Italian Journal of Animal Science

ISSN: 1828-051X (Online) Journal homepage: www.tandfonline.com/journals/tjas20

Mortality and spatial behaviour of farmed red deer after hard reintroduction

Nikica Šprem , Branimir Stankić , Pavao Gančević , Konstantinos Papakostas & Toni Safner

To cite this article: Nikica Šprem , Branimir Stankić , Pavao Gančević , Konstantinos Papakostas & Toni Safner (2026) Mortality and spatial behaviour of farmed red deer after hard reintroduction, Italian Journal of Animal Science, 25:1, 944-954, DOI: 10.1080/1828051X.2026.2699505

To link to this article: https://doi.org/10.1080/1828051X.2026.2699505

ITALIAN JOURNAL OF ANIMAL SCIENCE
2026, VOL. 25, NO. 1, 944–954
https://doi.org/10.1080/1828051X.2026.2699505

Taylor & Francis by informa

RESEARCH ARTICLE

OPEN ACCESS Check for updates

Mortality and spatial behaviour of farmed red deer after hard reintroduction

Nikica Šprem[a], Branimir Stankić[b], Pavao Gančević[c], Konstantinos Papakostas[d,e] and Toni Safner[f,g]

[a]Department of Fisheries, Apiculture, Wildlife Management and Special Zoology, University of Zagreb, Faculty of Agriculture, Zagreb, Croatia; [b]Croatian Hunting Federation, Zagreb, Croatia; [c]Agromediterranean Faculty, University of Split, Split, Croatia; [d]Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Koper, Slovenia; [e]Faculty of Environmental Protection, Velenje, Slovenia; [f]Department of Plant Breeding, Genetics, Biometrics and Experimentation, University of Zagreb, Faculty of Agriculture, Zagreb, Croatia; [g]Centre of Excellence for Biodiversity and Molecular Plant Breeding (CoE CroP-BioDiv), Zagreb, Croatia

ABSTRACT

Red deer, *Cervus elaphus*, is native to Europe and is one of the most frequently managed ungulate species. Reintroduction programmes often use farmed animals because they require less effort than live-captured wild animals, but farmed animals may struggle to acclimatise to life in the wild. We conducted this study in central Croatia from 2017 to 2024 and analysed the post-release spatial behaviour of 16 farmed red deer fitted with GPS collars (10 ♀ and six ♂) after a hard release (animals released from the trailer without acclimated period). Overall mortality reached 69% (11 animals) and poaching mortality showed a sex bias, with 100% mortality in males and 40% in females. Females had an average home range (minimum convex polygon, 95%) of 27.4 km^2 and males 98.4 km^2. We found no significant sex difference in the home range establishment period, defined as the time until stabilisation of post-release space use, although sample size was small (six out of 10 females, two out of six males). The high mortality rate supports that farmed deer struggle to adapt to the wild. Future work should evaluate if success is higher if using wild deer for reintroductions and evaluate soft release (animals released from the enclosure after acclimated period).

HIGHLIGHTS

- Hard reintroduction indicated a high mortality post-release rate of 69%.
- Poaching mortality showed a strong male bias.
- Mean survival time after release was 297 days.
- The mean home range size was 27.4 km^2 in females and 98.4 km^2 in males.

ARTICLE HISTORY
Received 11 April 2026
Revised 25 June 2026
Accepted 26 June 2026

KEYWORDS
Cervus elaphus; home range; poaching; restocking; telemetry

Introduction

Reintroduction or restocking refers to the process of translocation and releasing animals into areas where they were previously extirpated or considered endangered and where conditions are still favourable for their survival (Apollonio et al. 2014). This process is often carried out as part of conservation measures to restore natural ecological processes and biodiversity. At the same time, these interventions often have economic benefits such as hunting opportunities and wildlife watching (Chapagain and Poudyal 2020; Faure et al. 2024). Reintroduction measures usually require careful planning to ensure the survival and successful establishment of the wildlife population in its new or restored habitat (Parker et al. 2012; Apollonio et al. 2014). Prior to initiating reintroduction efforts, it is essential to conduct a series of preliminary assessments to enhance the likelihood of success. These should include habitat suitability assessments, SWOT (strengths, weaknesses, opportunities, threats) analyses and stakeholder opinion surveys, which collectively provide critical ecological, socio-economic and institutional insights for informed decision-making (White et al. 2015; Stadtmann and Seddon 2020; Marino et al. 2024). Successful reintroduction requires a good post-release monitoring program and assessment of ecological and environmental relationships (Torres et al. 2016; Valente et al. 2017). Reintroduction actions in Europe began in the nineteenth century, with most

CONTACT Nikica Šprem nsprem@agr.hr Department of Fisheries, Apiculture, Wildlife Management and Special Zoology, University of Zagreb, Faculty of Agriculture, Zagreb, Croatia

Supplemental data for this article can be accessed online at https://doi.org/10.1080/1828051X.2026.2699505.

major efforts occurring in the twentieth century, aiming to restore ecological balance and preserve biodiversity. Among the most successful ungulate reintroduction programmes in Europe are those involving the Alpine ibex (*Capra ibex*) (Stüwe and Nievergelt 1991), the European bison (*Bison bonasus*) (Krasinska and Krasinski 2007) and the Apennine chamois (*Rupicapra pyrenaica ornata*) (Antonucci et al. 2025). Without these interventions, it is likely that some of these species would become extinct (Apollonio et al. 2014).

The red deer, *Cervus elaphus*, is a deer species native to Europe and was an integral part of the European ecosystem in the past. It played a crucial role in shaping the ecosystem by influencing vegetation structure and composition through grazing and browsing (Schwegmann et al. 2024). In addition, red deer provided an important prey resource for large carnivores, thereby contributing to predator population persistence and influencing trophic interactions (Jędrzejewski et al. 2011). Through their effects on habitat structure, resource availability and nutrient cycling, deer also affected a wide range of associated taxa, highlighting their role as ecosystem engineers (Suominen et al. 2006).

The status of red deer in Europe is highly heterogeneous. While historical declines led to local extirpations and prompted numerous reintroduction and restocking programmes during the twentieth century, many populations have since recovered and expanded substantially (Mattioli et al. 2022). In several regions, particularly where natural predators are absent or occur at low densities and hunting pressure is limited, red deer populations have reached high abundances. Such increases have been associated with a range of ecological and management challenges, including excessive browsing pressure on forest regeneration, alterations in vegetation composition, agricultural damage, and conflicts with forestry and conservation objectives (Apollonio et al. 2010). Consequently, contemporary management of red deer in Europe often involves balancing conservation goals with the mitigation of ecological and socio-economic impacts arising from overabundant populations (Putman et al. 2011).

One of the main reasons for the numerous human interventions in the red deer population is the fact that it is a species of great hunting interest (Milner et al. 2006; Rivrud et al. 2013). In some cases, reintroduction was clearly dedicated to improving trophy quality, and this played an important role in the choice of source populations (Lowe and Gardiner 1974), while in other cases greater efforts were made to restore declining populations (Apollonio et al. 2014). Therefore, as a result of reintroduction and restocking programmes, and changes in land use across Europe, red deer has become one of the most widely distributed ungulate species on the continent (Cerri et al. 2026).

Managers often carry out deer reintroductions using farmed or captive animals because they require less effort than capturing wild animals alive, but these animals can struggle to acclimatise to life in the wild and to cope with predation risk (Nilsson et al. 2014). The genetic background of farm animals can also play an important role, as they can experience inbreeding depression and reduced genetic diversity (Frankham et al. 2004). As a result, they may show weaker selection for disease and parasite resistance (Apollonio et al. 2014).

The origin and number of animals used in reintroductions greatly affect the success of the action itself (Allendorf and Luikart 2007), and so wild source animals and a greater number of individuals have higher success rate than farm animals and fewer individuals (Fischer and Lindenmayer 2000; Lloyd et al. 2019; Beckmann and Soorae 2022). Furthermore, reintroduction can be done in a soft or hard way (Parker et al. 2012). Soft releases imply the construction of infrastructure (e.g. enclosures, fences) and therefore the financial investments are considerable before the start of the process. During soft release procedure, animals are acclimated for some period in enclosure to a novel area before release, while hard releases are without acclimated/holding period and animals are released immediately from the trailer (Bright and Morris 1994). Comparing these two methods, the soft method achieves much better results and is practiced more frequently (Ryckman et al. 2010).

According to the available literature, most documented red deer reintroduction programmes in Europe have resulted in the successful establishment and persistence of populations, as reported for reintroductions in the United Kingdom (Macdonald and Feber 1996), Italy (Mattioli et al. 2001), Portugal (Valente et al. 2017) and Lithuania (Balčiauskas and Yukichika 2022). However, reports of unsuccessful or only partially successful reintroductions are scarce, limiting the ability to evaluate the overall success rate of red deer reintroduction efforts across the species' European range and raising the possibility of publication bias (Mattioli et al. 2022).

Although red deer have featured in many reintroduction programmes, studies that examine post-release spatial behavioural ecology remain scarce

(Fischer and Lindenmayer 2000; La Morgia et al. 2011; Riga et al. 2022; Stankov et al. 2024). Information on mortality, post-release dispersal, home range and habitat use strongly influences population viability, reintroduction success and decisions about whether to release additional animals. This study aimed to describe the post-release survival and spatial behaviour of farmed red deer following a hard release, using GPS telemetry. We also assessed whether females and males differed in their post-release survival and spatial behaviour.

Materials and methods

Ethics statement

The study was conducted according to the ethical and welfare standards presented in the Official Gazette of the Republic of Croatia (OG 102/2017, Animal Protection Act) and Regulation on the Protection of Animals Used for Scientific Purposes (OG 55/13), with the approval of the Bioethical Committee for the Protection and Welfare of Animals of the University of Zagreb Faculty of Agriculture (UR.BR. 251-71-29-02/19-22-2).

Study area and red deer population history

The study was carried out in central Croatia, Sisak-Moslavina County, directly on the state border with Bosnia and Herzegovina (Figure 1). It covers the westernmost slopes and parts of the Zrinska Gora massif and takes its name from the Prolom forest complex. The study area is mountainous and mainly covered by forest. The entipredominatea slopes downwards towards the north, with the lowest altitude of 170 m, where the belt of climatic hornbeam *Carpinus betulus* forests predominates. The highest peak in the southern part is 529 m, where the belt of acidophilous beech *Fagus sylvatica* forests and Illyrian beech forests predominates. The water areas include streams that favour wildlife habitat and retention. The remainder consists of non-forested areas, namely neglected farmland, meadows and pastures. According to the Köppen classification, this area belongs to 'Cfwbx' climate, which means it has a warm and rainy climate with frost and snow in the (cold) winter part of the year (Zaninović et al. 2008). The annual rainfall is around 1079 mm.

The study area is inhabited by wild boar, *Sus scrofa* (15.3 ± 2.19 ind./km^2) at the highest densities, together with other ungulate species, namely: roe deer *Capreolus capreolus* (5.94 ± 1.2 ind./km^2), fallow deer *Dama dama* (less than 0.1 ind./km^2) and red deer *Cervus elaphus* (1.11 ± 0.23 ind./km^2). Density estimation in the study area is carried out continuously by camera traps and random encounter model (REM) (Rowcliffe et al. 2008). Large carnivores are also present, i.e. the grey wolf *Canis lupus* and occasionally the brown bear *Ursus arctos*. More details about density estimation methodology are described in a yearly report provided by Guerrasio et al. (2024).

In the past, red deer occupied the study area until the mid-1980s, when people eradicated them through several human related pressures, mainly poaching (Čelap M, personal communication). From then until 2015, the study area held no red deer, until some animals escaped from a nearby private enclosure. The reintroduction in the study area started in 2017 using farmed red deer, and by 2024 managers had released 67 individuals (six males and 61 females) aged one to five years (Table S1).

Breeders raise the deer used for reintroduction in an intensive lowland farm system, with a grazing area of 1.1 km^2 and a stocking density of 120–160 deer/km^2. Because stocking density remains high, staff feed deer intensively, mainly with grain, and handle them at least twice a year in a barn to apply antiparasitic treatment, cut antlers, separate herds by age, sex and live weight, and prepare animals for transport. In recent years, the recently established population has increased slightly, but poaching and, to a lesser extent, wolf predation have limited expected population growth (Šprem N, personal observation).

Sampling

During the reintroduction programme, 16 individuals (10 females and six males) were fitted with GPS collars prior to release for post-release monitoring (Table 1). We handled the animals at the farm without anaesthesia, and all animals were fitted with GPS telemetry collars (Survey, Vectronic Aerospace GmbH, Berlin, Germany). Before installation, we programmed the GPS collars to record the exact location of the animal twice a day (08:00 and 19:00) via satellite communication (Globalstar, Covington, LA). We marked the remaining released animals with different coloured ear tags (depending on the year of release) for better identification and tracking. After loading into the trailer (without sedation), we transported the animals to the study area (approximately a two-hour drive), and we hard released them at a suitable location. We chose the location based on its low anthropogenic

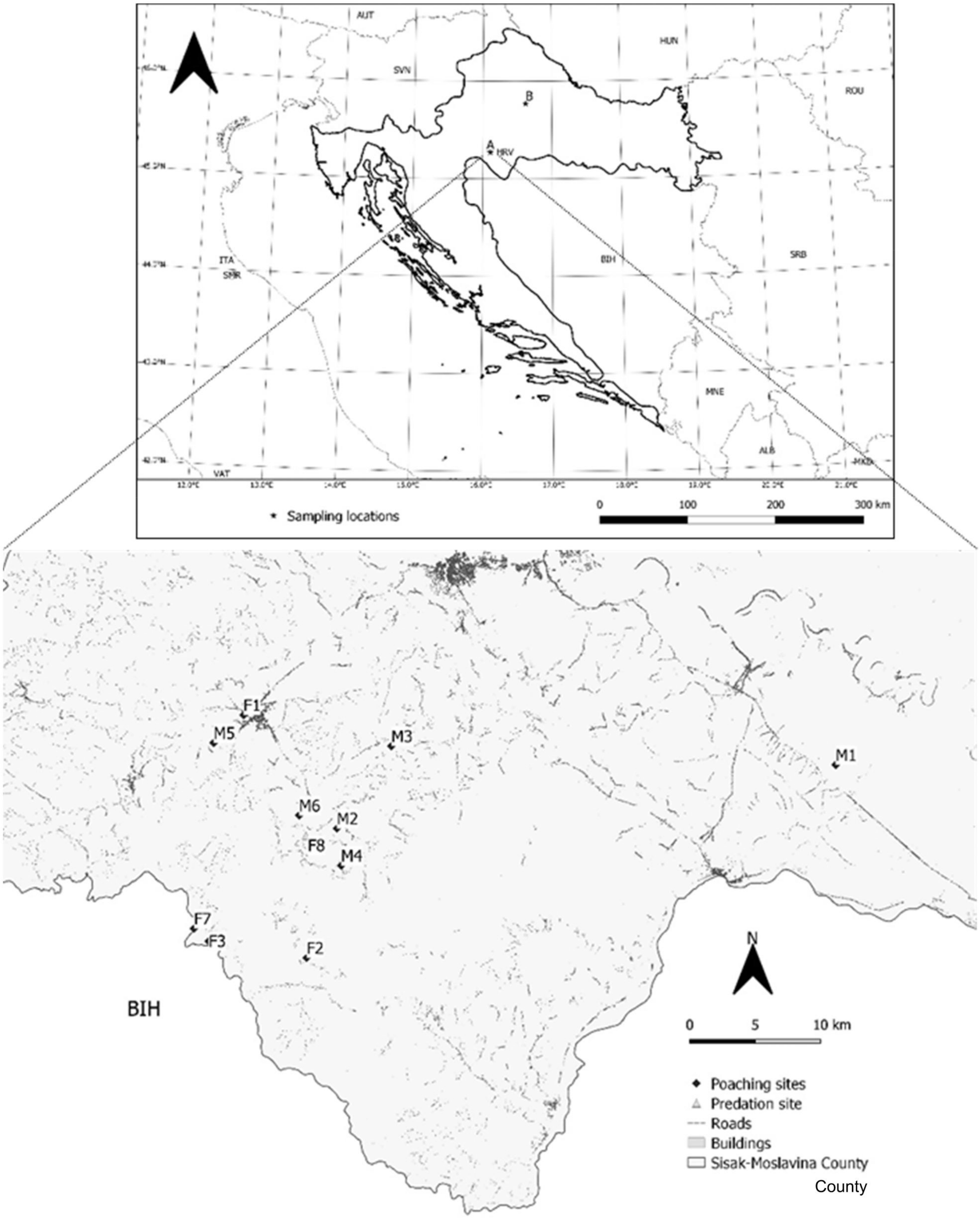

Figure 1. Location of the study areas in central Croatia; (A) study area for the hard reintroduction of farmed red deer *Cervus elaphus*; (B) red deer farm (source population) Poaching and predation sites in relation to the roads, settlements and the state border.

Table 1. Demographic and telemetry information for farmed red deer *Cervus elaphus* included in the reintroduction programme in central Croatia, including sex, estimated age, monitoring period (starting and ending GPS fix), number of active days, number of GPS fixes, MCP 95% home range area (km^2), final status and cause of death.

Animal ID	Gender	Estimated age	Starting GPS fix	Ending GPS fix	Days active	N of GPS fixes	Home range MCP 95%[a]	Status of the animal	Cause of death
F1	F	4	24 July 2018	29 January 2019	190	343	38.86	Poaching	Rifle
M1	M	3	24 July 2018	3 December 2018	133	205	362.5	Poaching	Rifle
F2	F	4	14 December 2018	1 May 2019	139	202	37.31	Poaching	Rifle
F3	F	4	14 December 2018	15 April 2019	123	221	6.12	Poaching	Snare
F4	F	4	27 February 2019	23 March 2022	1121	1785	64.94	Alive	–
F5	F	4	27 February 2020	27 June 2020	122	205	46.67	Alive	–
F6	F	4	27 February 2020	27 June 2020	122	201	8.31	Alive	–
M2	M	4	9 February 2022	1 October 2022	235	308	14.88	Poaching	Rifle
M3	M	4	9 February 2022	8 September 2023	576	935	102.79	Poaching	Rifle
M4	M	4	9 February 2022	21 December 2022	316	480	10.1	Poaching	Rifle
M5	M	2	22 March 2023	4 May 2023	44	85	82.41	Poaching	Rifle
F7	F	2	23 March 2023	7 August 2023	138	263	14.4	Poaching	Rifle
F8	F	2	19 April 2023	24 February 2025	678	1144	14.59	Predation	Wolf
M6	M	2	21 February 2024	9 January 2025	323	642	17.78	Poaching	Rifle
F9	F	3	21 February 2024	21 October 2025	609	663	18.46	Alive	–
F10	F	3	21 February 2024	27 January 2026[b]	707	704	24.83	Alive	–

[a]Home range values are in km^2.
[b]Still active.

pressure and mosaic landscape (meadows, forests, water, etc.), which are important for red deer.

Home range establishment analyses

To quantify home-range establishment, we calculated rolling 3-week 95% minimum convex polygon (MCP) home ranges for each individual, using the 'adehabitatHR' package in R (Calenge 2006). We used a moving window of three consecutive weeks, shifted forward by one week. To minimise instability caused by sparse telemetry data, we retained only 3-week windows with ≥30 GPS fixes (i.e. ≥10 fixes per week). We then quantified temporal stabilisation of space use using the Jaccard similarity index between consecutive 3-week home ranges (Equation (1)):

$$Jt = \text{Area } (H\_t \cap H\_\{t-1\})/\text{Area } (H\_t \cup H\_\{t-1\}). \quad (1)$$

where H_t denotes the 3-week MCP polygon for window t, and $H\_\{t-1\}$ denotes the polygon for the preceding window. J ranges from 0 (no overlap) to 1 (identical polygons). This index was suitable for our purpose because it is not calculated relative only to the previous or only to the current home range, but relative to the total area covered by both polygons. Therefore, low values may reflect either expansion into new areas, abandonment of previously used areas, or both, whereas high values indicate that consecutive home ranges share most of their spatial extent.

We defined establishment of a stable home range using a proportion-based criterion that allows occasional low-overlap windows during otherwise stabilised space use. Specifically, we considered a deer established when, over the following eight week-to-week comparisons, at least 75% of overlap values were ≥0.60. Because no established threshold exists for defining home-range establishment from rolling home-range overlap values, we treated these thresholds as an *a priori* operational definition developed for this study. The criterion was designed to identify sustained spatial overlap across most of an approximately two-month period, while allowing occasional low-overlap values caused by exploratory movements or temporary shifts in space use. We expressed establishment timing as days since release, based on the start week of the establishment window (7 × (week start − 1)).

Because sample size was limited and both response variables were categorical, we used Fisher's exact tests to assess sex differences in the categorical outcomes of poaching mortality and home range establishment (Kleinbaum and Klein 2012), and Kaplan–Meier's survival analysis with a log rank test to compare post-release survival over time between sexes (Agresti 2013). We interpreted the observed patterns and considered results statistically significant at $p < 0.05$. For the analysis, we used the R programming language (4.4.2) (R Core Team 2025). Finally, we examined all carcases to determine the cause of death, and all these cases were reported to the competent institutions, the Police and the Hunting Inspectorate for further action.

Dispersal distance and direction analyses

To quantify the maximum distance and the overall direction of post-release dispersal for each individual, we used the 'Near' tool in ArcGIS Pro (version 3.4.2). We estimated the maximum dispersal for each GPS fix by calculating the Euclidean distance from the release point to the most distant fix. Similarly, we also estimated the distance of the mortality sites to the closest road, state border and settlement based on public available 'Land use plans – Sisak-Moslavina County'. We also extracted the planar direction from the fix to the release point (reported as a planar angle with $0^\circ = $ East and values between -180° and 180°). Because we wanted the direction of movement from the release point to the fixes, we flipped each direction by 180° and expressed it as a standard 0–360° compass bearing. We then calculated, for each individual, the circular mean direction of the reversed angles (using mean sine and cosine) to obtain a single mean dispersal bearing. Finally, we classified each mean bearing into compass sectors (N, NE, E, etc.) to facilitate interpretation.

Results

We documented a high mortality rate of 69% (11 animals; five ♀ and six ♂) after hard release. Poachers killed 10 collared animals, whereas a predator, in this case a wolf, killed only one. Poaching mortality showed a clear male bias, as poachers killed all six males (100%) but only four females (40%) (Fisher's exact test, $p = 0.034$). Kaplan–Meier's survival curves also showed lower post-release survival in males than in females, although the difference in survival over time between sexes was not statistically significant (log rank test: $\chi^2 = 2.4$, $p = 0.10$). The animals that died survived for an average of 297 days (range: 44–1121) (Table 1).

The overall home range of females, calculated across the full monitoring period for each individual, ranged between 6.1 and 64.9 km^2, with a mean of 27.4 km^2, while males had a home range between 10.1 and 362.5 km^2, with a mean of 98.4 km^2 (Table 1, Figure 2). Eight of the 16 individuals (six females, two males) established a home range after release. They did so after a mean of 68 ± 33 days (range: 7–105 days). Females established home ranges after 70 ± 35 days (range: 7–105 days) and males after 63 ± 28 days (range: 35–91 days), with no statistically significant difference between the sexes (Fisher's exact test, $p = 0.608$). The rest of the animals died before establishing a home range.

Male red deer showed higher mean maximum dispersal distances (18.6 ± 13.9 km^2, range: 7.8–47.3 km^2)

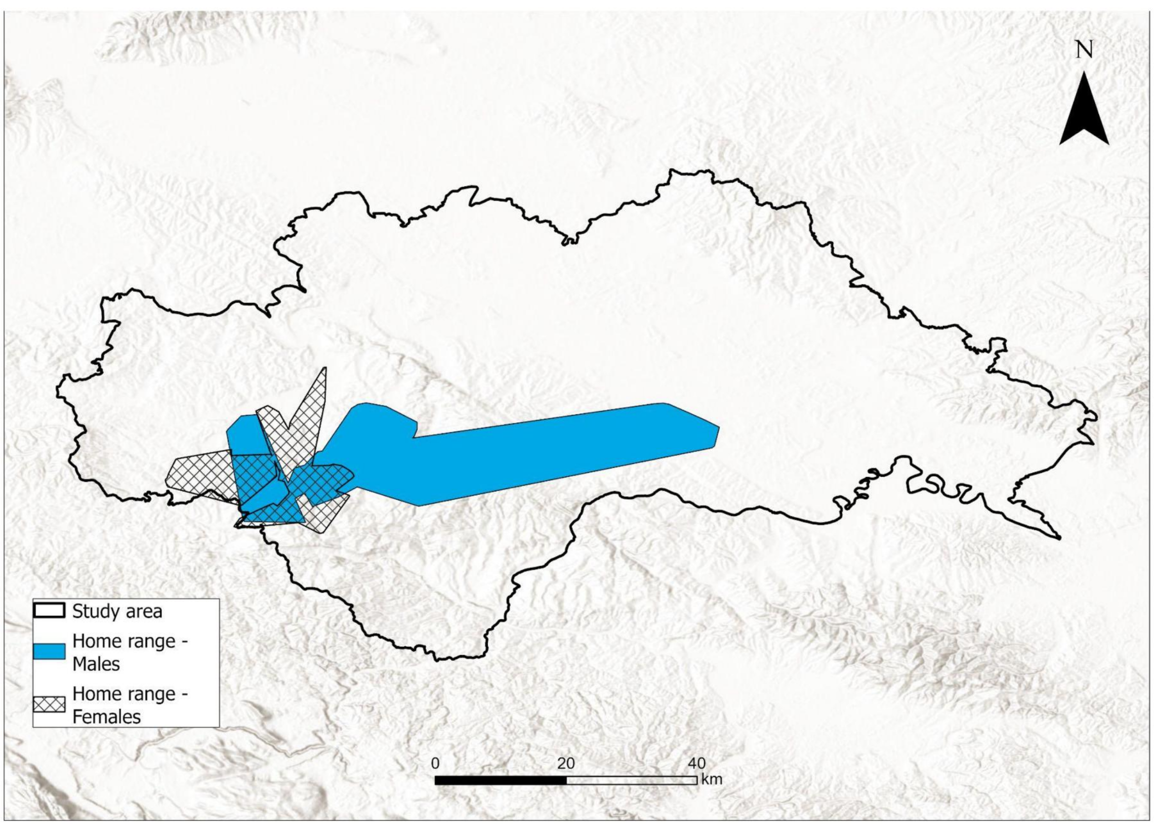

Figure 2. The overall home ranges of released females and males farmed red deer *Cervus elaphus* during hard reintroduction in central Croatia.

Table 2. Maximum dispersal distance (km) from the release point to the most distant GPS fix and mean dispersal direction for each reintroduced farmed red deer *Cervus elaphus* in central Croatia.

Animal ID	Maximum dispersal distance, km	Direction	Circular mean direction, °, East = 0
F1[a]	14.64	N	356.28
M1[a]	47.33	E	71.06
F2[a]	7.99	SE	138.54
F3[a]	4.33	S	197.53
F4	12.82	NW	297.19
F5	21.81	N	7.08
F6	5.44	N	20.71
M2[a]	8.42	NE	44.88
M3[a]	23.12	NE	38.33
M4[a]	9.33	NE	45.29
M5[a]	15.49	NW	321.24
F7[a]	6.42	W	254.38
F8[a]	9.39	N	14.86
M6[a]	7.84	N	11.61
F9	14.09	NW	293.24
F10	8.05	E	90.22

We report both a categorical direction (compass sector) and the circular mean bearing from the release point to all GPS fixes, with 0 degrees indicating east.
[a]Mortality.

Table 3. Distance of the mortality site from roads, settlements and the state border in reintroduced farmed red deer *Cervus elaphus* in central Croatia (see S1).

Animal ID	Distance of the mortality site from the road, km	Distance of the mortality site from the settlement, km	Distance of the mortality site from the state border, km
F1	0.16	0.39	14.10
M1	1.27	1.28	8.99
F2	0.19	18.15	6.01
F3	0.29	2.69	0.24
M2	0.59	0.83	12.87
M3	0.24	0.84	24.48
M4	0.24	0.66	11.61
M5	0.18	0.18	11.20
F7	0.67	1.15	0.31
F8[a]	0.43	0.45	10.37
M6	0.91	1.05	10.71
Study area	4.74 (±5.9)	4.67 (±5.56)	3.82 (±5.87)

The final row shows the mean distance ± standard deviation for each variable across the whole study area.
[a]Predator mortality.

than females (10.5 ± 5.1 km^2, range: 4.3–21.8 km^2). Eleven animals (six ♀ and five ♂) dispersed northward (N, NW, NE) after release, whereas only two females dispersed southward (S, SE) (Table 2).

The mortality site of six animals was less than 300 m away from the road. Other distances of mortality sites due to settlements and the state border are shown in Table 3.

Discussion

Our results clearly highlight poor survival of farmed animals used in reintroduction programmes. Farmed animals can lose antipredator behaviour, show less aggressive personalities, and display avoidance behaviour, which can increase mortality compared with wild animals (McDougall et al. 2006). Our results support this pattern. Of the 16 collared individuals, 11 died, with only one death caused by a predator and most deaths caused by poaching (Table 1). We also observed low wariness towards people. Several times, both GPS collared animals and individuals with ear tags allowed humans to approach to about 50 m before they moved slowly away. We also observed that newborn animals showed little fear of humans. This pattern probably reflects repeated handling on the farm several times per year, which may have made the animals easier targets for poachers. Evidence for low wariness also appeared at mortality sites, as most carcases occurred close to roads and settlements (Figure S1, Table 3). We explain the high mortality rate near roads and during night hours, based on the time when the collar mortality sensor activated, by the fact that many poachers operate from cars. They often drive at night and shoot using flashlights or night vision and thermal scopes. This problem appears to have worsened after 2018, when Croatian hunting law permitted night hunting to reduce wild boar numbers following the African swine fever outbreak.

Several studies report that farmed or captive bred animals generally show lower post-release survival than wild sourced animals (Griffith et al. 1989; Fischer and Lindenmayer 2000), and that failure often occurs (Watters and Meehan 2007). Studies also suggest that animals reared on large scale farms survive better than animals from small farms (Zidon et al. 2009). Hence, the high mortality we observed may partly reflect the small size of the source farm, which covered 1.1 km^2. The high mortality rate in our study aligns with the view that reintroductions succeed more often when managers translocate a larger number of wild animals rather than farmed animals (Parker et al. 2012; Apollonio et al. 2014). For example, in Portugal, managers reintroduced wild red deer and the population increased over two decades and spread across the area (Valente et al. 2017). In contrast, in the Omsk region of Russia, reintroductions that used farmed red deer resulted in semi wild animals and population growth did not meet expectations, similar to our case (Kassal 2015).

Poaching is recognised as a global problem and poses a serious threat especially to small and endangered populations (Goodrich et al. 2008; Liberg et al. 2012; Koen et al. 2017). The problem of poaching has also been recognised in Croatia (Hanley and Mikac 2020), in particular, a strong bias in sex-specific poaching mortality that likely reflects trophy killing, as previously suggested by Corlatti et al. (2019) for Italy. We hypothesise that intense poaching relates to the recent reintroduction of red deer to this area, as the species may represent a new target for local hunters and poachers for both meat and trophies. Of the 10 poached animals, rifles killed nine and a snare killed one. Supplementary material Figure S1 shows that poachers usually left the carcase at the site. We suggest that this happened because the animals did not die immediately after the shot and moved away before they collapsed or the poachers got scared when they saw the collar on the animal. In the case of deer M3, poachers removed only the antlers and left the carcase behind (Figure S1).

In our study, females used home ranges of 6.1–64.9 km^2, which they used to meet their needs for energy, cover and reproduction. Males used home ranges of 10.1–362.5 km^2 (Table 1, Figure 2). These values agree with previous reports (Mattioli et al. 2022; Jarnemo et al. 2023) and with the general tendency for males to use larger home ranges than females (Carranza et al. 2025). However, they contrast with results from soft released red deer in Serbia, where females had larger home ranges (20.6 km^2) than males (12.8 km^2) (Stankov et al. 2024). The higher average home range area for males in our study (98.4 km^2) likely reflects the highly dispersive male M1, which strongly influenced the results (Table 1). Males generally show greater dispersal capacity than females. Long distance and short distance movements in red deer also vary with the context in which a population lives, including changes in abiotic conditions that influence forage availability and quality, and physiological factors such as reproduction (Carranza et al. 2025).

Although our small sample size limited inference, we found no clear difference between females and males in the time required to establish a home range. Only half of the animals established a home range after release, including 60% of females and 33% of males. Introduced animals may need more time to stabilise space use because they perceive high risk in a novel environment (Maor-Cohen et al. 2021), especially after a hard release of farmed animals. The higher proportion of females that established a home range may partly reflect the stronger philopatric behaviour of females, compared to the higher dispersal ability of males (Carranza et al. 2025).

Researchers refer to consistent individual differences in behaviour as 'animal personality' (Nilsson et al. 2014). Reintroduced animals often explore unfamiliar environments and disperse over larger areas. Studies suggest that dispersal behaviour mainly reflects three traits: exploration and ambition, aggression and social behaviour (Cote et al. 2010). Our results for hard released farmed red deer showed relatively short dispersal distances between the release point and the most distant GPS fix (on average 10.5 km for females and 18.6 km for males). These values resemble those reported for hard released elk *Cervus canadensis* in Ontario, Canada, which dispersed 13.0–22.2 km (Haydon et al. 2008). Our dispersal distances were higher than those reported for soft released red deer in northern Serbia, averaging 6.4 km for females and 6.0 km for males (Stankov et al. 2024). A soft release group in our study area would have strengthened comparisons, because the contrast between studies may suggest that translocation alone can promote dispersal behaviour in deer (Ryckman et al. 2010). In addition, farmed animals released into unfamiliar habitats may also disperse less because they do not know local food sources or escape routes (Bright and Morris 1994). Dispersal directions also varied among individuals, which suggests that animals moved in different directions in a new and unfamiliar habitat, consistent with Haydon et al. (2008). Notably, individuals that lived together on the farm and that managers released at the same time often dispersed in different directions (Tables 1 and 2). Overall, dispersal direction did not relate to mortality, as deaths occurred across all directions (Table 2, Figure S1).

Conclusions

Managers should plan reintroduction and restocking carefully, and long-term behavioural, genetic and health monitoring after release is necessary to support success. Mortality is an expected part of these programmes, but it is typically higher in farmed animals than in wild animals. A key issue is that farmed animals can be 'naïve' because they often show reduced avoidance behaviour and weaker survival responses than wild animals. Ultimately, managers may improve the chances of success by combining strategies, including hard release of wild caught animals and soft release of farmed animals.

Research limitations

Although our study provides important insights for red deer reintroduction programmes, we acknowledge some limitations that should be considered when interpreting the results. First, dispersal distances were calculated as Euclidean distances from the release site and therefore represent straight line displacement rather than actual movement paths. Maximum dispersal distance was also based on the most distant GPS location recorded for each deer, which may be sensitive to outliers. Second, the sample size was limited, especially after post-release mortality, which reduced statistical power and limited our ability to test additional predictors of mortality or home range establishment, such as release year or season. Third, we used 95% MCPs to quantify rolling home ranges. MCPs may overestimate space use by including unused areas within the polygon and may therefore inflate overlap between consecutive home ranges. However, our aim was not to estimate fine scale intensity of space use, but to assess whether the outer spatial extent occupied by each deer became stable through time. For this purpose, MCPs provided a simple and comparable boundary-based estimator across individuals and time windows.

Acknowledgements

The authors would like to thank to all gamekeepers, hunters and Faculty stuff for great assistance during animal handling. We would like to thank the two reviewers for their valuable comments and suggestions, which have substantially improved and strengthened the manuscript.

Author contributions

CRediT: **Nikica Šprem**: Conceptualization, Resources, Supervision, Writing – original draft; **Branimir Stankić**: Data curation, Investigation, Writing – review & editing; **Pavao Gančević**: Data curation, Investigation, Writing – review & editing; **Konstantinos Papakostas**: Formal analysis, Writing – review & editing; **Toni Safner**: Formal analysis, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The study was supported by the Research Station of University of Zagreb Faculty of Agriculture 'Ban Josip Jelačić', the Ministry of Science, Education and Youth of the Republic of Croatia as part of the project for the popularisation of life science, European Union – Next Generation EU and Erasmus + SHUNTDIEM (Project: 2024-1-CZ01-KA220-HED-000253199).

Data availability statement

The data that support the findings of this study are available on request from the corresponding author, NŠ.

References

Agresti A. 2013. Categorical data analysis. 3rd ed. John Wiley & Sons Inc.

Allendorf FW, Luikart GH. 2007. Conservation and the genetics of populations. Blackwell Publishing.

Antonucci A et al. 2025. The reintroduction of Apennine chamois in the Majella National Park: an evaluation of long-term results. J Nat Conserv. 86:126950. https://doi.org/10.1016/j.jnc.2025.126950

Apollonio M, Andersen R, Putman R. 2010. European ungulates and their management in the 21st century. Cambridge University Press.

Apollonio M, Scandura M, Šprem N. 2014. Reintroduction as a management tool for European ungulates. In: Putman R, Apollonio M, editors. Behaviour and management of European ungulates. Whittles Publishing. p 46–77.

Balčiauskas L, Yukichika K. 2022. Red deer in Lithuania: history, status and management. Sustainability. 14(21):14091. https://doi.org/10.3390/su142114091

Beckmann KM, Soorae PS. 2022. Conservation translocations from the 'Global Reintroduction Perspectives' series: disease and other biological problems. Ecol Sol Evid. 3(3): e12163. https://doi.org/10.1002/2688-8319.12163

Bright PW, Morris PA. 1994. Animal translocation for conservation: performance of dormice in relation to release

methods, origin and season. J Appl Ecol. 31(4):699–708. https://doi.org/10.2307/2404160
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(3–4):516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017
Carranza J, Mattioli S, Putman R, Pérez-Barbería FJ, Gordon IJ. 2025. Red deer *Cervus elaphus* Linnaeus, 1758. In: Melletti M, Focardi S, editors. Deer of the world: ecology, conservation and management. Springer Nature. p 187–208.
Cerri J et al. 2026. Trends of ungulate species in Europe: not all stories are equal. Mammal Res. 71:19. https://doi.org/10.1007/s13364-025-00838-6
Chapagain BP, Poudyal NC. 2020. Economic benefit of wildlife reintroduction: a case of elk hunting in Tennessee, USA. J Environ Manage. 269:110808. https://doi.org/10.1016/j.jenvman.2020.110808
Corlatti L, Sanz-Aguilar A, Tavecchia G, Gugiatti A, Pedrotti L. 2019. Unravelling the sex- and age-specific impact of poaching mortality with multievent modelling. Front Zool. 16(1):20. https://doi.org/10.1186/s12983-019-0321-1
Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philos Trans R Soc Lond B Biol Sci. 365(1560):4065–4076. https://doi.org/10.1098/rstb.2010.0176
Faure E, Levrel H, Quétier F. 2024. Economics of rewilding. Ambio. 53(9):1367–1382. https://doi.org/10.1007/s13280-024-02019-2
Fischer J, Lindenmayer DB. 2000. An assessment of the published results of animal relocations. Biol Conserv. 96(1):1–11. https://doi.org/10.1016/S0006-3207(00)00048-3
Frankham R, Ballou JD, Briscoe DA. 2004. A primer of conservation genetics. Cambridge University Press.
Goodrich JM et al. 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin biosphere Zapovednik. J Zool. 276(4):323–329. https://doi.org/10.1111/j.1469-7998.2008.00458.x
Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: status and strategy. Science. 245(4917):477–480. https://doi.org/10.1126/science.245.4917.477
Guerrasio T et al. 2024. Generating wildlife density data across Europe in the framework of the European Observatory of Wildlife (EOW). EFSA Support Publ. 21(10):EN-9084. https://doi.org/10.2903/sp.efsa.2024.EN-9084
Hanley N, Mikac KM. 2020. Wildlife crime in Croatia. Forensic Sci Med Pathol. 16(4):702–704. https://doi.org/10.1007/s12024-020-00293-6
Haydon DT et al. 2008. Socially informed random walks: incorporating group dynamics into models of population spread and growth. Proc R Soc B. 275(1638):1101–1109. https://doi.org/10.1098/rspb.2007.1688
Jarnemo A, Nilsson L, Wikenros C. 2023. Home range sizes of red deer in relation to habitat composition: a review and implications for management in Sweden. Eur J Wildl Res. 69(5):92. https://doi.org/10.1007/s10344-023-01719-6
Jędrzejewski W, Apollonio M, Jędrzejewska B, Kojola I. 2011. Ungulate—large carnivore relationships in Europe. In: Putman R, Apollonio M, Andersen R, editors. Ungulate management in Europe: problems and practices. Cambridge University Press. p 284–318.
Kassal BY. 2015. Experience of reintroduction of Siberian red deer *Cervus elaphus sibiricus* in Omsk Oblast. Russ J Biol Invasions. 6(2):87–93. https://doi.org/10.1134/S2075111715020046
Kleinbaum DG, Klein M. 2012. Survival analysis: a self-learning text. Springer. New York. https://doi.org/10.1007/978-1-4419-6646-9_2
Koen H, de Villiers JP, Roodt H, de Waal A. 2017. An expert-driven causal model of the rhino poaching problem. Ecol Model. 347:29–39. https://doi.org/10.1016/j.ecolmodel.2016.12.007
Krasinska M, Krasinski Z. 2007. European bison: the nature monograph. Mammal Research Institute – Polish Academy of Sciences.
La Morgia V, Malenotti E, Badino G, Bona F. 2011. Where do we go from here? Dispersal simulations shed light on the role of landscape structure in determining animal redistribution after reintroduction. Landsc Ecol. 26(7):969–981. https://doi.org/10.1007/s10980-011-9621-3
Liberg O et al. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc R Soc B. 279(1730):910–915. https://doi.org/10.1098/rspb.2011.1275
Lloyd NA, Hostetter NJ, Jackson CL, Converse SJ, Moehrenschlager A. 2019. Optimizing release strategies: a stepping-stone approach to reintroduction. Anim Conserv. 22(2):105–115. https://doi.org/10.1111/acv.12448
Lowe VPM, Gardiner AS. 1974. A re-examination of the subspecies of red deer (*Cervus elaphus*) with particular reference to the stocks in Britain. J Zool. 174:185–201. https://doi.org/10.1111/j.1469-7998.1974.tb03151.x
Macdonald DW, Feber RE. 1996. Reintroducing red deer to Southern England: a preliminary assessment. Biol Conserv. 77:161–173.
Maor-Cohen M et al. 2021. Settling in: reintroduced Persian fallow deer adjust the borders and habitats of their home-range during the first 5 years post release. Front Conserv Sci. 2:733703. https://doi.org/10.3389/fcosc.2021.733703
Marino F, Crowley SL, Foley NAW, McDonald RA, Hodgson DJ. 2024. The transformative potential of local stakeholder engagement in the reintroduction of a contested species. Biol Conserv. 296:110688. https://doi.org/10.1016/j.biocon.2024.110688
Mattioli S, Meneguz PG, Brugnoli A, Nicoloso S. 2001. Red deer in Italy: recent changes in range and numbers. Hystrix. 12:27–35. https://doi.org/10.4404/hystrix-12.1-4168
Mattioli S, Zachos EF, Rossi L, Lister MA, Corlatti L. 2022. Red deer *Cervus elaphus* Linnaeus, 1758. In: Zachos EF, Hackländer K, editors. Handbook of the mammals of Europe. Springer Nature. p 51–86.
McDougall PT, Réale D, Sol D, Reader SM. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Anim Conserv. 9(1):39–48. https://doi.org/10.1111/j.1469-1795.2005.00004.x
Milner JM et al. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. J Appl Ecol. 43(4):721–734. https://doi.org/10.1111/j.1365-2664.2006.01183.x
Nilsson JÅ, Brönmark C, Hansson LA, Chapman BB. 2014. Individuality in movement: the role of animal personality.

In: Hansson LA, Åkesson S, editors. Animal movement across scales. Oxford Academic. p 90–109.

Parker K, Dickens M, Clarke R, Lovegrove T. 2012. The theory and practice of catching, holding, moving and releasing animals. In: Ewen J, Armstrong D, Parker K, Seddon P, editors. Reintroduction biology. Wiley-Blackwell. p 105–137.

Putman RJ, Apollonio M, Andersen R. 2011. Ungulate management in Europe: problems and practices. Cambridge University Press.

R Core Team. 2025. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Riga F, Mandas L, Putzu N, Murgia A. 2022. Reintroductions of the Corsican red deer (*Cervus elaphus corsicanus*): conservation projects and sanitary risk. Animals. 12(8):980. https://doi.org/10.3390/ani12080980

Rivrud IM et al. 2013. Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. J Appl Ecol. 50(1):168–180. https://doi.org/10.1111/1365-2664.12004

Rowcliffe MJ, Field J, Turvey ST, Carbone C. 2008. Estimating animal density using camera traps without the need for individual recognition. J Appl Ecol. 45(4):1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x

Ryckman MJ, Rosatte RC, Mcintosh T, Hamr T, Jenkins D. 2010. Postrelease dispersal of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. Restor Ecol. 18:173–180. https://doi.org/10.1111/j.1526-100X.2009.00523.x

Schwegmann S, Bhardwaj M, Storch I. 2024. The influence of native deer on forest fauna—a systematic map. Ecol Evol. 14(12):e70696. https://doi.org/10.1002/ece3.70696

Stadtmann S, Seddon PJ. 2020. Release site selection: reintroductions and the habitat concept. Oryx. 54(5):687–695. https://doi.org/10.1017/S0030605318001199

Stankov B, Cvetković Đ, Stamenković S, Gačić D. 2024. Post-release dispersal and home range of translocated red deer in the Vojvodina province (Serbia). Baltic For. 30:id763. https://doi.org/10.46490/BF763

Stüwe M, Nievergelt B. 1991. Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. Appl Anim Behav Sci. 29(1–4):379–387. https://doi.org/10.1016/0168-1591(91)90262-V

Suominen O, Danell K, Danell K. 2006. Effects of large herbivores on other fauna. In: Bergström R, Duncan P, Pastor J, editors. Large herbivore ecology, ecosystem dynamics and conservation. Conservation biology. Cambridge University Press. p 383–412.

Torres RT, Carvalho J, Fonseca C, Serrano E, López-Martín JM. 2016. Long term assessment of roe deer reintroductions in North East Spain: a case of success. Mamm Biol. 81(4): 415–422. https://doi.org/10.1016/j.mambio.2016.05.002

Valente A, Valente J, Fonseca C, Torres R. 2017. The success of species reintroductions: a case study of red deer in Portugal two decades after reintroduction. Int J Biodivers Sci Ecosyst Serv Manag. 13(1):134–138. https://doi.org/10.1080/21513732.2016.1277265

Watters JV, Meehan CL. 2007. Different strokes: can managing behavioral types increase post-release success? Appl Anim Behav Sci. 102(3–4):364–379. https://doi.org/10.1016/j.applanim.2006.05.036

White TH et al. 2015. Improving reintroduction planning and implementation through quantitative SWOT analysis. J Nat Conserv. 28:149–159. https://doi.org/10.1016/j.jnc.2015.10.002

Zaninović K et al. 2008. Klimatski atlas Hrvatske/Climate atlas of Croatia 1961–1990. DHMZ.

Zidon R, Saltz D, Shore LS, Motro U. 2009. Behavioural changes, stress, and survival following reintroduction of Persian fallow deer from two breeding facilities. Conserv Biol. 23(4):1026–1035. https://doi.org/10.1111/j.1523-1739.2008.01163.x