Home range size and spatio-temporal dynamics of male sika deer (Cervus nippon; Cervidae, Artiodactyla) in an introduced population

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Abstract. The sika deer (*Cervus nippon*) is native to Japan and East Asia and has been introduced almost worldwide. Despite the wide distribution of the species, only few studies on its home range in non-native areas have been conducted. We focused on home range size and its seasonal and spatial dynamics in an introduced sika deer population in the Doupovské hory Mts., north-western Czech Republic. The mean home range size, obtained from ten subadult and adult males, was 3620 ha using the minimum convex polygon method, 1163 ha using the Brownian bridges method, and 819 ha using kernel estimation. The mean intra-individual home range overlap from month to month was about 72 %, but decreased to 28 % when calculated for three-month periods. The unusually large home range sizes observed can be explained by a relatively low population density of the sika deer in the study area and possibly by the non-territorial mating strategy of males. The high values of seasonal home range overlap together with the time series of the monthly home range maps indicate some positional shifts but do not support presence of seasonal migration.

Key words: GPS wildlife tracking, non-native species, population density, utilization distribution

Introduction

Home range, its size, structure, and dynamics, represents one of the basic ecological characteristics of a species. The concept of home range was introduced by Burt (1943) and since that many factors have been shown to influence home range size and pattern in animals (e.g. McNab 1963, Mysterud et al. 2001, Anderson et al. 2005). Among them, environmental factors (climatic conditions, landscape structure, availability of food, predation risk, disturbances etc.) play a significant role (for instance in mammals: artiodactyls Larter & Gates 1990, Borkowski & Furubayashi 1998, rodents Lagos et al. 1995, primates Singleton & van Schaik 2001, carnivores Herfindal et al. 2005). Also introduction of a species in to a new habitat may affect its home range characteristics, as it de facto means considerable changes in the above mentioned environmental factors. Home range characteristics of a species occurring in a non-native environment may thus be of major importance and

may provide important information on its invasive potential (Swanson & Putman 2009).

The sika deer, *Cervus nippon* Temminck, 1836, is a medium-sized deer species native in Japan, Korea, south eastern Siberia, eastern China, Taiwan, and possibly Vietnam (Aramilev 2009, Kawamura 2009, McCullough 2009a, b, McCullough et al. 2009). The species was widely introduced during the 19th and 20th centuries and it currently occurs in the British Isles, mainland Europe (from France to western Russia), New Zealand, and the USA (Banwell 2009, Bartoš 2009, Feldhamer & Demarais 2009, Swanson & Putman 2009).

Home range size and spatial activity of the sika deer have been extensively studied within the Japanese part of its native range (Endo & Doi 1996, Borkowski & Furubayashi 1998, Sakuragi et al. 2003, Li et al. 2006, Yabe & Takatsuki 2009 and references therein). As far as we know, only four studies have been conducted within the areas of its introduction: USA
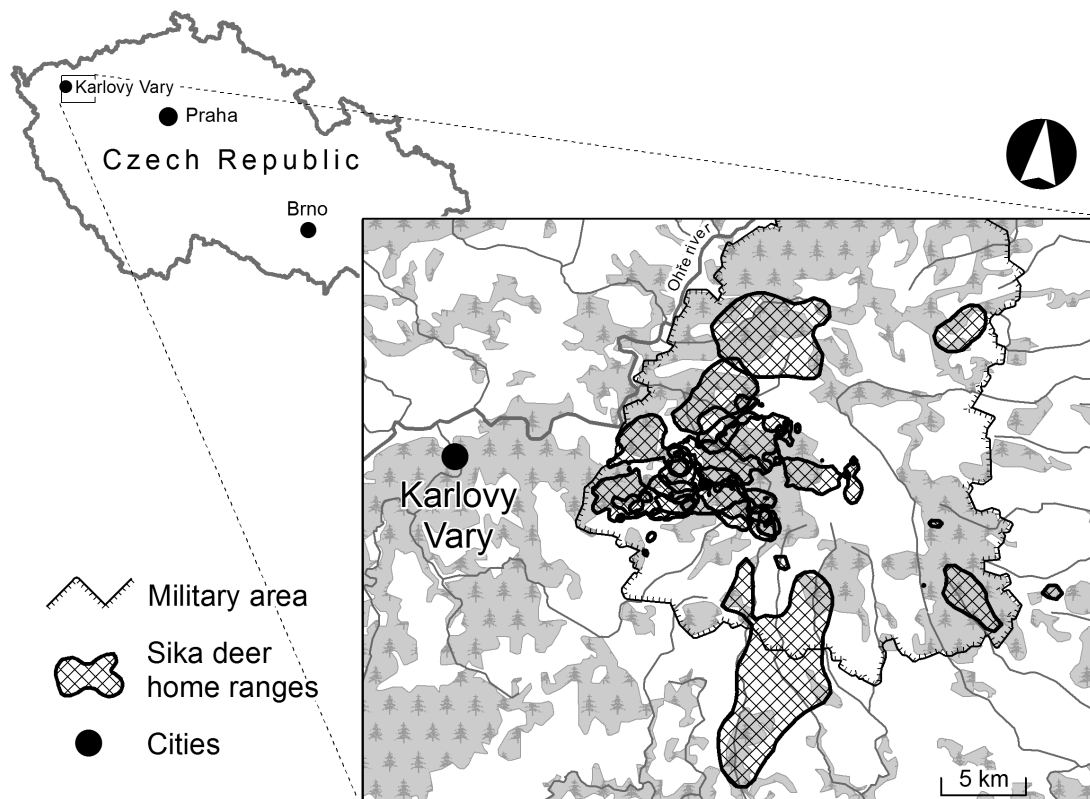
Fig. 1. Map of the study area with marked sika deer home ranges. Displayed home ranges are estimated using Brownian bridges method (see Material and Methods).

(Feldhamer et al. 1982, Kalb et al. 2013), England (Uzal et al. 2013), Ireland and Scotland – preliminary results mentioned by Swanson & Putman (2009). Moreover, majority of the studies were based on a low number of individuals – e.g. only a single male and a female in case of Feldhamer et al. (1982), but see Kalb et al. (2013); and all used the radio-tracking method. The GPS wildlife tracking, used in our study, provides some indisputable advantages in comparison to radio-tracking. Among them, usually an order higher number of animal locations and their higher accuracy are important, even though we are aware of the bias in the success of locations recorded in forest versus non-forest habitats (Graves & Waller 2006, Horne et al. 2007a). However, the most important advantage seems to be the regular recording of locations during the 24 hour period, as radio-telemetry in practice usually failed in this aspect and a substantial part of the previous home range studies is based only on data from a part of the day. For instance in the sika deer, Li et al. (2006), Kalb et al. (2013), and Uzal et al. (2013) used data collected regularly during the 24 hours, but Borkowski & Furubayashi (1998) and Sakuragi et al. (2003) used only daytime data and Endo & Doi (1996) did not provide information about time distribution of the sampling. Furthermore, the method of home-

range estimation suggested recently by Keating & Cherry (2009) enabled us to analyse and visualize the home-range spatio-temporal dynamics in great detail, depicting home-range size, its position and shape changes from month to month.

The main aims of our study were to: i) detect home range sizes of male sika deer in an introduced population using GPS wildlife tracking and ii) describe spatio-temporal dynamics of its home-ranges.

Material and Methods

Study area

The study was carried out in the Doupovské hory Mts., north-western Bohemia, the Czech Republic (ca. 50°16′ N, 13°7′ E; Fig. 1). The Doupovské hory Mts. are volcanic highlands with the area of 600 km² and elevation from 350 to 934 m a.s.l. The area consists of two parts, differing in various aspects. The central part of the mountain range (ca. 330 km²) is a military training area without any settlements. This area is comprised almost exclusively of broad-leaved and mixed forests, shrub formations, and meadows, each type covering approximately one third. The second, open access part of the mountains is covered by rural landscape, with patches of (in descending order of proportion) forests, meadows, fields, and – usually small – villages.

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Climatic conditions of the study area can be characterized as mild to cold with January and July mean temperatures varying with elevation from –4 to –2 °C and 15 to 19 °C respectively, annual precipitation from 650 to 1000 mm, and length of snow cover is from 40 to 120 days (Quitt 1971).

Occurrence of the sika deer in the Doupovské hory Mts. was first recorded in the mid-1960s. The first individuals migrated to this area from the Manětín region (western Bohemia), where sika deer had occurred in the wild since the Second World War (Bartoš 2009). In the first decades the abundance of the local sika population was low, but it gradually increased till the 1990s when the number of annually hunted individuals in the central (i.e. military) part exceeded two hundred. After that, sika deer abundance grew rapidly, currently estimated by the Military Forest Management to be 4000 to 6000 inds. – i.e. 12 to 18 inds./km^2 in the military training area (1500 inds. were hunted in 2012 – i.e. 25 to 37.5 % of estimated abundance; unpublished data of the Military Forest Management). Estimations of sika deer abundance are based on detailed counting of game in several ca. 100 ha areas and extrapolation of the data to the whole military area. Moreover, counts from winter enclosures and numbers of hunted individuals were also considered (Military Forest Management pers. comm.). Data for the open-access part of the Doupovské hory Mts. are not available as they are scattered among many hunting ground owners, but according to their reports, numbers of hunted individuals at these hunting grounds and our personal experience, the abundance seems to be lower. In the Doupovské hory Mts. sika deer occurs sympatrically with roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and partly also with fallow deer (*Dama dama*) and mouflon (*Ovis orientalis*). Natural predators are not present, but relatively intensive culling management (see above) is carried out from 1 September to 15 January. During the winter time, mainly from the end of November to the end of February, the game is provided with supplementary food – usually hay, silage, corn and beet. Feeding places are permanent and are evenly distributed with an approximate frequency of every 200 ha in the military area (unpublished data of the Military Forest Management) and even higher in the public part of the study area (own unpublished estimations).

Deer survey

Thirteen subadult and adult sika deer males (their estimated age based on tooth wear, body and antler size according to Wolf (1986) was 2 to 6 years, were equipped with GPS Plus collars (VECTRONIC Aerospace GmbH, Berlin) during the period 2009-2013. At first we used GPS Plus Collars 2D, later also the 3D and 4D types with GSM module. The collars are 600 to 980 g in weight, depending on the type, and they are able to record from 14940 to 52500 locations. The accuracy of the location, which in our case was

Table 1. Summary of home range sizes of the studied sika deer males (age of the animals refers to the time of collar attachment, MCP$_{0.95}$ – minimum convex polygon method, BB – Brownian bridges method, KC – Keating and Cherry's method). Bold values were not used in the calculation of the corresponding median, mean and standard deviation (see text for explanation).

Deer ID	Age (years)	Length of study (days)	MCP$_{0.95}$ (ha)	BB (ha)	Kernel$_{0.95}$ (ha)	Mean KC (ha)
7805	2	542	784.2	498.2	319.3	232
7806a	2	499	3681.6	554.8	458.5	254.1
7806b	4	238	238.5	175.6	114.3	90.6
7814a	2	603	2216.2	985.5	811.4	354.8
7817	4	182	890.1	579.9	294.5	287.2
8557	3	675	2982.7	1381.8	1079.3	385.5
8768a	5	415	1004.7	567.1	413.4	197.6
8768b	2	356	12670.9	1605.8	1401.2	270.1
8775	3	760	1744.6	453.2	283.3	139.8
9658	2	177	9986.4	4828.4	3017.8	423.3
7805b	2	**66**	**183.5**	**182.9**	**64.1**	**95**
11198a	6	**98**	**50.4**	**28**	**16.4**	**38.8**
11198b	3	**128**	**2163.6**	**728.3**	**536.2**	**284.9**
Mean ± SD		444.7 ± 195.5	3620.0 ± 4026.4	1163.0 ± 1292.1	819.3 ± 827.3	263.5 ± 100.0
Median		457	1980.4	573.5	435.9	232
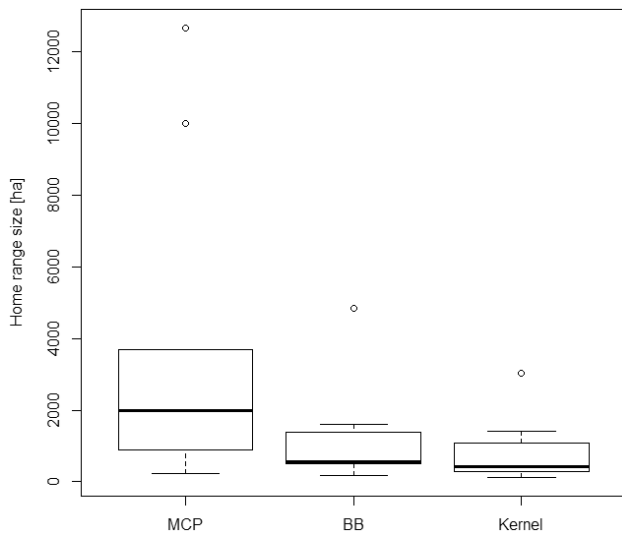
Fig. 2. Distributions of the sika deer home range sizes computed using the 95 % fixed kernel estimation, Brownian bridges (BB) and 95 % minimum convex polygon (MCP) methods (median indicated in bold).

automatically recorded every two hours, is about 5-10 m under optimal conditions and it is identical for all used collar types (VECTRONIC Aerospace GmbH pers. comm.).

The deer were immobilised by application of the ketamine-xylamine anaesthesia (Hellabrun mixture). Three millilitres of this mixture were injected into the muscles of a hind leg using an injection rifle (Pneu-Dart X-caliber Gauged CO_2 rifle; injections: Pneu-Dart 3.0 CC Type). Immediately after the deer became recumbent, it was fitted with a collar and basic data such as physical condition and age were recorded. After this procedure (usually less than 5 minute long), the deer were treated by intravenously applied antidote (yohimbine) and monitored until they recover and left the immobilisation site. The method was authorised by the Ethic committee of Czech University of Life Sciences, Prague; statement n. 0811. No animal was injured during the study.
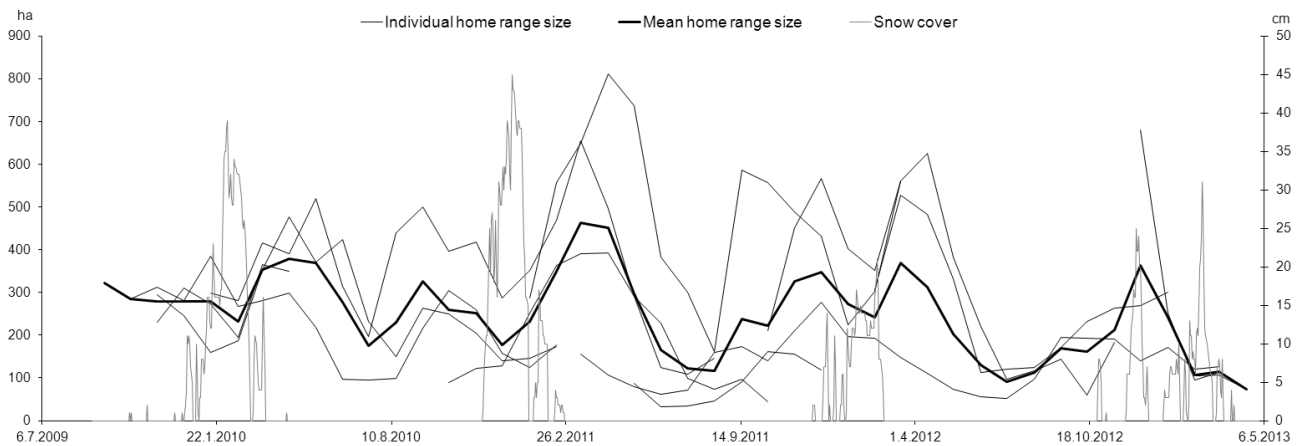
Fig. 3. Long-term variation of the individual sika deer monthly home range sizes, calculated using the KC method.
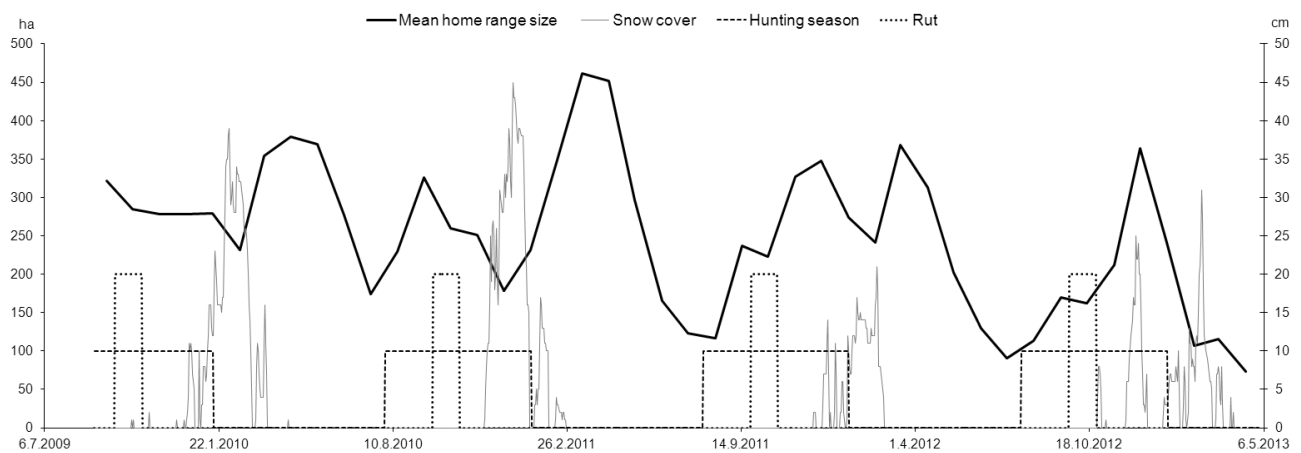
Fig. 4. Long-term variation of the sika deer mean monthly home range sizes (the same data as in Fig. 3) in relation to the depth of snow cover, hunting season and rut.

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Data management and statistical analyses

Before any analysis, we increased the accuracy of the positional data by removing all location estimates with the dilution of precision (DOP) greater than 6. This threshold was chosen arbitrarily, but in accordance with the range of values recommended in other studies (Lewis et al. 2007, Frair et al. 2010). Together with the location estimation failures, we reduced the original datasets by 1.6 to 25.4 percent, with the mean reduction (± SD) being 11.0 (± 7.1) percent. It is well documented that such a reduction can result in a considerable observation bias, as the locations under closed canopy cover and/or on steep terrain slopes are subject to higher DOP values (Lewis et al. 2007, Frair et al. 2010). Available correction techniques use the information about environmental conditions such as forest coverage to apply different probabilities of fix success to them (Horne et al. 2007b, Frair et al. 2010). Unfortunately, there is a lack of satisfactory map sources providing reliable information on canopy cover in the military area of the Doupovské hory Mts., particularly in the resolution we need. On the other hand, the use of the Brownian bridges approach for estimating the utilization distributions (Horne et al. 2007a, see below) can be also seen as a correction of the potential observation bias, as it effectively simulates movement trajectories between any two successive locations, and thus partially compensates for the missing observations (Frair et al. 2010). We therefore believe that not applying any explicit correction did not affect the resulting home ranges substantially.

We estimated home ranges of the sika deer using the Brownian bridges method (Horne et al. 2007b; referred here as the "BB" method). Regarding the biological assumptions inherent to it, this method has the same advantages over the traditional minimum convex polygon method as the well-known kernel method. This includes no assumptions about the shape and uni/multi-modality of the underlying utilization distribution and not over-emphasizing the less important observations near the distribution tails. Over the kernel method, it has an additional advantage of explicit dealing with the time-series nature of the data. This means that what presents a difficulty for the kernel method due to temporal autocorrelation is used as an important source of information in the Brownian bridges method, which makes the latter an appropriate alternative for GPS-telemetry data (Fischer et al. 2013).

We used 95 % volume contour for delineating the "life" home range (i.e. calculated from the whole observation period) from the utilization distribution

of each animal. The method has two key parameters: sigma1, the spatial variability related to the animal movement (i.e. a diffusion coefficient); and sigma2, the spatial variability caused by positional imprecision of GPS fixes. We estimated the sigma1 parameter using an approach suggested by Horne et al. (2007b), consisting in the maximum-likelihood estimation using intermediate locations. It means that only the odd observations were used as known positions (i.e. the "ends" of the Brownian bridges), whereas the even observations were used for the sigma1 parameter estimation (i.e. the "widths" of the Brownian bridges). Together with all the data reduction procedures mentioned above, this led to the mean (± SD) time interval between the odd observations being 5.1 (± 2.46) hours. We used the function liker from the AdehabitatHR package (see below for details on the software used) for the maximum-likelihood estimation of the sigma1 parameter. We set the value of the sigma2 parameter to 15 meters, which corresponds to the same positional accuracy of GPS fixes.

For facilitating comparisons of our results with older studies, we also estimated the home ranges using the minimum convex polygon method and using the fixed kernel method. The former was used with a correction for outliers consisting in the exclusion of 5 % of data points farthest away from the centroid determined as the arithmetic mean of the data points' coordinates (the technique mentioned e.g. in Worton 1995, Powell 2000; we refer to this method as "$MCP_{0.95}$"). For the fixed kernel method (Worton 1989; referred to as "K"), the smoothing parameter was estimated using the least squares cross validation technique, as suggested by Seaman & Powell (1996). Similarly to the BB method, also here we estimated the home ranges as 95 % volume contour from the utilization distribution.

To assess temporal dynamics of the home ranges, we adopted the methodology of Keating & Cherry (2009) (here referred to as the "KC" method). This methodology is based on the three-dimensional definition of utilization distribution, i.e. not only in two-dimensional space but also in time (and, if needed, also in the third spatial dimension), and estimates the utilization distribution using the product kernel method. We used the bi-weight kernel and treated the time as a linear variable (instead of a circular variable; see Keating & Cherry 2009). Apart from the spatial smoothing parameters (often called "bandwidths") commonly known from traditional kernel estimation methods (e.g. Worton 1989), the Keating and Cherry's method requires one additional, temporal smoothing

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parameter, to define the kernel "width" in the time dimension. We set both spatial smoothing parameters to 200 meters, and the temporal smoothing parameter to 30 days. Although the latter parameter was set so that the resulting home ranges would roughly represent the "month" estimates (see below), the former, spatial parameters were set only subjectively, by visual comparison of the resulting home ranges with the data (for justification of this approach for data exploratory purposes see Wand & Jones 1995 and Calenge et al. 2010). However, in the preliminary sensitivity analysis, we found this parameter to affect only the absolute values of home range sizes but not the structure of their relative differences in time.

The method enables to compute static two-dimensional "cuts" of the utilization distribution in predefined times, and thus to obtain standard-like two-dimensional distributions, from which the home range boundaries can be derived. In this manner, we estimated home range (as the 95 % volume contour) in the middle (i.e. 15th day) of each month during the whole study period for each animal. Finally, we plotted the time series of home range sizes into one plot, together with data on snow cover as well as the beginning and the end of the hunting season (1st of August to 15th of January) and peak of the rutting season (25th of September to 25th of October; unpublished data from 17 years of observation of the first author) so that we could display possible changes in home range size in relation to these factors. The snow cover data were obtained from the Czech Hydrometeorological Institute; Karlovy Vary station, 603 m a.s.l., ca. 11 km west from the centre of the studied area.

To quantify positional changes of home ranges over time, we estimated the overlap between any two successive utilization distributions calculated monthly using the Keating and Cherry's method (Keating & Cherry 2009). As a measure of the overlap, we used the Bhattacharyya´s affinity index as proposed by Fieberg & Kochanny (2005), who proved its benefits over other possible measures on simple illustrative
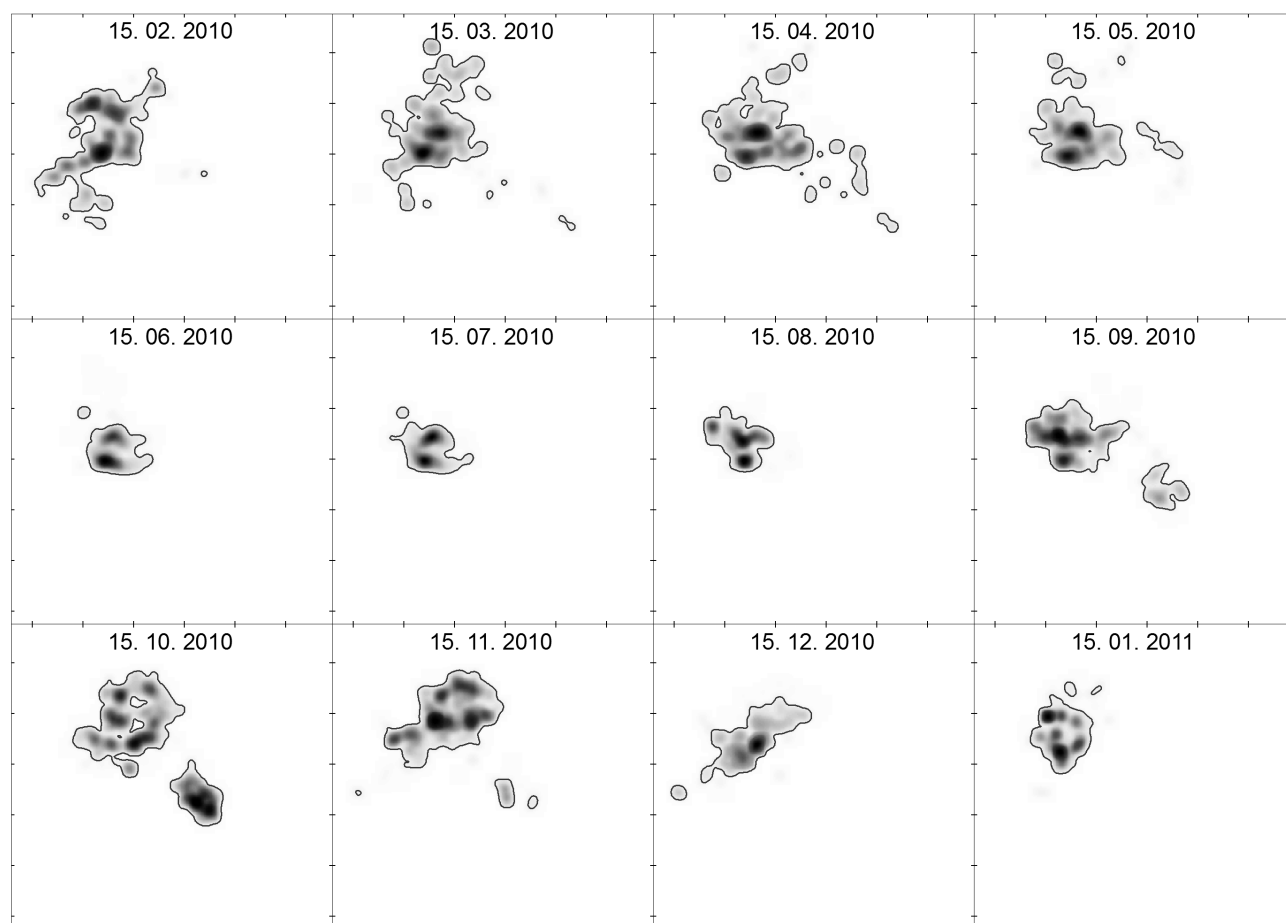
Fig. 5. Spatio-temporal dynamics of the monthly home range of the male 7805a, as an example of a "stable" behaviour. Twelve utilization distributions and 95 % home ranges, computed using the KC method, are displayed, covering the period from February 2010 to January 2011. The utilization distributions are in grey scale, with darker grey representing higher probability of occurrence. The corresponding 95 % home ranges are depicted as black solid lines. The marks on the borders are 1 km in width.

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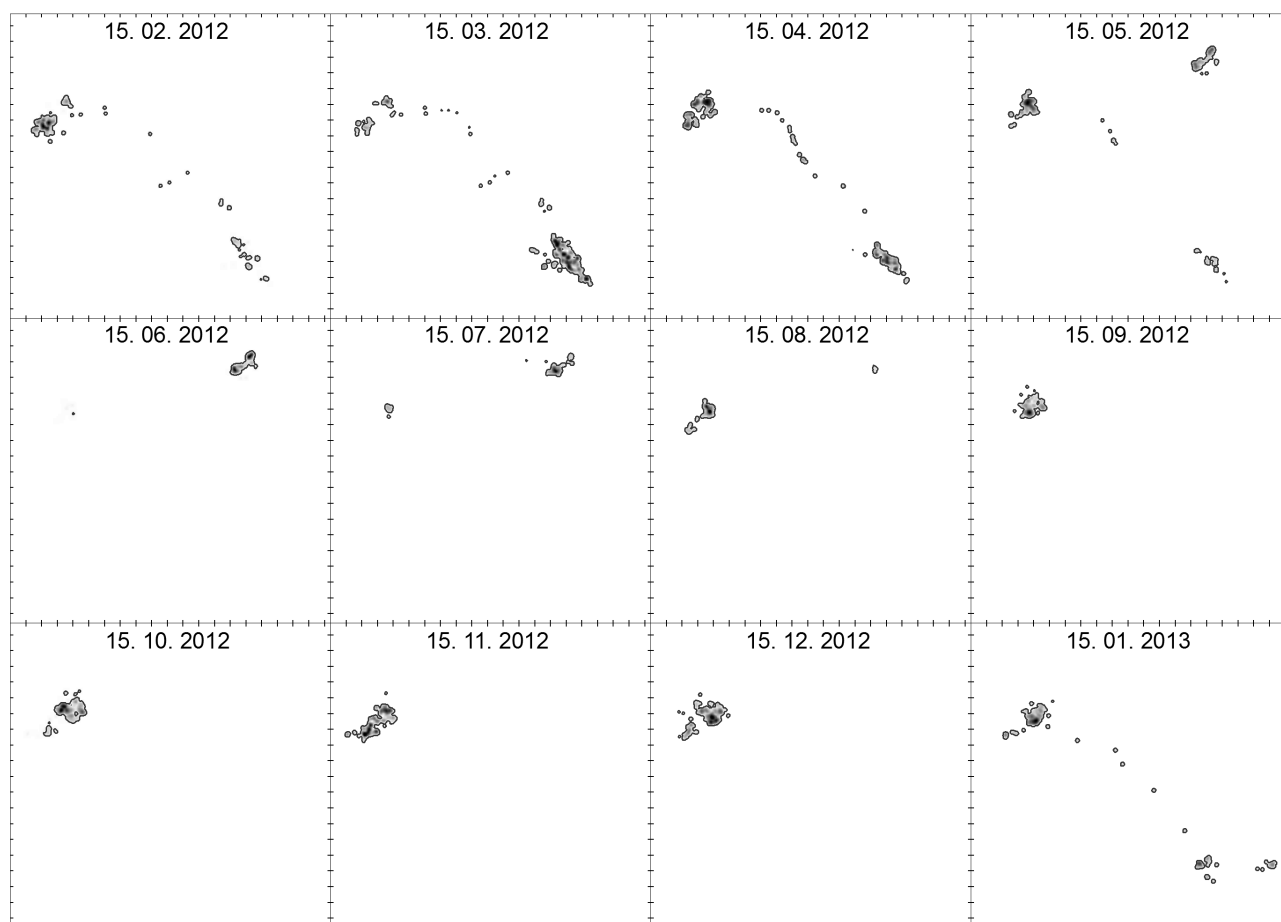
Fig. 6. Spatio-temporal dynamics of the monthly home range of the male 8768b, displaying periodical switches between three distinct patches. Twelve utilization distributions and 95 % home ranges, computed using the KC method, are displayed, covering the period from February 2012 to January 2013. The utilization distributions are in grey scale, with darker grey representing higher probability of occurrence. The corresponding 95 % home ranges are depicted as black solid lines. The marks on the borders are 1 km in width (note the different spatial scale than in Fig. 5).

examples (see their paper for the arguments as well as for the index formulation). We also calculated the overlap between January-April, April-July, July-October and October-January distributions, to assess the spatio-temporal dynamics on a larger temporal scale, as well as to ensure greater independence of the compared distributions (note that using the KC method, with the temporal smoothing parameter being 30 days, the successive distributions may be partly computed using the same data). The month pairs were chosen arbitrarily. However, January, April, July and October should represent periods of the year with different weather conditions and different stages of vegetation growth in the mild climatic zone. These months are also typically used in Czech climatic atlases (e.g. Quitt 1971, Hrnčiarová et al. 2009).

We performed all the computations using the R statistical programming language (R Development Core Team 2008), version 2.15, namely using the AdehabitatHR package (Calenge 2006), version 0.3.4.

For data manipulation and visualization, we used the Microsoft Office Excel 2003 (Microsoft, Redmond, WA, USA) and ArcGIS 9.3 (ESRI, Redlands, CA, USA).

Results

Data on home ranges were obtained for 13 males based on 66 to 760 days (mean 365 days, ca. 4380 locations) of observation. As the home range sizes calculated from the shortest data sets appeared to be unrealistically small when compared with the other values, we decided to set a minimum observation time of approximately six months as a criterion for inclusion of the dataset to the calculation of mean values. The exclusion of three individuals resulted in the mean observation length of 445 days (ca. 5340 locations on average), ranging from 177 to 760 days (see Table 1).

The mean home range size ($\pm$ SD) was 3620 ha $\pm$ 4026 ha (range from 239 to 12671 ha) using the $MCP_{0.95}$

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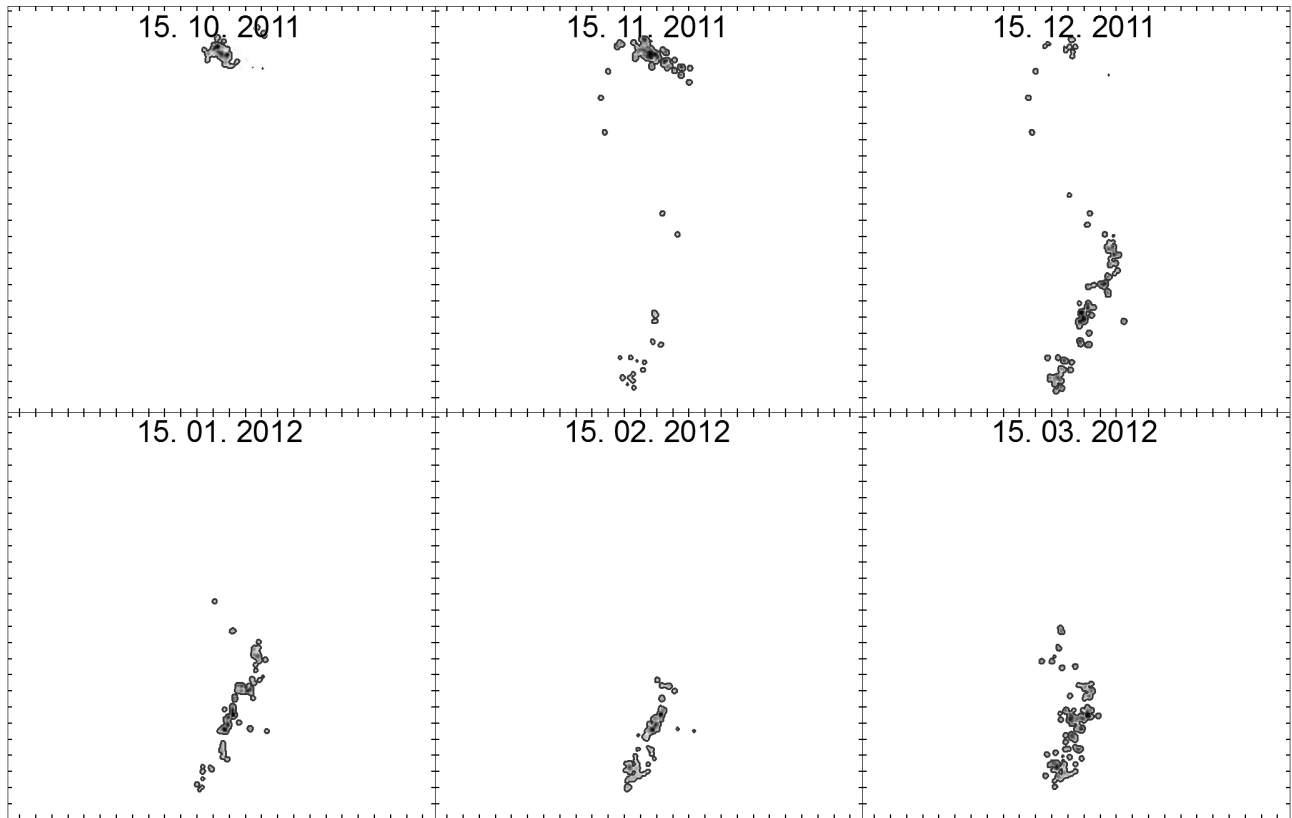
Fig. 7. Spatio-temporal dynamics of the monthly home range of the male 9658, recorded during a long distance movement. Six utilization distributions and 95 % home ranges, computed using the KC method, are displayed, covering the period from October 2011 to March 2012. The utilization distributions are in grey scale, with darker grey representing higher probability of occurrence. The corresponding 95 % home ranges are depicted as black solid lines. The marks on the borders are 1 km in width (note the different spatial scale than in Fig. 5).
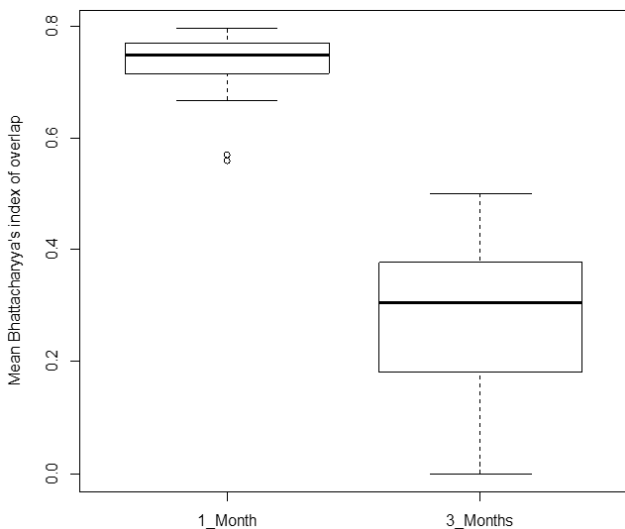
Fig. 8. Distributions of the intra-individual sika deer home range overlaps calculated using the Bhattacharyya's affinity index. The overlap is calculated from month to month (denoted as 1_Month method) as well as within three-month periods (i.e. between January-April, April-July, July-October and October-January utilization distributions; denoted as 3_Months method). The calculation is based on the utilization distributions estimated using the KC method (median indicated in bold).

method, 1163 ha $\pm$ 1292 ha (range from 176 to 4828 ha) using the BB method, and 819 $\pm$ 827 ha (range from 114 to 3018 ha) using the $K_{0.95}$ estimation (see Table 1). As expected, the $MCP_{0.95}$ method always produced considerably higher values than the BB and K methods (see Fig. 2). The monthly home range size calculated by the KC method varied individually from 91 to 423 ha with the mean ($\pm$ SD) being 264 $\pm$ 100 ha. The temporal dynamics (Figs. 3 and 4) also exhibited seasonal variations.

The spatio-temporal dynamics of the utilization distributions estimated using the KC method (Figs. 5 to 7) displayed both individual and seasonal variability. In most cases, the distributions were multimodal, resulting in home ranges consisting of one to three relatively stable distinct main patches (sometimes with a number of smaller patches around), usually one to three kilometers away from each other. In two individuals (nos. 8768b and 9658) the behaviour was slightly different. As shown in Fig. 6, the male 8768b occupied three distinct patches about 10 km away from each other. Although the BB method was able to capture this behaviour by creating multimodal

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utilization distribution and home range consisting of three main parts, the minimum convex polygon included the whole triangle between the three places, and thus mostly covered the area never visited by the deer. Similarly, the male n. 9658 was tracked during a movement between two distant patches (see Fig. 7), which resulted in the large home range estimate using all methods.

The relative spatio-temporal stability of most of the home ranges is also evident from relatively high values of the home range overlap during studied period (Fig. 8). The mean (± SD) value of the Bhattacharyya's index calculated for the pairs of subsequent months was 0.72 ± 0.07 (the range of individual means was 0.56 to 0.80, the absolute range was 0.24 to 0.98; n = 145 pairs in 13 inds.). As expected, the lowest overlaps were recorded for males with the largest home ranges (the males 8768b and 9658; see Figs. 6 and 7). In case of the three-month periods (i.e. comparisons between January-April, April-July, July-October and October-January distributions), the mean overlap was only 0.28 ± 0.13 (the range of individual means was 0.00 to 0.50, the absolute range was 0.00 to 0.78; n = 40 pairs in 10 inds.).

Discussion

Our study shows that male sika deer from an introduced population in north-western Bohemia use extensive home ranges, which exhibit some seasonal variability in size. There are some seasonal geographical shifts of home ranges; however, the deer do not display significant seasonal migration.

Most of the information about sika deer home range size comes from the species' native range. On the largest Japanese island, Honshu, home ranges of male deer reach 10 to 30 ha in the Shimane Prefecture, 40 to 70 ha in the Hyogo Prefecture, 50 to 80 ha in the Tanzawa Mts., 80 ha in the Nara Park, 70 to 140 ha in the Boso Peninsula, 150 ha in the Yamaguchi Prefecture, and 210 ha in the Odaigahara Mts. (Torii & Tatsuzawa 2009, Yabe & Takatsuki 2009 and references there in). A mean home range size of 192.52 ha calculated using the 95 % fixed kernel method (173.89 ha using $MCP_{0.95}$) was recorded in the Nikko National Park (Li et al. 2006). From the Kyushu Island, only a seasonal home range size of males is known with the mean of 50 ha (Yabe & Takatsuki 2009). The smallest home ranges were recorded in small island populations – for instance less than 100 ha in males from the Mage Island (Yabe & Takatsuki 2009), 10 to 20 ha in females from the Kinkazan Island (Yabe & Takatsuki 2009) or even 3 to 4 ha on the Nozaki Island (Endo & Doi 1996).

Outside Japan, data on home range sizes are available from the USA from the studies by Feldhamer et al. (1982) and Kalb et al. (2013), both focusing on young individuals. A single juvenile male studied by Feldhamer et al. (1982) was radio-tracked only during the summer months and its home range size was 182.5 ha (calculated by the harmonic mean method). Values reported by Kalb et al. (2013; 464 to 4121 ha) are generally congruent with our findings, although our study includes older males. As far as we know, the only other published data, describing sika deer home range size outside its native range, come from the British Isles (Swanson & Putman 2009, Uzal et al. 2013). Unfortunately, the published preliminary results (45 to 55 ha for adult and 60 to 70 ha for young males) from Ireland and Scotland are incomparable as no details on the methods used and the length of observation are provided in the publication by Swanson & Putman (2009) and the study by Uzal et al. (2013) from England focused only on females (mean home range sizes in two study areas were 87.37 and 107.76 ha, respectively).

Except for Kalb et al. (2013), all above mentioned values for males are about one order lower than our findings, but it should be noted that for example Li et al. (2006) and Feldhamer et al. (1982) carried out their studies only in a limited part of the year – in the summer season. In this case it may be more appropriate to compare their results with our mean monthly home range size (264 ha). The monthly home range size for both sexes in central Japan, specifically given by (Yabe & Takatsuki 2009), varies from 21 to 284 ha which is more or less congruent with our results. Nevertheless, it should be mentioned that the absolute value of monthly home range size in our study may be substantially biased by setting of the spatial smoothing parameters (see Methods).

If we compare our results with previous studies, the vast home ranges of sika deer observed in the Doupovské hory Mts. may have several explanations. The review by Yabe & Takatsuki (2009) showed that substantial variability in sika deer home range size depended on geographical and climatic conditions of the studied area. The variability is usually attributed to elevation and maximum snow depth, respectively, and thus migratory or sedentary life style of the deer (Yabe & Takatsuki 2009). Seasonal migration between two non-overlapping sites due to reduced food accessibility (McCullough 1985), typically under a snow cover, as known from some parts of the native area of distribution (e.g. Sakuragi et al. 2003, Li et al. 2006, Yabe & Takatsuki 2009), could

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be a possible cause of larger home ranges. Our data, however, do not clearly support this eventuality. Although the mean spatial overlaps of home ranges in the three-month pattern are much lower than those in the month-to-month pattern, they still are almost one third. Moreover, the maximum snow depth in the study area usually does not exceed 50 cm, which is thought to be limiting for sika deer locomotion (Takatsuki 1992) and which may be a possible break point between the sedentary and migratory life styles (Takatsuki 1992, Yabe & Takatsuki 2009). During winter months, game in the study area was provided with supplementary food, which may affect deer movements and home range size (Jerina 2012). The places where supplementary food is provided are distributed throughout the study area (see Material and Methods) and the sika deer are thus not forced to long seasonal migrations to fulfil their nutritional requirements. Based on our data, the sika deer in the Doupovské hory Mts. seem to be sedentary.

The two possible exceptions among the tracked animals, i.e. males with the largest home ranges and low home range overlaps (nos. 8768b and 9658), were recorded during long-distance movements between two or three distant sites (see Figs. 6 and 7). The limited length of observation, especially in case of the male no. 9658 (see Table 1), does not allow us to decide whether this behaviour is connected with their seasonal migration, dispersal from natal home range or whether they just possessed unusually large home ranges. Nevertheless, the periodical switches between two or more distinct (more or less distant) sites observed in several individuals including the deer 8768b (see Figs. 5 to 7) deserve further investigation, covering also local habitat data.

An alternative explanation of the large home range size of the sika deer recorded in our study may lie in a different, particularly low, habitat productivity of the studied area and wide dispersion of food sources (but see the opposite effect of winter supplementary feeding mentioned above) that may lead to extension of the home ranges. This was indicated by Endo & Doi (1996), Borkowski & Furubayashi (1998) and Uzal et al. (2013). Low habitat productivity/availability of food may be a possible reason of the observed seasonal changes in home range sizes (see Figs. 3 and 4), especially the enlargement of home ranges during spring when the deer need more energy for antler growth or after rut when they gather reserves for winter. By contrast, the late summer minimum of home range size may be related to high abundance of food and dense cover at the peak of the vegetation season (Borkowski & Furubayashi 1998). Also the winter minimum of home range size (Figs. 3 and 4) may be connected with nutritional requirements, particularly due to a limited rate of processing of the winter low-quality food available to large ungulates in the temperate zone that leads to the reduction of food intake and reduction of home range size (Irvin & Peak 1983, Clarke & Henderson 1984, Mysterud et al. 2001). Moreover, the winter home range size minimum is affected by supplementary feeding (see above), which possibly allows animals to meet their requirements almost at a single spot, and of course by higher energy expenses of locomotion in snow cover (Moen 1976). However, we do not expect that the lower productivity alone would lead to an order larger "annual" home range size, considering our preliminary data on females from the same area, which indicate much lower home range sizes – basically congruent with commonly reported values.

Another possibility is connected with population density of the deer and perhaps with male mating strategies. Among Cervidae it is usual that the size of an individual home range is negatively correlated with the density of individuals (e.g. Vincent et al. 1995, Kjellander et al. 2004, Jerina 2012). This effect is well pronounced in sika deer females where the lowest home range sizes were observed in very dense small island populations (Endo & Doi 1996). When compared to the published data (e.g. 10 to 40 inds./km^2 Mt. Ohdaigahara, central Japan – Ando & Shibata 2009; 27.6 inds./km^2 Kenting national park, Taiwan – Pei 2009; 11 to 12 inds./km^2 Lulworth, England; 14 to 44 inds./km^2 County Wicklow, Ireland; 42-45 inds./km^2 high density population in Scotland – Swanson & Putman 2009 and references there in; ca. 42 inds./km^2 Kinkazan island, Japan and ca. 56 inds./km^2 Mage island, Japan – Yabe & Takatsuki 2009 and references there in; 310 inds./km^2 Nozaki island, Japan – Endo & Doi 1996), the density of sika deer in the studied area is rather low and this alone may be a reason for the large home ranges.

Several mating tactics are known in sika deer males. They may maintain a "mating territory", keep a "harem", or use strategies such as "tending bond" and "sit and wait" (Endo 2009, Miami et al. 2009). The mentioned strategies may vary according to population density with a tendency of the "mating territoriality" to be positively related to the density. In low densities and diverse landscapes, the "tending bond" strategy (mating system where a male consorts an oestrus female) would thus be more advantageous (Miami et al. 2009 and references there in), and larger male

home ranges can be expected than in a population with territorial males. However, we observed no significant changes in home range size during the rut (see Fig. 4), which means that this explanation is not absolute. Moreover, most of the males in our study are below the age typical for dominant territorial males – 5 to 13 years according to Miami et al. (2009) – and thus their typical mating behaviour may have not become evident so far.

Home range size and spatial activity of deer is affected by human disturbances (Edge & Marcum 1985, Jeppesen 1987, Borkowski & Furubayashi 1998, Jerina 2012, Uzal et al. 2013), however, their impact can be different. Deer usually become accustomed to disturbances that are not in a direct conflict with them, such as traffic or other noise and light effects (e.g. Edge & Marcum 1985, Jeppesen 1987). This kind of disturbance typically does not affect home range size, but it does influence its spatial position or behaviour of the animals as they may for instance use the affected area only nocturnally (Jeppesen 1987, Uzal et al. 2013). Military training, which is intensive but occurs at the limited and relatively small invariable places of shooting ranges, and traffic thus probably have only a negligible effect on the home range size. On the contrary, the impact of disturbance caused by intensive hunting may be substantial. In areas where the deer are regularly hunted, their flight distances are longer (de Boer et al. 2004), they avoid open habitats (Kilgo et al. 1998) and their home ranges are significantly larger (Jeppesen 1987). Although our sample size precludes statistical testing, there seems to be a trend to enlarge home range during the hunting season (see Fig. 4 – especially the hunting seasons of 2011 and 2012).

In conclusion, our research showed that sika deer males from the introduced population in north-western Bohemia use vast annual home ranges, but they do not display significant seasonal migration. We suggest that the explanation of the unusual home range size may lie in the low population density and possibly in male mating system. However, future research, focussed especially on females and older males, is needed.

Acknowledgements

Literature

Anderson D.P., Forester J.D., Turner M.G., Frair J.L., Merrill E.H., Fortin D., Mao J.S. & Boyce M.S. 2005: Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecol. 20: 257–271.*

Ando M. & Shibata E. 2009: Bark-stripping preferences of sika deer and its seasonality on Mt. Ohdaigahara, central Japan. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 207–216.*

Aramilev V.V. 2009: Sika deer in Russsia. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 475–499.*

Banwell B.D. 2009: Sika deer in New Zealand. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 643–656.*

Bartoš L. 2009: Sika deer in continental Europe. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 573–594.*

Borkowski J. & Furubayashi K. 1998: Home range size and habitat use in radio-collared female sika deer at high altitudes in the Tanzawa Mountains, Japan. *Ann. Zool. Fenn. 35: 181–186.*

Burt W.H. 1943: Territoriality and home range concepts as applied to mammals. *J. Mammal. 24: 346–352.*

Calenge C. 2006: The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model. 197: 516–519.*

Calenge C., Guillemain M., Gauthier-Clerc M. & Simon G. 2010: A new exploratory approach to the study of the spatio-temporal distribution of ring recoveries: the example of teal (*Anas crecca*) ringed in Camargue, Southern France. *J. Ornithol. 151: 945–950.*

Clarke C.M.H. & Henderson J.R. 1984: Home range size and utilization by female chamois (*Rupicapra rupicapra*) in the Southern Alps, New Zealand. *Acta Zool. Fenn. 171: 287–291.*

De Boer H.Y., Van Breukelen L., Hootsmans M.J. & Van Wieren S.E. 2004: Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. *Wildlife Biol. 10: 35–41.*

Edge W.D. & Marcum C.L. 1985: Movements of elk in relation to logging disturbances. *J. Wildlife Manage. 49: 926–930.*

Endo A. 2009: Variation in mating behavior of sika deer: mating behavior of sika deer on Nozaki Island. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 285–296.*

Endo A. & Doi T. 1996: Home range of female sika deer *Cervus nippon* on Nozaki Island, the Goto Archipelago, Japan. *Mamm. Study* 21: 27–35.

Feldhamer G.A. & Demarais S. 2009: Free-ranging and confined sika deer in North America: current status, biology and management. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 615–641.*

Feldhamer G.A., Dixon K.R. & Chapman J.A. 1982: Home range and movement of sika deer (*Cervus nippon*) in Maryland. *Z. Säugetierkd. 47: 311–316.*

Fieberg J. & Kochanny C.O. 2005: Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildlife Manage.* 69: 1346–1359.

Fischer J.W., Walter W.D. & Avery M.L. 2013: Brownian bridge movement models to characterize birds' home ranges. *Condor* 115: 298–305.

Frair J.F., Fieberg J., Hebblewhite M., Cagnacci F., DeCesare N.J. & Pedrotti L. 2010: Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philos. T. R. Soc. B. 365: 2187–2200.*

Graves T.A. & Waller J.S. 2006: Understanding the causes of missed global positioning system telemetry fixes. *J. Wildlife Manage. 70: 844–851.*

Herfindal I., Linnell J.D.C., Odden J., Nilsen E.B. & Andersen R. 2005: Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *J. Zool. (Lond.) 265: 63–71.*

Horne J.S., Garton E.O. & Sager-Fradkin K.A. 2007a: Correcting home-range models for observation bias. *J. Wildlife Manage. 71: 996–1001.*

Horne J.S., Garton E.O., Krone S.M. & Lewis J.S. 2007b: Analyzing animal movements using Brownian bridges. *Ecology 88: 2354–2363.*

Hrnčiarová T., Mackovčin P., Zvara I. et al. 2009: Landscape atlas of the Czech Republic. *Ministry of Environment of the Czech Republic and The Silva Tarouca Research institute for landscape and ornamental gardening, p.r.i., Praha and Průhonice.*

Irwin L.L. & Peek J.M. 1983: Elk habitat use relative to forest succession in Idaho. *J. Wildlife Manage. 47: 664–672.*

Jeppesen J.L. 1987: Impact of human disturbances on home range, movements and activity of red deer (*Cervus elaphus*) in Danish environment. *Danish Review of Game Biology 13 (2): 1–38.*

Jerina K. 2012: Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *J. Mammal. 93: 1139–1148.*

Kalb D.M., Bowman J.L. & Eyler B.T. 2013: Dispersal and home-range dynamics of exotic, male sika deer in Maryland. *Wildlife Res. 40: 328–335.*

Kawamura Y. 2009: Fossil record of sika deer in Japan. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 11–25.*

Keating K.A. & Cherry S. 2009: Modelling utilization distributions in space and time. *Ecology 90: 1971–1980.*

Kilgo J.C., Labisky R.F. & Fritzen D.E. 1998: Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conserv. Biol. 12: 1359–1364.*

Kjellander P., Hewison A.J., Liberg O., Angibault J.M., Bideau E. & Cargnelutti B. 2004: Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. *Oecologia 139: 478–485.*

Lagos V.O., Contreras L.C., Meserve P.L., Gutiérrez J.R. & Jaksic F.M. 1995: Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. *Oikos 74: 259–264.*

Larter N.C. & Gates C.C. 1990: Home ranges of wood bison in an expanding population. *J. Mammal. 71: 604–607.*

Lewis J.S., Rachlow J.L., Garton E.O. & Vierling L.A. 2007: Effects of habitat on GPS collar performance: using data screening to reduce location error. *J. Appl. Ecol. 44: 663–671.*

Li Y., Homma K., Ohnaka K. & Koganezawa M. 2006: Summer home range size and inner structure of forest sika deer *Cervus nippon* in Nikko, Japan. *Acta. Zool. Sinica 52: 235–241.*

McCullough D.R. 1985: Long range movements of terrestrial mammals. *Contrib. Mar. Sci. 27: 444–465.*

McCullough D.R. 2009a: Sika deer in Korea and Vietnam. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 541–548.*

McCullough D.R. 2009b: Sika deer in Taiwan. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 549–560.*

McCullough D.R., Jiang Z.-G. & Li C.-W. 2009: Sika deer in mainland China. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 521–539.*

McNab K.B. 1963: Bioenergetics and the determination of home range size. *Am. Nat. 97: 133–140.*

Miami M., Ohnishi N., Okada A. & Takatsuki S. 2009: Reproductive ecology of sika deer on Kinkazan Island, northern Japan: reproductive success of males and multi-mating of females. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 297–317.*

Moen A.N. 1976: Energy conservation by white-tailed deer in the winter. *Ecology 55: 192–198.*

Mysterud A., Pérez-Barbería F.J. & Gordon I.J. 2001: The effect of season, sex and feeding style on home range area vs. body mass scaling of temperate ruminants. *Oecologia 127: 30–39.*

Pei K.J.C. 2009: The present status of the re-introduced sika deer in Kenting national park, southern Taiwan. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 561–570.*

Powell R.A. 2000: Animal home ranges and territories and home range estimators. In: Boitani L. & Fuller T. (eds.), Research techniques in animal ecology. *Columbia University Press, New York: 65–110.*

Quitt E. 1971: Climatic regions of Czechoslovakia. *Studia Geographica 16: 1–83. (in Czech with English summary)*

R Development Core Team 2008: R: a language and environment for statistical computing. Downloaded on 13 May 2013. *http://www.R-project.org*

Sakuragi M., Igota H., Uno H., Kaji K., Kaneko M., Akamatsu R. & Maekawa K. 2003: Seasonal habitat selection of an expanding sika deer *Cervus nippon* population in eastern Hokkaido, Japan. *Wildlife Biol. 9: 141–153.*

Seaman D.E. & Powell R.A. 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology 77: 2075–2085.*

Singleton I. & van Schaik C.P. 2001: Orangutan home range size and its determinants in a Sumatran swamp forest. *Int. J. Primatol. 22: 877–911.*

Swanson G.M. & Putman R. 2009: Sika deer in the British Isles. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 595–614.*

Takatsuki S. 1992: Foot morphology and distribution of s*ika deer* in relation to snow. *Ecol. Res. 7: 19–23.*

Torii H. & Tatsuzawa S. 2009: Sika deer in Nara park: unique human-wildlife relations. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 347–363.*

Uzal A., Walls S., Stillman R.A. & Diaz A. 2013: Sika deer distribution and habitat selection: the influence of the availability and distribution of food, cover, and threats. *Eur. J. Wildlife Res. 59: 563–572.*

Vincent J.P., Bideau E., Hewison A.J.M. & Angibault J.M. 1995: The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). *J. Zool. (Lond.) 236: 371–382.*

Wand M.P. & Jones M.C. 1995: Kernel smoothing. *Chapman and Hall/CRC, London.*

Wolf R. 1986: Sika deer. In: Husák F., Wolf R. & Lochman J. (eds.), Fallow deer, sika deer, white-tailed deer. *Státní zemědělské nakladatelství, Praha: 149–227. (in Czech with Russian and German summary)*

Worton B.J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. *Ecology 70: 164–168.*

Worton B.J. 1995: A convex hull-based estimator of home-range size. *Biometrics 51: 1206–1215.*

Yabe T. & Takatsuki S. 2009: Migratory and sedentary behavior patterns of sika deer in Honshu and Kyushu, Japan. In: McCullough D.R., Takatsuki S. & Kaji K. (eds.), Sika deer: biology and management of native and introduced populations. *Springer, Tokyo, Berlin, Heidelberg and New York: 273–283.*