

Seasonal patterns of resource selection by introduced sika deer (*Cervus nippon*) in Kaweka Forest Park Recreational Hunting Area, New Zealand

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Abstract: Sika deer (*Cervus nippon*) have attained high densities within their introduced range in the central North Island, New Zealand. They are an important big-game species for recreational hunters in New Zealand, but they can have unwanted impacts on native plants, such as reducing seedling growth rates. Management of sika deer requires detailed knowledge about which resources are important to them and how resource selection changes temporally. Using GPS location data, we assessed temporal (diel and seasonal) resource selection by male ($n = 10$) and female ($n = 16$) sika deer in Kaweka Forest Park Recreational Hunting Area, over a 15-month period. We found that sika deer were associated with ecotones comprising dense forest and open habitats, though the strength of selection for these habitats varied between sexes, time of day and season. Use of open habitats such as alpine and tussock by male and female deer showed complex temporal patterns that were presumably influenced by seasonal food availability and the risk of being seen and shot. Beech forest was an important habitat for sika deer, particularly in winter. Males and females showed strong selection for hollows (slips and guts on hillsides and small creeks with clearings) in most seasons, perhaps because palatable plant species are often associated with those areas. Males showed strong selection for forested terraces during the rut, possibly because these features provided defensible territories and a high number of mating opportunities. Our results indicate where and when aboveground and belowground impacts of sika deer may be highest, which can be used to guide impact monitoring protocols. Additionally, they indicate when sika deer most often use open habitats, where they are most easily observed; potentially increasing ground and helicopter hunting success.

Keywords: deer management; forest regeneration; GPS; habitat selection; mountain beech forest; resource selection functions

Introduction

Understanding how animals select the resources available to them can allow us to characterise their distribution and abundance, and therefore is an essential component of conservation biology, wildlife management and applied ecology (Rosenzweig 1981; McLoughlin et al. 2010). Resource selection by animals is a multifaceted process, requiring several variables to be considered simultaneously (Boyce & McDonald 1999). Until recently, multifaceted analyses of resource selection were difficult because of an inability to obtain sufficient location data for many species, match location data with environmental variables thought to influence species distribution, and analyse these data (Hebblewhite & Haydon 2010; Latham et al. 2015). However, advances in GPS and satellite technology, spatiotemporal resolution of environmental data and new quantitative analytical methods have enabled better characterisation of resource selection by animals (Guisan & Zimmermann 2000; Boyce 2006; Tomkiewicz et al. 2010). This has improved the ability to identify important resources for wildlife populations, model the spatial variation in animal abundance, and estimate potential range expansion and local impacts of introduced animals (Boyce & McDonald 1999; Forsyth et al. 2009; Hebblewhite & Haydon 2010). Here we use these methods to estimate resource selection by sika deer (*Cervus nippon*) in New Zealand.

Several species of deer have been introduced to many parts of the world, with many becoming invasive (King 2005; Wilson

& Mittermeier 2011). Sika deer were deliberately introduced into New Zealand in the early 1900s, and currently one main population now occupies a single near-continuous range concentrated in the central North Island (Banwell 2009). Similar to many species of native and introduced deer worldwide (Côte et al. 2004; King 2005; Latham et al. 2013), sika deer in New Zealand have attained high densities with unwanted impacts on native biodiversity. For example, intensive browsing by sika deer alters seedling growth and canopy replacement in mountain beech (*Fuscospora cliffortioides*) forests (Davidson & Fraser 1991; Allen & Allan 1997; Duncan et al. 2006). This selective browsing has changed the structure and composition of mountain beech forests, with an increasing amount of forest in an open state (Duncan et al. 2006) and forest understoreys becoming increasingly dominated by less palatable plants (Husheer et al. 2003; also see Takatsuki 2009).

Over the last 50 years, deer culling has occurred in most parts of sika deer range in New Zealand. Government-paid ground hunters were used initially, followed by commercial helicopter-based hunters (Davidson & Fraser 1991). However, commercial hunters focused primarily on red deer (*Cervus elaphus*) in unforested areas (Nugent 1992a), and thus their efforts did not adequately reduce sika deer numbers, or allow site- or habitat-specific seedling regeneration and canopy replacement (Coomes et al. 2003). Consequently, sika deer have also been periodically controlled since 1987 by the Department of Conservation (DOC; a department of the New Zealand Government) at a few high-priority sites

(Husheer & Robertson 2005; DH unpubl. data). Recreational hunting has also increased in many parts of sika deer range as hunters recognise their role in managing deer for both game management and conservation purposes (Kerr & Abell 2014).

Recreational ground hunters in New Zealand have been effective at controlling the abundances of deer and other wild ungulates in areas with low- to moderate-cover and close to a vehicle access (i.e. only at local scales; Batcheler & Logan 1963; Nugent 1988; Forsyth et al. 2003). However, they have been ineffective at reducing ungulate densities in remote, rugged terrain and in areas where initial densities of ungulates were high (Nugent 1988; Forsyth et al. 2013; also see Simard et al. 2013). Helicopter-based hunting is considered highly effective at reducing deer numbers in open habitats (e.g. Nugent & Fraser 2005) and moderately effective in forests with sufficient canopy openings to see and shoot deer, such as is the case with red deer and sika deer in the central North Island (Forsyth et al. 2013). The mixed efficacy of helicopter-based deer control programmes has been partially attributed to a lack of knowledge about deer ecology (Forsyth et al. 2013).

Sika deer ecology has been extensively studied within their native Japanese range (McCullough et al. 2009 and references therein), but less is known from elsewhere in their native range and in areas where they have been introduced (Dvořák et al. 2014). There is high variation in this paucity of information, for example, estimates of home range sizes vary from 4 to 800 ha depending on the geographical location and method used to estimate home ranges (Endo 2009; Mattioli 2011; Kalb et al. 2013). Additionally, the few studies that have described sika deer ecology in New Zealand, such as estimation

of home range sizes, dispersal distances and habitat use, were done prior to the advent of GPS and satellite technology and thus provide estimates derived from a limited amount of data (Davidson 1973a, 1979; Fraser & Leathwick 1990). Fine-scale descriptions of sika deer movements and habitat use will enable recreational hunters to target habitats with seasonally high deer use. They may also improve the efficacy of deer control operations by providing information about when and where to focus effort. Finally, detailed spatio-temporal assessments of resource selection by sika deer would provide information about how they use habitat in proportion to its availability. This could then be used to formulate hypotheses and predictions about the magnitude of impacts in habitats that are disproportionately used by sika deer (Forsyth et al. 2013).

The aim of this study was to assess temporal (diel and seasonal) resource selection by male and female sika deer in the central North Island, New Zealand. Specifically, we assessed the relative importance of environmental variables thought to influence sika deer distribution, with particular emphasis on fine-scale temporal trends in selection for open areas such as tussocks and alpine, because these represent areas where sika deer are most readily observed and easiest to manage (through helicopter and ground hunting). The intended management outcomes of this research are to (1) provide recreational and helicopter-based hunters with detailed information about which habitats are most likely to be used by sika deer at different times of the day and year and (2) highlight habitats used disproportionately by deer to allow hypothesis making regarding possible negative impacts within these habitats.

Methods

Study area

We assessed resource selection by sika deer in the northern portion of Kaweka Forest Park Recreational Hunting Area (Kaweka FPRHA; 39°16'S, 176°21'E), central North Island, New Zealand (Fig. 1). This park was gazetted in 1974 and covers an area of 59 000 ha. It is managed by DOC to preserve, among other values, some of the large tracts of indigenous mountain beech forest (Herries 2009, unpubl. rep., DOC DM-410423, DOC, Napier).

The park contains the Kaweka Range, which rises to 1724 m above sea level. The vegetation of the forest park is influenced predominantly by elevation, soils, herbivorous mammals, and fires (Elder 1959). The northern half of the park is largely forested with mountain beech, red beech (*Fuscospora fusca*) and podocarp species in the valleys. Alpine areas contain herb fields and snow tussocks (*Chionochloa* spp.), while red tussocks (*C. rubra*) occur in river valleys in the north-west.

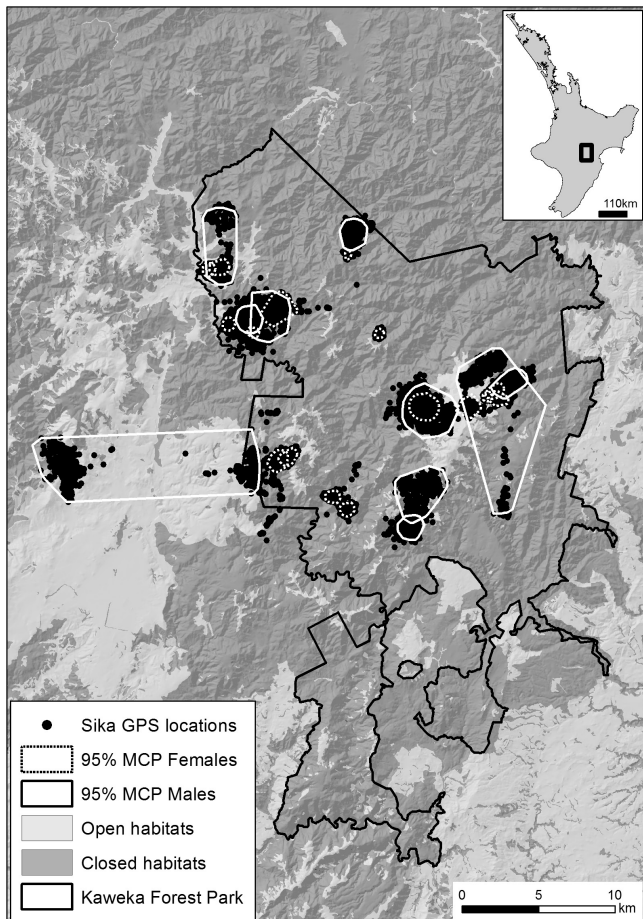


Figure 1. Location of study area in Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand. The area has rugged topography and is primarily covered by forested stands of beech (*Fuscospora* spp.), mānuka (*Leptospermum scoparium*) and lodgepole pine (*Pinus contorta*), interspersed with open areas of tussock. Within this area, we deployed GPS collars on 26 sika deer (*Cervus nippon*) between December 2010 and March 2012. The map shows the distribution of GPS locations obtained from collared animals and their home ranges estimated using 95% minimum convex polygons (MCP). Male MCPs are depicted in solid white lines, whereas female MCPs are depicted in dashed white lines.

Eastern areas have been affected by fires of anthropogenic origin and contain regenerating scrub, particularly mānuka (*Leptospermum scoparium*), kānuka (*Kunzea ericoides*) and pockets of beech/broadleaved forest (Elder 1959). Thickets of invasive lodgepole pine (*Pinus contorta*) occur over >5000 ha of the park (Ledgard 2001). A number of nationally threatened/at-risk plants occur in the park, including pua ō te reinga/wood rose (*Dactylanthus taylorii*), yellow mistletoe (*Alepis flavida*) and red mistletoe (*Peraxilla tetrapetala*).

A working group, comprising tangata whenua, the New Zealand Deer Stalkers' Association, Forest and Bird, the East Coast Hawke's Bay Conservation Board, helicopter operators, DOC and Landcare Research, was established in 1997 to determine how best to manage sika deer within the hunting area. The group used an analysis of canopy replacement under different levels of deer control (Duncan et al. 2006) as a basis to determine that deer numbers were too high and that a targeted aerial cull was required, to reduce numbers and thus level of impact. Aerial control of sika deer in Kaweka FP RHA started in 1998, with c. 4500 deer (2700 female sika deer, 1580 male sika deer and also 221 red deer) shot to date (DH unpubl. data). Since 2009, helicopter-based hunting has only targeted females. Additionally, open-access recreational hunting (i.e. hunting subject to minor permit requirements) is common in Kaweka FP RHA (Kerr & Abell 2014), and hunters have harvested a large but unknown number of sika deer annually (estimated to be 6845 in 1988; Nugent 1992b).

Sika deer telemetry data

Between December 2010 and March 2011, we captured and collared sika deer within Kaweka FP RHA, using nets fired from a Hughes 500D helicopter (DOC Animal Ethics Protocol No. 215). Captured animals were identified as sika deer from their physical appearance; however, some of these animals may have been sika–red deer hybrids (Ramón-Laca et al. 2014). We physically restrained captured animals (i.e. without the use of anaesthetics) and fitted them with a store-on-board GPS radio-collar (either a Kiwi Track collar (2010), Kiwi Track, Havelock North, Hawke's Bay, or a Wildlife GPS data-logger collar (2010), Sirtrack®, Havelock North, Hawke's Bay). We searched for animals to collar by flying above open areas (tussocks, shrubs and alpine) and gaps in the forest canopy. We attempted to collar a representative sample of animals from the northern part of Kaweka FP RHA where mountain beech forest was abundant. We did not target animals within the southern and eastern parts of the park because these areas are primarily forested by mānuka/kānuka (Fig. 1). Of the 30 animals captured, 18 (11 F, 7 M) were in tussock or alpine habitats, 10 were in beech or mānuka/kānuka forest (5 F, 5 M), and two males were in shrublands.

We programmed collars to obtain a location every 30 min between December 2010 and March 2012. We omitted from analyses location data obtained from the day of capture of each animal to avoid possible atypical behaviour immediately post-release (Northrup et al. 2014). We conducted data screening following Bjørneraas et al. (2010) to identify erroneous locations that were beyond the possible range of sika deer movements or that produced abnormal movement spikes. Finally, location data were rarefied to 2-h intervals to decrease autocorrelation between successive locations (Fieberg et al. 2010).

Landscape covariates

Explanatory variables included in our analyses were derived from a geographic information system (GIS) of the study area, using ArcGIS 10.1 (ESRI 2013), and included land-cover type, topography, and 'distance to' covariates. Recent studies highlighted that more useful insights into resource selection can be gained from considering habitat attributes at multiple, discrete scales (Boyce 2006; Leblond et al. 2011), so we collected landscape covariates at six discrete spatial scales (circular buffers of 25-, 50-, 100-, 250-, 500- and 1000-m radii). These were assumed to correspond to a range of hierarchical temporal (diel and seasonal) movement decisions (Leblond et al. 2011). The smallest scale corresponded to the average GPS location error, whereas the largest scale was assumed to correspond to larger ranges of perception by sika deer, such as home ranges (Mattioli 2011; Kalb et al. 2013). Within each buffer, we derived land-cover types from the Land Cover Database (LCDB version 3.3; www.lcdb.scinfo.org.nz), which had been ground-truthed by field personnel (DH unpubl. data). We classified land-cover types into: alpine; exotic forest plantations; broadleaved hardwood (podocarp); beech forest; mānuka forest (including mānuka and kānuka); shrubland; and tussock. Logged forestry blocks, exotic grasslands, gravel and rock, landslides, wetlands, and other landscape categories, such as land dominated by flax (*Phormium* spp.) or fern, were also present in Kaweka FP RHA; however, we omitted them from analyses because they only covered a small portion (<1% combined) of the study area. We converted land-cover types to a 25-m-resolution raster and included these in all analyses as the proportion of each land-cover type within the six discrete buffers around each GPS location.

Topographic variables were derived from a 25-m-resolution digital elevation model (DEM) of the study area and included aspect (eight categories, using north as the reference category), elevation (m), slope (°), and terrain ruggedness (standard deviation of elevation). Within the six different-sized buffers around each GPS location, we recorded the most common aspect, mean elevation, mean slope, and terrain ruggedness. Among the topographic variables, we also included the proportion of terraces and hollows within each of the six different-sized buffers; these landscape features were derived from the Landform Elements dataset (Barringer et al. 2008). Terraces (including benches) were flat or gently sloping surfaces usually associated with forest, and were included because they were considered to be areas important for defence of rutting territory, feeding, and bedding. Hollows comprised slips, guts and creeks on hillsides, and were considered to be particularly important for feeding. These landforms have previously been shown to influence habitat use by red deer in the South Island, New Zealand (Forsyth et al. 2010). 'Distance to-' variables comprised distance to nearest hollow, terrace, cover (including all forested cover types), and stream. Finally, we also included the density of streams within the six different-sized buffers around each GPS location.

Resource selection analysis

We evaluated third-order selection (sensu Johnson 1980) by sika deer, using resource selection functions (RSFs; Manly et al. 2002), by comparing landscape characteristics at used (GPS) and available (random) locations during four seasons: rut (1 April – 31 May), winter (1 June – 15 October), spring (16 October – 30 November), and summer (1 December – 31 March). The seasonal split was based on our ecological

knowledge of the system (as recommended by Basille et al. (2013)), and took into consideration temporal variation in sika deer behaviour and plant phenology. The rut captured the period of mating behaviour; winter represented the period with greatest snow cover and limited plant growth; spring captured the period when plant growth resumed; and summer the period of high forage availability and birthing and calf rearing. We conducted separate analyses for males and females. If individual deer were monitored for more than 1 year, data from separate years were combined. Areas used by each deer (i.e. the domain of availability; Manly et al. 2002) were defined by 95% minimum convex polygons (MCP) using the 'adehabitatHR' package (Calenge 2006) in R (R Core Team 2014). Within each 95% MCP, we randomly drew five locations per used location (which equated to an average of 94 (range: 1–379) random locations per hectare of 95% MCP) to describe habitat availability for each animal during each season.

Resource selection functions were fitted using mixed-effects logistic regression (Johnson et al. 2006) and the package lme4 (Bates et al. 2014) in R (R Core Team 2014). We included a random intercept for each individual deer to account for repeated observations obtained from the same animal, as well as an unbalanced sampling design (Gillies et al. 2006). Model building followed four steps for each sex–season combination. First, we assessed multi-collinearity between pairs of covariates, using Pearson correlation coefficients (r_p). For those pairs with $r_p \geq |0.7|$, we retained for further analyses the most biologically important variable of the pair (as recommended by Montgomery & Peck (1992)) determined from our understanding of sika deer biology in Kaweka FP RHA. Second, we identified the best scale to contextualise landscape variables in sika deer resource selection modelling, using Akaike Information Criterion (AIC; Burnham & Anderson 2002). To do this, we constructed six topographic models (one for each scale and each including all non-correlated topographic variables), six habitat models (each including all non-correlated habitat variables), and six stream density models, and identified the best scale for each group of variables as that of the model with the lowest AIC value. Third, the best topography, habitat, and stream density models were combined into one full model, to which we added the two remaining variables (distance to cover and distance to stream) only if this resulted in an overall lower AIC value. The fourth and final step was to add interaction terms between three landscape variables (distance to nearest hollow, proportion of alpine, and proportion of tussock) and time of day (t , recorded in decimal hours) to the full model, to assess diel variation in the strength of selection. Following Forester et al. (2009), we assessed diel patterns by including interaction terms with four harmonics of time of day, calculated as $s_1 = \sin(2\pi t/24)$, $s_2 = \sin(4\pi t/24)$, $c_1 = \cos(2\pi t/24)$ and $c_2 = \cos(4\pi t/24)$. For each sex–season combination, explanatory variables with 95% confidence intervals not overlapping zero were considered to have a significant influence on resource selection by sika deer.

Results

Between December 2010 and March 2011, we captured and collared 16 female (all adults) and 14 male (all adults; four of these collars failed shortly after deployment) sika deer within Kaweka FPRHA. We removed 635 telemetry locations (0.23% of the dataset) from the day of capture. After screening for erroneous locations, we removed a further 220 locations (i.e. <0.1% of the dataset). Finally, rarefaction to 2-h intervals

resulted in a reduction of 75% of the dataset. Once rarefied, we obtained 62 087 GPS locations from 26 radio-collared sika deer, with an average of 2388 (range: 91–4617) locations per individual. On average, individuals were monitored for 230 days (range: 8–428; Appendix 1). We obtained 36 653 locations from collared females, with 22% occurring during the rut, 40% during winter, 8% during spring, and 30% during summer. We obtained 25 434 locations from collared males, with 20% occurring during the rut, 37% during winter, 10% during spring, and 33% during summer. Collar location error was estimated at 30 m from stationary tests conducted prior to deployment (Frair et al. 2010); collar mean fix-rate success was 92% (SD = 7%, range = 70% to 100%).

Of 26 animals with functional collars, none dispersed outside of the study area. However, we recorded three long-distance movements (range: 4–12 km) by male sika deer (Fig. 1). In two of these events, one during early-summer and one during late-summer and the rut, males moved away from their original area of use (defined as the area where they were captured and GPS locations subsequently confirmed 'use' of the area), stayed in the new area for about two months, and then returned to the first area of use. The third event followed a similar pattern, with the animal moving into a new area at the start of the rut, and remaining there for the duration of the life of the collar battery halfway through the rut. We were unable to determine whether the animal subsequently returned to the original area of use.

The scale at which landscape covariates influenced resource selection by sika deer varied between sexes and seasons (Table 1). The buffer size that best explained the influence of landscape variables was generally smaller for females than for males. The rut was an exception, with male selection best described by the smallest buffer (50 m) and female selection for habitat and water best described by the largest buffer (1000 m). The scale at which landscape covariates influenced male resource selection was largest during spring and summer, whereas females showed less seasonal variation and were generally influenced by resources at scales of 50–250 m. Large spatial scales best explained female selection for habitat, whereas small spatial scales best explained their selection for topographic variables. The opposite pattern was observed for males in spring and summer but not during the rut or winter.

Male resource selection was strongly influenced by topography and habitat, but the influence of individual covariates changed between seasons (Table 2). Males selected areas closer to hollows in all seasons except winter, and selection for hollows was reasonably consistent across a 24-h period (Fig. 2, Appendix 2). Males selected areas close to terraces during the rut, whereas areas close to streams or with a high density of streams were important for males year-round. Males selected areas close to cover during winter, but further from cover during the spring. Northern aspects were selected during the rut, winter and summer, whereas southern aspects were also selected during spring. Males selected higher elevations during the rut and summer, but selected areas with lower terrain ruggedness and gentler slopes year-round. Areas with a higher proportion of alpine habitat were avoided during the rut and summer, but were selected during winter and spring. Males tended to select alpine areas during daylight, particularly during spring (Fig. 3, Appendix 2). Selection for beech forest, mānuka forest or shrublands was highest during winter, spring, and summer, whereas these were avoided during the rut (except beech forest which was not included in rut or summer models because it was negatively correlated

Table 1. Buffer radius size used in the best models explaining resource selection by sika deer (*Cervus nippon*) in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 – March 2012. Landscape covariates were collected at six spatial scales (circular buffers of 25-, 50-, 100-, 250-, 500- and 1000-m radii) around each location and the best scale was determined using AIC (Akaike Information Criterion). The results indicate that the ‘best’ buffer size describing resource selection by sika deer varied between sex, season, and resource-type (topography, habitat or stream density).

Variable	Buffer radii (m)							
	Rut		Winter		Spring		Summer	
	Male	Female	Male	Female	Male	Female	Male	Female
Topography	50	50	250	50	1000	50	1000	50
Habitat	50	1000	500	250	500	250	500	100
Stream density	na	1000	100	500	100	500	na	100

Table 2. Standardised parameter estimates (β) and standard errors (SE) for each explanatory variable explaining resource selection by male sika deer (*Cervus nippon*) during four seasons in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 – March 2012. Beta coefficients with 95% CI not overlapping zero are considered to have a significant influence on resource selection (indicated in bold). Selection for land-cover, topographic, and stream density variables is indicated by a positive coefficient, whereas selection for ‘distance to-’ variables is indicated by a negative coefficient. Parameter estimates (and SE) for interaction terms between some landscape variables and four harmonics of time of day are shown in Appendix 2.

Variable ^a	Rut (<i>n</i> = 5082)		Winter (<i>n</i> = 9487)		Spring (<i>n</i> = 2477)		Summer (<i>n</i> = 8388)	
	β	SE	β	SE	β	SE	β	SE
D hollow	-0.227	0.029	0.014	0.020	-0.412	0.048	-0.184	0.026
D terrace	-0.391	0.034	0.101	0.025	1.537	0.091	–	–
D cover	–	–	-0.083	0.020	0.105	0.053	–	–
D stream	-0.053	0.020	-0.447	0.023	–	–	-0.195	0.014
Stream density	–	–	0.009	0.019	0.367	0.029	–	–
Aspect north-east ^b	-0.335	0.066	-1.649	0.068	-3.533	0.338	-3.101	0.143
Aspect east ^b	-0.028	0.062	-0.409	0.050	-1.272	0.245	-0.673	0.081
Aspect south-east ^b	-0.126	0.059	-0.183	0.043	0.375	0.131	-0.824	0.058
Aspect south ^b	-0.691	0.064	-1.453	0.058	0.324	0.120	-1.456	0.063
Aspect south-west ^b	-0.607	0.068	-0.944	0.056	1.264	0.202	-0.024	0.061
Aspect west ^b	-0.413	0.068	-0.693	0.057	-4.082	0.321	-2.663	0.103
Aspect north-west ^b	-0.227	0.059	0.233	0.038	0.360	0.097	-0.705	0.046
Elevation	0.569	0.028	–	–	–	–	0.215	0.033
Slope	–	–	-0.066	0.023	-0.344	0.153	0.674	0.072
Terrain ruggedness	-0.208	0.023	–	–	-0.597	0.056	-0.134	0.029
P hollows	–	–	0.144	0.018	1.454	0.088	0.162	0.052
P terraces	-0.117	0.021	-1.080	0.101	-0.128	0.194	-0.352	0.050
P alpine	-0.351	0.030	9.808	0.467	6.569	0.780	-0.321	0.019
P exotic forest	-0.201	0.034	8.170	0.408	7.262	0.820	0.171	0.013
P broadleaved hardwood	-0.083	0.021	–	–	–	–	0.014	0.020
P beech forest	–	–	65.100	3.073	38.180	4.727	–	–
P mānuka forest	-0.307	0.022	45.960	2.146	21.680	2.642	0.080	0.019
P shrubland	-0.083	0.016	11.760	0.532	8.583	0.928	0.473	0.017
P tussock	-0.670	0.026	50.430	2.368	29.800	3.773	0.396	0.029

^a D = Distance to feature, in metres; P = Proportion within a buffer of varying radii (see Table 1) around a location

^b Categorical variable where reference category = Aspect north

with tussock). Males showed strong selection for tussock during winter, spring and summer; however, selection during spring and possibly summer appeared stronger during hours of darkness than during daylight hours (Fig. 4, Appendix 2). Male sika deer avoided areas with a high proportion of tussock during the rut, and particularly during daylight hours in that season (Fig. 4, Appendix 2).

Resource selection by females was often similar to males, but there were notable differences (Table 3). Females selected hollows during all seasons, with the strength of selection being

reasonably similar across a 24-h period (Fig. 2, Appendix 3). Areas closer to terraces were selected during winter and summer, used in proportion to their availability during the rut, and avoided during spring. Females selected areas closer to streams during the rut and winter; however, they consistently avoided areas with a high density of streams. Similar to males, females selected areas closer to forest cover during winter. Northern aspects were selected during the winter, whereas during the rut, spring and summer, selection for eastern aspects was also evident. Females selected higher elevations during the

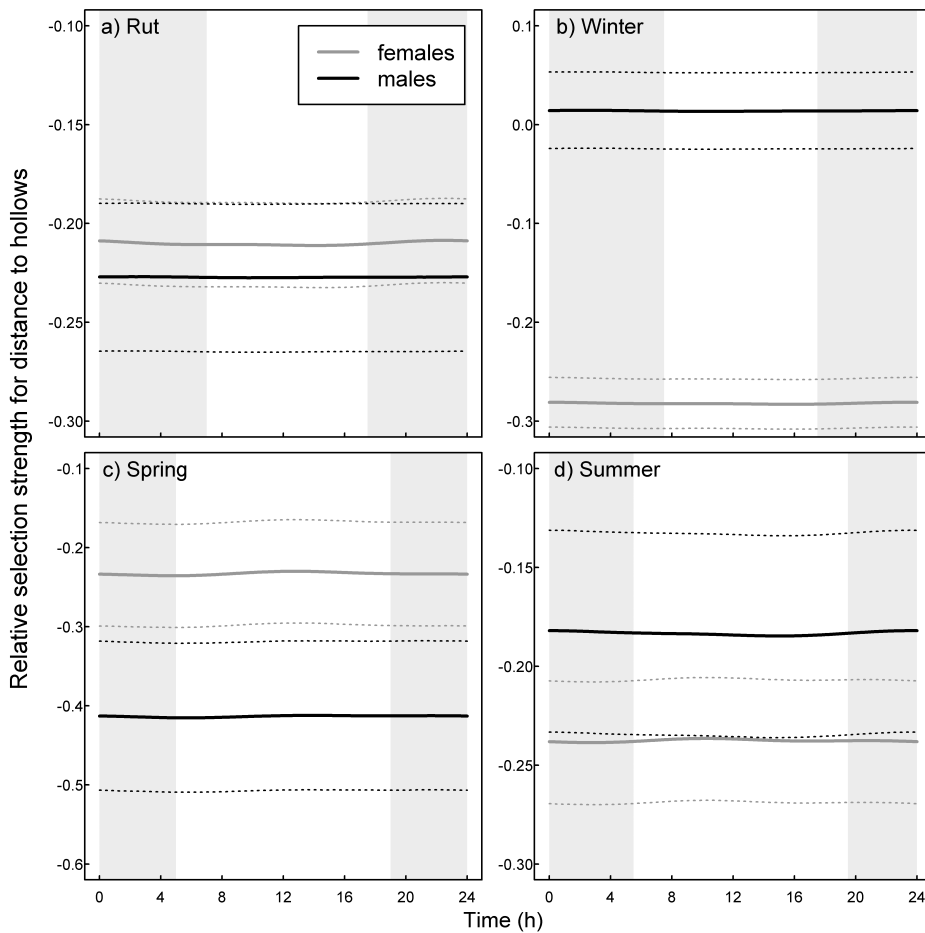
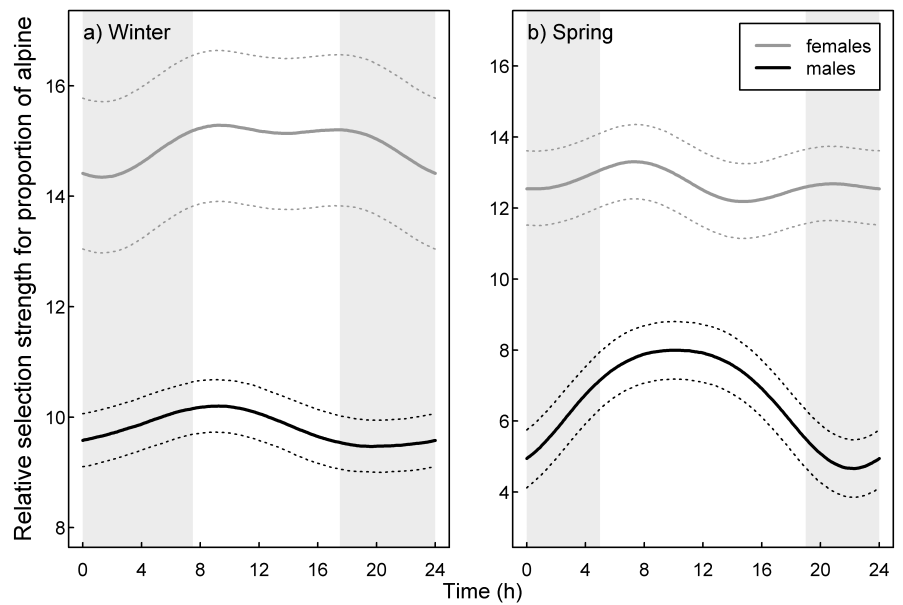


Figure 2. Strength of selection by male and female sika deer (*Cervus nippon*) for distance to hollows for all hours of the day during four distinct seasons in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 to March 2012. Dotted lines represent bootstrapped 95% confidence intervals around the median estimates (solid lines). Strength of selection was estimated using model coefficients presented in Tables 2 and 3. Areas shaded light grey represent hours of darkness determined from the times of sunrise and sunset for the date corresponding to the midpoint of each season in the hunting area (downloaded from <http://aa.usno.navy.mil/index.php>).

Figure 3. Strength of selection by male and female sika deer (*Cervus nippon*) for the proportion of alpine for all hours of the day during two distinct seasons in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 to March 2012. Dotted lines represent bootstrapped 95% confidence intervals (CIs) around the median estimates (solid lines). Strength of selection and CIs were estimated using model parameters presented in Tables 2 and 3, whereas proportion of alpine habitat was calculated within buffers of varying radii (see Table 1). Areas shaded light grey represent hours of darkness determined from the times of sunrise and sunset for the date corresponding to the midpoint of each season in the hunting area (downloaded from <http://aa.usno.navy.mil/index.php>).



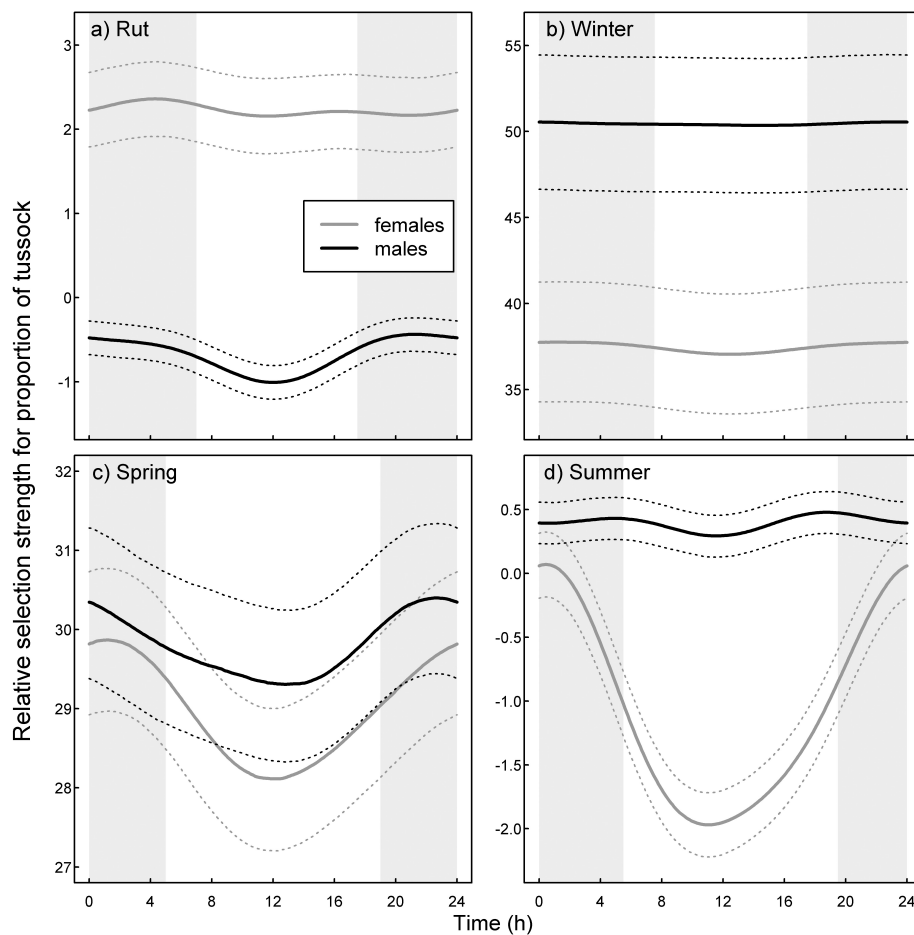


Figure 4. Strength of selection by male and female sika deer (*Cervus nippon*) for the proportion of tussocks for all hours of the day during two distinct seasons in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 to March 2012. Dotted lines represent bootstrapped 95% confidence intervals (CIs) around the median estimates (solid lines). Strength of selection and CIs were estimated using model parameters presented in Tables 2 and 3, whereas proportion of tussock habitat was calculated within buffers of varying radii (see Table 1). Areas shaded light grey represent hours of darkness determined from the times of sunrise and sunset for the date corresponding to the midpoint of each season in the hunting area (downloaded from <http://aa.usno.navy.mil/index.php>).

rut, but selected lower elevations during spring and summer. Selection for areas with high terrain ruggedness and steeper slopes was evident during the rut and winter. Females, like males, avoided areas with a higher proportion of alpine habitat during the rut and summer, but selected them during winter and spring. There was a weak trend towards increased selection for alpine during daylight hours in winter and at dawn during spring (Fig. 3, Appendix 3). Selection for beech forest and mānuka forest was evident during the rut, winter and spring, but these habitats were avoided during the summer. Shrublands were selected during winter and spring. Females showed strong selection for tussock during the rut, winter and spring. The strength of selection for tussock showed no discernible pattern during the rut or winter but, during spring, selection was highest during hours of darkness (Fig. 4, Appendix 3). During summer, females avoided areas with a high proportion of tussock during daylight hours, but used it in proportion to its availability during hours of darkness (Fig. 4, Appendix 3).

Discussion

Within their native range, sika deer are considered to be a species typical of woodland with dense undergrowth and adjacent open ground (Smith & Xie 2008; Mattioli 2011). In Europe, where they have been introduced and are widespread, sika deer similarly establish home ranges in areas with a mixture of forested-cover and open grazing habitat (Uzal et al. 2013). We found that sika deer in the Kaweka FP RHA also were associated with ecotones comprising dense forest and open

habitats (Davidson 1973a), though the strength of selection for these habitats varied with time of day, season and sex. Additionally, we found that some uncommon habitats, such as hollows, were strongly selected by sika deer during most of the year. To our knowledge, this is the first comprehensive analysis of seasonal and sex-specific resource selection for a deer species in New Zealand undertaken using GPS data and environmental variables derived from GIS.

Sika deer in the Kaweka FP RHA have historically been exposed to high predation pressure from recreational and helicopter-based hunters (Davidson 1973a; Davidson & Fraser 1991; Kerr & Abell 2014). Deer were targeted and killed primarily in open areas, such as grassy river valleys, open tussock faces and above the treeline, and this has likely shaped their current use of habitats (Fraser & Leathwick 1990). We found patterns of resource selection that similarly suggested male and female sika deer were attempting to maximise foraging opportunities while minimising predation risk in open areas. Sika deer showed strong selection for areas with a high proportion of tussock during spring, presumably in response to the new growth of forbs and grasses at that time of year (Davidson 1973b). However, the strength of selection for this open habitat differed significantly between day and night. Specifically, sika deer selection for tussock increased significantly in the early evening, remained high throughout the night, decreased significantly around sunrise, and remained low throughout the day (also see Mattioli 2011).

Additionally, both sexes selected tussock in winter, but unlike in spring, they showed no discernible daily patterns in the strength of selection for this habitat. Rather they tended

Table 3. Standardised parameter estimates (β) and standard errors (SE) for each explanatory variable explaining resource selection by female sika deer (*Cervus nippon*) during four seasons in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 – March 2012. Beta coefficients with 95% CI not overlapping zero are considered to have a significant influence on resource selection (indicated in bold). Selection for land-cover, topographic, and stream density variables is indicated by a positive coefficient, whereas selection for ‘distance to-’ variables is indicated by a negative coefficient. Parameter estimates (and SE) for interaction terms between some landscape variables and four harmonics of time of day are shown in Appendix 3.

Variable ^a	Rut (<i>n</i> = 7955)		Winter (<i>n</i> = 14 935)		Spring (<i>n</i> = 2828)		Summer (<i>n</i> = 10 935)	
	β	SE	β	SE	β	SE	β	SE
D hollow	-0.210	0.017	-0.282	0.013	-0.233	0.033	-0.238	0.016
D terrace	-0.032	0.045	-0.081	0.032	0.982	0.089	-0.162	0.029
D cover	-0.025	0.024	-0.037	0.019	–	–	–	–
D stream	-0.161	0.016	-0.112	0.011	0.265	0.031	–	–
Stream density	-0.344	0.031	-0.007	0.014	-0.210	0.044	-0.170	0.014
Aspect north-east ^b	-0.233	0.061	-0.101	0.045	0.195	0.114	0.300	0.057
Aspect east ^b	0.052	0.057	-0.199	0.042	0.364	0.113	0.520	0.051
Aspect south-east ^b	-0.001	0.053	-0.194	0.038	0.462	0.101	0.356	0.047
Aspect south ^b	-0.459	0.057	-0.506	0.039	-0.261	0.108	-0.035	0.049
Aspect south-west ^b	-0.114	0.053	-0.651	0.040	-0.189	0.103	-0.136	0.050
Aspect west ^b	-0.200	0.055	-0.497	0.040	0.091	0.100	-0.080	0.045
Aspect north-west ^b	-0.223	0.049	-0.455	0.036	-0.224	0.101	-0.126	0.043
Elevation	0.294	0.033	–	–	-1.662	0.080	-0.132	0.025
Slope	–	–	0.217	0.015	0.021	0.044	-0.009	0.017
Terrain ruggedness	0.063	0.016	–	–	–	–	–	–
P hollows	–	–	–	–	–	–	–	–
P terraces	–	–	–	–	–	–	–	–
P alpine	-0.804	0.074	14.943	2.030	12.700	1.526	-0.438	0.036
P exotic forest	–	–	–	–	–	–	–	–
P broadleaved hardwood	–	–	–	–	–	–	–	–
P beech forest	2.598	0.238	47.037	6.538	25.780	3.326	-1.460	0.131
P mānuka forest	2.580	0.227	46.630	6.468	31.250	3.840	-0.945	0.128
P shrubland	–	–	4.022	0.534	3.831	0.453	–	–
P tussock	2.231	0.204	37.452	5.150	28.980	3.568	-1.072	0.096

^a D = Distance to feature, in metres; P = Proportion within a buffer of varying radii (see Table 1) around a location

^b Categorical variable where reference category = Aspect north

to use open tussock-covered hillsides but only if they were in close proximity to forested cover (also see Takatsuki 1989; Chadwick et al. 1996), a pattern that may also have been driven by ground- and/or helicopter-based hunting pressure (Davidson 1973a). Alternatively, reduced use of tussocks away from forest during winter could be linked to an increased need for close proximity to thermal cover and decreased locomotory costs associated with deep snow in open areas, as has been shown for red deer (Forsyth et al. 2010). Although females also selected tussock during the rut, their strength of selection did not change noticeably across a 24-h period, nor was it related to distance to cover. Selection for tussock by females at this time of year may have been primarily driven by nutritional requirements; however, selection during daylight hours would also presumably make them more conspicuous, and thus easily observed by hunters. Interestingly, males generally avoided tussock during the rut, instead presumably encountering females for breeding opportunities most often in other habitats (particularly forested terraces). Sexual segregation in wild ungulates is common, particularly outside the rut, and has been linked to different reproductive strategies by males and females (Main 2008) and to population abundance (Forsyth et al. 2010).

Sika deer can negatively impact regeneration and growth of some plant species in native and plantation forests in New Zealand (McKelvey 1959; Allen & Allan 1997; Husheer & Robertson 2005) and in their native range (Takatsuki 2009).

We found that males and females selected mountain beech forest in winter and spring, and that females (and possibly males) also selected it during the rut. Although sika deer browse mountain beech saplings, which may retard regeneration of beech forests, these are not a preferred food (Husheer et al. 2003; Ramsey et al. 2012). In Kaweka FPRHA, preferred graminoids are most available seasonally (spring and summer), whereas preferred broadleaved plants are always scarce because of overbrowsing by abundant deer (Allen & Allan 1997). Thus, sika deer may have selected beech forest in winter because they were food limited, with sparse palatable food (such as deer-preferred edible litterfall) available to them at that time of year (also see Campos-Arceiz & Takatsuki 2005). Alternatively, food availability may not have been the primary driver for selection of beech forest. For example, they may have used beech forest as thermal cover, as has previously been shown for ungulates in temperate regions in winter (Forsyth et al. 2005; Cook et al. 2013). In these regions, ungulates often survive by metabolising fat reserves accumulated during spring–autumn and selecting habitats (i.e. forests) that minimise thermal costs. In addition, sika deer may have selected forests because it provided escape habitat from hunting pressure (as has been shown in other systems, e.g. Kilgo et al. 1998). Notably, they selected open areas such as tussock, and slips and gullies on hillsides (i.e. distance to hollow) when food was available in those areas, but primarily during hours of darkness and in areas close to tree or scrub cover. This could result in heterogeneous use of

beech forest, whereby deer use of beech forest decreases with increasing distance from an open habitat edge. If, in addition to resting, deer also feed when hiding in forest margins, then their impacts on forest regeneration in those areas could be disproportionately high.

Weather and aspect may also have influenced deer use of indigenous forest through two non-mutually exclusive mechanisms. First, plant species preferred by deer may be more common or palatable on some aspects than others and, second, deer may prefer some aspects over others because these provide shelter from adverse weather conditions (Igota et al. 2004). We found that deer preferred north- and east-facing aspects, and generally avoided south- and west-facing aspects that were more exposed to the prevailing cold weather patterns. This was particularly evident in winter when north was selected over all other aspects, a strategy that may have minimised exposure to severe cold temperatures and deep snow on colder faces (Davidson 1973a; Mattioli 2011). Comparable patterns of winter resource selection have been shown for many ungulates living in other temperate regions (e.g. Pearson et al. 1995). Selection for north-facing aspects by sika deer may explain why some unpalatable plants (e.g. *Pseudowintera colorata*) have been shown to increase in numbers in the presence of sika deer on north-facing aspects in Kaweka FPRHA (Husheer et al. 2003; also see Speedy 1992).

Male and female sika deer showed strong selection for some uncommon habitats/eco-types in Kaweka FP RHA. Hollows (slips and guts on hillsides and small creeks with clearings) were strongly selected by both sexes in all seasons except winter, when it was avoided by males. Although we did not determine the plant species associated with those habitats, deer likely selected them because they contained palatable species such as putaputawētā (*Carpodetus serratus*), wineberry (*Aristotelia serrata*), patē (*Schefflera digitata*), broadleaf (*Griselinia littoralis*), fivefinger (*Pseudopanax arboreus*), and many species of *Coprosma*, grasses and forbs (Husheer et al. 2003; Fraser 2005). These species are more palatable than mountain beech to sika deer (Husheer et al. 2003; Ramsey et al. 2012) and, although significantly overbrowsed in Kaweka FP RHA (Allen & Allan 1997), the biomass of these preferred plant species per unit area likely remains higher in hollows than in interior indigenous forest. Consequently, despite making up only c. 7% of Kaweka FP RHA, hollows are likely to be an important habitat for deer in this area. Selection for topographic landforms, such as hollows and spurs, has also been reported for red deer in the South Island (Forsyth et al. 2010). Strong selection for hollows may mean greater above- and below-ground impacts of deer in those areas and, consequently, we recommend that impact monitoring protocols be stratified to ensure sufficient data are obtained from these uncommon landscape features. This result also suggests that slips and forest openings associated with hollows might be good places to hunt deer, both because deer are commonly associated with these features (this study) and are often readily observable on slip faces and other openings (Forsyth et al. 2013).

Male sika deer showed strong selection for terraces during the rut, possibly because these areas provided defensible rutting territories, as well as habitat suitable to make scrapes in the ground in which they urinate or sometimes wallow to advertise their presence to other deer (Fraser 2005). Indeed, with the exception of hollows and streams, males avoided most other habitats during the rut, indicating their high fidelity to terraces. This pattern was further supported by our assessment

of optimal buffer sizes (Leblond et al. 2011), in which we found that during the rut smaller-sized buffers best contextualised habitats selected by males. We suspect that this was not related to the distances moved by individuals (which in some cases were quite large), but rather to their fidelity to a clearly defined geographical feature (terraces), which presumably provided a high number of mating opportunities. Male sika deer adopt many strategies that would result in high fidelity to these features during the rut, including defending rutting territories, collecting a harem, and even displaying lekking behaviour in some introduced populations (Bartoš et al. 1998; Fraser 2005). The strategy chosen by an individual would likely be dependent upon their ability to defend a territory with high mating opportunities. Presumably, less dominant individuals would be likely to travel more during the rut as they seek mates opportunistically, although mature males may also move large distances if they are following a female in oestrus (Fraser 2005). Transitioning into winter, male sika deer moved away from forested terraces, instead selecting other areas within exotic and indigenous forests, as well as mānuka, shrubland and tussock.

Our study used GPS data to describe patterns of resource selection by introduced sika deer from which we inferred potential impacts to native vegetation. However, a limitation of trying to identify habitats disproportionately used by deer is the resolution of available habitat layers. We used a version of the LCDB that had been corrected to reflect gaps in the forest canopy and open areas not captured by the original layer. This provided a one-off snapshot of the vegetation in the study area. It is likely that the resolution, both spatial and temporal, of this land-cover layer might not be detailed enough to reflect any fine-scale impacts of sika deer on specific plant communities; however, we believe that it is sufficient to formulate predictions about where such impacts might occur. We monitored 26 animals for a period of 15 months. This meant that we were unable to replicate each of the seasons we analysed and we do not know whether or not there is inter-annual variation in the selection patterns that we have reported. Despite this, Forsyth et al. (2010) found that resource use of red deer in the South Island did not change over a 5-year period, implying that, at least in some deer systems, inter-annual variation may be low. Further, our sample of collared animals was similar to what is often recommended for resource selection studies (Leban et al. 2001). However, when analysed separately by sex and season, the actual sample sizes (i.e. number of collared animals) decreased, even though there remained sufficient GPS locations to allow a high number of covariates to be included in models (Harrell 2001). Sample size limitations are difficult to overcome in most studies using GPS or satellite-based technologies, primarily because of high cost of the hardware and potential for units to fail before yielding data (Latham et al. 2015). In our case, this limitation means that we can only assume that the sample of collared animals is representative of the average population-level response for sika deer in Kaweka FP RHA.

Sika deer purportedly have a greater ability to digest fibrous plant material than most other deer species introduced into New Zealand (Fraser 1996), and this adaptation may increase the severity of their impacts to native vegetation (McKelvey 1959). Our findings have significantly increased our understanding of spatial and temporal patterns of selection by sika deer, and thus have improved managers' ability to identify where and when their impacts are likely to be highest and to determine where and when they will be most susceptible to helicopter-based control. Additionally, our results indicate

where recreational hunters are more likely to encounter sika deer during different times of the day and seasons. However, frequent use of a habitat by sika deer does not necessarily mean that a hunter will be most likely to kill a deer in that habitat, because deer may be more easily seen and shot in less frequently used habitats (Lima & Dill 1990). Our results do, however, indicate when sika deer most commonly use open habitats where they are usually most easily observed (Davidson 1973a), potentially increasing kill rates and hunter success in these areas. In summary, this study provides the first quantitative assessment of resource selection by any species of deer in New Zealand determined using GPS data in combination with environmental data, and demonstrates the utility of this approach for understanding fine-scale spatio-temporal patterns of habitat use for deer management.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Monitoring periods for 26 GPS-collared sika deer (*Cervus nippon*) in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, from December 2010 to March 2012.

Appendix S2. Standardised parameter estimates (β) and standard errors (SE) for interaction terms between landscape variables and four harmonics of time of day included in a model describing resource selection by male sika deer (*Cervus nippon*) in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 – March 2012.

Appendix S3. Standardised parameter estimates (β) and standard errors (SE) for interaction terms between landscape variables and four harmonics of time of day included in a model describing resource selection by female sika deer (*Cervus nippon*) in the Kaweka Forest Park Recreational Hunting Area, central North Island, New Zealand, December 2010 – March 2012.

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