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Future perspectives for the monitoring of red deer populations – a case study of a transboundary population in the Bohemian Forest ecosystem

Maik Henrich[1,2,*], Frederik Franke[3], Tomáš Peterka[4,5], Kai Bödeker[6], Jaroslav Červenka[5], Cornelia Ebert[7], Ulrich Franke[8], Jitka Zenáhlíková[5], Martin Starý[5], Wibke Peters[3], Marco Heurich[1,2,9]

[1] *Chair of Wildlife Ecology and Wildlife Management, University of Freiburg, D-79106 Freiburg, Germany*

[2] *Bavarian Forest National Park, Freyunger Str. 2, D-94481 Grafenau, Germany*

[3] *Department of Biodiversity, Conservation & Wildlife Management, Bavarian State Institute of Forestry, Hans-Carl-von-Carlowitz-Platz 1, D-85354 Freising, Germany*

[4] *Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ-165 21 Prague, Czech Republic*

[5] *Šumava National Park, 1. máje 260, CZ-38501 Vimperk, Czech Republic*

[6] *Department of Ecology and Ecosystem Management, Technical University of Munich, Emil-Ramann-Straße 6, D-85354 Freising, Germany*

[7] *Department Wildlife Genetics, Seq-IT GmbH & Co. KG, Pfaffplatz 10, D-67655 Kaiserslautern, Germany*

[8] *Wildlifemonitoring by aerosense, Ludwigstrasse 80, D-67483 Edesheim, Germany*

[9] *Institute for Forest and Wildlife Management, Inland Norway University of Applied Sciences, Evenstad, NO-2480 Koppang, Norway*

[*] Maik.Henrich@npv-bw.bayern.de

Abstract

Red deer is an important game species in Europe and of interest to ecotourism. However, as a major ecosystem engineer, red deer not only have positive effects on biodiversity, but also cause economic damage to managed forests and agriculture. Data obtained from effective and precise monitoring of red deer populations are therefore needed to provide a baseline for the establishment of adaptive management strategies that consider the interests of the different stakeholders. To date, counts of animals at winter feeding sites have been frequently used as an index of abundance. Because the proportion of red deer overwintering at feeding sites may correlate with winter severity, this method strongly depends on weather conditions and may not be suitable under conditions of a changing climate. Here, we present three alternative field methods to estimate deer population densities, which we tested in the Bohemian Forest: faeces genotyping, camera trapping and aerial surveys. The spatial use and the individual behaviours of the deer can be taken into account by the further addition of GPS telemetry. Our discussion of the study design, preliminary findings and future perspectives includes a consideration of the relationship between red deer distribution and both browsing survey results and hunting bags.

Key words: deer, monitoring, sampling design, wildlife management

Introduction

The interactions of humans and wildlife are complex. The presence of wildlife promotes overall biodiversity, directly benefits humans by providing ecosystem services and is appreciated as a source of cultural and recreational value (Soulsbury & White 2015). Conversely, wildlife can benefit from human activities, such as through intentional or unintentional improvements in habitat quality and forage availability (Geisser & Reyer 2005). Yet, while wildlife populations are expanding, the availability of suitable habitats is shrinking due to human encroachment, including for recreational purposes (Ciuti et al. 2012, Apollonio et al. 2017). Wildlife managers are therefore increasingly being asked to intervene in human-wildlife conflicts, most commonly for economic reasons (Barua et al. 2013). Ungulates, for example, can cause substantial damage through their foraging activities (Messmer 2000, Gordon et al. 2004) such that their populations in Europe are usually regulated by hunting (Apollonio et al. 2017). However, climate change is posing an additional challenge for wildlife management by altering population abundances and distributions, which in turn needs to be integrated in effective management strategies (Mawdsley et al. 2009). A prerequisite for adaptive management planning are reliable population density estimates that are able to reflect both climatic and anthropogenic changes.

Red deer (*Cervus elaphus* Linnaeus, 1758) is an iconic species that has fascinated humankind for centuries and accordingly has a high socio-cultural value (Leroi-Gourhan 1982, Soderberg 2004). Due to its large body size and wide distribution throughout Europe, red deer is an important game species (Mitchell-Jones 1999), but it also contributes to wildlife tourism, which has become an increasingly important source of revenue (Macmillan & Phillip 2008) for rural economies. From an ecological perspective, browsing by red deer can lead to an increase in plant species richness by suppressing the dominance of competitive tall-growing species (Schütz et al. 2003). The forest openings created by browsing and trampling may benefit thermophilous insects and birds associated with pasture woodlands (Fuller 2001, Stewart 2001), while bark stripping increases the supply of deadwood and thus provides additional habitat for many rare species of lichens, bryophytes, invertebrates, birds and mammals (Radu 2006). Red deer are also important agents for the dispersal of plant seeds over distances of several kilometres (Pellerin et al. 2016) and adequate deer populations are essential to the conservation of large carnivores in Europe (Linell et al. 2005, Jedrezejewski et al. 2006). In addition, the faeces of red deer are valuable resources for coprophagic organisms whereas their carcasses provide a rich food source for vertebrate scavengers and a variety of invertebrates (Stewart 2001, Barton et al. 2013, Stiegler et al. 2020).

Nonetheless, in managed forests and agricultural landscapes, red deer activities such as browsing, bark stripping and the scoring of trees by the deer's antlers may lead to extensive damage with a high economic cost (Putman & Moore 1998). Furthermore, wildlife-vehicle collisions involving red deer in areas with dense red deer populations are not uncommon, and in addition to the death of the deer cause substantial vehicle damage and possibly serious human injury (Mysterud 2004). Red deer may also facilitate the spread of diseases to livestock, such as foot-and-mouth disease or bovine tuberculosis (Gibbs et al. 1975, Zanella et al. 2008, Dorn-In et al. 2020), but also host the ticks associated with Lyme disease in humans (Ruiz-Fons & Gilbert 2010). Accelerated red deer population growth may negatively affect biodiversity, especially that of the invertebrates and birds that breed or feed within the shrub layer (Fuller 2001, Stewart 2001). For these reasons, effective management is essential to maintain healthy and sustainable red deer populations while considering the interests of local stakeholders.

Global climate change may affect the population dynamics of red deer in several ways. Milder winters with less snow are expected to increase in frequency (Marty 2013) and may decrease natural mortality while increasing reproductive success through improved food availability and reduced energy expenditure (Langvatn et al. 1996, Bonardi et al. 2017). Warmer weather at the beginning of the vegetation season would also enhance population growth by increasing the available biomass and therefore the nutritional supply (Langvatn et al. 1996). Additionally, the growth of early seral stands following disturbances due to windthrows and bark beetle outbreaks also increases forage productivity and thus potentially red deer populations as well (Senn et al. 2002, Kuijper et al. 2009). Conversely, higher temperatures later in the vegetation season can impair reproductive rates, because faster plant development accelerates the decline in forage quality (Langvatn et al. 1996). Furthermore, the variable winter conditions that characterise climate change, with unexpected heavy snow falls at high elevations and northern latitudes (Post et al. 1997, Laternser & Schneebeli 2003, Stoffel & Corona 2018), may hamper population growth.

Most populations of large carnivores in Europe have been stable or increasing since the beginning of this century (Chapron et al. 2014). In Germany, the wolf (*Canis lupus* Linnaeus, 1758) population has grown continuously since the establishment of the first pack in 2000 (Reinhardt et al. 2019), and red deer are among the preferred prey of these predators (Ansorge et al. 2006, Jędrzejewski et al. 2012). Besides direct effects on the population sizes of deer, the presence of wolves alters their spatial use and browsing patterns (Kuijper et al. 2013).

Human land use and disturbance may further affect animal behaviour by altering distributions and local population densities. Red deer tend to avoid trails in areas of intense human recreational activities, particularly during the day (Sibbald et al. 2011, Coppes et al. 2017, Scholten et al. 2018). Such changes in habitat selection may have important economic implications due to increases in the browsing of young trees and bark stripping by red deer using dense forest stands instead of open patches with abundant forage located close to trails (Jayakody et al. 2011, Coppes et al. 2017). Humans also impact red deer through the definition of hunting season, as Rivrud et al. (2016a) showed that the onset of the autumn migration of red deer was significantly related to hunting.

The complexity of the aforementioned factors and their interactions has made predicting red deer population growth and distribution in Europe a challenging task. This is also the case in our study area, the Bohemian Forest, which comprises two national parks, forming the largest forested area without human intervention in Central Europe (Krojerová-Prokešová et al. 2010), as well as managed public forests in their vicinity. The management of the transboundary population of red deer in the Bohemian Forest must include a consideration of the different aims of the various stakeholders, which range from preserving natural processes in the national parks to minimizing economic damage in the managed forests. Reconciling these different interests requires scientifically sound information. The presumed red deer density gradients across management zones and the competing management aims make the study area and its red deer population an ideal case study system.

To date, the red deer population in the Bohemian Fores has been estimated by unstandardized counts at fenced feeding stations and at baiting sites. However, because the number of animals using supplementary food sources is influenced by winter severity (Ossi et al. 2017), such counts may not be a reliable index of population densities. With the recent and predicted future increase in the frequency of warmer winters due to climate change, counting according to this method is likely to miss a substantial part of the red deer population and thus underestimate its size. The number of harvested animals per unit area is also an unreliable surrogate for densities, because harvest rates are subject to local hunting regulations, hunting efforts and the success of different hunting strategies (Pettorelli et al. 2007). Seasonal migrations, which may also differ between male and female red deer, further complicate the interpretation of hunting statistics when animals are hunted in rutting areas, overwintering areas and at sites in between (Jarnemo 2011, Loe et al. 2016). Browsing surveys provide another index for ungulate abundance and are often used by public authorities to set hunting quotas (Morellet et al. 2007, Forstliches Gutachten 2018), but with multiple sympatric browser species, eDNA analyses might be necessary to attribute browsing damages to a specific deer species (Van Beeck Calkoen et al. 2019). Annual management plans aimed at establishing effective population regulation and sustainable harvest rates require accurate estimates of the density and distribution of red deer populations. Thus, in the present study, part of the Interreg Project "New ways towards a cross-border red deer management in times of climate change", we explored different methods to monitor the red deer population in the Bohemian Forest. Herein we aim to answer the following questions:

i) Which population parameters can be derived from the results of each methodology and how do the methods differ with regards to the costs and effort needed?
ii) How do the results of these methods compare to the distribution of browsing pressure and hunting bags?
iii) Which methods can be used in the future for accurate long-time monitoring of red deer population development?

Material and methods

Study area

Our study area covered the Bavarian Forest National Park (BFNP, 245 km²), the state forest of Neureichenau (SFNR, 152 km²) and the Šumava National Park (SNP, 684 km²). The elevation within this area ranges from 570 m to 1453 m above sea level and the most prevalent land cover types are coniferous forests (60%), mixed forests (20%) and grasslands (14%), including pastures and open areas in the forest that were created by bark beetle (*Ips typographus* L.) outbreaks (Pflugmacher et al. 2019). The bark beetle outbreaks started in 1992, reached a peak in 1996 and 1997 and continue today (Lausch et al. 2011). Other land cover types present in the area include broadleaved forests (6%), shrublands (<1%) and surfaces covered with buildings and extensive pavement (<1%) (Pflugmacher et al. 2019) (Fig. 1).

The forest composition is dominated by Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.) in the wet valley floors and transitions to mixed forests with an abundance of European beech (*Fagus sylvatica* L.) on the mountain slopes. The forest in the upper montane zone is less dense but, rich in Norway spruce. On the mountain tops and high plateaus, sub-alpine spruce forests are interspersed with mountain ash (*Sorbus aucuparia* L.) and sycamore (*Acer pseudoplatanus* L.) (Elling et al. 1987, Heurich & Neufanger 2005). In the SNP, natural forests have been replaced by Norway spruce in more extensive areas than in the BFNP (Krojerová-Prokešová et al. 2010)

Natural predators of red deer within the study area include wolves, with a first pair of wild wolves having recolonised the area in 2016 (Heurich, pers. comm.), as well as Eurasian lynx (*Lynx lynx* Linnaeus, 1758), which occasionally prey on red deer females and calves (Belotti et al. 2014). As of 2018, hunting has been prohibited within 23% of the study area, and within 19% hiking is restricted to marked trails. The 16 winter enclosures in the BFNP (n = 4), SFNR (n = 2) and SNP (n = 10) were established to provide food for red deer during the winter months and thus prevent browsing in commercial forests as well as damage to agricultural fields (Wotschikowsky 1981). Depending on the weather conditions and the advancement of the vegetation season, the enclosures are shut between October and January and opened between late March and mid-May (Möst et al. 2015).

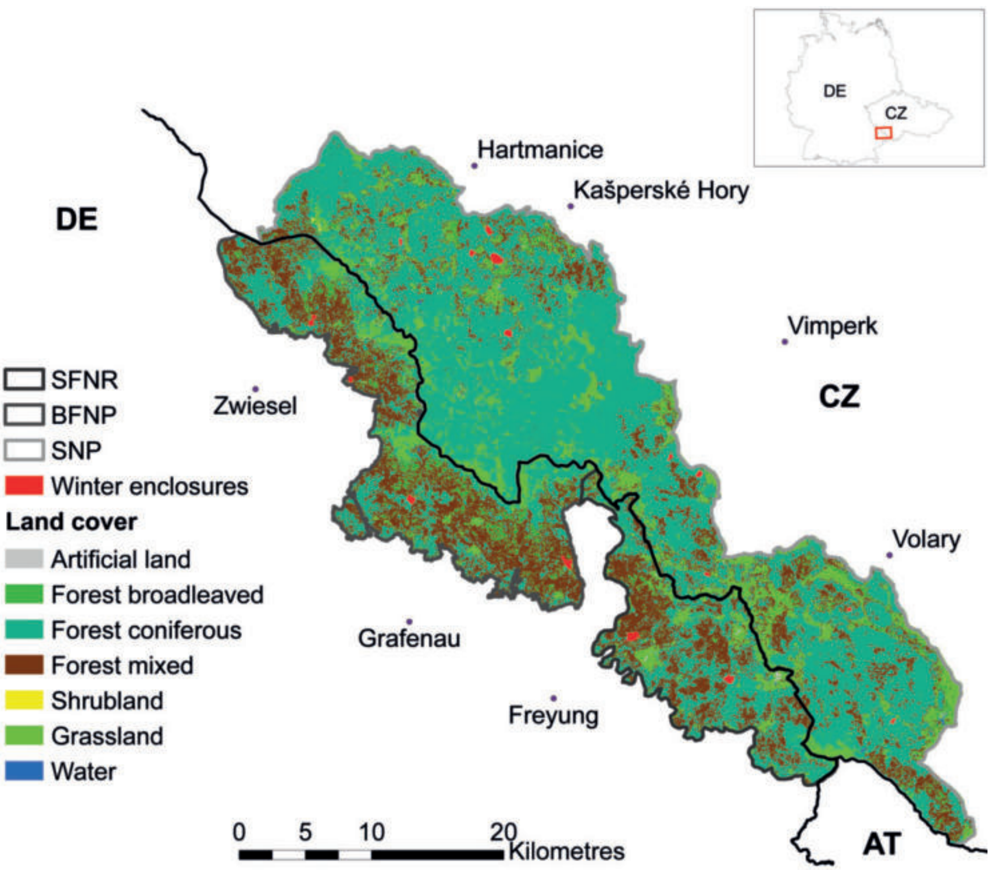

Fig. 1. The map of the study area shows the outlines of the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP) as well as the land cover categories as depicted by Pflugmacher et al. (2019).

Red deer counts

The annual red deer counts used in this study were recorded by the game wardens at baiting sites and winter enclosures on predefined days in February or March of each year from 2002 to 2020 in the BFNP, from 2006 to 2020 in the SFNR and from 2001 to 2020 in the SNP. The number of enclosures differed slightly between years due to variations in maintenance or natural disturbance (e.g. damage due to windthrows), which may have affected the counts (see Appendix 1). The game wardens recorded the numbers of adult males, adult females and calves less than one year old. In our analysis of these data, we used Spearman's rank correlation coefficient to test for an increase in the number of counted individuals and the Benjamini-Hochberg procedure to check for a false discovery rate at a threshold of 5% (Benjamini & Hochberg 1995).

Faeces sampling and processing

A 1 km^2 grid fully located within the boundaries of the BFNP, SFNR and SNP and covering a small part of the state forest Boubín (Kubany) was created using ArcGIS Desktop 10.5.1. (ESRI 2017). Due to the very large survey area, we needed to reduce the proportion of the area to be sampled. In a first step 42 grid cells were omitted because more than half of their area was covered by settlements, fenced areas, water bodies or very steep terrain. Based on a simulation study that included variation in home-range size, search effort and population size (sensu Milleret et al. 2020), we randomly discarded further grid cells until the coverage of the original area reached 80%, but to allow for even coverage avoided discarding adjacent grid cells. The final grid that was searched for red deer faeces contained 543 cells.

From June 5 to August 10, 2018, all grid cells were searched systematically for red deer faeces. To ensure homogeneous coverage, the grid cells were subdivided into 16 smaller units of 250×250 m, which were sampled with a similar intensity (Fig. 2). Due to DNA degradation,

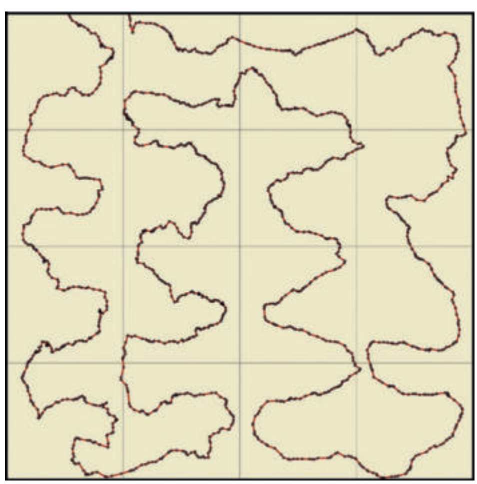

Fig. 2. Example of a faeces search path within one grid cell subdivided into 16 units of 250×250 m that were sampled with similar intensity.

genotyping of fresh samples has a higher success rate and samplers were advised to only collect pellet groups that were still moist and had an intact surface. In areas with low detection rates, older pellets with a relatively intact surface were also included. Sampling of faeces from the same individual at the same spot twice was avoided by allowing a minimum distance of 2 m between successive piles. From each of these individual pellet groups, two pellets were sampled. For every sample, a new toothpick or plastic bag was used to avoid cross-contamination. The samples were placed in a freezer at −20°C at the end of each sampling day. The search effort was accounted for by recording the sampling spots as well as the tracks of the observers using handheld GPS devices.

Genetic analyses were performed 1–5 months after sample collection. Details of the DNA extraction, PCR and data analysis are provided in Ebert et al. (in press). The presence of the X- and Y-chromosome-specific forms of the amelogenin gene was used for sex determination and eight dinucleotide microsatellites were selected for the identification of individual animals: IDVGA55, BMC1009, TGLA53, BM203, CSSM16, CSSM19, Haut14 and ETH225 (Frantz et al. 2006, Valière et al. 2006, Gurgul et al. 2010).

Camera trapping and photo processing

A subset of 248 grid cells was randomly selected from the 543 cells used for faeces sampling and camera traps (C2, Cuddeback, USA) were installed at their centre coordinates. A random sample of 100 replacement grid cells was used in the given order if a point within a 15 m radius around the centre coordinate of the originally selected cell could not be reached in the field. As Henrich et al. (2020) found no evidence that infrared flash causes avoidance in deer, the camera traps were equipped with infrared flash units, which cover a wider range than black flash. The camera traps were set to record a series of five photos per trigger without any delay between photos within or between series. The range of the infrared flash was set to ”far”' and the field of the pyroelectric infrared sensor to ”wide”. In addition to the triggered photos, the field of view of the camera trap was monitored with photos taken daily from November 2018 onwards, which helped for example to keep track of snow cover.

The camera trap deployments started on May 7, 2018 and were completed on August 19, 2019, with each camera trap remaining at the same position for at least one year. The cameras were mounted on tree trunks and poles 60–70 cm above ground level with the direction of view ranging from northeast to northwest. The vertical angle was adjusted to match the slope of the terrain.

Photos were collected from the camera traps at regular intervals, and all photo series were tagged with the animal species, number of animals and, if red deer were visible, also with the number of adult males, adult females, adults of unknown sex and calves, using the free software digiKam 5.7.0 (Giles et al. 2017). Young animals were defined as calves until the March 31 of the year following their birth, while older animals including yearlings were considered adults. All photos of one series were tagged with identical information. The total number of males, females and calves visible on the photos of a series was summed whenever all animals could be individually tracked within the five photos of a series. Otherwise, all photos of a series were tagged with the maximum number of animals visible on one of the five images.

Photos from several series were grouped as one event if an animal or a group of animals was present in front of the camera continuously. Events were differentiated by a time gap between two consecutive photo series of more than 5 min. For each camera trapping event, the number of males, females and calves corresponded to the maximum number of individuals detected on one of the included photo series. The package camtrapR (Niedballa et al. 2016) in R 3.6.0 (R Core Team 2019) was used to create a table of all events that was sorted by camera trap location, animal species and time. The camera traps were considered active from setup to de-installation, except when empty batteries, full SD cards or technical problems were discovered during checks. If time-lapse photos were available, they were used as an indicator of the duration of the malfunction, otherwise, it was assumed that the camera trap had stopped working the day after the last photo was triggered. Time periods during which parts of the camera trap lenses were covered by snow were also removed from the analysis. The camera trapping rate was defined as the number of events per 100 camera trapping days. Sex ratios were calculated for June, in line with the time period of the faeces search and following the findings of Heurich et al. (2016). Cow-calf ratio was determined for the period from June to October when calves are easily recognizable.

Aerial survey

Red deer were detected from the air using an ultralight aeroplane equipped with a camera system consisting of a thermal camera (Jenoptic VarioCam HD) and a high-resolution visual camera (Sony ILCE 7R) (Franke et al. 2012). Two blocks of approximately 29 km² each were selected for the aerial survey. Within these areas, the plane followed parallel transects separated by a distance of 150–200 m. The northern block, east of the town of Zwiesel, was overflown on July 21, 2018 between 9:10 and 11:11 UTC along west-easterly and east-westerly transects with a total length of 195 km and a mean swath width of 128 m. The other block, located close to the village of Waldhäuser, was overflown on July 22, 2018 between 16:28 and 18:00 UTC along north-southerly and south-northerly transects with a total length of 136 km and a mean swath width of 113 m. The videos of the thermal camera were used to detect animals manually and the images from the visual camera were consulted for verification and species identification. Red deer detections and ambiguous detections were documented with the respective number of individuals counted, together with their spatial localisation.

GPS telemetry

Between February 6 and April 4, 2018, 55 female red deer (24 in the BFNP, 11 in the SFNR, 20 in the SNP) were collared in 12 different winter enclosures (4 in the BFNP, 2 in the SFNR, 6 in the SNP) across the study area. Between February 7 and March 25, 2019, 16 additional females were collared (2 in the BFNP, 3 in the SFNR, 11 in the SNP). In two of the enclosures the animals were captured in narrow wooden pens and handled without anaesthesia. In all other cases, the deer were immobilised using 3 ml of Hellabrunner mixture (Wiesner 1998), injected using an air pressure rifle. In addition to the GPS collars (Vertex plus or GPS+, Vectronic Aerospace, Germany), the red deer were fitted with ear tags. For each animal, body length, hindfoot length and neck circumference were measured and a hair and/or faeces sample was taken for genetic analysis. The collars were programmed to record the deer's position every hour and for animals collared in the BFNP and the SFNR also during a 15 min interval every eighth day. After two years of GPS collar deployment, the automatic drop off mechanism was activated.

To test for differences in the ranging behaviour of the deer between management areas (BFNP, SFNR, SNP), annual home ranges were calculated using data collected between March 31, 2018 and April 1, 2019 for those individuals that had GPS positions for at least 360 days within this period. The estimated 95% autocorrelated kernel density home range (Fleming et al. 2015) was calculated using the R package ctmm (Calabrese et al. 2016). Differences in home range sizes between the three study locations were assessed with a Mann-Whitney U test and checked against a false discovery rate of 5% using the Benjamini-Hochberg procedure (Benjamini & Hochberg 1995).

Hunting data

During the 2018/19 hunting season (in Germany from June 1 to January 31, in the Czech Republic from August 1 to January 15 and for calves extended to March 31), the sex, age and location of hunted deer and deer that were found dead were recorded for all animals in the BFNP and the SFNR and for 71% of the animals in the SNP. The number of individuals harvested in the BFNP, SFNR and SNP was compared.

Browsing survey

The browsing survey was designed based on the guidelines of the Bavarian Forest Administration (Forstliches Gutachten 2018). The survey was done in 2018 at the beginning of the vegetation season (April 16–July 10, 2018) and focussed on the damage detected after the 2017 vegetation season. A raster of 800×800 m grid cells used in previous years in the BFNP was superimposed also on the area of the SFNR. In the SNP, a raster of 1000×1000 m was implemented. Crossing points of raster cells were defined as initial points for the survey. Starting from these points, the closest regeneration area with a density of at least 1300 trees of >20 cm height per hectare and a length of at least 50 m was then selected for sampling (Hothorn & Müller 2010) . Along a transect with a length of at least 50 m, five poles were placed at regular intervals and the cardinal direction of the transect was noted. At each of these points, the sizes of the 15 closest trees with a height in the range of 20–200 cm were measured. For each tree, the species, a browsed leading shoot, browsing in the upper third of the tree and fraying were noted. The outermost of these 15 trees marked the outer circumference of the sampling plot. Within this plot, the number of larger trees was documented, along with their species and the presence of fraying damage.

Results

Red deer counts

Annual counts of red deer in the BFNP suggested an increase in population size since 2002 (rho = 0.60, $p<0.05$). In the BFNP, the number of calves closely followed the number of females, while the trend for males followed that for females, albeit with a certain delay (Fig. 3a). The number of red deer counted in the SFNR was stable from 2006 until the end of the study period, and females were always more numerous than males (Fig. 3b). There was no significant trend in the winter enclosure counts in the SNP (Fig. 3c).

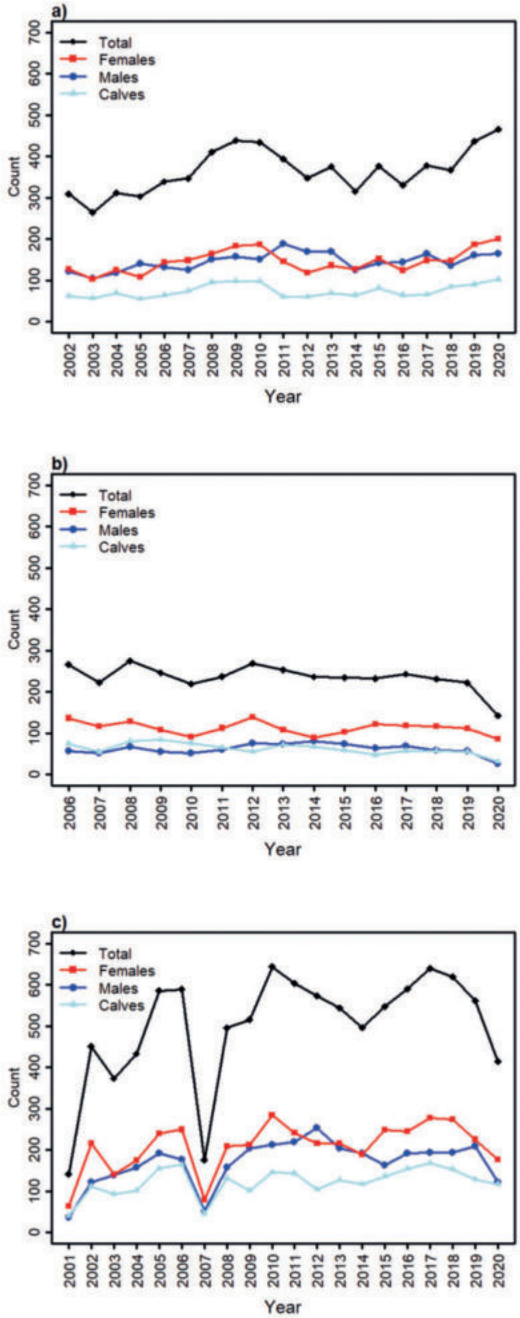

Fig. 3. Number of red deer counted in the winter enclosures and at feeding stations in the three sub-areas of the study site: a) Bavarian Forest National Park between 2002 and 2020, b) state forest of Neureichenau between 2006 and 2020 and c) Šumava National Park between 2001 and 2020.

Faeces sampling

Based on the 3234 faeces samples collected in summer 2018, faeces densities were higher in the SNP (6.67 samples/km²) than in the BFNP (6.25 samples/km²) and lowest in the SFNR (3.86 samples/km²) (Fig. 4). A cluster with high faeces densities was detected at high elevations of the SNP and the neighbouring parts of the BFNP. Of the collected samples, 53.6% could not be genotyped successfully. The 1578 successfully genotyped samples were assigned to 1120 different red deer individuals, of which 1060 could be sexed. The male: female ratio in the genotyped samples was nearly balanced (Table 1). Up to six samples from a single individual were collected and 28.5% of the individuals were detected more than once. The resampling rate differed between the sexes, with 33.7% of the detected males and 25.9% of the detected females sampled at least twice.

Camera trapping

Red deer were the most frequently photographed animal species during the camera trapping period of more than one year (Table 1). Red deer trapping rates were nearly twice as high in

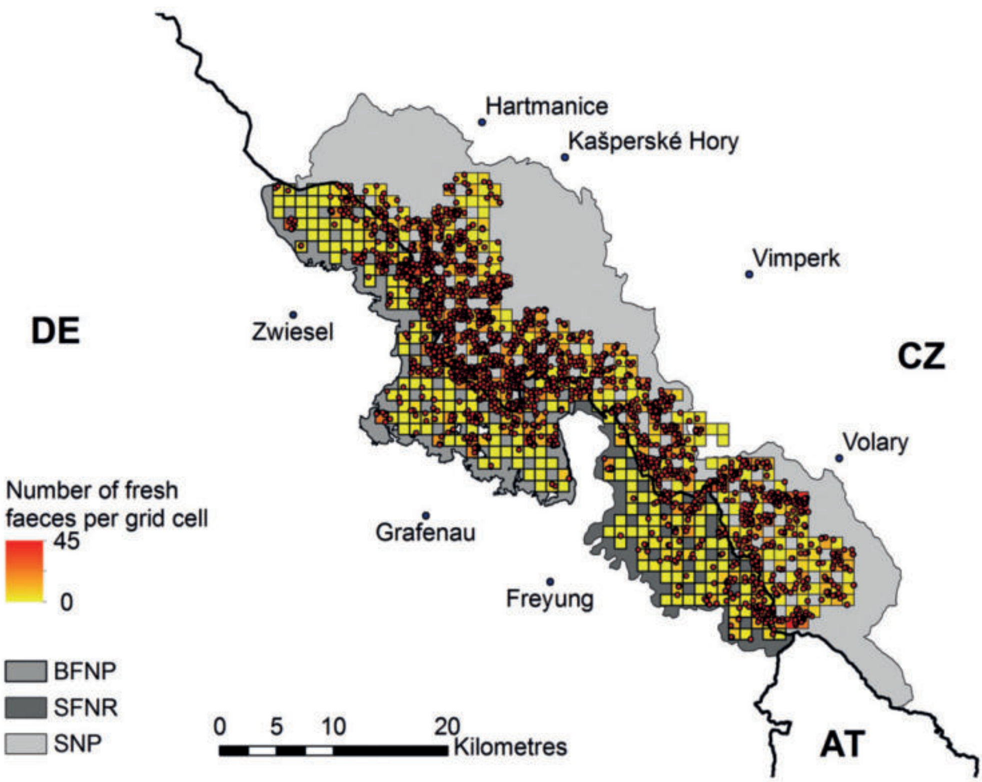

Fig. 4. Distribution of red deer faeces sampled in the Bavarian Forest National Park, the state forest of Neureichenau and Šumava National Park. The search-grid cells are coloured according to the number of collected samples in the respective cell.

Table 1. Sex ratio and cow-calf ratio estimates obtained from different sources. For camera trapping, the ratios are given considering only the sexed females and all adults that were not classified as males (in brackets) as females.

	Sex ratio (m:f) Winter enclosure counts 2019	Sex ratio (m:f) camera trapping	Sex ratio (m:f) genotyping	Cow-calf ratio camera trapping
BFNP	1:1.16	1:1.39 (1:1.58)	1:1.10	1:0.37 (1:0.33)
SFNR	1:1.98	1:0.67 (1:0.84)	1:0.40	1:0.55 (1:0.46)
SNP	1:1.08	1:0.27 (1:1)	1:0.85	1:1.14 (1:0.32)
Total	**1:1.23**	**1:0.53 (1:1.10)**	**1:0.9**	**1:0.66 (1:0.34)**

the SNP than in either the BFNP or the SFNR. The second most common species was roe deer (*Capreolus capreolus* Linnaeus, 1758) in the SNP and SFNR. In the BFNP, roe deer camera trapping rates were only roughly half as high as those in the SNP (Table 2). Instead, the second most frequent species in the BFNP was wild boar (*Sus scrofa* Linnaeus, 1758), which showed very low trapping rates in the SFNR.

Two red deer hot spots were identified, one in the central part of the SNP, close to the country border, and another further to the north (Fig. 5). Camera traps east of the most northern part of the SFNR were also triggered frequently by red deer. In the BFNP, many red deer occurrences were recorded by a cluster of camera traps located east of the village of Zwiesel. These observations were largely in accordance with the faeces distribution.

Most of the observed red deer (97%) could be categorised as calf or adult. Among the 76% of the adult individuals that were sexed (BFNP: 96%, SFNR: 94%, SNP: 66%), 35% of those detected in June were females. The male bias is attributable to the observations in the SNP. If all adults not classified as males are assumed to be females however, the sex ratio is balanced in the SNP, but biased towards males in the SFNR and towards females in the BFNP (Table 1). The number of calves observed from June to October reached nearly half the number of adult females from the same period in the SFNR, but stayed around one third in the BFNP and SNP (Table 1). 78% of the events were triggered by just a single animal, 16% by two animals and the maximum observed group size was 14 (Fig. 6).

The distribution of red deer observations during the day showed a distinct daily activity pattern, with peaks at dawn and dusk and an activity minimum around midday. This pattern was most pronounced in the SFNR and was relatively weak in the SNP (Fig. 7).

Aerial survey

During the aerial survey, 91 red deer individuals within 57 observation events were recorded (Fig. 8). The survey revealed red deer hot spots at higher elevations within the two observation blocks. These observations coincided with the results of the faeces sampling. The median number of red deer per event was 1 (lower quartile: 1, upper quartile: 2, max: 11).

Table 2. Camera trapping rates of 248 camera traps deployed in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and in Šumava National Park (SNP) for more than 12 months in 2018/19.

	Species	Area	Events/100 days
Ungulates	Red deer (*Cervus elaphus*)	BFNP	7.420
		SFNR	5.348
		SNP	16.213
	Roe deer (*Capreolus capreolus*)	BFNP	1.609
		SFNR	2.595
		SNP	3.146
	Fallow deer (*Dama dama*)	BFNP	0.000
		SFNR	0.000
		SNP	0.003
	Wild boar (*Sus scrofa*)	BFNP	3.023
		SFNR	0.453
		SNP	2.096
Carnivores	Eurasian lynx (*Lynx lynx*)	BFNP	0.091
		SFNR	0.055
		SNP	0.046
	European wildcat (*Felis sylvestris*)	BFNP	0.003
		SFNR	0.005
		SNP	0.005
	European badger (*Meles meles*)	BFNP	0.046
		SFNR	0.027
		SNP	0.035
	Pine marten (*Martes martes*)	BFNP	0.212
		SFNR	0.098
		SNP	0.025
	Red fox (*Vulpes vulpes*)	BFNP	0.287
		SFNR	0.459
		SNP	0.497
	Wolf (*Canis lupus*)	BFNP	0.013
		SFNR	0.000
		SNP	0.008
	Raccoon dog (*Nyctereutes procyonoides*)	BFNP	0.000
		SFNR	0.000
		SNP	0.003
Rodents and lagomorphs	European hare (*Lepus europaeus*)	BFNP	0.134
		SFNR	0.246
		SNP	0.186
	Eurasian red squirrel (*Sciurus vulgaris*)	BFNP	0.441
		SFNR	0.317
		SNP	0.453
Grouse	Hazel grouse (*Tetrastes bonasia*)	BFNP	0.003
		SFNR	0.000
		SNP	0.000
	Western capercaillie (*Tetrao urogallus*)	BFNP	0.013
		SFNR	0.005
		SNP	0.052

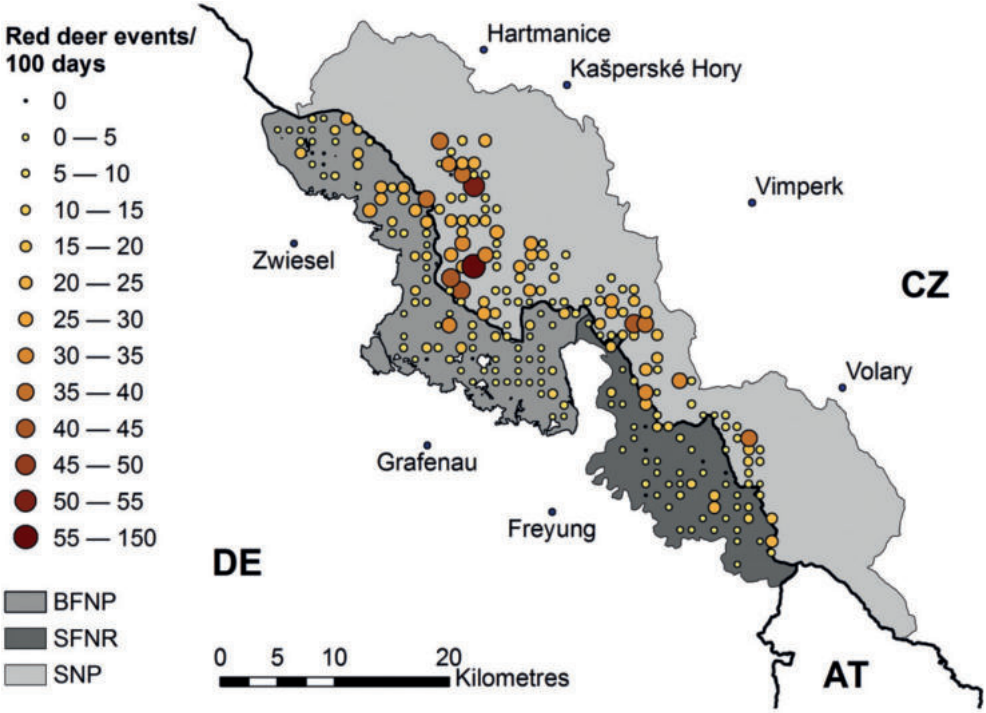

Fig. 5. Spatial distribution of the red deer camera trapping events across the Bavarian Forest National Park, the state forest of Neureichenau and Šumava National Park.

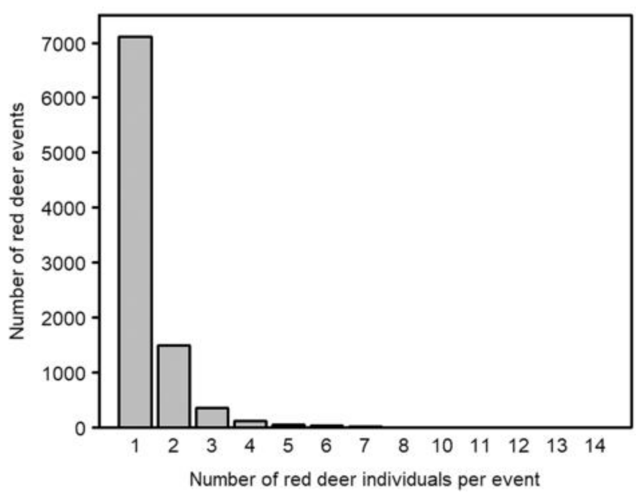

Fig. 6. Number of red deer individuals observed per camera trap event in the Bavarian Forest National Park, the state forest of Neureichenau and Šumava National Park during a period of >12 months in 2018/19.

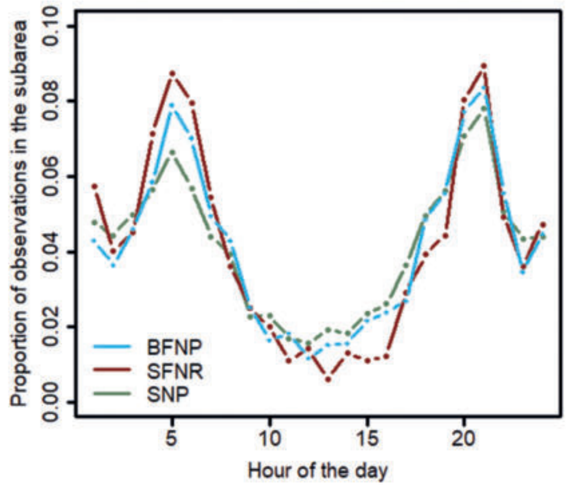

Fig. 7. Daily distribution of red deer camera trapping events in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP) during a period of >12 months in 2018/19.

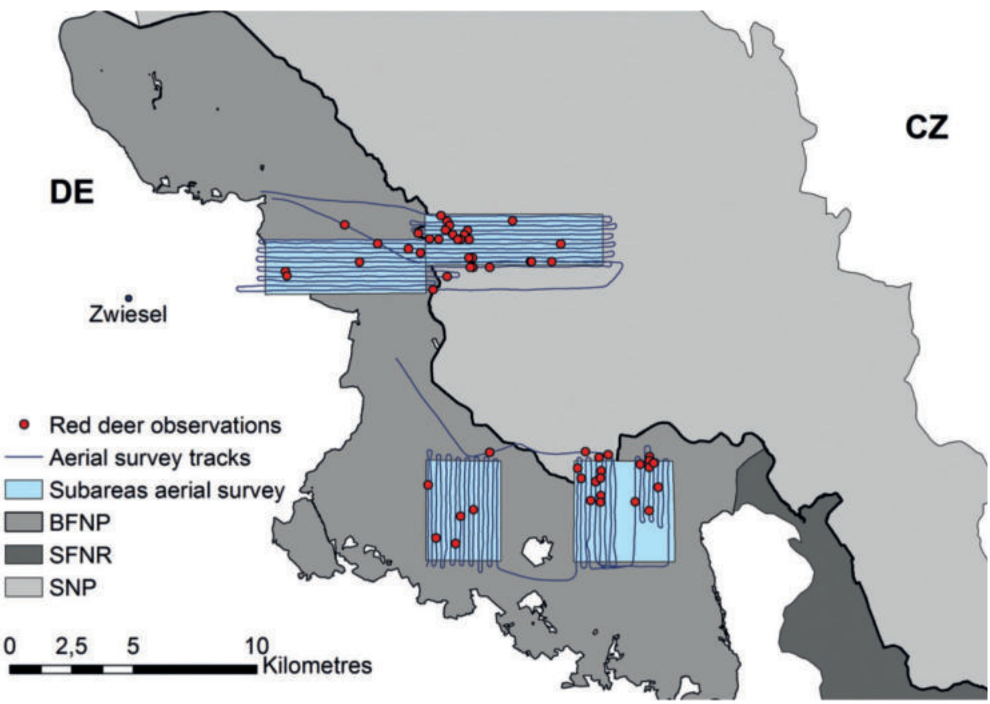

Fig. 8. Aerial survey observation blocks and red deer detection events in the Bavarian Forest National Park (BFNP) and Šumava National Park (SNP). The state forest of Neureichenau (SFNR) was not included in the aerial survey.

GPS telemetry

The annual home ranges of red deer females differed between the winter enclosures in which the deer were collared. Animals that over-wintered in the enclosures Buchenau, Neuhüttenwiese, Březová Lada and Špičák had especially small home ranges (<8 km^2, Table 3, Fig. 9). The four largest home ranges of 500 km^2 and more were found for animals collared within the SFNR, which clearly reflected the seasonal migration patterns. In general, the home ranges of animals using enclosures in the BFNP were significantly smaller than those of animals using enclosures in the SFNR ($p<0.01$). The differences to the SNP were not significant.

Hunting data

Of the 1017 red deer reported dead during the 2018/19 hunting season, 904 were hunted, at least 8 were killed in vehicle accidents and 12 died due to other reasons. The highest number of animals hunted per square kilometre was recorded in the SNP (1.05 animals per km^2), followed by the SFNR (0.53 animals per km^2) and the BFNP (0.43 animals per km^2). The male: female ratio of the hunted animals was 1:0.94 (BFNP: 1:0.67, SFNR: 1:0.98, SNP: 1:0.99), 46.11% of the culled red deer were calves, 41.11% were adults and 12.52% were yearlings. The cow: calf ratio of the hunted animals was 1:2.17.

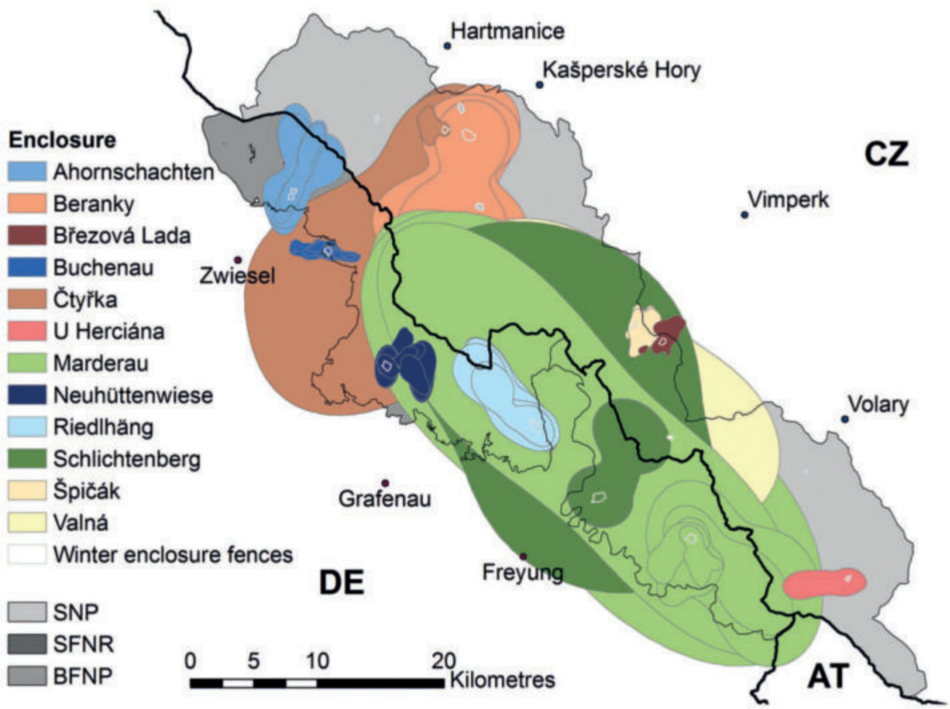

Fig. 9. The 95% autocorrelated kernel density of the annual home ranges of female red deer separated by winter enclosures in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP). The non-filled areas (white in the legend) mark the location of the winter enclosures.

Table 3. Mean annual home range sizes (95% AKDE) of female red deer collared in different winter enclosures within the Bohemian Forest.

Sub-area	Winter enclosure of origin	Area (km²)	Standard deviation (km²)	Sample size
BFNP	Ahornschachten	20.25	11.35	4
BFNP	Buchenau	3.33	2.09	4
BFNP	Neuhüttenwiese	7.48	4.91	6
BFNP	Riedlhäng	23.96	6.40	4
SFNR	Marderau	245.99	285.80	8
SFNR	Schlichtenberg	212.18	287.37	3
SNP	Beranky	115.17	23.92	4
SNP	Březová Lada	5.56	NA	1
SNP	Čtyřka	117.60	155.31	6
SNP	U Herciana	12.45	NA	1
SNP	Špičák	7.24	1.13	3
SNP	Valná	376.16	NA	1

Most of the red deer were hunted in the northern part of the SNP, which coincided with the high relative densities determined by faeces sampling and camera trapping (Fig. 10). Another hunting hot spot was located in the lower elevations close to the winter enclosure Buchenau, where the camera trapping rates were also high.

Browsing survey

The percentage of browsed trees was lowest in the managed forest (SFNR) but relatively similar for the most common tree species in the BFNP (Fig. 11, Fig. 12). By contrast, browsing pressure in the SNP was up to seven times higher for Mountain ash, Norway spruce and European beech (Fig. 12). The percentage of browsed trees at the survey plots reflected the prevalence of Norway spruce, as the browsing pressure was lower when this species dominated the tree species composition at a plot (Fig. 11). Although Norway spruce made up >50% of the recorded tree regeneration, <6% of its leading shoots were browsed (Fig. 12). The high red deer densities determined by faeces sampling and camera trapping were partly reflected in the distribution of browsing pressure, especially in the north-east SNP and the areas of the SNP near the northern part of the SFNR. However, browsing pressure was relatively low at the high elevations between Mt. Rachel and Mt. Lusen despite the high relative abundance of red deer in this region (Fig. 4, 5 and 11).

For a comprehensive overview of the costs, efforts and potential outcomes of the methods described here please refer to Table 4.

Discussion

The aim of the Interreg project "New ways towards a cross-border red deer management in times of climate change" is to assess the distribution and structure of the red deer population in the Bohemian Forest. Although winter enclosure counting has been used to estimate the red deer population size in this area, this approach may not reliably reflect the relative abundances as annual variations in the counts may be related to varying weather conditions. For example, the strong decline in the SNP counts in 2007 could be attributed to the storm "Kyrill", which destroyed the fences of many winter enclosures such that the deer escaped before they could be counted. Between enclosures the counts are also not standardised in terms of timing and effort. The alternative approaches used within the project can be applied under changing climatic conditions. Here, we present our study design, the preliminary results obtained with these approaches and a comparison with the results from the traditional counting method. While some of the alternative methods were shown to yield similar raw results, they nonetheless differ in their spatial and temporal resolution and in the ancillary information they provide.

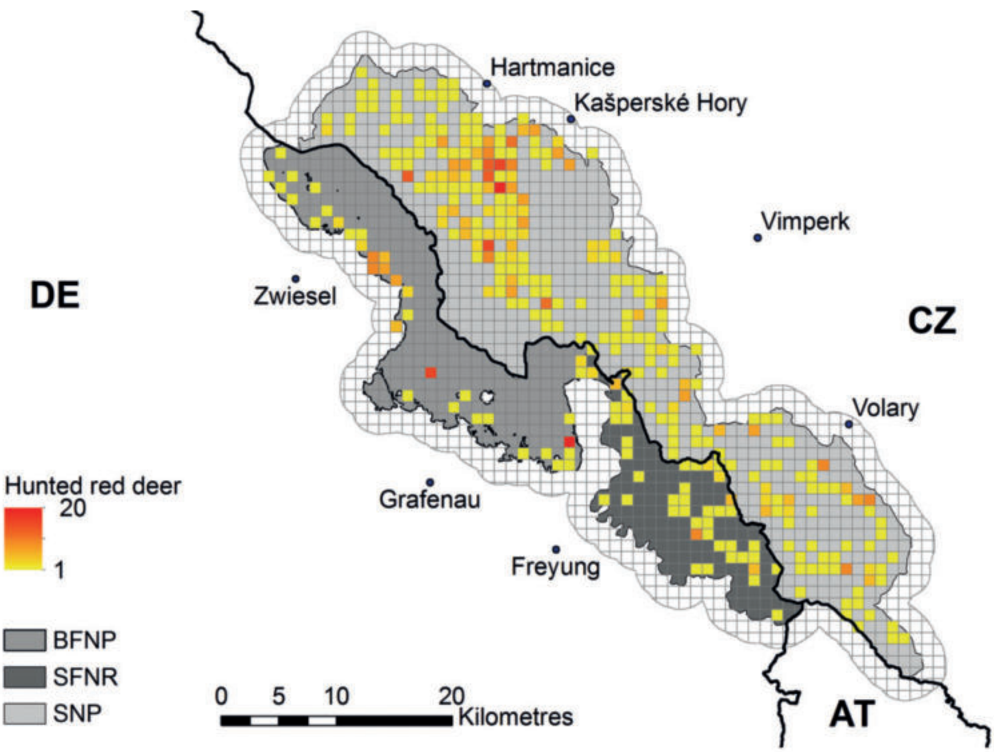

Fig. 10. Number of culled red deer within a 1 km² grid during the 2018/19 hunting season in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP), shown with a 2 km border zone.

Systematic faeces sampling offered the best spatial resolution with respect to the red deer distribution, since 8688 250×250 m cells were searched with similar effort over the whole project area. Only those cells (<2%) in very difficult terrain, characterised by steep slopes, very dense young stands, swamps and deadwood, were omitted. However, the density of ground vegetation, the weather conditions and observer experience can affect the detection probability of faeces in the field. The percentage of successfully genotyped samples was relatively low (<47%) compared to samples collected in similar studies and analysed in the same laboratory, where genotyping was possible for 50–80% (Ebert et al. in press). Our low genotyping rate can likely be explained by the rapid degradation of the DNA in the faeces due to the warm temperatures and moist conditions during the sampling period in early summer (mean air temperature between 6 a.m. and 8 p.m. at the weather station near the village Waldhäuser at 945 m above sea level during the search period: 18.2 ± 4.8°C). In general, faecal sampling is best conducted during the cooler and drier conditions of winter. However, since red deer overwinter in the enclosures in the study area and deep snow often covers large parts of the higher elevations for an extended period, sampling in winter is not feasible. In spring, migration from the winter enclosures and lower elevations follows the vegetation greenup (Rivrud et al. 2016b). Because single-session surveys are best conducted when populations are fairly stable, i.e. not during migration or during other times when wide-ranging movements are common (Royle et al. 2016) sampling in late autumn, just before migration

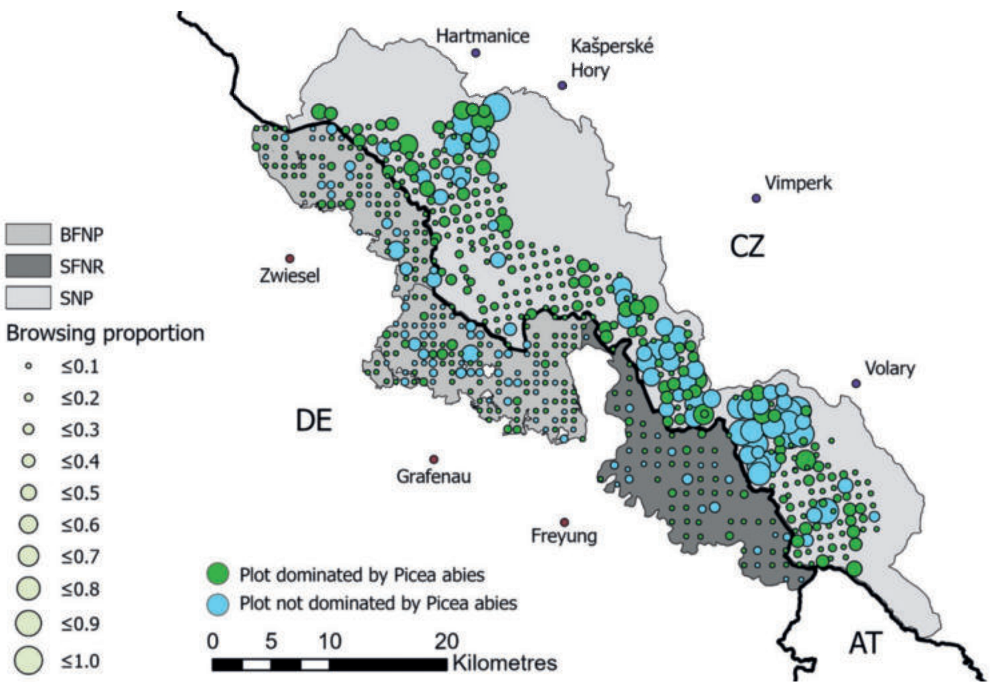

Fig. 11. Proportion of browsed trees divided into plots dominated by Norway spruce or not in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP).

and after the rut might be the only alternative to the sampling period used in the current study. The low frequency of resampling the same individuals indicated that a considerable part of to be close to the true sex ratio of the studied population, due to the large sample size. Yet, statistical analyses using spatially explicit capture recapture methods (Royle et al. 2014) that account for sex-specific detection rates may yield different sex ratio estimates compared to the sample. A slight skew towards males and their higher resampling rates indicated that a higher percentage of male than female individuals of the population was sampled. This sampling bias can be attributed to the larger size of the pellets of male red deer that makes them more conspicuous and easier to distinguish from roe deer pellets (Spitzer et al. 2019).

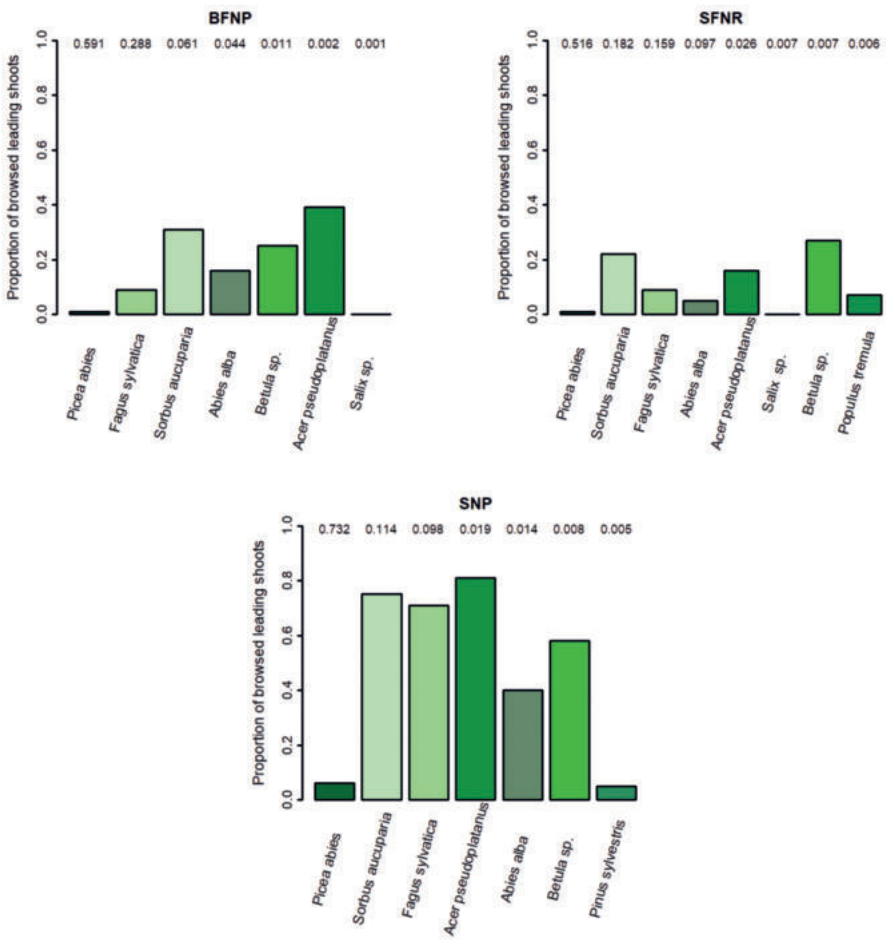

Fig. 12. Proportion of tree saplings with browsed leading shoots for all recorded tree species representing at least 0.1% of the regeneration community in the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP). The tree species within each plot were sorted by their prevalence. The numbers above the bars indicate the number of saplings of the tree species as a proportion of the total number of surveyed saplings in the respective sub-area.

Table 4. Comparison of costs and efforts associated with the methodologies applied within this study with the goal to obtain data on the population density, distribution and structure of ungulates and browsing pressure.

Method	**Material and service costs*** ***(total project area)***	**Field effort**	**Data preparation effort**	**External service needed**	**Outputs**	**Options for further analyses**
Winter enclosure counts	–	2 persons for 4 h each	–	no	- Approximation of the number of deer per enclosure - Approximation of the sex ratio	–
Faeces sampling and genotyping	Material per sample: <1 € (*<3234 €*) Genotyping per sample: 35 € (*113190 €*)	1 day per 1 km^2 and person	1 h per grid cell	yes	- Spatial distribution of faeces - Number of sampled individuals - Sex ratio in the sample	- Population density and sex ratio: Spatially explicit capture-recapture[1] - Home range[1] Population genetic diversity and patterns
Camera trapping	1 Camera trap and housing: 250–300 € (*74400 €*) 2 SD cards: ca. 8 € (*1984 €*) Batteries per camera trap and year: 60–10 € (*2480 €*)	3–4 visits during a yearly camera trap deployment, effort per visit strongly depends on the accessibility of the locations	Strongly depends on the number of photos (ca. 1 min per photo)	no	- Spatial and temporal distribution of trapping rates - Daily and seasonal activity patterns - Sex ratio - Cow-calf-ratio - Group sizes - Behaviour (also for other animal species simultaneously)	- Population density: REM[2] (movement rate as an required parameter often derived from external sources) - Population density: Distance Sampling[3] - Population density: REST[4]

* *Costs do not include labour costs for field and data preparation effort, because work was done by paid personnel, interns or student helpers. Thus, labour costs might be quite substantial. Especially for faeces searches and for camera trapping numerous work hours are required.*

Table 4. Continued.

Method	Material and service costs* *(total project area)*	Field effort	Data preparation effort	External service needed	Outputs	Options for further analyses
Aerial survey	Flight with a sampled area of 20 km² and associated video evaluation: 10000 € (*10000 €*)	–	Done externally, included in costs	yes	- Spatial distribution of red deer observations/ habitat use - Group size (also for other large mammals simultaneously) - Approximation of the sex ratio	- Population density: Animals/ filmed area, considering habitat--specific detection probabilities
GPS telemetry	1 GPS collar: 2500 € (*165000 €*) Data transmission via GSM per collar and month: 5–8 € (*12672 € for 66 collars with a deployment period of 2 years*)	Collaring: At least 2 persons for 1 day to collar 1 animal	–	License and equipment for distance immobilization; supervision by a vet is needed	- Trajectory of individual animals - Additional data depending on collar type (e.g. activity data)	- Home range (MCP, KDE, AKDE)[5] - Habitat selection (RSF, SSF)[6,7] - Migratory behaviour[8] - Cause specific survival[9] - Activity patterns[10]
Browsing survey	–	Per day a 2 person team manages 5–10 plots	–	no	- Percentage of browsed trees per species and per unit area - Spatial distribution of browsing pressure	- Could be advanced to estimate and monitor habitat quality for ungulates as indicator of ecological change[11]

1 Royle *et al.* 2014
2 Rowcliffe *et al.* 2008
3 Howe *et al.* 2017
4 Nakashima *et al.* 2018
5 Fleming *et al.* 2015
6 Boyce *et al.* 2002
7 Thurfjell *et al.* 2014
8 Rivrud *et al.* 2016a
9 Murray 2009
10 Owen-Smith *et al.* 2012
11 Morellet *et al.* 2007

Further, the typically larger home ranges of males (KAMLER et al. 2008) may increase their recapture rate due to the different distribution patterns of their faeces. As the survey was conducted just after calving, the faeces of red deer offspring were unlikely to have been sampled due to their much smaller size, it can thus be assumed that faecal sampling yields pre-birth estimates. The raw genotyping data from the faeces sampling presented here provide a first estimate of the red deer distribution and minimum abundance and will be used to build spatially explicit capture-recapture models (ROYLE et al. 2014). Spatial, sex-specific information as well as covariates on density (e.g. elevation or land cover) will be incorporated to determine sex-specific population sizes.

The advantage of camera trapping is its ability to document multiple species over long periods with a high temporal resolution, therefore yielding insights into seasonal as well as diurnal patterns. While the observed area is limited to the cone-shaped detection zone of the camera, random placement of multiple cameras with respect to environmental variables ensures that landscape features are sampled in close accordance with their availability (WEARN et al. 2013). The data can then be analysed statistically to draw conclusions about the larger-scale distributions of the animals and their population densities (e.g. ROWCLIFFE et al. 2008). A minimum of 30 days of camera trapping per location can probably be regarded as a good recommendation to obtain population density estimates for most species, but this also depends on the density itself (WEARN and GLOVER-KAPFER 2017). Additional information, including sex ratio, cow: calf ratio, group size, behaviour and the occurrence of other species, can also be derived from the observations. Red deer were the most numerous species in our study area, but it is important to keep in mind that large-bodied animal species have a higher probability of triggering the camera trap than do smaller ones (HOFMEESTER et al. 2017). Moreover, there may be within-species variations in detectability. For example, daily movement rates differ between red deer sexes, with the travel speeds of males being much faster in autumn during the rutting season (HEURICH et al. 2016), leading to higher camera trapping rates. When only June was included in the analysis, the proportions of males and females were skewed towards females and males in the BFNP and SFNR respectively. The larger proportion of tagged males in the SNP was likely due to the smaller proportion of sexed individuals and to the higher certainty of observers in recognizing males, as the comparison between males and adult animals not classified as males shows. The genotyping results support this notion. Camera trapping and winter enclosure counts are not directly comparable, which is demonstrated by large sex ratio differences in the SFNR (Table 1). Calves may be less likely to be detected by camera traps than adult females, because of differences in size and behaviour. Despite this shortcoming, differences in the cow-calf ratio between the SFNR and the other two subareas could indicate that females with calves are less likely to migrate out of the subarea. Beyond these indices the camera trapping data obtained in our study will be used for multiple approaches to estimate the red deer population density (Table 4).

With an aerial survey, a large area can be monitored for red deer within a narrow time window, causing minimal disturbances for the animals and their habitats, as nobody has to enter the survey area on foot. However, dense canopy cover may prevent detection, which might explain the low detection rate in the mixed forests at lower elevations. Nonetheless, the findings of our aerial survey were roughly consistent with the low red deer densities in these areas as indicated by faeces sampling and camera trapping and were thus considered representative of the study area. Estimates of visibility per habitat type, especially for gradients of canopy cover, can be used to account for differences in detection probabilities (POTVIN & BRETON 2005).

While the aforementioned methods provide information on animal distributions at relatively coarse spatio-temporal scales, GPS telemetry provides a picture of the behaviour and movement patterns of specific individual animals at high spatio-temporal resolution (Nathan et al. 2008) and is thus commonly used to investigate inter-individual differences with respect to spatial use and behaviour. Moreover, information on home range size and movement rate can help to interpret the results of other methods such as camera trapping (Dillon & Kelly 2008, Rowcliffe et al. 2008) or spatially explicit capture recapture data (Royle et al. 2013). Additionally, it can be used to evaluate changes in habitat quality and the associated shifts in density and distribution (Said & Servanty 2005, Gaillard et al. 2010).

For ungulates, habitat selection, and thus the distribution and abundance of these animals, is mainly driven by the trade-off between forage and predation (Fryxell et al. 1988). In general, this was reflected in the density patterns observed in our study. The high percentage of dense conifer forest cover across the study area and the fairly low productivity during long periods of the year at higher elevations, where snow cover is typically present for up to 200 days (Heurich & Neufanger 2005), leads to seasonal shifts in distribution (Rivrud et al. 2016a) and may depress population growth. Forage availability is the main factor explaining the red deer distribution characterised by high densities at higher elevations and in areas with abundant deciduous regeneration. Nutrient-poor, waterlogged sites in colder conditions with low coniferous cover become areas of high herb biomass in summer and are especially attractive for red deer. By contrast, beech-dominated montane forests are the habitats least favoured by red deer (Ewald et al. 2014). Fewer disturbances by hunting and forestry in the nature zones of the national parks and reduced human recreational activities in the core zones (Heurich et al. 2011) may also support an increase in local red deer densities, even in habitats of lower quality (Lone et al. 2015).

In the absence of a significant predation risk, hunting is by far the most important cause of mortality for wild ungulates in Europe (Apollonio et al. 2017) Predation by lynx plays a much smaller role for red deer than for roe deer (Belotti et al. 2014) and the current number of wolves is still too low to significantly influence population development, but this may change in the future. The significant reduction in red deer population densities during the first years after the founding of the BFNP (Heurich et al. 2011) suggests a considerable impact of hunting, the success of which may be related to harsh winters that force the animals to descend to lower elevations and to visit baiting sites. Nonetheless, the annual counts indicated a stable to positive population development since the beginning of this century and therefore a favourable effect of environmental changes in these years. For wide-ranging species such as red deer, coordinated wildlife management strategies across management jurisdictions are necessary to meet future population goals while incorporating stakeholder interests (Meisingset et al. 2017).

The sizes of the home ranges of red deer differed substantially between the BFNP and the SFNR. In addition to forage availability, this difference can be partly explained by the hunting regime. Intensive hunting was shown to increase the movement and home range sizes of red deer in Denmark (Jeppesen 1987) but no hunting is allowed within 75% of the BFNP. A common response to hunting pressure is moving into areas with restricted hunting or no hunting at all, such as national parks, as shown for North American elk (Conner et al. 2001, Proffitt et al. 2010). In our study, four of the red deer collared in the SFNR had shifted a part of their annual home ranges into the non-hunting zones of the national parks. In addition, the daily activity patterns recorded in the SFNR suggested that anthropogenic disturbances had increased the nocturnality of red deer. Similar reactions were observed in roe deer, as their diurnal activity decreased in areas more strongly impacted by human activities (Bonnot et al. 2020).

The distribution of hunted deer matched the spatial pattern determined by camera trapping in the BFNP and SNP. In these two national parks, the proportion of camera trapping rates in relation to the average over the whole study area (BFNP: 69%, SNP: 151%) was higher than the proportion of hunted deer densities compared to the average (BFNP: 51%, SNP: 126%). In the managed forest of the SFNR, camera trapping rates were 50% of the average, but the proportion of hunted deer per square kilometre was 64% of the average. The sex ratio of the hunted deer was nearly balanced, consistent with the estimates for the population (Table 1). Relative to their abundance in the population estimated from the camera trapping rate, calves were overrepresented in the hunting bags, indicative of their selective targeting by hunters.

The assumption that red deer population densities are reflected in the results of browsing surveys (Ward et al. 2008) was largely confirmed in our study. Yet, the relative occurrences of preferentially browsed tree species should be taken into account when drawing inferences on relationships between browsing and deer density (Díaz-Yáñez et al. 2017). Ungulates in the Bohemian Forest favour common rowan over silver fir and European beech while Norway spruce is strongly avoided (Möst et al. 2015). Spruce is browsed intensively only if other, more palatable forage sources are depleted or not available (Motta 2003). Thus, plots with a high proportion of spruce may show low browsing intensities even under high deer densities, which must be taken into account in interpretations of overall spatial browsing patterns. Möst et al. (2015) found an increase in browsing pressure with decreasing distance to winter enclosures regardless of tree species. The two sites with the highest browsing pressure in the BFNP were indeed located close to the two winter enclosures Neuhüttenwiese and Buchenau. The same study found that less-preferred tree species were more rarely browsed in the ungulate management zone than in the non-hunting zone of the BFNP and browsing decreased closer to trails or roads (Möst et al. 2015). The high population densities but relatively low browsing pressures in the mountain spruce forests close to Mt. Rachel can be explained by the large availability of grass in the open areas created by the extensive bark beetle outbreaks and the absence of preferred tree species. Grasses constitute up to 90% of the red deer diet at high elevations (Krojerová-Prokešová et al. 2010) and therefore relieve the browsing pressure on regenerating trees.

Conclusions

Several methods are available to assess red deer population densities and structures, each with its own advantages and disadvantages regarding practical implementations and potential biases in the results. Most importantly, the method considered must yield the specific data needs posed by the ecological or management questions at hand. Researchers and managers must consider the trade-off between accuracy and precision and costs and first determine which parameters, e.g. precise density estimates versus relative abundance in time and/or space, are needed (Morellet et al. 2011). Aerial surveys work best in areas with fairly low canopy cover or need habitat-specific visibility correction factors to account for heterogeneous and sometimes dense forest cover, as it was the case in our study area. Camera trapping is especially versatile in obtaining different population parameters, after differences in detection probabilities are considered. The most precise estimates of the structure and density of the red deer population will likely be obtained by genotyping faecal samples, especially if very fresh faeces can be collected.

With regards to economic feasibility, aerial surveys can offer an efficient one-time snapshot for large areas independent of animal density, while camera trapping is very cost-effective in the long-term with regards to field work. Further analyses aimed at optimising the study design will be conducted to obtain reliable results while keeping the number of camera traps needed and the deployment period to a minimum. While the manual classification of photos and videos can be very time-consuming, the automatization of this process using machine learning approaches will increase its efficiency and make this method even more attractive to managers (Tabak et al. 2019). The costs for the genotyping of non-invasive samples are largely determined by the amount of samples that depends on the population density (Table 4). Especially when spatio-temporal dynamics in population size and distribution are of interest, it may be most advisable to consider a combination of methods. For example, periodically conducted faecal genotyping can be used to validate and augment continuous camera trapping data, regular aerial surveys or indices for population densities from winter enclosure counts or browsing surveys. Subsequent analyses during the Interreg-Project "New ways towards a cross-border red deer management in times of climate change" will provide further insights into the precision and accuracy of each method based on calculations of population estimators using robust statistical methods.

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Appendix 1. Active enclosures in the study area, including the Bavarian Forest National Park (BFNP), the state forest of Neureichenau (SFNR) and Šumava National Park (SNP) between 2001 and 2020. The years refer to the time period of counting the animals in the enclosures.
x = enclosure active without recorded complications, count data is available
O = enclosure opened during the winter (opening of the gates or damages to the fence)
D = disturbances in the vicinity of the enclosure, likely preventing deer from entering
NA = no count data available
An empty cell indicates that the enclosure was not operational.

Subarea	Winter enclosure	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	Avg. animals/year
BFNP	Ahornschachten	NA	x	x	x	x	x	O	x	x	x	O	x	x	x	x	x	x	x	x	x	30
BFNP	Buchenau	NA	x	D	x	x	x	x	x	x	D	x	x	x	x	x	x	x	x	x	x	58
BFNP	Neuhüttenwiese	NA	x	D	x	x	O	x	x	x	x	x	x	x	x	x	O	x	x	x	x	114
BFNP	Riedlhäng	NA	x	x	x	x	x	O	O	x	x	x	x	x	x	x	x	x	x	x	x	89
SFNR	Marderau	NA	NA	NA	NA	NA	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	148
SFNR	Schlichtenberg	NA	NA	NA	NA	NA	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	86
SNP	Hejhal	x	x	x	x	x	x															7
SNP	Ctyrka	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	80
SNP	Wastl	x	x	x	x	x	x	O	x	x	x	x	x	x	x	x	x	x	x	x	x	23
SNP	Dobronin	x	x	x	x	x																15
SNP	Zadni Chalupy		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	25
SNP	Rokyta		x	x	x	x	x	O	x	x	x	x	x	x	x	x	x	x	x	x	x	30
SNP	Beranky		x	x	x	x	x	O	x	x	x	x	x	x	x	x	x	x	x	x	x	125
SNP	Frantiskov		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x					7
SNP	Spicak	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	87
SNP	Brezova Lada	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	40
SNP	Obecni Les		x	x	x	x	x	O	O	x	x	x										35
SNP	Valna												x	x	x	x	x	x	x	x	x	27
SNP	Kohouti						x	O	x	x	x	x	x	x	x	x	x					8
SNP	Planyrka	x	x	x	x	x	x	O	O	O	x	x	x	O	O	x	x	x	x	x	x	9
SNP	Kostelni	x	x	x	x	x	x															5
SNP	Hucinka	x	x	x	x	x	x															5
SNP	U Herciana	x	x	x	x	x	x	O	x	x	x	x	x	x	x	x	x	x	x	x	x	45