific competition for paddock resources, some hinds may have chosen or been forced to use this vegetation type. Red tussock in itself would not have faced competition for pasture-dominant vegetation more than in proportion to its availability, thus, could also in face of potentially strong intra-speci competition for the most preferred vegetation resources for each animal was low. Under strong intra-specific competition, the availability of the most preferred vegetation may be reduced to such an extent that it becomes not energetically worthwhile for some hinds to search for and use these areas, forcing them instead to use more readily available but nutritionally poorer vegetation types (Clutton-Brock et al. 1982). The amount of pasture vegetation available to each hind, thus, could also influence their selection for other vegetation types such as tussock, which would provide a similar resource. This would explain why for all of the hinds that used pasture less than in proportion to its availability, they generally instead used tussock vegetation, and, to a lesser extent, shrubland, considerably more than in proportion to its availability (Table 3).

Only one of nine GPS-tracked hinds used shrubland vegetation more than in proportion to its availability, indicating that this vegetation type is not placed under as greater pressure than the others by the hinds over late gestation and lactation (Table 3). A long-term management implication of the low selection pressure for shrubland-dominated vegetation is that this may allow it to expand into other higher forage-value vegetation, negatively affecting the paddock’s overall deer-carrying capacity. Other livestock species, such as cattle, could be used to help control any shrubland ingress, but care would need to be taken to ensure that they did not damage other highly valued vegetation types such as tussocks. Given that indications are that the shrubland vegetation is not a major forage source, then its level of browse damage could also be used as an indicator of whether the herbaceous forage available within the paddock is enough relative to hind stocking rate, with high amounts of shrubland browsing indicating that stocking rates are restricting hind intakes of higher-quality forage and, similarly, designated tussock patches could be used in a similar manner.

Given that the low-altitude (401–500 m) and arable (0–11°) hill-slope areas of the study paddocks contained comparable levels of high- and low-quality pasture to the other altitude and hill-slope classes (Fig. 1a, b), it is unlikely that forage quality was a major factor for the hinds generally using them less than in proportion to their availability (Table 4). However, low-altitude and arable land may have been avoided because of its exposed nature, with steeper and higher-altitude terrain providing the hinds with a more suitable habitat for escaping and finding refuge in if required, especially given their need for keeping their offspring safe. This would also lend support to why the GPS-tracked hinds actively selected hill land (12–28°), while using steepland (>28°) and mid-altitude (501–600 m) to upper-altitude (601–700 m) hill slopes in proportion their availability (Table 4). Overall, the results indicated that, in particular, hill slopes (12–28°) are more consistently put under pressure from the hinds and, thus, would also be a good place to monitor forage availability and any signs of overgrazing. They also indicated that, at the stocking rates currently used, this topography is highly valued by the breeding hinds over parturition and lactation.

The south-east- to north-west-facing aspects of the study paddocks were generally used by the GPS-tracked hinds in proportion to their availability (Table 5), indicating that they were all being put under similar pressure by the hinds. Conversely, the north- to east-facing aspects were used less than in proportion to their availability (Table 5), which may have been related to the low-quality pasture vegetation and bare ground areas being centred on these aspects (Fig. 1a, b), thus deterring their use by the hinds.

Hind daily (24-h) cyclic movement patterns

The predominantly bimodal daily rhythm, with peak movement velocities, especially at dawn and dusk, exhibited by eight of nine GPS-tracked hinds (Fig. 3a, b) has previously been widely reported for other red deer populations (Berger et al. 2002; Pépin et al. 2009) and other cervids such as elk (Ager et al. 2003). Kie et al. (2005) hypothesised that for elk, higher rates of movement at dawn and dusk reflected their attraction to particular vegetation patches with desirable forage. In contrast,
movement velocities were lower during periods of rest and rumination. Other studies, specifically measuring the actual foraging activities of red deer and elk, have shown that the hours approximately at dawn and dusk are normally associated with peak grazing times of each 24-h daily cycle (Craighead et al. 1973; Green and Bear 1990; Clarke et al. 1995; Hester et al. 1996).

All of the GPS-tracked hinds were more active during the day than at night, with a particularly prolonged period of elevated movement occurring during the morning (Fig. 3a, b). This differs from the stricter crepuscular or more elevated nocturnal patterns reported for red deer subjected to regular daytime anthropogenic disturbances (Georgii 1981; Berger et al. 2002). Greater daytime activity has been observed in undisturbed populations of wild red

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**Fig. 5.** Daily (24-h) cyclical patterns of vegetation usage for individual hinds and mean values ± standard error. Hinds: OR146 (---), OR385 (-----), Y1184 (--), Y22 (--), Y6 (--), Y81 (--), Y85 (--), Y116 (--), and Y121 (--). Timing of sunrise and sunset over study period was 0550 hours to 0720 hours and 2040 hours to 2140 hours respectively.
deer (Clutton-Brock et al. 1982; Kamler et al. 2007), indicating that set-stocking the farmed red deer hinds in the large tussock grassland paddock provided them with a safe and secure environment from human disturbances. This could reduce the stress levels incurred by these hinds over parturition, which has been shown to be an important requirement for ensuring high calf-survival rates from deer-farming systems (Asher and Pearse 2002).

The increase in shrubland usage, particularly at midday and early afternoon (Fig. 3e, f), coincided with when the GPS-tracked hinds were generally less active (Fig. 3a, b), providing evidence that this vegetation may have been used as a concealment cover for non-grazing activities such as resting and ruminating and calf nurturing or for thermal protection. Most previous research has shown that especially during the day, deer select concealment cover for resting and ruminating (Clarke et al. 1995; Hester et al. 1999; Ager et al. 2003) and young calves are known to seek cover while their dams forage (Guinness et al. 1979; Wass et al. 2004). Overall, these results have reiterated that even though shrubland-dominant vegetation does not make up a large part of the HR of most hinds (Table 2), nor is it highly selected for in relation to its availability (Table 3), it is still likely to be a ‘valued’ habitat by the hinds for possibly thermal protection or as a secure site from disturbances. The tussock vegetation would also provide a similar habitat, especially for the latter, and this may explain why it was also used by some of the GPS-tracked hinds during periods of reduced activity at night (Figs 3a, 5c).

A long-term management implication of this daily (24-h) behaviour is the potential for soil-fertility transfer from pasture patches to mid-altitude shrubland and upper-slope tussock patches if the hinds defecate more shortly after rising from resting and ruminating. The dominant woody-shrub species at the site, Matagouri, has more vigorous growth on soils with high phosphate and sulfur concentrations (Daly 1969). Thus, disproportionally greater levels of hind defecation among the shrubland vegetation could encourage the expansion of Matagouri shrubs into adjacent areas, which, if left unabated, would potentially have a negative impact on the long-term carrying capacity of the paddocks for farming deer.

Conclusions
Pasture-dominant vegetation made up the greatest proportion of the majority of hind HRs and this vegetation type was consistently used for a high proportion of each day. However, likely owing to strong intra-specific competition, some hinds used primarily tussock-dominated vegetation as a substitute for pasture-dominant vegetation. While all of the GPS-tracked hinds consistently had a small component of shrub-dominant vegetation within their HR, this vegetation type was generally used less than in proportion to its availability, indicating that it was not being placed under as much grazing or foraging pressure as were the pasture- and tussock-dominated areas of the paddocks. This lack of grazing or foraging pressure has implications for further ingestion of this vegetation type over time, which, if left unabated, could reduce the overall livestock carrying capacity of these tussock grassland paddocks in the future. Both tussock- and shrub-dominant vegetation was used by the hinds when they were least active, indicating that these vegetation types may have been used for resting and sheltering within, which also has implications for soil-fertility transfer away from the pasture-dominated vegetation areas. Given that indications from the present study are that tussock- and shrubland-dominant vegetation types are less preferred as a forage source, than are pasture-dominated areas, designated patches of the two former vegetation types could be regularly monitored to indicate whether hind stocking rates are appropriate, with severe signs of grazing or browsing signifying that either hind-stocking rates should be reduced or additional feed supplements should be provided to the hinds.

Conflicts of interest
The authors declare no conflicts of interest.

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References
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