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RESEARCH

Home ranges and movement of sika deer (*Cervus nippon*) in central North Island, New Zealand

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Abstract: Sika deer (*Cervus nippon*) were introduced into the central North Island, New Zealand, in the early 1900s. They rapidly established, increased in numbers, and extended their geographic range, eventually displacing sympatric red deer (*Cervus elaphus*). Sika deer are an important game species, but they can also severely damage native forest, especially where they occur at high densities. Here, we provide the first comprehensive assessment of annual and seasonal home range and movement ecology of adult male and adult female sika deer in New Zealand. Using kernel density estimation, we found that the average annual home range size of males (mean = 446.5 ha, SD = 273.0) was significantly larger than that of females (mean = 77.0 ha, SD = 48.6; Mann–Whitney $U = 6$, $p < 0.05$). This pattern was consistent across seasons, but was least pronounced in spring and most pronounced in autumn, when males seek mating opportunities. We found some males moved between non-overlapping seasonal ranges, whereas no females displayed this behaviour. On average, males used slightly higher elevations (c. 80 m higher) than females in all seasons, but there was high individual variability for both sexes. We did not find evidence that sika deer in central North Island make altitudinal migrations to avoid inclement weather in winter like sika deer do in colder regions of their native range. Information about home range and movement ecology can guide management strategies that aim to prevent further geographic spread of sika deer from their current range in the central North Island.

Keywords: GPS wildlife tracking; home range ecology; introduced deer; kernel density estimator; minimum convex polygon; seasonal home range overlap; seasonal migration; utilisation distribution

Introduction

Sika deer are an originally east Asian species of cervid. With the exception of Japan, where they remain common and widespread, sika deer have been extirpated from much of their native range (Mattioli 2011; Nugent & Speedy 2021). Introduced populations of sika deer occur in the British Isles (Pérez-Espona et al. 2009; Swanson & Putman 2009), continental Europe (Bartoš 2009), Russia (Aramilev 2009), North America (Feldhamer & Demarais 2009), and New Zealand (Nugent & Speedy 2021; also see Nugent et al. 2025). Within their native and introduced ranges, many populations of sika deer have hybridised with other subspecies of sika deer (Banwell 1999, 2009; Grubb 2005), or with closely related red deer (*Cervus elaphus*) (McDevitt et al. 2009; Smith et al. 2018). Hybridisation has implications for the conservation status of native populations of *Cervus* spp. (Biedrzycka et al. 2012) and could alter the ecology, and therefore the unwanted impacts and management, of introduced populations (Fraser 1996).

Sika deer were introduced into the Kaimanawa Mountains, central North Island, New Zealand, in 1905 (Donne 1924). The central North Island sika deer originated from Woburn Abbey Deer Park in England, and were initially thought to be the Manchurian subspecies (*C. n. mantschuricus*), but were subsequently found to be a mix of various subspecies of sika deer held at that park (Davidson 1973a; Banwell 2009). Red deer were also introduced to the central North Island during the late 1800s and early 1900s, and occurred sympatrically with sika deer (Nugent & Forsyth 2021). Although red deer were initially more widespread than sika deer, sika deer progressively expanded their geographic range, eventually becoming significantly more prevalent than red deer where their populations overlapped. For example, 10–20% of deer shot in official control operations in the Kaweka Range in the early 1960s were sika deer, whereas this percentage increased to 70% by the late 1980s (Davidson & Fraser 1991).

Currently, sika deer have largely replaced red deer in the Kaimanawa Mountains and Kaweka Range (Nugent & Speedy 2021). One explanation for this is that sika deer competitively displaced red deer by virtue of having a rumen morphology that is better able to digest the low-quality fibrous forage that is typical within their central North Island range (Fraser 1996). An alternative explanation is that red deer may have been more susceptible to being seen and shot in official control operations than were sika deer.

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To what extent sika deer and red deer have hybridised in the wild in New Zealand is largely unknown (Nugent & Speedy 2021). Although some sika deer may currently be hybrids in the central North Island, studies assessing the ecology of sika deer in this area have assumed, based on phenotype, that sampled deer are sika deer, not sika deer–red deer hybrids (e.g. Fraser 1996; Latham et al. 2015a, 2018).

Despite being present in the central North Island for about 120 years, some important aspects of sika deer ecology remain poorly understood. Their habitat use/selection has been reported (Davidson 1973b; Latham et al. 2015a), as have crude measurements of movement of marked (not telemetered) individuals (Davidson 1979). However, the home range ecology of sika deer in New Zealand has received scant attention, being reported only once, using annual 95% minimum convex polygons (MCP) (M.C. Latham, unpubl. analyses, reported in Nugent & Speedy 2021). The advent of GPS and satellite technology for tracking animals, and statistical methods for analysing location data, have enabled detailed assessments of home range and movement ecology (Latham et al. 2015b). For example, GPS collars have been used to assess home ranges and movement of introduced sika deer in the Czech Republic (Dvořák et al. 2014) and native sika deer in Japan (Takii et al. 2012; Takafumi et al. 2017; Laneng et al. 2023).

Overseas studies have found that the home range sizes of sika deer vary between and within sexes, that they often make long-distance movements between non-overlapping seasonal home ranges (especially males), and that populations in temperate mountainous areas often make altitudinal migrations (e.g. Takatsuki et al. 2000; Eyler 2001; Igota et al. 2004; Takii et al. 2012; Kalb et al. 2013; Kim et al. 2016; Dhakal et al. 2023; Laneng et al. 2023). This important information on home range ecology, movement between seasonal home ranges, and altitudinal migrations is lacking for sika deer in New Zealand. Understanding seasonal home range and movement ecology has important implications for understanding unwanted impacts caused by sika deer, and can aid management to mitigate these impacts (e.g. Kalb et al. 2013).

Here, we use GPS data collected from sika deer in the Kaweka Forest Park, supplemented with a lesser amount of VHF location data collected from the northeast Kaimanawa Mountains, central North Island, to describe home range and movement ecology of sika deer in New Zealand. Based on overseas studies on sika deer, we tested three predictions. First, we predicted that annual and seasonal home ranges of males would, on average, be larger than those of females. This could be driven by the greater nutritional requirements of larger-bodied males (especially for antler growth and post-rut when they gather fat reserves for winter), or be related to males seeking mating opportunities with multiple females during the rut (Dvořák et al. 2014; Reinecke et al. 2014). Second, we predicted that males would, on average, make larger seasonal migrations or movements between non-overlapping seasonal home ranges than females. This might also be related to moving between areas that provide mating opportunities and food accessibility or quality (McCullough 1985; Dvořák et al. 2014). Third, we predicted that sika deer in the central North Island would make altitudinal migrations. This could be driven by deer following food availability downslope during the winter and upslope in spring, and/or moving down from higher elevations because of high snow accumulation in winter (Takatsuki et al. 2000; Sakuragi et al. 2003; Igota et al. 2004; Yabe & Takatsuki 2009).

Methods

Study area

We conducted tracking of sika deer in the central North Island in two geographically separate locations within the greater contiguous sika deer population. First, we GPS-collared 30 sika deer in Kaweka Forest Park (39°16′ S, 176°21′ E) on the eastern side of the central North Island, New Zealand, between 2010 and 2012 (Fig. 1). The 59 000 ha Kaweka Forest Park was gazetted in 1974 and is managed by the New Zealand Department of Conservation (DOC). The vegetation in the park is comprised of forests dominated by mountain beech (*Fuscospora cliffortioides*), red beech (*Fuscospora fusca*), and podocarp species, and alpine areas containing herb fields and snow tussocks (*Chionochloa* spp.). Red tussocks (*Chionochloa rubra*) are common in river valleys on the northwest of the park. Eastern parts of the park have been affected by fires of anthropogenic origin and contain regenerating scrub dominated by mānuka (*Leptospermum scoparium*) and kanuka (*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). The highest point in the park is Kaweka J at 1724 m above sea level. Sika deer in the Kaweka Forest Park are hunted recreationally, subject to minor permit requirements. Sustained control operations using helicopter-based shooting have occurred since 1998 (targeting only females since 2009) (see Latham et al. 2015a, 2018; Nugent & Speedy 2021 for more details).

Second, we VHF-collared male sika deer in an area comprising the northeast Kaimanawa Mountains, the northern Kaweka Range, and the western Ahimanawa Range (general centroid location c. 39°02′ S, 176°17′ E) from 2009–2012 (Fig. 1). Hereafter, we use the term 'northeast Kaimanawa Mountains' to capture the geographic location where these three ranges converge. This study area was a mix of privately owned land, including farmland, and public conservation land managed by DOC. The vegetation and topographic relief within this study area were broadly comparable to those of Kaweka Forest Park. The northeast Kaimanawa Mountains were typified by rugged, forested mountains, with some scrub, tussock, and alpine herbfields (although these were less common in the northeast of the Kaimanawa Mountains than they were further to the southwest). The mountains are dissected by a number of large rivers. Beech trees, especially red and silver (*Lophozonia menziesii*) beech, dominate the forest at higher elevations in the northern portion of the Kaimanawa Mountains, whereas podocarp broadleaved forest dominates lower elevations. The elevational range in this area is c. 800–1500 m above sea level. Recreational hunting is also permitted in the DOC managed estate in the Kaimanawa and Ahimanawa mountains.

Deer capture and collaring

Between December 2010 and March 2011, we used nets fired from a Hughes 500D helicopter to capture sika deer in Kaweka Forest Park. We targeted open areas in tussocks, shrubs, and alpine environments, and gaps in the forest canopy to capture deer. Captured deer were identified as sika deer (rather than sika deer-red deer hybrids) based on their physical appearance. We physically restrained captured deer (i.e. we did not use anaesthetics) and fitted them with a store-on-board GPS 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

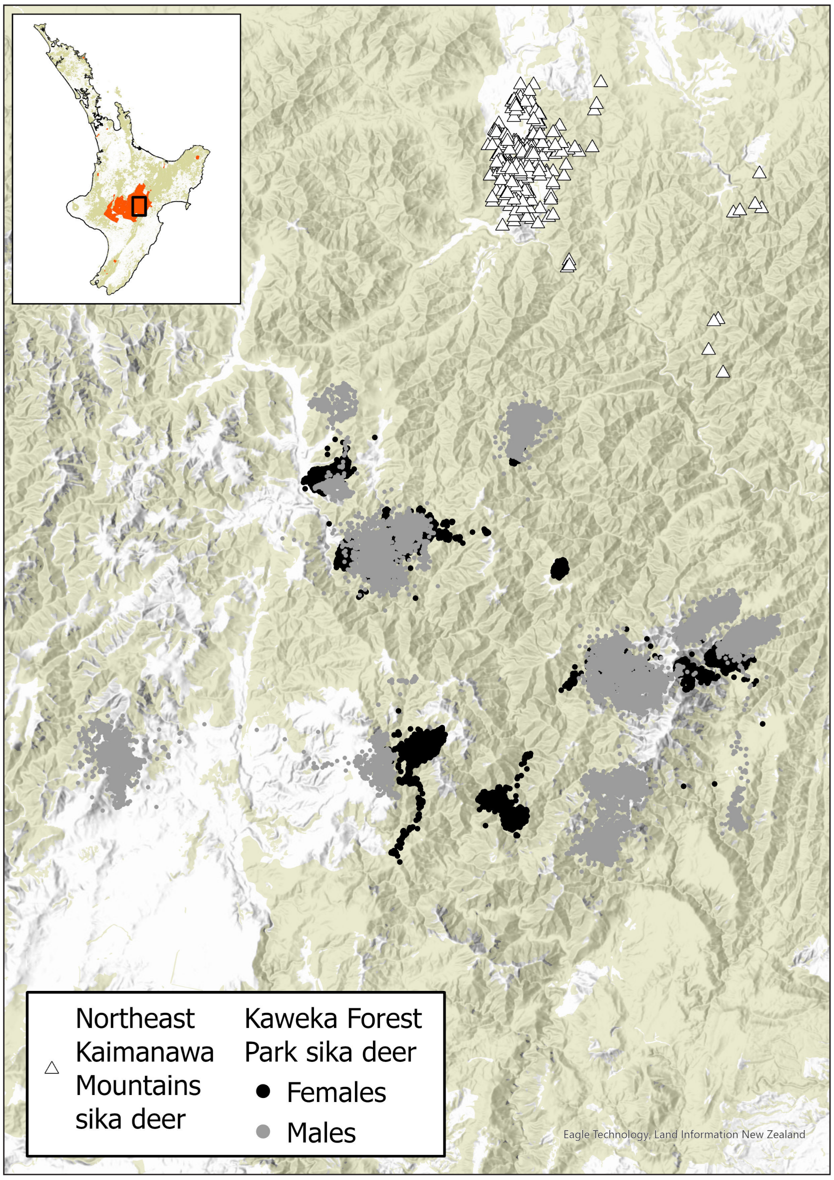

Figure 1. Locations of sika deer (*Cervus nippon*) collared in two study areas within the geographic range (red polygon in map insert) of the sika deer herd in the central North Island, New Zealand. The black and grey dots in the southern portion of the map correspond to 26 adult sika deer monitored between 2010–2012 in the Kaweka Forest Park. The white tringles in the northern portion of the map correspond to 15 adult male sika deer monitored between 2009–2012 within portions of three mountain ranges: the northeast Kaimanawa Mountains, northern Kaweka Range, and western Ahimanawa Range.

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 GPS locations that were beyond the possible range of sika deer movements or that produced abnormal movement spikes.

We applied the method of Bjørneraas et al. (2010) by using three consecutive filters to identify erroneous locations that needed to be omitted from further analyses. First, we identified impossible locations, i.e. those locations that were > 100 km from the median of the X and Y coordinates of the ten previous and ten subsequent locations. These points represented movement distances that sika deer could not travel in 30 minutes. Second, we identified unlikely locations, i.e. those points that were > 10 km from the mean of the X and Y coordinates of the ten previous and ten subsequent locations. Because 99.98% of the 30-min steps were < 10 km, larger movements were considered erroneous, despite being biologically plausible. Third, we examined for erroneous spikes, i.e. locations where outgoing and incoming speed exceeded 1.5 km in 30 min (99.87% of the 30-min steps were < 1.5 km) and the turning angle associated with that movement was larger than 165°. We visually assessed errors identified during screening to determine whether they were biologically plausible. Based on screening and subsequent visual assessment, 220 GPS locations (< 0.1% of the dataset) were considered to be erroneous and were removed from the dataset (also see Latham et al. 2015a). Additionally, we removed 635 GPS locations (0.23% of the dataset) from the day of capture. Based on stationary tests conducted prior to collar deployment, we estimated that GPS location error was a maximum of 30 m. The mean fix-rate success of GPS collars was 79% (SD = 14%), with males (mean = 82%, SD = 11%) having a slightly higher fix-rate success rate than females (mean = 78%, SD = 16%).

Between September 2009 and November 2010, we used nets fired from a Robinson R22 helicopter to capture sika deer on Poronui Station adjacent to the northeastern Kaimanawa Forest Park. We targeted open areas in grassland or cut-over plantation (pine and eucalyptus) forest to capture deer. Captured deer were identified as male sika deer (rather than female sika deer or sika deer-red deer hybrids) based on their physical appearance. We physically restrained captured deer (i.e. we did not use anaesthetics) and fitted them with a standard ungulate VHF tracking collar from Kiwi Track, Havelock North, Hawke's Bay. We estimated locations of radio-marked male deer by triangulation (minimum two fixes from different positions) and occasional physical sightings between two and three times per month while collars were functional. Where fixes could not be obtained from ground telemetry for two consecutive visits, aerial telemetry from a helicopter (Hughes 500D) or fixed-wing aircraft (Cessna 172) with wing-mounted aerials was used to provide coarse geographic locations that were subsequently followed up for ground telemetry.

We found that the recorded VHF locations were less accurate than the locations derived from GPS collars (e.g. Amelon et al. 2009). Based on those occasions when telemetered deer were physically sighted (c. 45 observations during the monitoring period) relative to the location that was derived from triangulation, we estimate that the linear error was between c. 50–200 m (the maximum estimated linear error was c. 200 m). Bartolommei et al. (2012) estimated the mean linear error for VHF telemetered roe deer (*Capreolus capreolus*) was about 43 m. This equates to an area error of 0.57 ha (Bartolommei et al. 2012). For our maximum linear error of 200 m, the area error would be c. 12 ha.

Home range and movement analyses

We used location data from GPS- and VHF-collared sika deer to describe annual and seasonal home range sizes. Home range estimates are sensitive to sample size and estimation method (Boyle et al. 2008). Therefore, we excluded individual deer for which we had fewer than 30 locations; however, we acknowledge that home range sizes might not be adequately described for animals with between 30–40 locations (Girard et al. 2002). This possible limitation was exclusively related to VHF-collared males, for which we had a limited dataset (11–53 relocations over the monitoring period).

We estimated annual 95% MCPs for all individuals for which we had > 30 locations. We also estimated annual and seasonal kernel density estimators (KDEs; Worton 1989) for the animals fitted with GPS collars. Our seasonal definitions were autumn, i.e. the rut or breeding season (16 March–31 May), winter (01 June–15 October), spring (16 October–15 December), and summer (16 December–15 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 (based on expert knowledge and visual inspection of the location data) and plant phenology.

We derived KDEs using the "amt" package (version 0.2.2.0; Signer et al. 2019) in R (version 4.4.2; R Core Team 2024). We used the KDEs to create a utilisation distribution (UD) for each GPS-monitored deer and then estimated home range area based on the 95% UD. Two key parameter choices need to be made to estimate the UD: the overall shape of the distribution of the animal's relocations (the density kernel) and the bandwidth (h). The bandwidth determines the smoothness of the kernel such that larger h values tend to result in unimodal UDs, whereas smaller h values result in multimodal UDs. We used a bivariate normal density kernel to represent the UD (Worton 1989). Because KDEs can differ based on the algorithm used to estimate the bandwidth, we tested three alternative methods: (1) the reference bandwidth, (2) the least-square cross-validation bandwidth, and (3) the plug-in bandwidth. We visually inspected the results of the different bandwidth estimation methods (as recommended by Worton 1989) and retained home range estimates obtained using the reference bandwidth approach. We chose the reference bandwidth because the outputs represented cohesive home ranges (i.e. unimodal UDs) rather than disjointed areas (i.e. multiple small polygons or multimodal UDs) of greatest use within a home range.

To assess migrations or movements between seasonal home ranges, we estimated KDEs for the GPS-monitored deer in Kaweka Forest Park for the seasons described in the paragraph above. For each individual deer, we calculated the area of overlap of pairs of seasonal UDs (i.e. spring vs. summer, spring vs. rut, and so on). If these areas of overlap were 0, we deemed the seasonal home ranges to be disjunct and estimated the straight-line distance between the centroid of each seasonal UD polygon.

To determine whether sika deer displayed altitudinal migrations between seasons, we collected the elevation, in metres above sea level, for each GPS location that we had for each of the GPS-collared deer in Kaweka Forest Park. Elevation was obtained from a 25 m resolution digital elevation model of the study area downloaded from the Land Information New Zealand data service (https://data.linz.govt.nz/data/). We subsequently summarised median elevation for each individual deer and statistically compared these values between sexes and seasons using a generalised linear model with a gaussian distribution. Pair-wise comparisons were performed using the package "emmeans" (version 1.11.1; Lenth 2023) in R.

Results

We GPS-collared 16 adult female and 14 adult male sika deer in Kaweka Forest Park between December 2010 and March 2011. Four of the GPS collars deployed on males failed shortly after deployment and did not provide useable data. We VHF-collared 15 adult male sika deer in the northeast Kaimanawa Mountains, six of which we excluded from subsequent analyses because they had < 30 relocations.

Home range sizes varied between study areas, sexes, and individual animals (Tables 1 & 2). The annual home range sizes of males estimated using 95% MCPs were, on average, larger at Kaweka Forest Park (mean = 1415.7 ha, SD = 1878.5, range = 215.6–5868.8 ha) than in the northeast Kaimanawa Mountains (mean = 252.0 ha, SD = 148.2, range = 72.0–479.1 ha). While collar type (GPS vs. VHF) can affect home range size estimates, the estimated maximum area error (12 ha) associated with VHF locations was well below the reported difference in home range size between sites. In Kaweka Forest Park, annual home range sizes (estimated using kernel density) were

Table 1. Individual annual and seasonal home range sizes (ha) estimated from GPS data from 26 adult sika deer (*Cervus nippon*) in Kaweka Forest Park, North Island, New Zealand, 2010–2012. 'Nb.days' represents the number of days that the animal was monitored. 'Nb.points' is the number of GPS locations obtained for that animal. Annual home ranges were estimated using 95% minimum convex polygons (MCPs) and 95% utilisation distributions of kernel density estimators (KDEs), whereas seasonal home ranges were estimated using only KDEs. Note: In deer ID tags, 'H' denotes hinds (females) and 'S' denotes stags (males), while the number represents the order in which individuals were collared and the lower case letter represents the area within the study region where the deer was captured.

Deer ID	Nb. days	Nb. points	Annual		Seasonal			
			95% MCPs	95% KDEs	Rut	Winter	Spring	Summer
H1a	389	17899	57.9	49.3	48.6	54.8	35.3	35.3
H1b	427	17620	141.4	95.9	73.2	68.0	85.8	77.7
H1c	260	10502	95.1	92.6	60.8	69.5	–	104.8
H1d	247	3564	66.4	70.7	66.5	73.6	–	54.2
H1e	273	10924	63.3	58.3	76.3	41.1	32.4	59.8
H2a	244	8369	39.4	39.5	41.7	37.5	–	33.9
H2b	284	10218	333.9	172.7	128.3	66.2	–	327.1
H2c	323	10822	107.0	91.9	108.3	87.5	62.9	50.5
H2d	154	5462	54.5	54.7	57.8	52.7	–	51.4
H2e	7	358	18.5	18.5	25.7	–	–	0.8
H3a	271	11582	88.2	61.0	66.1	35.7	31.9	62.5
H3b	189	6750	154.4	95.8	55.5	154.3	–	89.2
H3c	292	13010	269.6	196.9	119.1	185.9	85.9	338.9
H3d	16	712	33.1	34.6	17.9	34.9	–	–
H3e	32	1251	27.1	31.8	31.4	–	–	28.2
H3f	277	8563	92.5	67.7	80.9	44.0	30.3	23.3
S1a	126	4746	5868.8	899.5	591.2	240.1	–	462.3
S1b	355	13005	215.6	154.8	226.9	99.5	74.3	92.8
S1c	152	6547	866.9	597.9	783.2	199.6	–	122.7
S1e	31	1454	962.7	646.6	113.0	350.3	–	202.2
S2a	376	10036	247.7	143.2	200.9	129.0	47.2	51.9
S2b	406	17377	288.9	169.3	176.1	67.7	47.1	172.7
S2d	225	9338	729.7	384.1	744.6	137.1	114.5	41.9
S3a	124	4478	291.7	284.8	267.3	63.3	–	109.6
S3b	382	16808	947.1	787.0	870.9	546.3	475.7	588.1
S3d	360	14429	3738.2	397.1	246.0	222.5	39.5	75.5

Table 2. Individual annual home range sizes (ha) estimated from VHF data from nine adult male sika deer (*Cervus nippon*) in an area encompassing the northeast Kaimanawa Mountains, northern Kaweka Range, and western Ahimanawa Range, North Island, New Zealand, 2009–2012. 'Monitoring period' represents the time that the VHF collared deer was monitored. 'Nb.points' is the number of VHF points obtained for each VHF collared deer. Home ranges were estimated using 95% minimum convex polygons (MCPs). Note: we excluded six VHF-collared males for whom we had < 30 relocations.

Deer ID	Monitoring period	Nb. points	95% MCP
1	October 2009–November 2011	36	80.5
5	September 2009–April 2011	35	364.5
14	November 2010–June 2012	32	330.5
36	June 2010–June 2012	37	231.5
87	November 2009–June 2012	53	377.5
89	November 2009–June 2012	47	245.0
91	November 2009–August 2011	35	87.0
97	November 2009–June 2012	52	479.1
852	June 2010–June 2012	37	72.0

significantly larger for males (mean = 446.5 ha, SD = 273.0) than for females (mean = 77.0 ha, SD = 48.6; Mann–Whitney $U = 6$, $p < 0.05$ two-tailed). All annual home ranges of males were > 100 ha, whereas all but two home ranges of females were < 100 ha. This pattern was consistent when comparing between sexes over the four different seasons (Fig. 2), although the difference between male and female home range size in spring was not statistically significant ($U_{rut} = 2$, $p < 0.05$; $U_{winter} = 19$, $p < 0.05$; $U_{spring} = 11$, $p = 0.181$; $U_{summer} = 34$, $p < 0.05$). The home range sizes of females were similar across seasons (Kruskal-Wallis $\chi^2 = 1.30$, $p = 0.728$), but the home range sizes of males differed significantly between seasons (Kruskal-Wallis $\chi^2 = 10.978$, $p = 0.018$). The largest home range sizes of males were recorded during the rut (range = 113.0–870.9 ha), whereas the smallest home range sizes were recorded during spring (range = 39.5–475.7 ha). We found high variability in annual home range sizes (c. 72.0–479.1 ha) of males in the northeast Kaimanawa Mountains (Table 2).

We recorded migrations between non-overlapping seasonal home ranges for three males (Fig. 3; Appendix S1 & S2), whereas all females showed comparatively high home range site fidelity (i.e. their home ranges overlapped across all seasons; Appendix S1 & S3). For Kaweka Forest Park individuals S1a and S1e, disjunct home ranges were observed during the rut, whereas their winter and summer home ranges overlapped. Conversely, individual S3d had a home range in spring that did not overlap with the rut, winter, or summer ranges. The straight-line distance between non-overlapping home range centroids was 12 km, 9 km, and 4 km for S1a, S1e, and S3d, respectively. Interestingly, four additional males (S1c, S2a, S2d, and S3a) had comparatively large home ranges during the rut (Fig. 3). These ranges encapsulated the other seasonal home ranges of these individuals and also included large areas that were unused during the other seasons (at least during the period that we monitored them).

There was large variation between individuals in the median elevation used, with males, on average, using slightly higher elevations (c. 80 m higher) than females in all seasons (Fig. 4). However, the difference between sexes was not statistically significant ($\beta_{female\text{-}male} = 52.43$, $p = 0.1$). The median seasonal patterns of elevational use for males and females were similar, with both sexes showing a decrease in the median elevation used in spring. Overall, the difference in elevation used between seasons was not statistically significant ($\beta_{rut\text{-}winter} = 1.77$, $p = 0.99$; $\beta_{rut\text{-}spring} = 69.57$, $p = 0.49$; $\beta_{rut\text{-}summer} = -5.98$, $p = 0.99$; $\beta_{winter\text{-}spring} = 67.80$, $p = 0.52$; $\beta_{winter\text{-}summer} = -7.75$, $p = 0.99$; $\beta_{spring\text{-}summer} = -75.55$, $p = 0.42$). At the individual level, about half of the females displayed use of high elevation (c. 1100–1350 m a.s.l.) areas commonly used by males, but only one male used the lower elevations (< 950 m a.s.l.) that were often used by females.

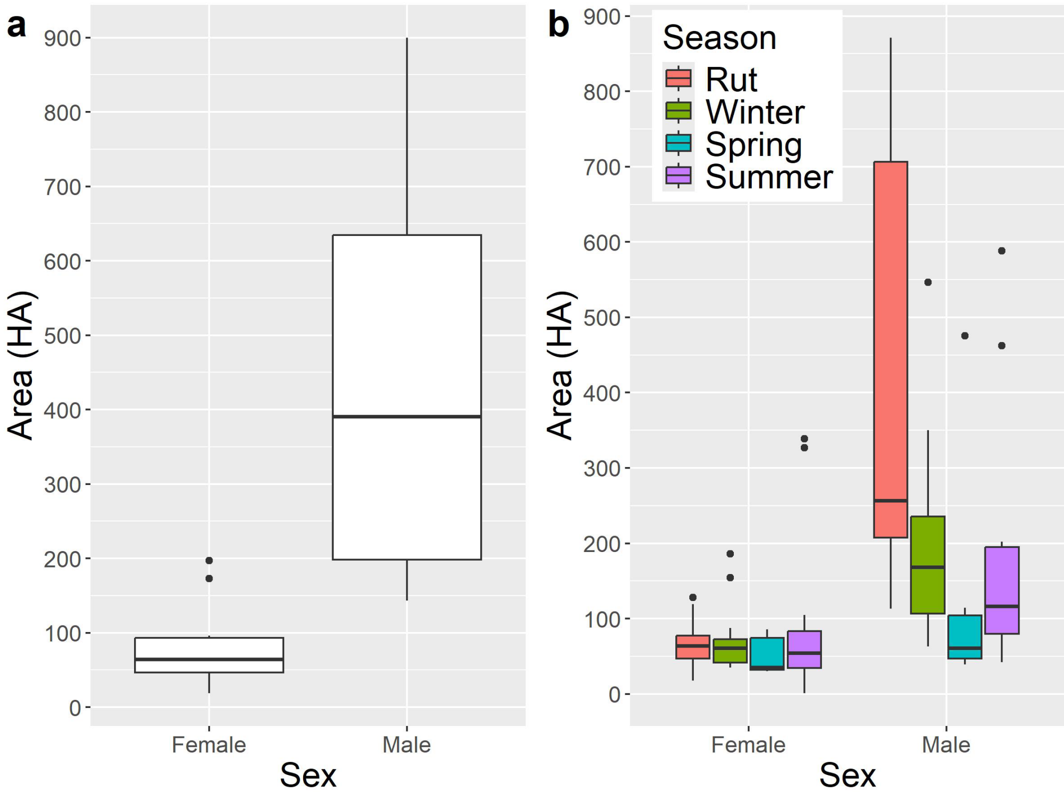

Figure 2. Box plots for the home range size of male and female sika deer (*Cervus nippon*) monitored using GPS-collars in Kaweka Forest Park, central North Island, New Zealand. Home ranges were estimated using the 95% utilisation distribution of a kernel density estimator. Annual home ranges were estimated using all location data available for each individual, 2010–2012 (a), as well as by splitting the location data into four seasons: rut (autumn), winter, spring, and summer (b). The median home range size is shown by the solid horizontal line in the box. The hinges represent the first and third quartiles (i.e. the 25th and 75th percentiles, respectively). The vertical lines (whiskers) extending from the hinges of the box represent the smallest and largest values no further than 1.5 times the inter-quartile range (i.e. the distance between the first and third quartiles, respectively). The black dots represent outlying points in the dataset.

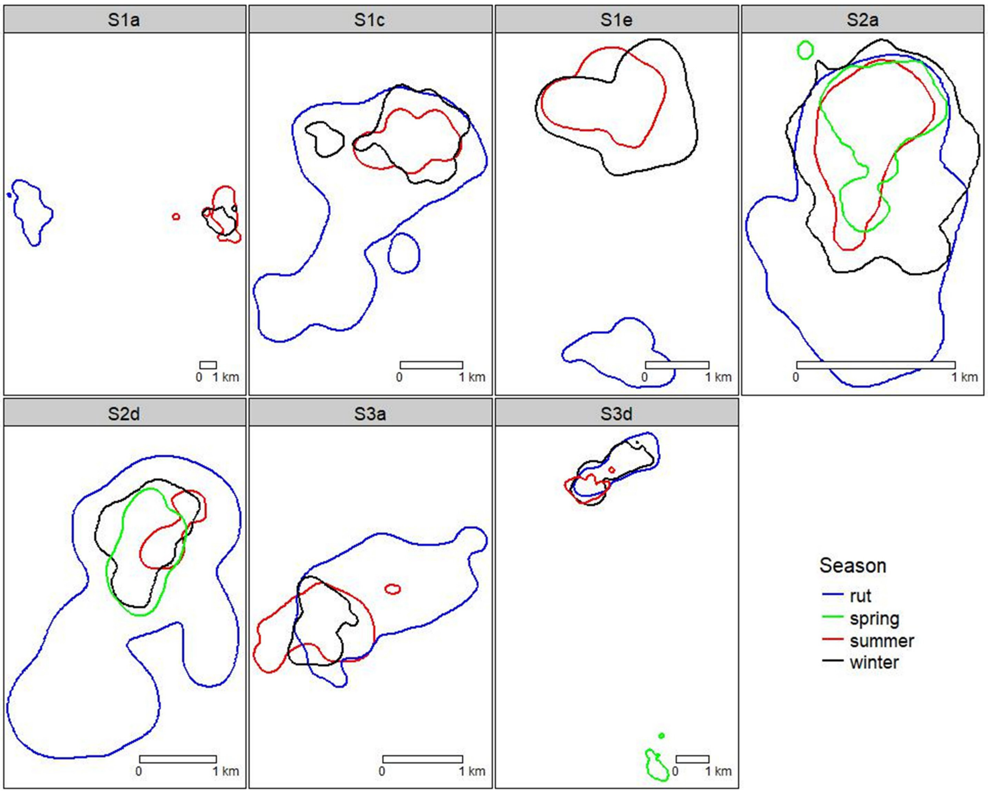

Figure 3. Seasonal home ranges for seven male sika deer (*Cervus nippon*) that displayed non-overlapping seasonal home ranges, or that showed enlarged home ranges during the rut (i.e. the breeding season in autumn). Individuals were monitored using GPS-collars in Kaweka Forest Park, central North Island, New Zealand, 2010–2012. Home ranges were estimated using the 95% utilisation distribution of a kernel density estimator.

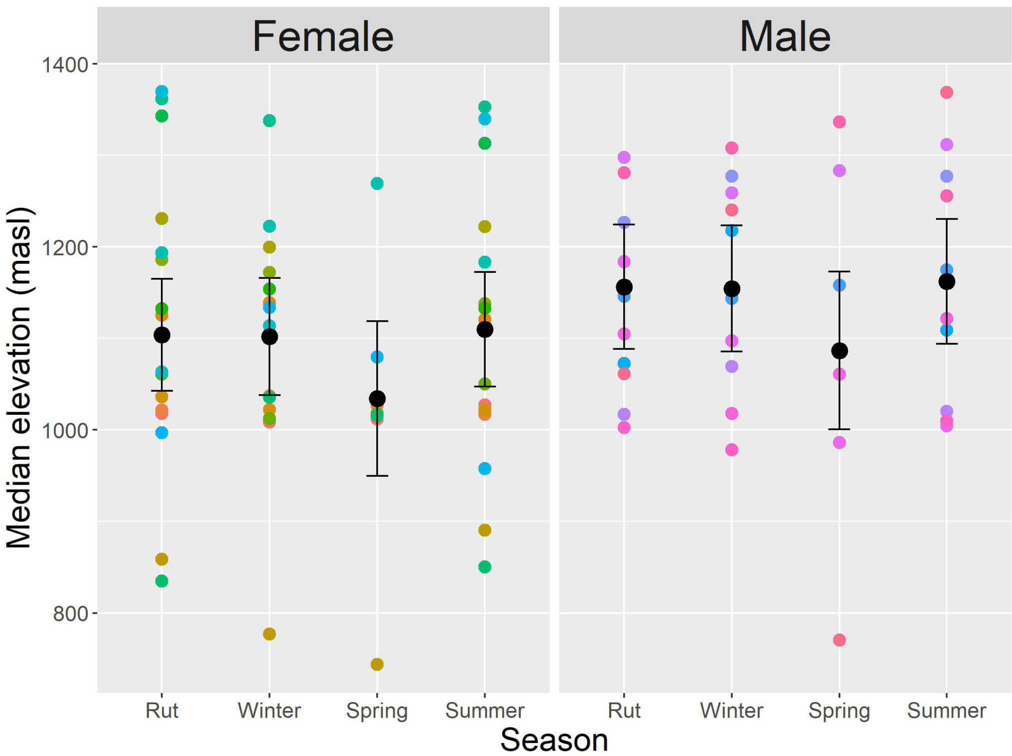

Figure 4. Median elevation recorded from 235 276 locations obtained from 26 GPS-collared sika deer (*Cervus nippon*; 16 adult females and 10 adult males) in Kaweka Forest Park, central North Island, New Zealand, 2010–2012. Elevation was summarised for each individual (different coloured dots) for each of four seasons (rut/autumn, winter, spring, and summer) and compared between sexes. Mean trends (black dots) were estimated using a generalised linear model with a gaussian distribution. Error bars show a 95% confidence interval for the predicted mean.

Discussion

We tested three predictions related to the seasonal home range ecology and movement of male and female sika deer in the central North Island, New Zealand. These predictions stemmed from overseas studies of both native and introduced populations of sika deer. Our aim was to determine whether sika deer in New Zealand displayed similar patterns of home range use and movement to overseas populations that have been studied, and to relate observed patterns to suspected drivers of movement and space use.

We found strong support for our first prediction, that annual and seasonal home ranges of males would, on average, be larger than those of females. Both annual and seasonal home range sizes were significantly larger for males, with the possible exception of spring, when the home range sizes of males were at their smallest (c. 75 ha, compared to a mean of c. 446 ha for the annual home range size of males using the KDE method; Fig. 2). The home range sizes of males were largest and most variable during the rut (autumn). The range for the 25th to 75th percentiles using the KDE method was c. 200–700 ha (Fig. 2). Only two females had annual home ranges > 100 ha in size (H2b = 173 ha and H3c = 197 ha). The remainder ranged from 19–96 ha (Table 1).

The difference in home range sizes of invasive male and female sika deer in Maryland, USA, was slightly lower than that reported in this study. Non-migratory males in Maryland had home ranges about three times larger than those of females (Eyler 2001), whereas they were about five and a half times larger in Kaweka Forest Park, although this included three males that made seasonal home range shifts. It is also well-established that the home ranges of males are much larger than those of females in Japan (Yokoyama et al. 2022) and South Korea (Kim et al. 2016). For example, the average home range size (based on 95% MCPs) was 294 ha (range = 108–417 ha) for males in Korea, whereas it was 153 ha (range = 76–293 ha) for females (see Table 2 in Kim et al. 2016; note that the abstract of the paper contains an error that contradicts this table). Most southern and coastal populations of female sika deer in Japan have small home ranges relative to most other native and introduced populations (either sex) that have been studied, e.g. seasonal home ranges of between 3.0 and 3.6 ha on Nozaki Island, Goto Archipelago (Endo & Doi 1996), and annual home ranges of between 10 and 20 ha on Kinkazan Island, northeastern Honshu (Yabe & Takatsuki 2009) and between 11.2 and 20.2 ha in the Tanzawa Mountains, central Honshu (Borkowski & Furubayashi 1998).

The sika deer population in Japan spans from c. 26° N in the southern subtropical part of the country to c. 44° N in the northern temperate region (Kobu 2014). The body weights of sika deer vary substantially from northern to southern Japanese populations, e.g. adult females weigh about 75 kg in Hokkaido, about 45 kg in central-eastern Honshu, and about 32 kg on Nozaki Island to the south of Kyushu (Kaji et al. 1988; Endo & Doi 1996). On average, heavier deer need home ranges that are larger than those of smaller-bodied conspecifics, as larger deer have greater nutritional requirements (Reinecke et al. 2014). Similarly, winter severity and seasonal food availability also vary from north to south (Endo & Doi 1996). Winters in Hokkaido and mountainous Honshu are comparatively severe, resulting in home ranges that need to be large enough to provide food throughout the year, or deer needing to make altitudinal migrations in search of food, especially dwarf bamboo (e.g. *Sasa* spp.), at lower elevations (Maruyama et al. 1976; Endo & Doi 1996; Takatsuki et al. 2000). Home range sizes also seem to be smaller for populations at high densities (50–310 km^{-2}) and that are geographically constrained, e.g. small islands (Kaji et al. 1988; Endo & Doi 1996; also see Kalb et al. 2013).

This complex, interconnected suite of factors affecting home range sizes and movement of sika deer in Japan may explain the comparatively large (non-migratory or nomadic) home range sizes of sika deer in the central North Island. Notably, the nutritional quality, and in some areas the availability, of browse and forage in the central North Island is low (Fraser 1996; Nugent & Speedy 2021). Moreover, the temperate, mountainous terrain (that occurs at a latitude of c. 39° S) of the central North Island is more similar to the northern parts of Japan, where sika deer have large home ranges and occur at lower densities (e.g. Maruyama et al. 1976; Endo & Doi 1996; Takatsuki et al. 2000). The estimated densities (16–20 deer km^{-2}; Husheer & Robertson 2005; Morriss & Nugent 2017) of sika deer in the central North Island are substantially lower than in areas of Japan where deer home range sizes are small (e.g. Endo & Doi 1996). Similarly, the mean weights of sika deer in the central North Island (mean for males = 62.5 kg, range = 41.0–82.5 kg; and mean for females = 49.5 kg, range = 36.5–70.0 kg; Davidson 1990) are in the intermediate to upper bracket of sika deer weights recorded from Japan. This suggests that, similar to northern Japan (e.g. Borkowski & Furubayashi 1998), the comparatively large home range sizes in the central North Island may be related to the nutritional requirements of comparatively large-bodied deer that occur in a temperate region with low-quality food (Reinecke et al. 2014). Nutritional quality and availability of food, in conjunction with breeding opportunities during the rut, will also likely influence the seasonal movements of males.

The smaller home ranges (based on MCPs) for males in the northeast Kaimanawa Mountains, relative to males in Kaweka Forest Park, could also be related to food availability. Some deer in the northeast Kaimanawa Mountains had access to forage on farmland, whereas the marked deer in Kaweka Forest Park did not. The high variability in home range size (c. 72–480 ha) for males in the northeast Kaimanawa Mountains appeared to be related to the availability of farmland in their home ranges. That is, males with the smallest home ranges tended to overlap, or were immediately adjacent to farmland. An alternative explanation is that the number of relocations obtained from some VHF collared individuals resulted in marginal sample sizes that did not adequately describe the full extent of home ranges (see Table 2). Nevertheless, males with the smallest home ranges had access to nearby pasture.

We found that males made larger movements between seasonal home ranges than did females, thereby providing support for our second prediction (albeit based on a small sample size of three individuals; also see Davidson 1979). This pattern primarily occurred during the rut when home ranges were either spatially distinct and non-overlapping with individuals' home ranges in winter, spring, and summer, or were so large that they encapsulated their winter, spring, and summer home ranges. The high variability in the rut home range size and movement of males could be related to differences in breeding strategies. For example, some males adopt breeding strategies that result in high site fidelity during the rut, e.g. keeping a harem, defending rutting territories, and even displaying lekking behaviour in some introduced populations (Bartoš et al. 1998; Fraser 2005; Endo 2009). Conversely, some males, perhaps less dominant individuals, might travel large distances during the rut as they seek mates opportunistically, or as they move large distances following a female in oestrus (Fraser 2005). This behaviour would produce the especially large rutting ranges (relative to other seasonal ranges) of some of our marked sample of males.

Males with rutting home ranges that overlapped their other seasonal ranges presumably also had prime areas of forage and browse within the greater area in which they sought mates, and did not need to move (migrate) to alternative feeding areas post-rut. Given that we did not have collars deployed over multiple years, we do not know if males that moved between non-overlapping ranges between the rut and other seasons did so consistently across years. Qualitatively, however, three males from the northeast Kaimanawa Mountains moved to rut ranges that were spatially segregated from their other seasonal ranges for the two years that they were monitored. In both years, the males moved to the same rut ranges that they had previously used; distances of c. 6 km, 7 km, and 14 km between their rut and non-rut ranges.

Male sika deer in the central North Island, similar to those in the Czech Republic (Dvořák et al. 2014), did not display significant seasonal migration, with the greatest linear movements being c. 12–14 km. In some parts of Japan, especially Hokkaido and central mountainous Honshu, male and female sika deer are reported to migrate average distances of about 15–35 km, which is variously attributed to factors including availability of winter forage, snow depth, and human disturbance (Igota et al. 2004; Takii et al. 2012). From a sample of 60 telemetered male sika deer in Maryland, USA, 14 deer migrations (average linear distance = 6.2 km) were observed between winter and summer home ranges; however, most deer were considered non-migratory (Kalb et al. 2013).

We did not find evidence to support our third prediction, that sika deer make movements to lower elevations to avoid deep snow in winter, as there were no significant seasonal differences in the median elevations used. However, our results showed that both males and females used slightly lower elevations during spring, albeit with high individual variability. A biological explanation for sika deer using lower elevations in spring is that green-up, on average, occurs earlier at lower elevations than it does at higher elevations (Piao et al. 2011), although other factors, such as aspect, will confound this relationship. Given that we only had one year's data to assess altitudinal migrations by sika deer, it is possible that altitudinal migrations in the central North Island might occur in years with atypically high snowfall that forces deer to lower elevations to find food, as has been found in some parts of native ranges (Takatsuki et al. 2000; Sakuragi et al. 2003; Igota et al. 2004; Li et al. 2006; Yabe & Takatsuki 2009). Snowfall in our study area in winter 2011 was not atypical, at least based on nearby historic weather data from Mount Ruapehu, which showed snowfall (c. 900 mm) was average or slightly above average (www.worldweatheronline.com; accessed on 18 September 2024). An alternative explanation is that sika deer in the central North Island do not make altitudinal migrations in response to inclement winter weather and that the small observed differences in elevational use in spring are not biologically significant.

Despite the importance of introduced sika deer as a hunting resource and the economic benefit associated with this (Kerr & Abell 2014; Nugent & Speedy 2022), sika deer can cause significant damage to native vegetation (Husheer & Tanentzap 2024). Although densities of sika deer need to be substantially reduced to mitigate this damage in some parts of the central North Island, preventing further geographic spread (natural and human-assisted) is also a key management strategy. The information provided in this current study shows that males make large movements, but females are less likely to do so (also see Davidson 1979). Davidson (1973a) reports an average annual dispersal distance by the central North Island sika deer population of 1.6 km from 1905–1962. These movement/dispersal distances suggest that the invasion front of the breeding population is a comparatively narrow band. Including the potential for long distance movements by males would substantially broaden the invasion front, but unless males encountered errant females well outside the breeding range, extraterritorial forays by males will not extend the breeding population. Controlling sika deer to moderate- to low-densities in a buffer at the periphery of their geographic range would further prevent/slow geographic spread, assuming that dispersal is density dependent. This could be done using a combination of recreational hunting and, in more inaccessible areas, formal hunter- or DOC-led sustained control operations.

Our results provide the first comprehensive assessment of annual and seasonal home range use by sika deer in New Zealand. We found that the patterns of home range and movement ecology of introduced sika deer in the central North Island were broadly similar to those of native and introduced populations of sika deer in other temperate, but not tropical, locations. Spatial and temporal patterns of habitat use by sika deer in temperate areas are likely driven by many of the same factors, e.g. seasonal food availability, searching for mating opportunities, and inclement weather. Information about home range sizes and movement distances may be important for management strategies that aim to prevent further geographic spread of sika deer from their current range in central North Island.

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Additional information and declarations

Author contributions: DH, MCL, CS, and ADML conceived the idea and designed the study. DH and CS carried out data collection. MCL and ADML conducted analysis, and ADML wrote the manuscript, with editorial contributions from DH, MCL, and CS.

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Data and code availability: The sika deer data from the Kaweka Forest Park can be accessed by contacting the corresponding author. The sika deer data from the northeast Kaimanawa Mountains cannot be shared as a condition of our access agreement.

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Supplementary Material

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

Appendix S1. Area of overlap between seasonal home ranges for 26 sika deer monitored using GPS collars in Kaweka Forest Park.

Appendix S2. Seasonal home ranges for ten male sika deer.

Appendix S3. Seasonal home ranges for 16 female sika deer.

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