

Alternative strategies of space use of female red deer in a mountainous habitat

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Alternative strategies of space use may be present in a species or in a population as a response to different environmental parameters, especially in mountainous habitats, where heavy snowfalls in winter may determine important variations of habitat quality. The spatial behaviour of 20 radiotagged red deer hinds was assessed in a mountainous habitat in the eastern Italian Alps from 2002 to 2004. Two groups of hinds were identified: ‘resident’ females remained in the same area throughout the year; ‘shifter’ females showed separated winter and summer areas. No significant difference was found in seasonal home-range sizes between resident and shifter hinds in 2002 and in 2003. Each year, in summer, home-range quality of shifter hinds was significantly better than that of resident ones, while, in winter home ranges, habitat diversity was similar in the two groups. During the severe winter 2003–2004, 33% of females summering in lower quality habitat died, whereas mild winters did not influence the survival of our collared hinds.

Introduction

The availability, distribution and quality of resources (e.g. food, thermal cover, escape terrain, partners for reproduction) influence the space use of animals (Lott 1990). These features of natural resources are heavily dependent on environmental variables, and they may show great spatial and seasonal variation, especially in areas with a strongly seasonal climate (Shackleton & Bunnell 1987, Ferguson & Messier 1996, Ferguson & Elkie 2004).

In mountains, winter severity is the main limiting factor regulating ungulate space use (e.g. Boyce 1991, Brown 1992). In winter, food availability is decreasing (Parker *et al.* 1984, Sweeney & Sweeney 1984) and energetic costs of locomotion and thermoregulation are the highest (Gates & Hudson 1978, Parker *et al.* 1984). It is then important for each individual to select an appropriate summer range and to accumulate sufficient fat reserves by the end of autumn. Quality of winter ranges is also important in reducing energetic costs of movement and thermoregulation.

tion (e.g. wooded slopes, south-oriented) and in providing sufficient food supply (Parker *et al.* 1984, Poole & Mowat 2005). Thus, in mountains, as well as in all populations living in a strongly seasonal climate, summer and winter ranges are important elements of space use.

Diverse strategies of space use may be present in a species as a response to different environmental situations (Fryxell & Sinclair 1988): resident populations, living in the same area all year round, and populations using allopatric seasonal home ranges (Hebblewhite *et al.* 2006). However, the definition of what may be called “migration” has not been formulated yet (for a review *see* Berger 2004). Seasonal movements will develop as a function of changes in the environment, i.e. when natural resources are spatially variable and seasonally-dependent (Boyce 1991). Risks and energetic costs of moving through a relatively unknown terrain (Nicholson *et al.* 1997, Szemethy *et al.* 2003a) are balanced by better foraging opportunities (McCullough 1985, Boyce 1991, Albon & Langvatn 1992), as well as by reduced snow depth (e.g. Tierson *et al.* 1985, Poole & Mowat 2005) and by better thermal cover (e.g. Verme 1973, Kearney & Gilbert 1976). Hunting by man can also be a factor determining local distribution and movements of individuals (Irwin 2002). Different strategies of space use may also be present in the same population (e.g. Nicholson *et al.* 1997, Lovari *et al.* 2006) or, more rarely, applied by the same individual at different times (e.g. Myslenkov & Miquelle 2001, Sabine *et al.* 2002). Movement patterns may be learned by calves from their mothers (Clutton-Brock *et al.* 1982), whereby the same summer and winter areas are used every year (Knight 1970, Craighead *et al.* 1972, Andersen 1991, Boyce 1991).

There is a wealth of information on the spatial behaviour of the North American wapiti (*Cervus canadensis*) (e.g. Craighead *et al.* 1973, Irwin & Peek 1983, Boyce 1991, Van Dyke *et al.* 1998, Ager *et al.* 2003). Ranging movements of the red deer (*Cervus elaphus*) are relatively well documented in central and northern Europe (e.g. Catt & Staines 1987, Clutton-Brock & Albon 1989, Albon & Langvatn 1992, Szemethy *et al.* 1998, Klein & Hamann 1999, Szemethy

et al. 2003a), but not sufficiently known in the Mediterranean area (Carranza *et al.* 1991, Lovari *et al.* 2007). Information on spatial movements of red deer in mountainous habitats, where heavy snowfalls in winter may determine important variations in habitat quality, is also poor (Blankenhorn *et al.* 1978, Georgii 1980, Georgii & Schröder 1983, Schmidt 1993, Luccarini *et al.* 2006). Blankenhorn *et al.* (1978), Georgii (1980), Georgii and Schröder (1983) and Luccarini *et al.* (2006) described seasonal, usually altitudinal, movements of red deer in autumn/early winter and in spring, in the European Alps. Yet, all previous information on “migrant” red deer was derived from small samples of individuals and from a small number of fixes/month [Georgii (1980): $N = 10$ hinds, 11 fixes/ind./month; Luccarini *et al.* (2006): $N = 6-8$ hinds, 12 fixes/ind./month, pooled together with stags]; other methods [capture-mark-resight (Blankenhorn *et al.* 1978, but *see* Fattorini *et al.* 2007); direct and indirect observations on unmarked deer (Schmidt 1993)] were also used.

The aim of our study was to answer the following questions: (i) Do all individuals follow the same pattern of habitat use? (ii) If not, is there a prevalent strategy? (iii) Is phenology of spatial behaviour an age-dependent event?

Study area

Our research was carried out in the Dolomites, between the regions of Veneto and Trentino, Italian Alps. The area of our main study site in the upper Travignolo valley (Natural Park of Paneveggio-Pale di San Martino, 12°00'E, 46°30'N; 1210–2500 m a.s.l.) was ca. 118 km². The site is covered with spruce (34%) at lower altitudes, and larch (18%) forests at the upper altitudes with clearings (20%), rocks (14%) and shrubland (9%) in the remaining parts. Hunting was prohibited in 39% of the Travignolo valley, corresponding mostly to the spruce forest, but it was permitted in the remainder of the area between September and December.

A secondary study area (ca. 488 km², 600–3200 m a.s.l.; used only in late spring, summer and early autumn) extended around the eastern boundary of the main study site, with a variety of

habitats, e.g. Alpine meadows, moor and shrubland.

The climate is pre-alpine continental (Gafta & Pedrotti 1998), with snowy winters and short summers. January is the coldest month (mean temp. = -4.9 °C), whereas July is the warmest one (mean temp. = 12.9 °C).

During our experiment, the local density of the red deer in spring, estimated by spotlight counts, was 6 ind./100 ha (Amministrazione Provinciale di Trento unpubl. data). Hunting was allowed during Sep.–Dec., except within protected areas (46 km² for the Travignolo valley; at least 87 km² in the secondary study area). No meso/large predators were present.

Material and methods

Twenty hinds (four 1–3 years old, nine 4–9 years old, and seven > 9 years old; age based on tooth eruption and wear) were trapped in three corrals, in the winters 2001, 2002 and 2003, in the main study area of the upper Travignolo valley. All were radiotagged with VHF transmitters (150–151 MHz; Televilt Int.[®], Sweden, mod. TXH-3).

We collected a mean number of 20.1 fixes (SD = 4.8)/individual/month, evenly distributed around the clock (each hind was located at least 20 days/month, a maximum number of 4 days elapsed between measurements). At least three bearings (loudest signal method, Springer 1979) were used to locate red deer. A minimum time of six hours elapsed between two consecutive fixes. Hinds moving out of the main study area were followed continuously (i.e. located every 15–30 minutes, when on the move).

Home range (hereafter, HR) features were assessed with the fixed 90% kernel method (Worton 1989). When a deer used two distinct areas in the same period (*see below*), separated by a gap greater than the median daily distance covered during seasonal movements, the two sub-HRs were calculated separately to avoid shortcomings of the method, i.e. an artificial increase of size of each sub-HRs. Seasonal analyses were carried out for summer (June–August) and winter (December–February).

HR centres/individual/period were calculated as the centre of 90% of locations, using the

Weighted Mean of Points ver. 1.2c for ArcView (Jenness 2004). The distance of HR centres/individual, between seasons, the interfix distance (i.e. the linear distance between successive locations) in each season and the overlap percentage of winter–summer HRs in the same year, as well as winter–winter and summer–summer HRs in subsequent years (as a measure of site fidelity), were assessed. The overlap percentage of these HRs was calculated as the mean of the overlaps in relation to the size of the corresponding home range, e.g. two or more overlapping HRs (e.g. home range A and home range B). The percentage of overlap between HRs (A and B) varies for each HR in relation to its size. The fixes collected by continuous monitoring of individual deer moving outside the winter range were used to determine the daily median distance covered.

Seasonal movements were defined in various ways on the basis of the percentage of overlap of home ranges in the warm (summer) and in the cold (winter) seasons (*see e.g. Sabine et al. 2002, Berger 2004, Hebblewhite et al. 2006*). Some authors used the distance between the summer and winter HR centres (*see e.g. Nicholson et al. 1997, Szemethy et al. 2003b, Poole and Mowat 2005*). We used the distance between summer and winter HR centres, i.e. the ratio (D) of the linear distance between seasonal HR centres (D_c) and the median inter-fix distance in the warm and in the cold seasons (d_{it}), to describe spatial behaviour. The use of percentage overlap of seasonal HRs could be biased by the conventional, i.e. astronomic, definition of seasons, independent of the individual responses to the variation of environmental parameters (Ferguson & Elkie 2004) among years. Thus, some individuals could show a temporary overlap between seasonal HRs (but with a great distance between HR centres) because moving away from their winter ranges very late in summer or coming back very early in autumn, in respect to other individuals of the same population. On the other hand, when the ratio of the distance between HR centres and the median inter-fix distance in both seasons is greater than the threshold value 2, it means that the hind used 2 seasonal areas, separated by twice the median distance covered during bouts of spatial mobility in summer and winter. In this context, the term migration (“typically of

relatively long distance from one area, stratum or climate to another", Lincoln *et al.* 1982) may be inappropriate as seasonal animal movements can be short and long-distance ones. Thus, we have preferred to term as "shifters" (not "migrants") the hinds which used two seasonal HRs, even if adjacent ones. Females that switched their spatial behaviour during the study period ($N = 2$, cf. Results) were pooled with shifters or residents, in relation to their movements in that year. We removed them from the data set to avoid pseudoreplication when features of residents and shifters were compared.

Radiotracking data were spatially analysed (i.e. home range analyses, interfix distance) using the software Animal Movement ver. 2.0 beta for ArcView 3.2 (Hooge & Eichenlaub 1997).

We used the k -means cluster analysis on the percentage overlap between HRs of hinds, in the same period, but in successive years, to assess site fidelity (cluster number = 2; 1 = site faithful, 2 = no site faithful).

Red deer are "ecotonal" species, i.e. adapted to feeding on a mixed diet of browse and graze (Clutton-Brock *et al.* 1982). Environmental diversity increases ecotonal habitats. Thus we assumed that it could be used to provide a measure of habitat quality (e.g. Oberdorfer 1957, Lucherini & Lovari 1996) for red deer. Habitat heterogeneity was assessed using Shannon's index (Magurran 1988), which is based on the relative abundance of vegetation categories:

$$H' = -\sum p_i \log_2 p_i$$

where p_i = proportion of a vegetation category (Corine Land Cover — level four; Image & Corine Land Cover 2000, EU; vegetation categories: Alpine meadows, rocks, man-managed pastures and dispersed greenery, spruce forest, mixed woodland, shrubwood) in the seasonal HR of each individual.

Climatic data were provided by the Istituto Agrario di San Michele all'Adige (TN, Italy) and collected at the meteorological station in Paneveggio.

We used Spearman's rank correlation coefficient to test associations. Medians (hereafter, M) were used in all our analyses as they are less

influenced by large outliers; quartiles (Q_1 and Q_3) were used to assess the variability range. All tests were non-parametric, two-tailed (Siegel & Castellan 1988). All p values were considered significant at the level of 0.05, except for Spearman's rank correlation coefficient to which the Bonferroni correction was applied.

Results

For all hinds, the index of spatial behaviour (D) was directly associated to habitat diversity, within the summer HRs (Spearman's rank correlation coefficient: $r_s = 0.751$, $N = 39$, $p < 0.001$), but not to that in winter HRs ($r_s = 0.118$, $N = 39$, $p = 0.474$).

Two main categories of hinds were found on the basis of the distance ratio (D) between HR centres (D_c) and the median inter-fix distance (d_{if}) in both seasons (summer and winter; Fig. 1). 'Resident' females (R, 2002: $N = 5$; 2003: $N = 3$; 2004: $N = 6$) showed $D_c \leq 2d_{if}$ (Fig. 1) and spent both the winter and the summer in the same area; therefore they showed a relatively high overlap between home ranges of different seasons (median of overlap: 42%, range: 12%–69%), as well as a small distance between the centres of their summer and winter ranges (median: 0.6 km; range: 0.2–1.1 km; Fig. 2). 'Shifter' females (S, 2002: $N = 6$; 2003: $N = 9$; 2004: $N = 10$) showed $D_c > 2d_{if}$ (Fig. 1), thus a very small or no seasonal overlap in HR, as well as widely-separated centres of summer and winter ranges (median: 7.7 km, range: 0.9–31.0 km; Fig. 2). The median daily distance covered during seasonal movements was 7.5 km ($Q_1 = 5.7$ km, $Q_3 = 13.0$ km). The percentage of shifters differed annually (2002: $N = 11$ radiotagged females, 55% shifters; 2003: $N = 12$ radiotagged females, 75% shifters; 2004: $N = 16$ radiotagged females, 63% shifters).

Ninety percent of hinds showed a consistent spatial behaviour all throughout our study. Only two hinds switched yearly their spatial strategies. No significant age difference was found each year between residents and shifters (Mann-Whitney U -test: $U \leq 29.0$, $N_1 = 3-6$, $N_2 = 6-10$, $p \geq 0.139$).

Home-range sizes (pooled data) in summer were significantly greater than those in the previ-

Fig. 1. Spatial behaviour of hinds (R = residents, S = shifters). D_c = distance between home range centres, d_{if} = mean interfur distance.

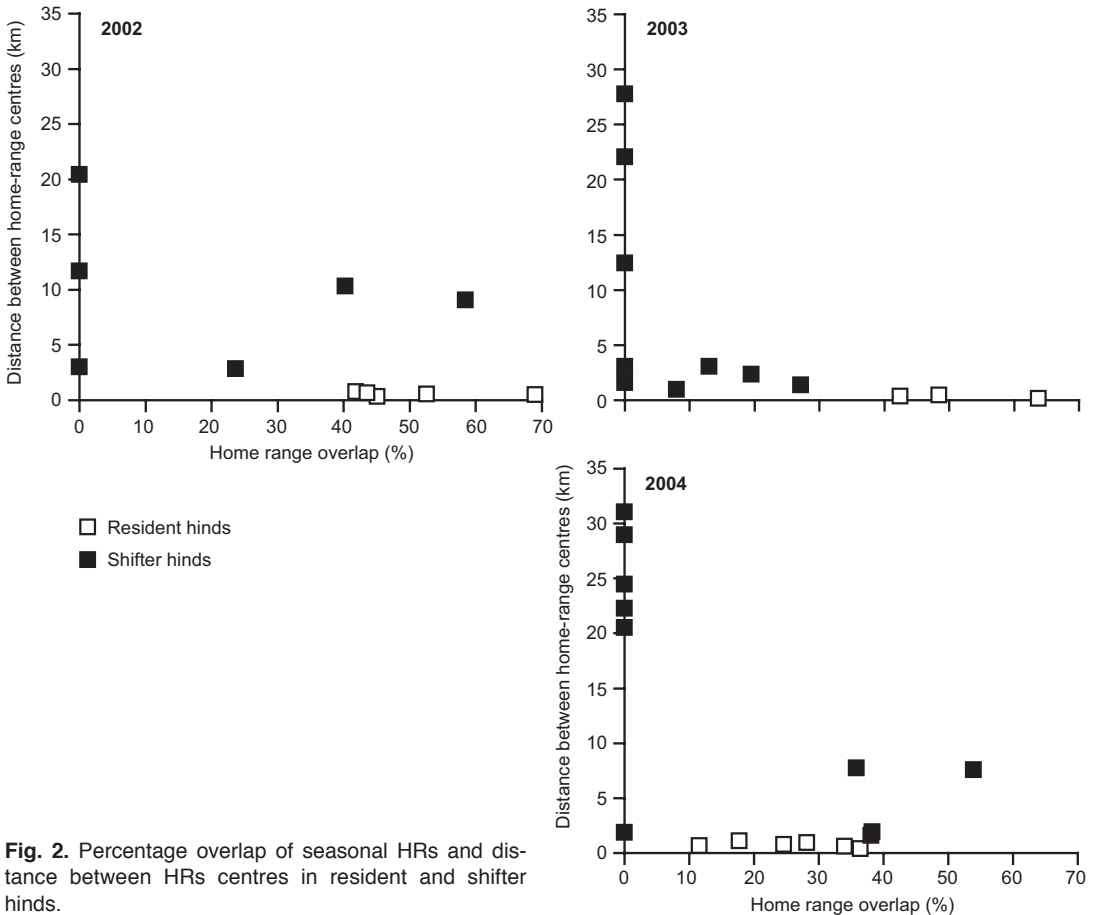
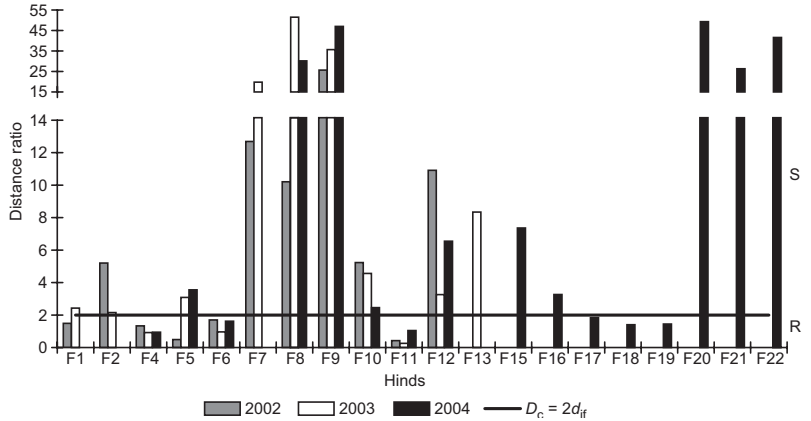


Fig. 2. Percentage overlap of seasonal HRs and distance between HRs centres in resident and shifter hinds.

ous winters of 2002 (Wilcoxon’s matched pairs test: $Z = 2.05$, $N = 11$, $p = 0.041$) and 2004 (Wilcoxon’s matched pairs test: $Z = 2.79$, $N = 16$, $p = 0.005$; Table 1), but not in the winter of 2003 (Wilcoxon’s matched pairs test: $Z = 0.00$, $N = 12$, $p = 1.000$). Mainly shifter hinds were responsi-

ble for this difference in 2002 and 2004 (Wilcoxon’s matched pairs test: 2002, $Z = 2.20$, $N = 6$, $p = 0.028$; 2004, $Z = 2.40$, $N = 10$, $p = 0.017$).

No significant difference was found in winter HR sizes (Wilcoxon’s matched pairs test: $Z \leq 1.68$, $N = 8-11$, $p \geq 0.093$), as well as in summer

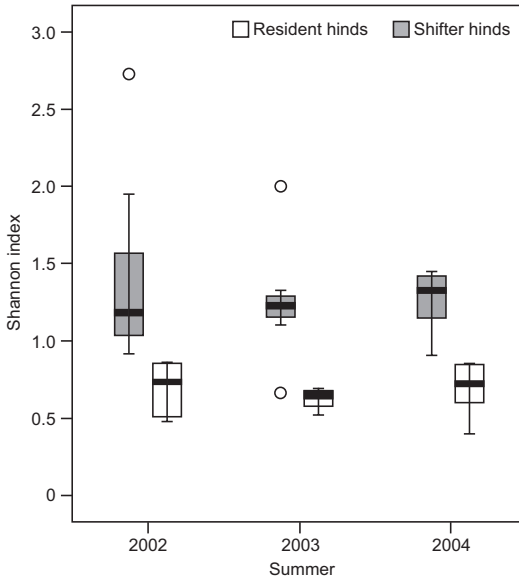


Fig. 3. Habitat diversity in HRs of resident and shifter hinds, during summer (medians and interquartile ranges; o = outliers).

HR sizes (Wilcoxon's matched pairs test: $Z \leq 1.68$, $N = 8-11$, $p \geq 0.093$) between years. No significant difference was also found in seasonal (summer and winter) HR sizes between resident and shifter hinds in 2002 and 2003 (Mann-Whitney U -test: $U \leq 10.0$, $N_1 = 3$, $N_2 = 6-7$, $p \geq 0.067$; Table 1); in 2004, ranges of shifter hinds in winter and in summer were greater than those of residents (Mann-Whitney U -test: $U = 8.0$, $N_1 = 6$, $N_2 = 9$, $p = 0.026$; and $U = 9.0$, $N_1 = 6$, $N_2 = 9$, $p = 0.036$; respectively).

In summer, HRs of shifter hinds showed a significantly greater habitat diversity than that of

residents (Mann-Whitney U -test: 2002, $U = 0.0$, $N_1 = 5$, $N_2 = 6$, $p = 0.004$; 2003, $U = 1.0$, $N_1 = 3$, $N_2 = 9$, $p = 0.018$; 2004, $U = 0.0$, $N_1 = 6$, $N_2 = 10$, $p < 0.001$; Fig. 3). In winter, habitat diversity in HRs was similar for shifter and resident females, when they were occupying the same area in the upper Travnigolo valley (Mann-Whitney U -test: $U \leq 25.0$, $N_1 = 3-6$, $N_2 = 6-9$, $p = 0.548$).

No difference was detected in altitude at which shifter and resident hinds were found in winter (Mann-Whitney U -test: 2002-2004, $U \leq 20.0$, $N_1 = 3-6$, $N_2 = 6-9$, $p \geq 0.095$) and summer (Mann-Whitney U -test: 2002-2004, $U \leq 11.0$, $N_1 = 3-6$, $N_2 = 6-9$, $p \geq 0.066$). Twenty-five percent of shifter hinds ($N = 14$) summered at lower altitudes than resident hinds.

The highest maximum daily temperatures (mean temp. = 22.4 °C) occurred in the summer of 2003 (Student's t -test: 2002/2003, $t = -6.114$, $N = 87$ days, $p < 0.001$; 2003/2004, $t = 12.090$, $N = 87$ days, $p < 0.001$). Snow depth showed a great variability between winter and spring, as well as between the years (Table 2). No winter mortality of hinds moving outside the winter range (i.e. the Travnigolo valley) was recorded, whereas 33% of the others ($N = 9$) died of starvation at the end of the severe winter of 2003/2004.

The k -means cluster analysis on percentage of overlap between HRs of hinds, in the same period but in consecutive years, suggested a great overall site fidelity ($F = 78.822$, $N = 38$, $p < 0.001$; Fig. 4).

In the first week of the hunting season, most (80%-100%) of our shifter hinds were back from their summer areas to the protected part of their winter range or to other protected areas,

Table 1. Home range sizes (ha) of radiotagged hinds.

Year	N	Annual		Winter		Summer	
		Median	Range	Median	Range	Median	Range
Shifter hinds							
2002	6	374	329-964	151	40-308	408	296-903
2003	9	475	390-1098	169	26-872	173	49-485
2004	10	760	142-1699	117	80-210	451	30-2231
Resident hinds							
2002	5	189	99-379	134	102-189	78	30-469
2003	3	137	64-593	148	100-242	53	30-98
2004	6	212	74-471	58	35-190	96	56-319

suggesting that this return was encouraged by the disturbance associated with hunting.

Discussion

Two patterns of space use have been found amongst hinds: ‘shifter’ females, with separated summer and winter ranges, and ‘resident’ ones, living in the same area throughout the years. All groups of hinds wintered in the Travignolo valley, where they were caught during the cold season. By contrast, Schmidt (1993) described only resident (“non-migratory”) deer in the Central Austrian Alps, less than 200 km from our study area, although some “migrant” deer have been reported for other Alpine regions (Swiss Alps: Blankenhorn *et al.* 1978; Bavaria: Georgii 1980; two areas of the Italian Alps: Luccarini *et al.* 2006). In our study area, yearly HRs, as well as winter ranges, were smaller than those found by Luccarini *et al.* (2006) in the Susa valley and in the Tarvisio forest for both, shifter and resident hinds. Conversely, summer HR size was greater in our study area than in the Tarvisio Forest for shifter hinds (Luccarini *et al.* 2006). HRs were significantly smaller in winter than in summer. Georgii (1980) and Luccarini *et al.* (2006) suggested that snow cover on the ground may limit winter movements. Although snowfalls were comparable in their and in our study areas, we cannot confirm their statement. By contrast, no significant variation in seasonal HR size was found in our study area in 2003, when the warmest summer in the whole study period occurred.

There were no significant differences between seasonal HR sizes of shifter and resident hinds. Shifter females only moved to separate summer ranges, but, when there, they showed HRs of sizes comparable to those of residents, although individual variation was great. Hinds were reported to perform altitudinal seasonal movements, with summer ranges at greater altitudes (Georgii 1980, Luccarini *et al.* 2006), but, in our study area, some shifter hinds (25%; $N = 14$) had their summer ranges at lower altitudes than those of their winter ranges. Seasonal movements may not be determined only by altitude: other factors are likely involved, e.g. habitat richness, aspect, human harassment.

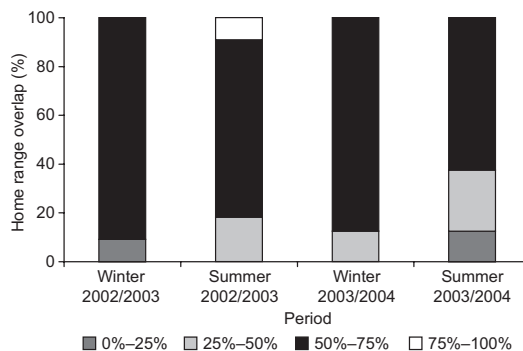


Fig. 4. Site fidelity of hinds in winter and summer, assessed as the percentage of HR overlap in the same seasons, in successive years.

Every year, resident and shifter hinds used the same summer and winter ranges. Only two adult hinds changed their spatial behaviour throughout 2002–2004.

Animal movements appear to be strongly dependent on seasonal availability and quality of resources (Georgii 1980, Fryxell & Sinclair 1988, Boyce 1991, Albon & Langvatn 1992, Myrsterud *et al.* 2001). The size of patches or amounts of a given type of environment (i.e. habitat heterogeneity) present in a landscape directly affect colonisation of individuals, persistence of individuals and breeding units (Morrison *et al.* 1992). We estimated habitat quality in terms of environmental heterogeneity, e.g. the plant community patches are not evenly distributed in a qualitatively rich habitat (Oberdorfer 1957, Kollmann & Fischer 2003). In summer, shifter hinds showed more heterogeneous HRs than residents, who did not leave the spruce forest. After shifter hinds moved to their summer grounds, residents benefited from reduced competition as compared to that in winter. Furthermore, the resident seg-

Table 2. Mean snow depth (cm; Paneveggio meteorological station) in winter (Dec.–Feb.) and in spring (Mar.–May).

Year	Winter		Spring	
	<i>N</i>	Mean ± S.D.	<i>N</i>	Mean ± S.D.
2002	89	2.37 ± 5.42	91	2.54 ± 7.95
2003	84	20.79 ± 11.88	92	2.63 ± 6.98
2004	82	36.64 ± 18.54	85	22.43 ± 29.63

ment of the deer population, remaining behind, may have compensated for the relatively homogeneous quality of habitat with a greater plant selection (Nicholson *et al.* 1997).

Movement patterns have often been assumed to enhance access to high quality food resources and/or to reduce the risk of predation (Fryxell & Sinclair 1988). In our study area with no natural predators, most likely habitat quality (assessed in terms of habitat diversity) determined summer movements of shifter hinds to more heterogeneous areas than those where residents remained. Conversely, winter ranges of both behavioural groups were within the Travignolo valley and their HRs did not significantly differ in heterogeneity.

From an evolutionary viewpoint, both strategies, i.e. the shifter and the resident ones, provide benefits and costs to hinds. Usually shifter individuals have access to better food resources than resident ones (*see* Fryxell & Sinclair 1988 for large herbivores), but moving is expensive energetically and potentially dangerous, especially when in late pregnancy or with a very young calf at heel, as distant areas have to be reached (Gates & Hudson 1978). Furthermore, in some areas, accident and predation risks (i.e. Nicholson *et al.* 1997) may be greater for shifters and their calves, when unknown areas are crossed during migrations and knowledge of escape terrain may be vital (Albon & Langvatn 1992). In our study area, "predation" risks are mimicked by hunting, although the risk to be shot seems to concern mainly males, because of trophy hunting (1/3 of radiotagged stags, $N = 21$). Presumably, resident hinds may benefit both from a greater familiarity with their habitat, when this information is needed, and from protection accorded to the area (i.e. hunting prohibited). Blankenhorn *et al.* (1978), Georgii (1980) and Luccarini *et al.* (2006) reported altitudinal and horizontal migratory movements for red deer in the Alps as a winter migration (i.e. individuals moved towards their summer and winter ranges with yearly snowfalls). In our study area, most hinds moved back from their summer ranges to their winter ranges (Travignolo valley) in September, when snowfalls were still negligible (summer migration). Hinds may come back to the coniferous forest in the Travignolo valley, because it is

a traditional rutting area and/or a better winter range (e.g. forage quality, shelter from wind and snow) than their respective summer ranges or, as the timing of return movements in our study suggests, when disturbed by hunting activities in their summer ranges.

It is a striking feature of our data that two alternative spatial strategies (year-round residency and seasonal movements between discrete winter and summer ranges) coexist in the same population. These alternative strategies should each have evolutionary advantages and disadvantages. Presumably, in order to persist in the behavioural repertoire of red deer, each pattern should be differentially advantageous in different contexts, e.g. years and areas (Fretwell 1972, *see also* Lovari *et al.* 2006). Rates of survival and reproduction need not to be similar in all years for a mixed strategy to be maintained in a population (Nicholson *et al.* 1997). The spatial strategy could in fact be related to a differential yearly mortality in relation with snowfall, which may suggest that moving to summer ranges of a better quality could improve autumn body condition and winter survival. This pattern of space use could also be linked to the reproductive success, with a potential different mortality rate of calves.

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References

- Ager, A. A., Johnson, B. K., Kern, J. W. & Kie, J. G. 2003: Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. — *Journal of Mammalogy* 84: 1076–1088.
- Albon, S. D. & Langvatn, R. 1992: Plant phenology and the benefits of migration in a temperate ungulate. — *Oikos* 65: 502–513.
- Andersen, R. 1991: Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. — *The Journal of Applied Ecology* 28: 102–108.
- Berger, J. 2004: The last mile: how to sustain long-distance migration in mammals. — *Conservation Biology* 18: 320–331.
- Blankenhorn, H. J., Buchli, C. H. & Voser, P. 1978: Wanderungen und jahreszeitliches Verteilungsmuster der Rothirschpopulationen (*Cervus elaphus* L.) im Engadin, Munstertal und Schweizerischen Nationalpark. — *Revue Suisse de Zoologie* 85: 779–789.
- Boyce, M. S. 1991: Migratory behavior and management of elk (*Cervus elaphus*). — *Applied Animal Behaviour Science* 29: 239–250.
- Brown, C. G. 1992: Movement and migration patterns of mule deer in southeastern Idaho. — *The Journal of Wildlife Management* 56: 246–253.
- Carranza, J., Hidalgo De Trucios, S. J., Medina, R., Valencia, J. & Delgado, J. 1991: Space use by red deer in a Mediterranean ecosystem as determined by radio-tracking. — *Applied Animal Behaviour Science* 30: 363–371.
- Catt, D. C. & Staines, B. W. 1987: Home range use and habitat selection by red deer (*Cervus elaphus*) in a Sitka spruce plantation as determined by radio-tracking. — *Journal of Zoology* 211: 681–693.
- Clutton-Brock, T. H. & Albon, S. D. 1989: *Red deer in the Highlands*. — BSP Professional Books, Oxford.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982: *Red deer: behaviour and ecology of two sexes*. — The University of Chicago Press, Chicago.
- Craighead, J. J., Atwell, G. & O’Gara, B. W. 1972: Elk migrations in and near Yellowstone National Park. — *Wildlife Monographs* 29: 1–48.
- Craighead, J. J., Craighead, R. L. Jr. & O’Gara, B. W. 1973: Home range and activity patterns of nonmigratory elk of the Madison Drainage Herd as determined by biotelemetry. — *Wildlife Monographs* 33: 1–55.
- Fattorini, L., Marcheselli, M., Monaco, A. & Pisani, C. 2007: A critical look at some widely used estimators in mark-resighting experiments. — *The Journal of Animal Ecology* 76: 957–965.
- Ferguson, S. H. & Messier, F. 1996: Ecological implications of a latitudinal gradient in inter-annual climatic variability: a test using fractal and chaos theories. — *Ecography* 19: 382–392.
- Ferguson, S. H. & Elkie, P. C. 2004: Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). — *Journal of Zoology* 262: 125–134.
- Fretwell, S. D. 1972: *Populations in a seasonal environment*. — Princeton University Press, Princeton.
- Fryxell, J. M. & Sinclair, A. R. E. 1988: Causes and consequences of migration by large herbivores. — *Trends in Ecology & Evolution* 3: 237–241.
- Gafta, D. & Pedrotti, F. 1998: Fitoclima del Trentino — Alto Adige. — *Studi Trentini di Scienze Naturali, Acta Biologica* 73: 55–111.
- Gates, C. & Hudson, R. J. 1978: Energy costs of locomotion in wapiti. — *Acta Theriologica* 23: 365–370.
- Georgii, B. 1980: Home range patterns of female red deer (*Cervus elaphus* L.) in the Alps. — *Oecologia* 47: 278–285.
- Georgii, B. & Schröder, W. 1983: Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the Alps. — *Oecologia* 58: 238–248.
- Hebblewhite, M., Merrill, E. H., Morgantini, L. E., White, C. A., Allen, J. R., Bruns, E., Thrston, L. & Hurd, T. E. 2006: Is the migratory behaviour of montane elk herds in peril? The case of Alberta’s Ya Ha Tinda elk herd. — *Wildlife Society Bulletin* 34: 1280–1294.
- Hooge, P. N. & Eichenlaub, B. 1997: *Animal movement extension to ArcView, ver. 1.1*. — Alaska Biological Science Center, U.S., Geological Survey, Anchorage, AK, USA.
- Irwin, L. L. 2002: Migration. — In: Towell, D. & Thomas, W. J. (eds), *North American elk. Ecology and management*, 2nd ed.: 493–513. Smithsonian Institution Press, Washington DC.
- Irwin, L. L. & Peek, J. M. 1983: Elk habitat use relative to forest succession in Idaho. — *The Journal of Wildlife Management* 47: 664–672.
- Jenness, J. 2004: *Weighted mean of point (weightmean.avx) extension for ArcView 3.x, v. 1.2c*. — Jenness Enterprises.
- Kearney, S. R. & Gilbert, F. F. 1976: Habitat use by white-tailed deer and moose on sympatric range. — *The Journal of Wildlife Management* 40: 645–657.
- Klein, F. & Hamann, J. L. 1999: Domaines vitaux diurnes et déplacements de cerfs males (*Cervus elaphus*) sur le secteur de la petite Pierre (bas-Rhin). — *Gibier Faune Sauvage* 16: 251–271.
- Knight, R. R. 1970: The Sun river elk herd. — *Wildlife Monographs* 23: 1–66.
- Kollmann, J. & Fischer, A. 2003: Vegetation as indicator for habitat quality. — *Basic and Applied Ecology* 4: 489–491.
- Lincoln, R. J., Boxshall, G. A. & Clark, P. F. 1982: *A dictionary of ecology, evolution and systematics*. — Cambridge University Press, Cambridge.
- Lott, D. F. 1990: *Intraspecific variation in the social systems of the wild vertebrates*. — Cambridge University Press, Cambridge.
- Lovari, S., Sacconi, F. & Trivellini, G. 2006: Do alternative strategies of space use occur in male Alpine chamois? — *Ethology, Ecology and Evolution* 18: 221–231.
- Lovari, S., Cuccus, P., Murgia, A., Murgia, C. & Plantamura, G. 2007: Space use, habitat selection and browsing effects of red deer in Sardinia. — *The Italian Journal of Zoology* 74: 179–189.
- Luccarini, S., Mauri, L., Ciuti, S., Lamberti, P. & Apollonio, M. 2006: Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeling. — *Ethology*,

- Ecology and Evolution* 18: 127–145.
- Lucherini, M. & Lovari, S. 1996: Habitat richness affects home range size in the red fox *Vulpes vulpes*. — *Behavioural Processes* 36: 103–106.
- Magurran, A. E. 1988: *Ecological diversity and its measurement*. — Croom Helm, London.
- McCullough, D. R. 1985: Long range movement of large terrestrial mammals. — *Contributions in Marine Sciences* 27: 444–465.
- Morrison, M. L., Marcot, B. G. & Mannan, R. W. 1992: *Wildlife-habitat relationships. Concepts and applications*. — University of Wisconsin Press, Madison.
- Myslenkov, A. I. & Miquelle, D. 2001: Migrations of red deer in Sikhote-Alin Reserve, Russian far east. — In: *Proceedings of the 15th International Congress of the International Union of Game Biologists. Abstracts*: 36. Government Printing Office, Nicosia, Cyprus.
- Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stanseth, N. C. 2001: Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. — *The Journal of Animal Ecology* 70: 915–923.
- Nicholson, M. C., Bowyer, R. T. & Kie, J. G. 1997: Habitat selection and survival of mule deer: tradeoffs associated with migration. — *Journal of Mammalogy* 78: 483–504.
- Oberdorfer, E. 1957: *Suddeutsche Pflanzengesellschaften*. — Gustav Fischer, Jena.
- Parker, K. L., Robbins, C. T. & Hanley, T. A. 1984: Energy expenditure for locomotion by mule deer and elk. — *The Journal of Wildlife Management* 48: 474–488.
- Poole, K. G. & Mowat, G. 2005: Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. — *Wildlife Society Bulletin* 33: 1288–1302.
- Sabine, D. L., Morrison, S. F., Whitlaw, H. A., Ballard, W. B., Forbes, G. J. & Bowman, J. 2002: Migration behaviour of white-tailed deer under varying winter climate regimes in New Brunswick. — *The Journal of Wildlife Management* 66: 718–728.
- Schmidt, K. 1993: Winter ecology of nonmigratory Alpine red deer. — *Oecologia* 95: 226–233.
- Shackleton, D. M. & Bunnell, F. L. 1987: Natural factors affecting productivity of mountain ungulates: a risky existence? — In: *Proceedings of the Conference on the Reintroduction of Predators to protected Areas*: 46–57. University of Turin Press, Turin, Italy.
- Siegel, S. & Castellan, N. J. 1988: *Nonparametric statistics for the behavioural sciences*. — McGraw-Hill, New York.
- Springer, J. T. 1979: Some sources of bias and sampling error in radio triangulation. — *The Journal of Wildlife Management* 43: 926–935.
- Sweeney, J. M. & Sweeney, J. A. 1984: Snow depths influencing winter movements of elk. — *Journal of Mammalogy* 65: 524–526.
- Szemethy, L., Heltai, M., Mátrai, K. & Pető, Z. 1998: Home range and habitat selection of red deer (*Cervus elaphus*) on a lowland area. — *Gibier Faune Sauvage* 15: 607–615.
- Szemethy, L., Mátrai, K., Katona, K. & Orosz, S. 2003a: Seasonal home range shift of red deer hinds, *Cervus elaphus*: are there feeding reasons? — *Folia Zoologica* 52: 249–258.
- Szemethy, L., Mátrai, K., Bíró, Z. & Katona, K. 2003b: Seasonal home range shift of red deer in a forest-agriculture area in southern Hungary. — *Acta Theriologica* 48: 547–556.
- Tierson, W. C., Mattfield, G. F., Sage, R. W. Jr. & Behrend, D. E. 1985: Seasonal movements and home range of white-tailed deer in Adirondacks. — *The Journal of Wildlife Management* 49: 760–769.
- Van Dyke, F. G., Klein, W. C. & Stewart, S. T. 1998: Long-term range fidelity in rocky mountain elk. — *The Journal of Wildlife Management* 62: 1020–1035.
- Verme, L. J. 1973: Movements of white-tailed deer in upper Michigan. — *The Journal of Wildlife Management* 37: 545–552.
- Worton, B. J. 1989: Kernel methods for estimating the utilization distribution in home range studies. — *Ecology* 70: 164–168.