Animal Biotelemetry

TELEMETRY CASE REPORT

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Spatial behavior of red deer (*Cervus elaphus*) in Northern Apennines: are we managing them correctly?

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Abstract

Background: Throughout their range, red deer are a well-studied species. In Italy, this species occupies two ecologically different ranges: the Alps and the Apennines. Although several studies have described the spatial behaviour of red deer in the Italian Alps, no data are available for the Apennine population.

Results: The spatial behaviours of 13 deer from the Northern Apennines range were analysed for the first time using GPS-GSM telemetry from 2011 to 2017. Red deer displayed two coexisting strategies, i.e., migratory and stationary. In our sample, females tended to migrate more than males. We found a high level of interindividual variability in the date of migration/return, while each migratory deer was very conservative during the study period. The migration ranges were on average 12 ± 4.2 km from the resident range. Both migratory and resident deer displayed high site fidelity. No switch from the migratory to stationary strategy was observed for any deer during the study period; however, the period could have been too short to detect any switch. At the management level, over 18 management cycles occurred during the study period, and a spatial mismatch was found between deer range and management units (districts) in 38.9% (7) of the cases. Merging the districts belonging to each province to obtain an area of approximately 1000 km^2 would partially address such spatial mismatch, reducing its occurrence to 22%.

Conclusions: Despite the small sample size, these results can guide future management actions. However, an in-depth study with a larger sample size is required to better understand and manage the red deer Apennines population.

Keywords: *Cervus elaphus*, Apennines, Spatial behaviour, Management

Background

Ungulate spatial behaviour is a complex process shaped by climate, species life-history strategies, population density, and other factors, such as predation pressure and human disturbance (hunting, recreation; [12, 57, 69]. Thus, strategies displayed by individuals related to space use, as the result of different pressures, aim to maximize individual fitness under different ecological conditions. In this regard, migration plays a central role in use of space since it is thought to be mainly an adaptation to changing resource availability and quality [2, 34, 37], a response to competition when density increases [59] but see also [55] or a way to prevent predation on offspring without any clear relation to population density [4, 8]. However, according to Mysterud et al. [56] and several hypotheses, a combination of ecological triggers can explain the same migration pattern. Therefore, migration is a complex process, with behavioural plasticity making seasonal movements very flexible, further blurring the line between discrete categories of residency and migration [17].

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The red deer (*Cervus elaphus*) is a well-studied species that exhibits differences in its use of space across its distributional range. In the northern hemisphere, where resource availability and climate are markedly seasonal, populations are partial migrants, including both migratory and resident individuals [55, 56], with a negative density dependence on the likelihood of migration [55]. Partial migration is known to occur in several other large herbivores (for a review see [7].

In Italy, red deer are found both in the Alps and in the Apennines, where they face very different environmental conditions mainly associated with climate and food quality, availability, and accessibility throughout the year. These conditions affect the species' feeding habits, as suggested by tooth wear, which occurs much faster in Alpines than in Apennine for red deer of the same age class [25]. When compared to Alpine deer, Apennine red deer are generally similar in weight (eviscerated weight ± sd,adult, male: 130.4 ± 15.6 kg, female: 72.6 ± 10.0 kg—[5], adult, male: 140.71 ± 22.26, female: 73.68 ± 9.55 kg—Apollonio et al. [3]; for the Apennines and Trentino Alps, respectively) or heavier (adult, male: 110.87 ± 21.36 kg; female: 68.19 ± 10.93 kg, [35], Stelvio National Park, eastern sector).

During the last 20 years, in the northern region of the Apennines, the species distribution range and density have increased. Thus, its management has become increasingly important and mainly aimed at reducing conflicts between human activities and deer presence, namely, road accidents, damage to agricultural activity and impact on forest renovation. Management objectives are pursued by setting hunting quotas based upon population size, which is assessed through direct counts. Management is therefore particularly challenging when the target is moving, as in the case of a migratory population, because both the functional population unit (sensu [21] and the corresponding management area cannot be properly defined.

We present the first data on the spatial ecology of red deer from the northern Apennines. In the Alps, red deer have been found to behave as partially migrant (i.e., only part of the population migrates; [10, 11, 14, 50], while in the Apennines, this has never been investigated. Considering the high migration propensity shown by the species populations spanning environmental gradients across Europe Peter et al. [63], we expected that red deer in the Apennines would also exhibit partial migration.

Moreover, we assessed whether the space-use strategy displayed by the red deer affects their management in the study area. Since population-level management is difficult to achieve if individuals cross the administrative limits of management units, we also discussed (i) whether the current deer management approach is consistent with the population unit principle (i.e., the management unit should encompass a population unit and both resident and migratory ranges) and effective to meet management objectives and (ii) what possible solutions exist for improving the species management in the northern Italian Apennines.

Materials and methods

Study site

The study area is located in the Italian Northern Apennines within the provinces of Parma (PR), Modena (MO), and Reggio-Emilia (RE, Emilia Romagna region) to the north and the provinces of Lucca (LU) and Massa Carrara (MS, Tuscany region—Fig. 1) to the south.

The area is characterized by a continental climate, with dry hot summers and cold, snowy winters. Between October and March, snow cover occurs from 14.9 to 207.9 days, while snow depth varies between 1.5 and 104.3 cm (1961–1990; [24]. The abundance of snowfall is negatively correlated with altitude, and below 100 m asl., it becomes negligible.

The area is mainly hilly and mountainous, with elevations ranging from 265 (Langhirano, PR) to 2165 m (Monte Cimone, MO). Sixty percent of the study area is covered by forests dominated by beech wood (*Fagus sylvatica*) at higher altitudes and oak wood (*Quercus sp.*) at lower altitudes. Approximately 38% of the area is covered by agricultural pastures, arable land, and orchards (mainly olive and cherry groves). Urban areas are limited to the valleys where the road density is also higher; however, a few mountain villages are scattered at higher altitudes.

Five ungulate species are present in the area: in addition to red deer, roe deer (*Capreolus capreolus*), mouflon (*Ovis aries*, distributed mainly along the border with the Tuscany region, with small and isolated groups in the province of Reggio Emilia), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) are also present. Wolf (*Canis lupus*) and red fox (*Vulpes vulpes*) are the only predators of red deer in the area.

Deer population and management

The presence of red deer in the area is due to several reintroductions carried out mainly during the 1980s and the beginning of 2000, coupled with occasional escapes from enclosures [30, 51, 61]. Since early 2000, regional administrations (Tuscany and Emilia Romagna), which share the population, have monitored the presence of this species, and in 2011, the first distribution map was generated, with the population being quantified therein. In 2012, 3500–3900 deer were estimated to be present in the area (1.9–2.2 n/km^2), and hunting was allowed for the first time [32]. Since 2012, the minimum population

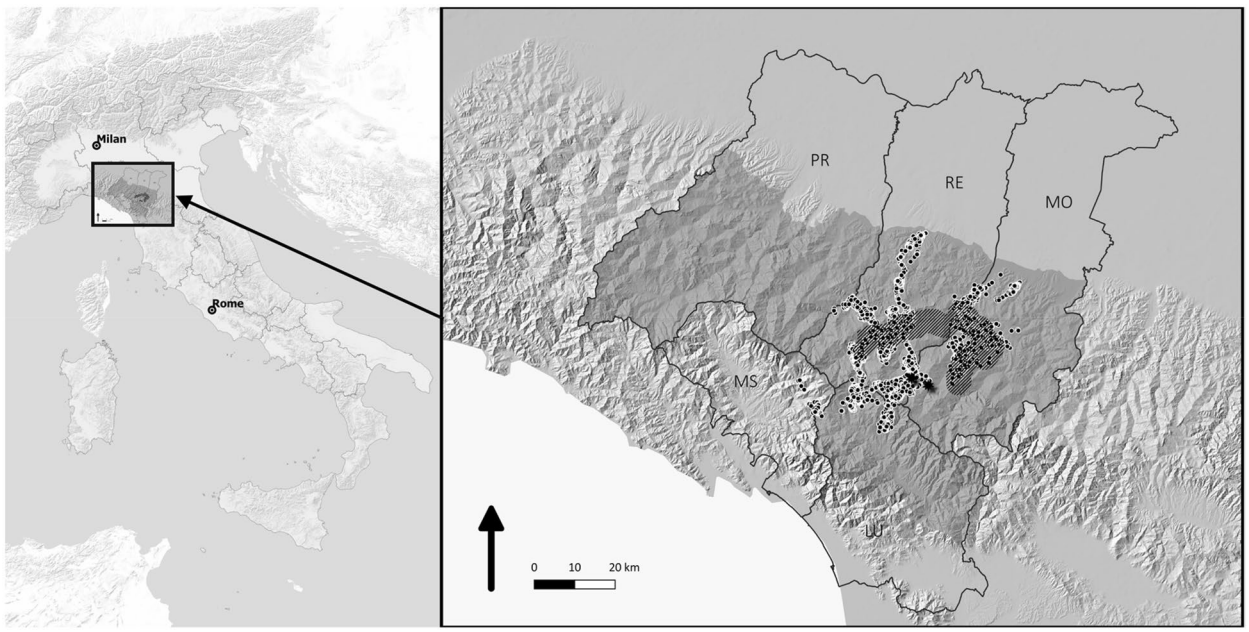

Fig. 1 Shaded relief map of the study site showing deer GPS locations, ACATER (dark grey), corral trap location (black stars), capture area (dithered area) and province borders (PR, RE, MO, MS, and LU)

size has been quantified yearly through observation point counts in spring, carried out at dawn and dusk in agricultural areas and forest edges. To date, the red deer population has continued to increase and expand in distribution. The annual hunting quota varies between 19.9% and 34.6% of the minimum population size quantified in the spring.

In both Emilia Romagna and Tuscany, red deer management is carried out in wide management areas (ACATER) that encompass the deer population unit distribution range. Currently, there are three deer management ACATERs ranging from 3900 to 5840 km^2 shared by Emilia Romagna and Tuscany [76].

Within such areas, annual population monitoring is carried out, and annual management plans are prepared and agreed upon by a management committee representing public and private stakeholders. A 5-year management plan is also prepared for each ACATER, which determines the main objectives for red deer management. Hunting is carried out in subunits within each ACATER (called "districts") ranging from 170 to 432 km^2, and the hunting plan is assigned per district. Each management plan specifies the target (red deer population estimate, culls, impacts on habitat and crops, road accidents, etc.), the methods (monitoring of both populations and impacts, hunting, crop protection, etc.) and the management objectives, which are primarily aimed at reducing deer impacts. Reducing these impacts is also achieved by setting appropriate annual hunting quotas (split into sex and age classes), which are spatially allocated among hunting units (districts) based on the results of the direct counts in each district. Thus, during the hunting season, red deer are expected to occur the same district in which they have been counted, allowing the quotas to be met.

The study site is in western ACATER (5840 km^2, including the abovementioned regional administrations and four provinces, Fig. 1).

At the study site, the hunting season occurs from October until mid-March and from January to mid-March for males and females, respectively. Spring counts are carried out after the end of the hunting season (late March—late April). The period between the 16th of March of one year and the 15th of March of the following year is therefore considered the management time unit, hereafter referred to as the "management cycle". Each management cycle falls during two calendar years, starting with the spring counts and ending with the implementation of the hunting plan, for which its quotas are based on the results of these counts.

Deer capture and tracking

Deer were captured within the Secchia River catchment area (Fig. 1) through telenarcosis and baited corrals traps. Telenarcosis was carried out at night, and animals were located using a spotlight mounted on a 4×4 vehicle. Darts were equipped with a radio transmitter (TeleDart®

Transmitter Dart-TDS), and darted animals were located through a directional, four-element YAGI antenna and an ICOM-IC-R20 radio receiver. Sedation was induced by a veterinary doctor using a pharmacological mix of tiletamine hydrochloride, zolazepam hydrochloride and xylazine [42]. An antagonist of xylazine (atipamezole) was used to reverse sedation [54]. Two corral traps were set up in the valleys of Dolo (Costalta, Reggio Emilia) and Dragone rivers (Riccovolto, Modena, Fig. 1). Captured deer were sedated before handling using the same protocol as telenarcosis.

Captured deer were sexed, measured, and fitted with ear tags and GPS-GSM collars (Vectronic Aerospace—GPS PRO Light-2 model TARIC 8526 91 20) if older than one year of age. This device model has been used in different studies [39], as it allows data to be collected remotely using dedicated hardware (Vectronic Aerospace GSM-2 Ground Station) and provides the accuracy of the locations through the dilution of precision (DOP), a measure of the quality of satellite geometry, which is assigned to each location [47].

The collars were programmed to collect 4 locations per day (every 6 h) for the first 13 months of tracking and 2 locations (every 12 h) afterwards.

Only data from deer followed for at least one year were used for the analysis, and only locations obtained from the triangulation of at least four satellites (validation GPS-3D) were retained for the analysis [6, 39]. To assess pregnancy and the presence of fawns, tagged females were periodically located and observed as long as necessary to assess their status. Tagged deer were excluded from culling based on local regulations.

Data analysis

Home range estimation and site fidelity

Home ranges were calculated using continuous-time stochastic movement models and autocorrelated kernel density estimation (AKDE, [28, 29]. This estimator allows the calculation of rigorous HR estimations accounting for autocorrelation and irregular sampled fixes while providing an optimal weighting of the data, giving appropriate weight to time-isolated relocations corresponding to gaps in the data. It also accounts for the accuracy of each relocation using the corresponding DOP. AKDE however only works for stationary data,i.e., it is not suitable to describe dispersing, migrating, or shifting home ranges. Therefore, before computing 95% home ranges, we first detected stationary subsets of positions using variograms (see below).

We classified animals as "migrants" if they displayed regular movements between two or more discrete areas that, even at a short distance < 10–50 km, did not overlap [7], while "residents" were animals that displayed a continuous, overlapping use of the same range [1, 38, 52].

We calculated variograms and movement models, and estimated home range sizes using the *ctmm* package in R [18]. Deer residency was evaluated using variograms. For resident individuals, the variogram reached an asymptote at a timescale roughly corresponding to the home range crossing time. When semivariance did not reach an asymptote, as in the case of dispersers, individuals were not assumed to be residents [58] and therefore excluded from the analysis. Both variogram analysis [27] and model selection were used to confirm that there was evidence of range residency in the data and that it was therefore reasonable to perform the home-range estimation.

When the variogram showed spikes or regular patterns of variation, some level of migration or spatial instability was exhibited. In such cases, we used R software [68] to perform a cluster analysis (Package segclust2d, [62] on latitude and longitude to identify the locations that clustered in space and time. This analysis allows for segmentation of multivariate time series, obtaining clusters that correspond to different stationary phases. When all the locations were assigned to one cluster, the individual was considered resident; otherwise, it was considered migratory (i.e., locations were assigned to more than one cluster).

We also classified deer as "migrant" if their GPS relocations clustered in disjointed areas, as detected by visual inspection. Such areas were clearly identifiable on the map and used recursively by the same deer in different years for some time and represented stationary phases. Relocations falling in these clusters were used to calculate the home range, excluding positions pertaining to the migration route.

The parameters of the variogram and its shape produce different movement models whose SVFs (semivariance function, [27] fit is evaluated via maximum likelihood. Models were compared, and the best fitting model was selected using the Akaike information criterion (AIC, see [18] for a thorough description of the method). Once the appropriate model was selected, AKDE was used to calculate the home range [18].

For individuals who expressed migratory behaviour, the total home range was calculated as the sum of the disjoined home ranges, i.e., each temporary residency subarea, without including the positions along the migration routes. Such areas were referred to as the "primary resident" and "migration" ranges hereafter, where the first was the area where an individual spent most of his time (> 50%) and the latter was the area where it moved for a shorter period. In migrants, the distance between the migration and primary seasonal ranges was calculated as

the Euclidean distance between the centroids of the two ranges.

To quantify the site fidelity displayed by migrant deer in different years, AKDE home range pairwise overlap was calculated with the Bhattacharyya coefficient (BC, also called the Bhattacharyya Affinity, [9, 75], which has several advantages [75]. This coefficient varies between 0 (no overlap) and 1 (full overlap) and was calculated with the ctmm package, which also provides the CI. Given that the migration ranges were identified spatially and not temporally, one year corresponded to the migration event, i.e., the period spent in the migration (and the primary seasonal) range each time the primary seasonal range was left to move into the migration range and vice versa.

The range altitude for migrating deer was calculated as the average altitude value of the locations falling into each range (migration and primary seasonal). The altitude values were obtained from the regional topographic online database [70], whose metadata are available for consultation.

Deer movement in relation to management units

To verify whether current deer management units (both ACATER and districts) are spatially appropriate and effective, we assessed whether deer were present in the same district (the smaller management unit) during both the spring counts and the following hunting season.

For each management cycle, if the district where the individual deer were counted during annual monitoring proved to be the same as the district that accounted for at least 95% of its locations during the following hunting season, then the match between count and hunting districts was considered positive, and it was negative otherwise (mismatch between counting and hunting districts). Thus, if a deer during the hunting season visited the same district where it was counted during annual monitoring, then we considered the match between count and hunting district to be positive. For each management cycle, only deer positions collected during the concerned periods (counts and hunting, see "Deer population and management" section) were used. We also quantified the percentage overlap between deer home ranges and the districts and calculated the number of districts used by each deer. The analysis was carried out using the free source software QGIS [66].

Results

Deer GPS data, home ranges and space-use strategy

From August 2011 to January 2016, 23 deer were captured, 78% through telenarcosis and 22% with baited corral traps. Only 22 individuals were old enough to be fitted with radio collars. However, some collars ($N=4$) stopped working after a very short period, and other animals died shortly after capture ($N=5$). The cause of death was assessed only for two deer: one died because of preexisting pathologies, while the other, a male, showed signs of fight injuries.

Thirteen individuals, tracked for 12–55 months with an average of one location every 8.14 h, were considered for the analysis. The average dilution of precision (DOP see "Materials and Methods") for the retained locations ($N=21{,}244$) was 3.43 m (95th percentile 7.2 m); 87% of the locations used for the analysis had a DOP value < 5 m.

Six deer were identified as residents (46.2%, 4 males and 2 females), five as migrants (38.4%, 4 females and 1 male), and two as dispersers (15.4%, 1 male and 1 female, Table 1).

Migration started in spring (April, $N=2$), summer (August, $N=2$) and autumn (October, $N=1$). Spring migrants were back in the primary seasonal range (i.e., where the deer spent most of their time > 50%, see "Methods") in summer (August), while later migrants spent most of their time there between October and December.

Despite the high interindividual variability, the dates of migration did not vary as much for each deer in different years (Table 1). Migrant deer tracked for longer than one year showed little variation in departure dates (23.8 ± 8.9 and 3.5 ± 2.5 days, maximum and minimum average difference ± sd) among years. The return dates, on the other hand, were more variable (the maximum and minimum average differences were 58 ± 73.8 and 11.8 ± 14.1 days, respectively). Migratory deer spent on average (± sd) 263 days (± 26) in the primary seasonal range and 92 days (± 24) in the migration range.

Overall, migratory deer used larger home ranges than resident deer (35.06 km^2 ± 15.55 and 18.73 km^2 ± 11.33, respectively), although the difference was not significant (Welch two-sample t test, t = 2.08, df = 9.14, p value = 0.06). Migration and primary seasonal ranges were on average (± sd) 12.04 ± 4.2 km apart (Table 1).

Migrant deer tracked for more than one year (at least two years of data: N = 4 for the primary seasonal range, and N = 5 for the migration range) were very traditional in their range choice, using generally the same primary seasonal and migration ranges every year (BC = 0.89 CI 0.83–0.94 and BC = 0.78, CI 0.64–0.94, respectively).

Almost all the tracked deer used one discrete primary seasonal and migratory range, except one female, which used two disjoined subareas in both the primary and migratory ranges (Fig. 2).

The mean altitude (± sd) of the migratory ranges was quite variable (788.6 m asl ± 547.9; 338.6–1776.4 m asl, minimum and maximum, respectively) and not significantly different from that of the primary seasonal ranges (760.3 ± 296.1 m asl; 341.4–1169.6 m asl, minimum

Table 1 Data on red deer monitored in the Northern Apennines 2011–2017

ID	Capture date	Sex	Age[1]	Monitoring in months	GPS locations (n)	Category	Total HR (km^2)	Primary seasonal range (km^2)	Migration range (km^2)	Onset migration[2]	Return month[2]	BC Resident range	BC Migration range	Distance between ranges (Km)
9049	24/08/2011	F	Y	28	1407	Migrant	16.56	10.66	5.89	August	October	0.94	0.91	9.812
9046	14/09/2011	M	A	13	1204	Resident	10.13	–	–					
8806	10/09/2012	F	A	33	1037	Migrant	25.04	19.18	5.85	April	August	0.93	0.82	13.029
9044	25/09/2012	M	Y	21	1479	Disperser	166.88	–	–					
9052	09/10/2012	M	A	12	629	Resident	25.98	–	–					
9050	10/02/2013	F	Y	12	594	Resident	16.29	–	–					
11,289	05/09/2013	F	Y	16	1350	Disperser	29.52	19.70	9.82	October	No return			10.282
11,760	18/09/2013	F	A	55	3467	Migrant	38.20	18.34	19.86	April	August	0.83	0.82	20.100
11,762	10/12/2013	F	A	27	2233	Resident	5.11	–	–					
11,759	12/12/2013	F	A	55	3214	Migrant	61.63	46.60	15.03	October	December	0.87	0.73	10.291
11,765	25/09/2014	M	A	15	1543	Resident	36.73	–	–					
11,766	25/09/2014	M	A	17	1651	Migrant	39.43	33.12	6.31	August	November		0.64	8.740
11,746	23/10/2015	M	A	24	1946	Resident	18.15	–	–					

AKDE HR: Autocorrelated Density Kernel Estimator home range (see text for explanation). BC: Bhattacharyya Affinity expressing spatial overlap

[1] Upon capture: Y: 8–22 months; A: females > 22 months; males > 5 years

[2] For multiple years, the median month is given

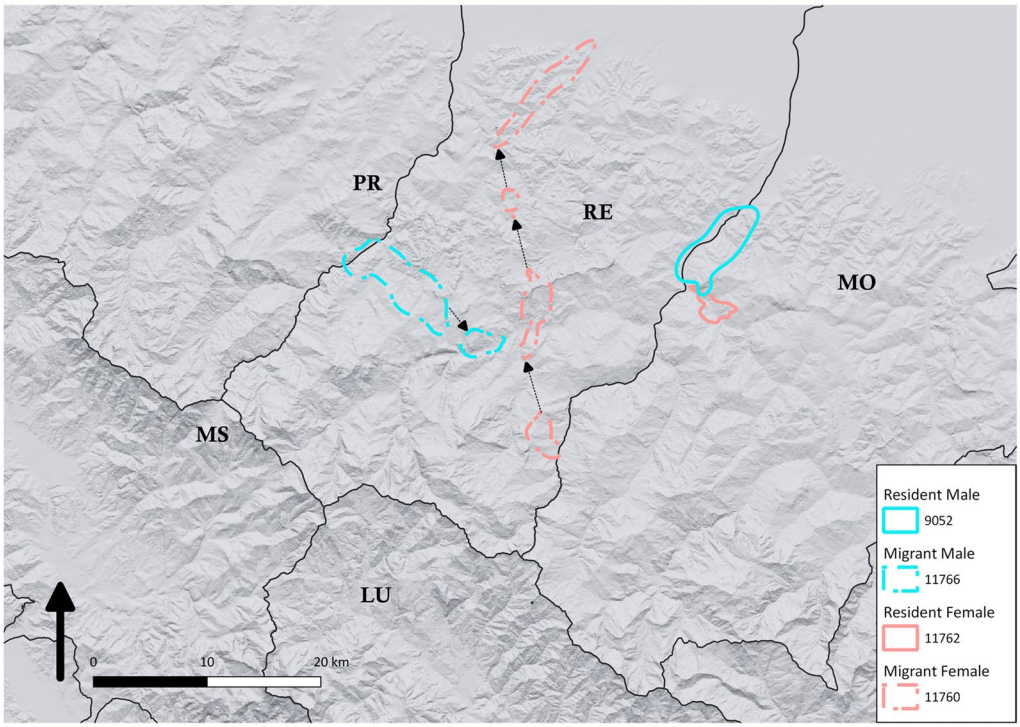

Fig. 2 Home ranges for two migratory (11,760 female; 11,766 male) and two resident (11,762 female; 9052 male) deer. Migration trajectories are also shown (arrows). Provinces are also shown

and maximum, respectively; Wilcoxon test, $W = 14$, p value $= 0.5887$).

Mismatch between deer range and management units

Migrant and resident deer used on average ($\pm$sd) 2.8 ± 0.98 and 2 ± 0.89 districts, respectively. The home ranges of both migrant and resident deer showed substantial overlap with only one district (mean overlap home range vs. district 73.18% vs. 91.91%, respectively), limiting the use of the other districts (min–max overlap: 0–30% for migrant; 0–18% for resident).

Analysing data collected over 6 years for 13 deer (some of them followed for more than one year), corresponding to a total of 18 management cycles, in 38.9% of the cases (7 over 18), a mismatch occurred between the districts (which are the operative management units) and the deer distribution (negative match; Fig. 3, Table 2). If provincial borders were considered instead, then the mismatch was reduced to 22% (4 over 18), while ACATER (*Areale del Cervo dell'Appennino Tosco-Emiliano-Romagnolo*) borders encompassed all but one (11,289) monitored deer.

Discussion

According to our data, red deer in the Apennines are partially migrant; migration dates vary among individuals but remain constant at the individual level across years. Females tend to migrate more than males and show fidelity to both the strategy adopted and the ranges used.

The partial migration strategy is described for ungulates [7] and documented in several European red deer populations [45] for a review), including northern countries (Norway, [53],Sweden, [43]. Partial migration has also been found to be a strategy for red deer in the Italian Alps (Tarvisio and Val Susa, [50],Stelvio National Park, [14], Paneveggio Natural Park, [11]. Both Alpine and Apennine populations also display range fidelity and no switching between strategies (but see [11].

The migration distances found in this study (12 ± 4.2 km) are comparable in magnitude to migration distances displayed by several alpine populations (Italian Alps: 8–10 km, [50],5.20 ± 3.25 km, [14],7.7 km, -only females, range 0.9–31 km, [11].

Although our results were limited by the small sample size, migration seemed to be displayed more by females than by males, as also found in the Italian Alps [50], in contrast to the results of Bocci et al. [11], who found 87% of stags and 49% of hinds were migrants (shifters, Italian north-eastern Alps). In fact, Peters et al. [63] found that the probability of migration was higher in males than in females. Under the forage maturation hypothesis, red deer, as mixed feeders, are expected to migrate, and under the body size

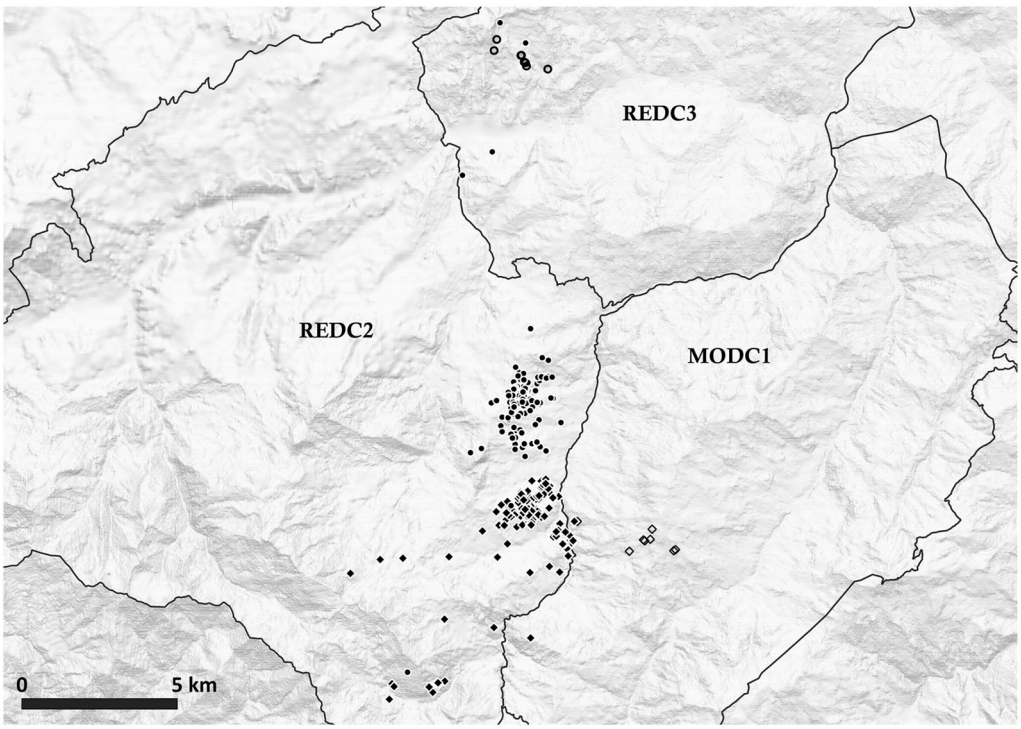

Fig. 3 Example of mismatch for deer 11,759 (diamond) and 11,760 (circle). During the hunting season, both deer were not present in the district they were counted. Open symbols: GPS positions during the annual counts; filled symbols: GPS positions during the hunting season. REDC2, MODC1, and REDC3: districts'names within Modena (MO) and Reggio Emilia (RE) provinces

constraint hypothesis, the propensity to migrate should be biased towards males [63]. However, the only migratory male in our study moved in late summer from west to east, keeping an average constant altitude in both the migratory (551 m a. s. l.) and the resident (582 m a. s. l.) ranges, thus possibly not driven by forage maturation. It is possible that the movements during late summer displayed by two individuals (the only migratory male and one female) were linked to the search for mating opportunities. Notably, these individuals reached two well-established mating territories in two different areas where the male remained until the end of the mating season while the female remained until mid-October. Female red deer have been reported to make substantial movements, including changing harems when in oestrus [73]. Female movements among mating areas have been observed in the red deer *Cervus elaphus hispanicus* in Doñana (Spain, [20], where rutting males can defend mating territories [19], a mating strategy—also recorded in our study site—that coexists with the defence of mobile harems described for red deer in northern Europe [22]. Movements to mate have also been reported for female roe deer *Capreolus capreolus* [49, 71], which are known to perform rut excursions (lasting from hours to days) that provide the opportunity for active mate choice. In the present study, movement to mating areas could have been carried out within a migration framework.

Two females left at the onset of spring, in April, to give birth away from the primary seasonal range (20 and 13 km, Table 1) and came back at the end of August, when the calves were able to follow the mother [22]. No altitudinal variation characterized these movements, and the timing of forage maturation was likely the same in both areas, which are characterized by very similar habitats. Therefore, it seems that the hypothesis of access to better quality resources for parturition and lactation was not supported [37]. On the other hand, altitudinal variations characterize the movements of female red deer in Stelvio National Park, where females move towards summer ranges between half April and half May (median May 2nd, min-max April 5th–June 7th, [14]. These movements are likely due to the search for plants at a relatively early stage of growth [14], which have greater palatability and nutritive value [40]. Migration towards wintering ranges was more variable over time (median November 10th, min-max August 22nd–December 26th), probably due to weather conditions, notably snowfall [14].

A later migration date was exhibited by a female, who started the migration in a period when rutting

Table 2 List of management cycles (by the two solar years covered) per deer

ID	Management cycle	Category	District		Percentage locations	Match at district level	Province		Match at province level
			during counts	during hunting season			during counts	during hunting season	
9049	2012–13	M	REDC2	REDC2	100 (77/77)	Positive	RE	RE	Positive
9044	2013–14	D	MODC4	MODC1	8.7 (38/347)	Negative	MO	MO	Positive
8806	2013–14	M	MODC5	MODC5	96.7 (59/61)	Positive	MO	MO	Positive
9052	2013–14	R	MODC5	MODC5	100 (251/251)	Positive	MO	MO	Positive
9050	2013–14	R	REDC2	REDC2	100 (93/93)	Positive	RE	RE	Positive
11,289	2014–15	D	LUDC1	Outside ACTER	1.9 (1/52)	Negative	LU	MS	Negative
11,760	2014–15	M	REDC3	REDC2, REDC3	3.15 (4/127)	Negative	RE	RE	Positive
11,760	2015–16	M	REDC2	REDC2, REDC3	94.9 (132/139)	Positive	RE	RE	Positive
11,760	2016–17	M	REDC3, REDC4	REDC3, REDC2	95.2 (119/125)	Positive	RE	RE	Positive
11,762	2014–15	R	MODC5	MODC5	100 (127/127)	Positive	MO	MO	Positive
11,762	2015–16	R	MODC5	MODC5	100 (140/140)	Positive	MO	MO	Positive
11,759	2014–15	M	MODC1	REDC2, MODC1	2.2 (3/137)	Negative	MO	RE, MO	Negative
11,759	2015–16	M	MODC1	REDC2, MODC1	39 (50/128)	Negative	MO	RE, MO	Negative
11,759	2016–17	M	MODC1	LUDC1	0 (0/131)	Negative	MO	LU	Negative
11,765	2015–16	R	REDC2	REDC2	100 (140/140)	Positive	RE	RE	Positive
11,766	2015–16	M	REDC1	REDC1, REDC2	60.9 (148/243)	Negative	RE	RE	Positive
11,746	2016–17	R	REDC2	REDC2	100 (343/343)	Positive	RE	RE	Positive
11,746	2017–18	R	REDC2	REDC2	100 (22/22)	Positive	RE	RE	Positive

The districts and provinces used by each deer during the spring count and the corresponding hunting season are reported. Match at the district and province levels during both periods is also shown. Percentage locations: percentage of locations of each deer during the hunting season within the district they were counted

M migrant, *D*: disperser, *R* resident, *RE* Reggio Emilia, *MO* Modena (Emilia Romagna region), *LU* Lucca, *MS* Massa-Carrara (Tuscany region)

is generally over in the Apennines. The only possible explanation for this movement was the access to abundant, predictable, and heavily localized food resources (chestnut).

Hunting represents an important tool to regulate ungulate populations [16, 36, 46, 64, 65], and seasonal migration complicates harvest management. At the same time, hunting can affect migratory and sedentary deer differently, i.e., when the movement involves a migration from a protected area to hunting grounds, resulting in overexploitation of migrants [13, 43]. The efficacy of red deer management depends upon the capacity of managing a deer functional population unit to affect population dynamics [46] in accordance with management goals. A management unit's size is therefore important and should encompass an entire population unit during both monitoring and hunting. This study shows that this principle is not fully accomplished by the district design in our study area. The evidence that deer use more than one district supports the need to increase the area of this operative hunting unit. Bocci et al. [11] proposed a circular area with a radius equal to the maximum distance covered by a deer during migration: an area of 1300 km^2 would include 75% of the monitored deer. In our study, merging the districts belonging to each province to obtain an area of approximately 1000 km^2 would reduce the mismatch highlighted in this study from 38.9% to 22%.

Conclusions

Although the small sample size did not allow for more in-depth analyses, the variability among dates of migration found in the present study suggests that migration in the Apennines might be triggered by several drivers and that any of the current hypotheses alone, including the forage maturation hypothesis, is unlikely to fully support all the observed migration movements. A cultural, learned component could play a role in the observed timing of migration and in the choice of the migratory area itself. In fact, migration in ungulates has been recognized as a learned behaviour, the result of knowledge acquired from experience and culturally transmitted information [44]. Evidence of migration as a learnt behaviour transmitted from mother to young has been reported in moose and white-tailed deer [60, 74], underlining the importance of the early social environment, rather than the physical environment, to determine behaviour in adulthood.

There was no switch from migration to sedentary behaviour across the study period. However, time scale is crucial to detecting any switching, and our temporal window was not large enough to observe any variations

in factors sufficient to encourage switching. It has been demonstrated that migratory behaviour is characterized by flexibility in response to factors such as density [55], predation risk, and a combination of both to maximize lifetime reproductive success [26]. Switching behaviour has been reported in several species of large herbivores (but see [72], such as elk [26], roe deer [63], and red deer, where it is more pronounced in males than in females (23% and 1%, respectively, [63],in addition, red deer can also switch behaviour in response to winter severity [12].

Both migrants and resident red deer displayed site fidelity across the study period. Site fidelity is a behavioural adaptation whose fitness benefits have been explained by the advantage of already acquired knowledge of resource and security cover distributions, which can increase survival and reproductive success [15, 33].

This study highlights the need for management at a larger scale, comparable with the home range used by the species. An increase in district size, however, should not compromise the effectiveness of coordination among the administrations involved in red deer management. Solutions envisaged by other authors, such as coordination between management units [53], have already been applied within the ACATER, but as shown in the present study, they have not resolved the issue of mismatch. The hunting season in Italy is differentiated between males and females. The female hunting season is among the shortest in Europe, while the male one is comparable with that in most European countries [65]. Extending the hunting season as suggested by other authors [48] would not resolve the problems and would generate other issues. For example, extending the hunting season in spring would imply hunting during late pregnancy, when the young are still dependent on the mother and/or in the presence of antlerless deer [65, 67]. We found that by merging the districts within provincial borders, the mismatch was reduced.

Factors that could influence the spatial behaviour of deer (e.g., ecological and environmental barriers; [41] should also be identified to improve red deer management in the Apennines. The spatial distribution of roads in our study area (in particular, if they are at the bottom of a valley and flanked by a river) could also play a role in shaping the home ranges and their size. Further studies are thus required to clarify these important aspects of the red deer ecology in the Apennines, which could help in identifying more functional management units.

Our findings are limited by the small sample size, which was primarily due to deer capture difficulties. A pilot study carried out in the provinces of Modena [31] has already shown extremely low deer capture success with corral traps: in four winter seasons, one corral trap, active for 182 nights, captured only three individuals (0.02 deer per night). At the study site, hunting has been permitted since 2012. Since then, deer have changed their behaviour by becoming increasingly wary (as also documented in [23]. This decreased the effectiveness of telenarcosis as a capture method: nine individuals were captured in the two years before 2012, while only eight were captured in the four years after 2012.

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Author contributions
RF and AL conceived and designed the study; EA provided veterinary support in handling and sedation procedures; ERP supervised the scientific efforts; RF, AL and EA collected the data; LC, ERP and RF analysed the data; ERP, LC and RF wrote the paper. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets analysed during the current study are available in the MoveBank repository: https://www.movebank.org/cms/movebank-mainrepository.

Declarations

Ethics approval and consent to participate
All data reported in this study were collected in accordance with a protocol approved first by Istituto Nazionale per la Fauna Selvatica (2010/12) and then by the Istituto Superiore per la Protezione e la Ricerca Ambientale (2013/09).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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