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# Home Range Patterns of Female Red Deer (*Cervus elaphus L.*) in the Alps

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**Summary.** From 1976 to 1978, ten female red deer in the northern parts of the Bavarian Alps (Southern West Germany) were fitted with transmitter collars. Seasonal movements, the home range patterns, and habitat utilization as a function of the habitat structure were examined. While some animals remained in the lowlands throughout the year, others move between two or even three different areas seasonally. The average size of the home range was 65 ha during winter, 167 ha in spring and autumn and 121 ha in summer. The overlap of home ranges of different individuals ranged from 18 to 100%. In habitats with a patchy vegetation structure the home ranges were used more uniformly, whereas in habitats with a distinct separation of large woods and meadows home ranges show diurnal and nocturnal activity centres respectively.

## 1. Introduction

Data on the habitat used by red deer in the Alps is lacking. Sporadic records (e.g. Kobell 1859) report extensive migrations between summer mountain areas and wintering areas in the lowlands. Similar seasonal migrations are made by red deer in the Swiss National Park (Blankenhorn et al. 1978). Darling (1937) had already documented these vertical migrations between high summer areas and low winter areas. Similar findings have been reported by Stevens (1970) on moose (*Alces alces*), Robin (1975) on roe deer (*Capreolus capreolus*), Bertram and Rempel (1977) on mule deer (*Odocoileus hemionus*), Craighead et al. (1973) on wapiti (*Cervus canadensis = elaphus*), and Geist (1968) and Nievergelt (1966) on various Bovine species. In many areas of their alpine distribution the characteristic migrations of the red deer today are changed because of intensive human land use and artificial winter feeding of deer within the mountain valleys.

This report deals with the habitat utilization of red deer under these present conditions. It should provide basic information for further investigations of the habitat assessment of the species in alpine regions. The assumption is made that red deer follow special strategies to meet the topographical and climatical extremes of the alps in order to achieve optimal habitat utilization. Some aspects of the resulting spatial behaviour will be discussed. The study of home ranges of individuals during the course of the year is expected to give the best information concerning the space-time-system (Hediger 1950) of this species. The term "home range" is understood in its classical definition of Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young."

The home range patterns of North American cervids have been extensively studied (e.g., Miller 1970; Craighead et al. 1973; Phillips et al. 1973; Franklin et al. 1975; Drolet 1976). However, the only treatment of this subject in the European red deer are those of the Scottish highlands. The home range estimates of 400 ha (Lowe 1966) to over 6,000 ha (Staines 1970) are presumably not transferable to other environmental conditions. For the management of such a large game species in a habitat utilized very intensively by man, however, this kind of biotop-specific data promisses to be very advantageous.

## 2. Study Area

The study area of approximately 12,000 ha lies on the northern edge of the Bavarian Alps between 10°50′ and 11°05′ E, 47°30′ and 47°36′ N at an altitude from 850 to 2185 meters NN above sea level. The average annual precipitation ranges from 1,600 mm in the lowlands to 2,500 mm in the highlands, the average snow cover from 60 cm to 200 cm respectively. Sudden warm periods caused by the "Föhn", a southerly gale, are frequent.

The landscape ranges from pronounced rugged massives of high mountains to rounded ridges of medium size (Fig. 1). The vegetation is varied (see Feldner 1978) and in most cases reaches up to the mountain ridges. The area is 70% forested with stands of spruce, firs and beeches. In the lowlands the forests alternate with wide pastures, while the highlands show relatively natural stands of open mixed mountain woods.

The red deer is indigenous to the research area, which is part of the large alpine distribution of this species. The average population density is estimated to be 3–4 animals per 100 ha. During the winter 30–50 individuals concentrate near artificial feeding places in the main valleys. In spring, they split into small groups of 3–7 individuals for the coming summer. The composition and size of these groups varies constantly. In the long run only doe, yearling and calf form a stable social unit. The males form separate herds as a rule (see also Schröder 1978).

## 3. Material and Methods

For this study ten female red deer have been radiomarked. They were caught during winter at the feeding places within the research area. A drug mixture of Rompun, Vetalar and Kinetin was applied by using an immobilizing gun (for details see Wiesner 1977). Table 1 presents information about age, date of marking, observation period and number of radio locations per animal.

The telemetry system utilized has been developed by the Messerschmidt-Boelkow-Blohm company (Munich). The transmitter collars

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Fig. 1. View of the study area

Table 1. Some individual data of the ten radio-marked red deer hinds

| Animal number | Age (years)[a] | First marking | Observation period | Number of radio locations |
|---|---|---|---|---|
| ♀ 1 | 5–6 | April 1977 | 1977 | 107 |
| ♀ 2 | 5–6 | May 1976 | 1976–1977 | 104 |
| ♀ 3 | 8–9 | April 1977 | 1977 | 48 |
| ♀ 4 | 8–9 | March 1976 | 1976 | 51 |
| ♀ 5 | 10+ | April 1977 | 1977–1978 | 320 |
| ♀ 6 | 2–3 | March 1976 | 1976–1978 | 596 |
| ♀ 7 | 10+ | April 1976 | 1976 | 84 |
| ♀ 8 | 5–6 | April 1976 | 1976 | 45 |
| ♀ 9 | 2–3 | May 1976 | 1976–1978 | 376 |
| ♀ 10 | 5–6 | January 1978 | 1978 | 186 |

[a] Estimated according to teeth wear of the immobilized animal at the time of the first marking

weighed 450 grams, and function in the 37 MHz range. The receiver unit consisted of a conveniently sized receiver with 12 channels and a ring-antenna with an angular accuracy of 2°–3° (for details see Sonnberger et al. 1977). The location of the animals was determined by triangulation of 3 to 5 bearings, as described by Heezen and Tester (1967). Each animal was located daily or every few days at randomly selected times. In addition, they were located at 2–3 h intervals for an entire day every month.

This analysis is based on 1,917 radio location fixes in 1976–1978. The data was analysed for the most part using computer programmes by Klein und Georgii (1979, unpublished). A quadrate procedure, with a grid size of 200 × 200 m, was used for the description of the home range and complete area calculations. In addition, chronologically ordered locations were connected by straight lines, and then only the grids actually used and those intersected by these lines were taken. The "daily home ranges" were determined in the same way. In order to achieve greater accuracy, however, with this "graphical procedure" the grid size was reduced to 100 × 100 m. This method seemed to be advantageous in our mountaineous study area over the more mathematical methods reviewed by Van Winkle (1975). Because of the limited number of observations for certain animals (see Table 1), the estimated home range sizes were tested by the procedure of Odum and Kuenzler (1955). Accordingly, at least 50–100 fixes are necessary for reliable estimates of home range size and therefore some sets of data are insufficient.

## 4. Results

### 4.1 Spatial and Seasonal Variation of Home Ranges

Two patterns of habitat utilization have become apparent regarding the position and extension of the home range of the ten observed female red deer. An example of each pattern using data of one individual in each case is shown in Fig. 2. The general patterns are as follows:

*Non-migratory animals* which stay all the year round in the valleys (Hind No. 1, 3, 4, 5, – Fig. 2, I). Besides the valley bottoms their home ranges include only the lower parts of the mountain slopes. In late autumn they reduce the size of their home ranges following the first snowfall. In the spring the animals react in reverse to the new growth of vegetation with an expansion of the winter range. Therefore the winter home range is only a small fraction of the area roamed about in the other seasons.

*Migratory animals* which during autumn, winter and spring have a home range in the valleys too, reducing and expanding it in the same way as described above. However, during summer these animals have a fully separate home range in the highlands (Hind No. 2, 6, 8, 9, 10 – Fig. 2, II). It was characteristic that in autumn as well as in spring the animals used the same area; therefore in the further discussion a destinction between the two will not be made.

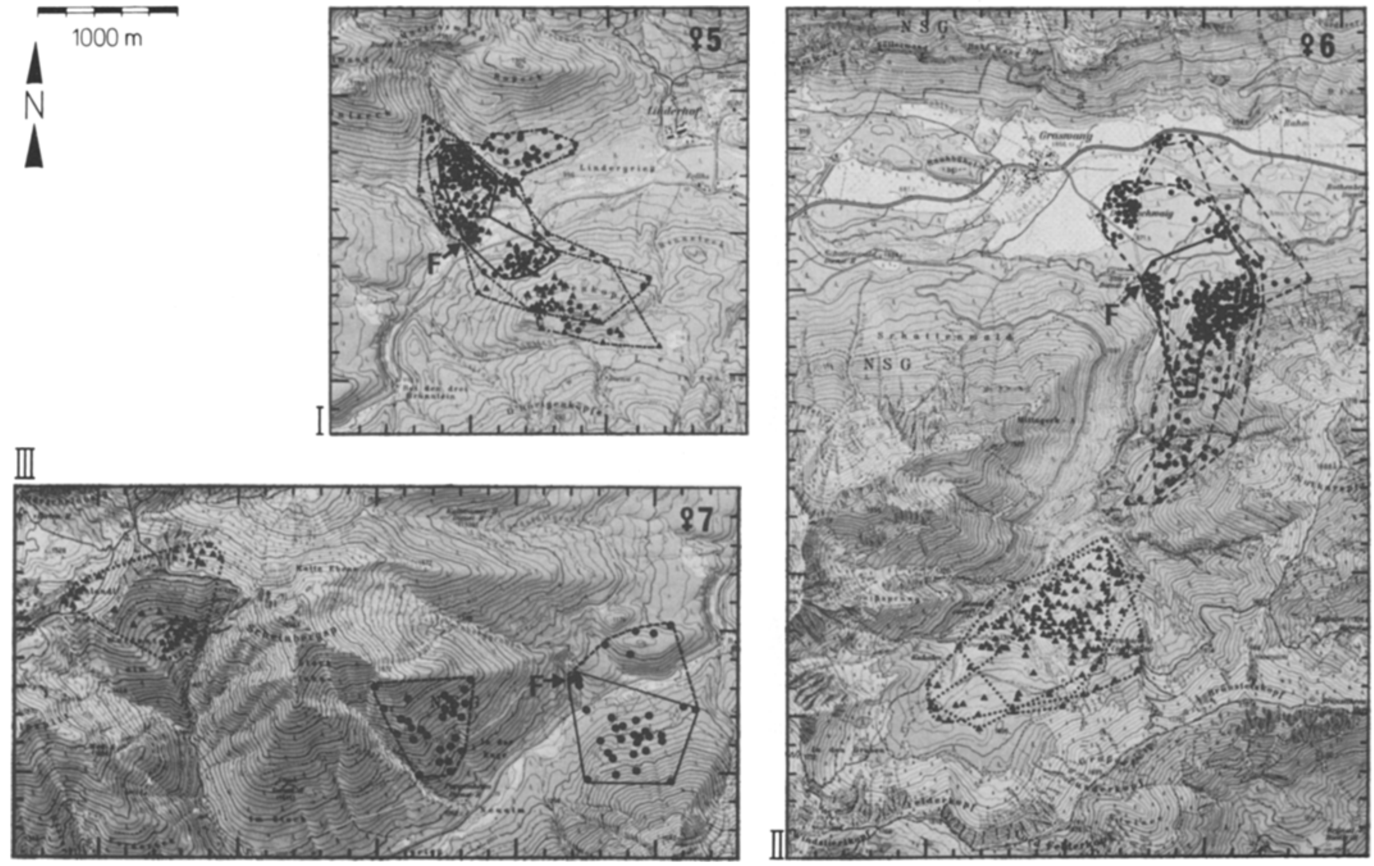

**Fig. 2.** Examples of animals with only one (I), two (II) and three (III) home ranges. Original distribution of radio locations; points = autumn, winter and spring telemetry fixes, triangles = summer fixes. —— winter ranges, – – – – autumn/spring ranges, · · · · summer ranges, –·–·–·– range used from spring to autumn. Different outlines of the home ranges correspond to observation periods lasting two (I) and three (II) successive years respectively. $F$ = position of feeding stations

In some cases the second pattern appears to be modified, as is demonstrated by hind No. 7 and in 1978 also by hind No. 9 (Fig. 2, III; see also Fig. 3, III). Hind No. 7 left her winter range earlier than those animals exhibiting pattern II but delayed her migration to the summering grounds at medium altitudes establishing there a further home range for about three to four weeks. Later she changed to the summer range at the upper timber line. These "holding areas" (Bertram and Rempel 1977) or "intermediate ranges" (Robinette 1966) may also be used during autumn.

To date it remains uncertain whether only these two home range patterns apply or whether they are linked by a continuum of other patterns. For example hind No. 9 altered her behaviour from 1977 to 1978 (see Fig. 3).

The spatial position of the different seasonal ranges of the animals remained surprisingly similar from year to year although the boundaries vary slightly as is shown in Fig. 2. Therefore distances between the ranges also remain similar. A specific pattern in their shapes cannot be detected. Usually their borders are determined by geographic features such as ditches, streambeds, ridges, roads or by the position of winter feeding places.

Just so, as in the spatial position of the home ranges, so also are the seasonal changes between them very similar in consecutive years. As Fig. 3, II and III shows, most of the animals leave their spring home range at the end of May, beginning of June ($\bar{x}$ = June 3, SD = 12 days, $n = 11$). Only rarely does an animal leave notably earlier (No. $2_{76}$) or considerably later (No. $9_{78}$ and No. $10_{78}$). The period during which animals leave the summer range extends from end of July to late September ($\bar{x}$ = September 2, SD = 19 days, $n = 11$), although the data must be interpreted with caution due to many transmitter failures. Thus, the stay on the summer home range is quite variable, extending from just under two months to more than four months ($\bar{x}$ = 80 days, SD = 31 days, $n = 11$).

As Fig. 3 suggests, all migrations between seasonal home ranges occur within one day, sometimes even within a few hours, depending on the distances between the home ranges, which vary from some 250 m to aproximately 3,000 m. By contrast, the reduction of the autumn range and the expansion of the winter range, observed in type I as well as in type II, lasts over a period of up to two weeks. Normally the animals (of types II and III) do not leave their home ranges until the next seasonal range change. Only two short-time excursions out of a given home range were observed: No. 6 made a one-day trip in both 1976 and 1978 from the spring to the summer home range a week before the definite home range change ("test trips" Bertram and Rempel 1977).

### 4.2. *Size of the Home Ranges*

The size of home ranges goes through a characteristic annual change, as analysis of both the entire sample of animals and the intra-individual comparison of the seasonal home ranges shows (Fig. 4). The smallest ranges were found during winter, averaging

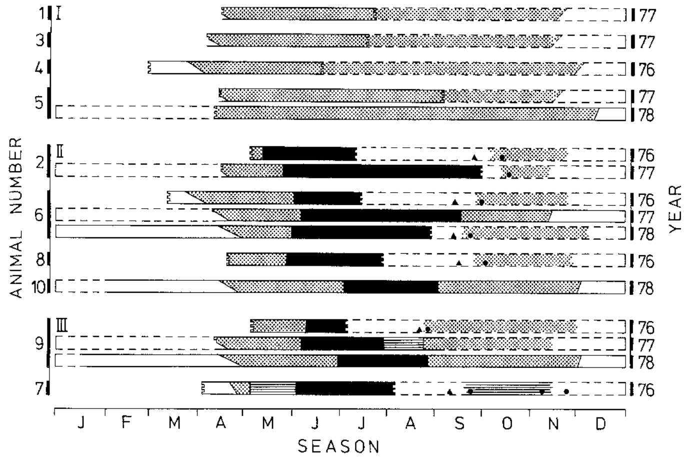

**Fig. 3.** Duration of seasonal home range maintenance by the ten observed red deer hinds. Animals with one (I) two (II) and three (III) home ranges. White = winter ranges, shaded = home range used from spring to autumn (I) or only during spring and autumn (II) in the valleys, black = summer ranges in the mountains, hatched = home ranges of hind No. 7 and No. 9 at medium altitudes. [ ] beginning of telemetry work with the animals or break-down of the transmitters respectively. ⌶ change of home ranges within one day or only some hours. ⊻ ⊼ time period of expanding the winter range and reducing the autumn range respectively. Broken lines = completed by visual observations after transmitter failures. Triangles = last observation in summer ranges, points = first observation in fall ranges; an exact timing for the range change is not possible in these cases

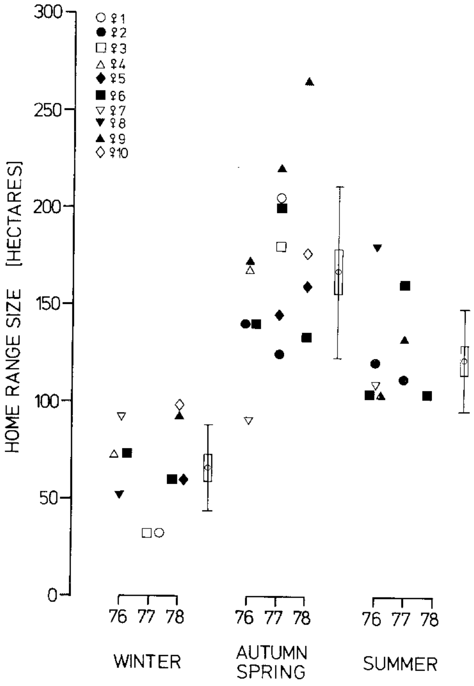

**Fig. 4.** Size of seasonal home ranges in the three observation years; individual values as well as averages with standard error and standard deviation

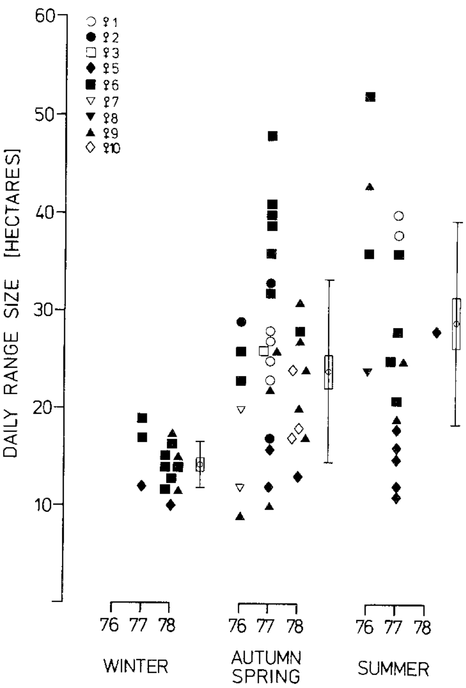

**Fig. 5.** Size of areas roamed about within one day; individual values as well as averages with standard error and standard deviation. For comparison, see Fig. 4

65±22 ha ($n=10$). The autumn/spring ranges measured two to three times as much, with an average size of 167±45 ha ($n=15$). In contrast, the summer ranges are again somewhat smaller averaging 121±26 ha ($n=9$). The size differences between the three types of seasonal home ranges were highly significant (U-tests, $P<0.005$).

The same seasonal differences in the size of the home ranges were observed in different years for the individual animals. In five of the six animals with two seasonal areas, the size of the ranges increased significantly from winter to spring ($P<0.005$), but declined in summer ($P<0.001$, $t$-test for paired differences). An exception is No. 7 which had three ranges, the autumn/spring range being the smallest.

The home range of those animals for which only a single area could be defined (hinds No. 1, 3, 4, 5), had an average extension of 171±20 ha ($n=4$). This size is similar to that of the autumn/spring home ranges of the remaining individuals and it possibly delimits an upper boundary of economical habitat use for the animals in the study area.

On the basis of these data it does not appear very reasonable to combine the different seasonal ranges of the animals to "annual" or even "lifetime ranges" (Jewell 1966). Furthermore, the migratory routes were not considered part of the home ranges because the migration often lasts only some hours and therefore these "corridors" would disproportionately enlarge the calculated range sizes.

In conclusion it has to be pointed out that some of the home range estimates are based only on very few measurements (see Table 1). Therefore the given figures should only be considered as preliminary values.

### *4.3. Size of Daily Ranges*

Only relatively small sections of the home ranges were traversed by the animals within a 24-h span (Fig. 5). The size of the section used during a given day undergoes a change in the course of a year. The smallest daily spatial requirements are found in winter

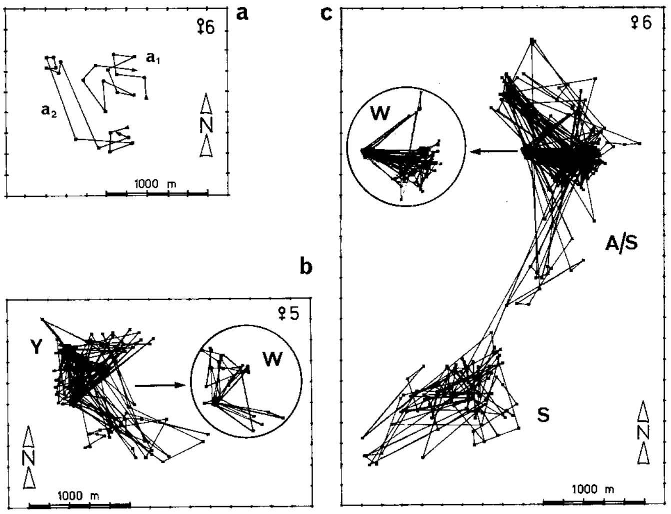

**Fig. 6a–c.** Movement patterns within the home ranges obtained by connecting consecutive fixes. Examples for two animals (compare with Fig. 2, I and II). **a** Site changes of hind No. 6 within 24 h (time intervals between fixes approximately 2 h); $a_1$ during summer, $a_2$ during spring. **b** Day-to-day movements of hind No. 5 within her annual range (Y, 1978). **c** Day-to-day movements of hind No. 6 within her autumn/spring range (A/S, 1977/78) and summer range (S, 1977). The movements within the winter ranges (W) are drawn in a circle beside the autumn/spring range and annual range, respectively, in which they are actually incorporated

averaging 14 ± 2.4 ha ($n = 13$). The animals only move to the feeding stations in the evenings, and mornings they move back again into the cover, where activity is minimal. In contrast, during the remaining seasons, they roam around extensively. Thus during spring and autumn the daily range requirements reached mean sizes of 24 ± 9.4 ha ($n = 34$). This is significantly larger than in winter ($P < 0.005$). In comparison to the reduction of home range sizes in summer (see Fig. 4), the size of the areas used daily further enlarges from spring to summer (mean size = 29 ± 10.4 ha, $n = 18$) although this enlargment is not statistically significant ($P > 0.02$; U-test).

### *4.4. Internal Use of Home Ranges*

The internal use of home ranges may be regarded from different aspects: (1) how the red deer hinds roam about within their home ranges, (2) whether they use different places during day and during night or (3) for feeding and resting respectively and (4) whether they prefer some areas more than others. Regarding the movements of the animals within their home ranges, one can distinguish more regular patterns from random ones. This is shown in Fig. 6 for two daily routes of hind No. 6, revealed by 13–14 fixes per 24 h (Fig. 6a), and the day-to-day travels of hinds No. 5 and 6, resulting from connections between chronological locations taken on successive days (Fig. 6, b and c). As Hediger (1950) already has pointed out, these patterns may depend on the "internal anatomy" of the home ranges. This appears to hold true also for red deer hinds. Thus, in uniformly structured habitats the animals roamed about in a somewhat directionless way (Fig. 6$a_1$; Fig. 6b, Y; Fig. 6c, S), whereas in those parts of the research area in which places for feeding and sheltering are far apart from one another movements into preferred directions are recognizable (Fig. 6$a_2$; Fig. 6c, A/S; Fig. 6b and c, W).

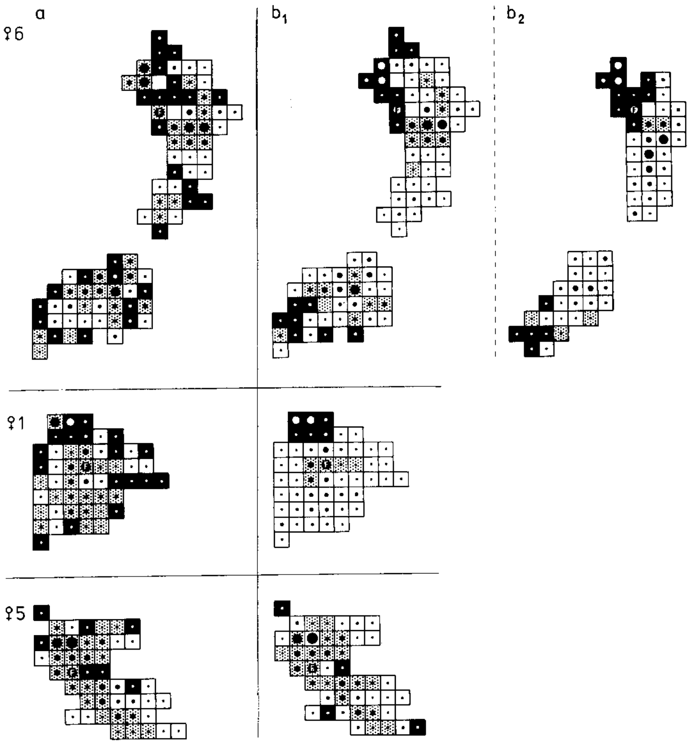

**Fig. 7.** Internal use of home ranges shown by examples of three animals; hind No. 6 with both the autumn/spring range (top) and summer range (bottom); hind No. 1 and No. 5 with annual ranges. **a**: grid cells indicating areas only used for feeding (black) and used only during rest (white) or used in both activities (shaded). **b**: grid cells indicating areas used only at night (black) and used only during daytime (white) or used day and night (shaded). For hind No. 6 comparison is made between 1977 ($b_1$) and 1978 ($b_2$). Smallest points = one or two radio locations per grid cell; size of points increases according to the number of fixes per grid cell; largest points more than twenty radio locations per grid cell; F = feeding stations

As is shown in Fig. 7b, often some of these areas (especially the more open ones) are visited exclusively during night (black) whereas others are used mainly during day (white). Between these are areas frequented both days and nights (shaded). There is a remarkable similarity in these patterns from year to year (Fig. 7$b_1$ and $b_2$). Hinds No. 1 and 6 demonstrate a good example for this situation. However, as hind No. 5 elucidates, clear separation of day- and night-use areas may be missing in the home range of other animals. In such cases the vegetational structure of the range seems to be more homogeneous than in the habitats described above.

On the other hand, a definite separation of areas for performing different activities appears to be not so marked (Fig. 7a). Most feeding places are used also for resting and *vice versa*. Therefore the grid cells used only for feeding (black) and only for rest (white), or those used in both activities (shaded) show a relatively uniform or random distribution. This was typical for the majority of the animals.

As already seen from the original and rather irregular distribution of fixes (see Fig. 2), the home ranges are not uniformly used, but some parts are preferred. This preference results in one or more activity centres (Hayne 1949), seen in every home range, and marked by large points in Fig. 7. These coincide in the valleys with either the small winter home ranges in the vicinity of the feeding stations, or with the large valley meadows. In the alpine

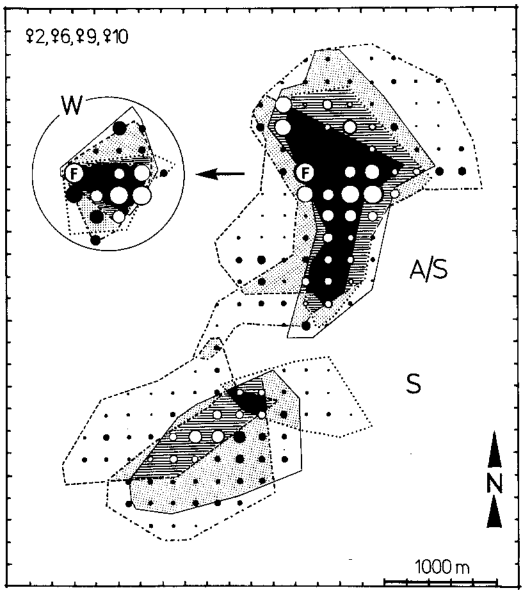

**Fig. 8.** Overlapping of winter ranges (*W*) autumn/spring ranges (*A*/*S*) and summer ranges (*S*) for four animals; black = fourfold, hatched = threefold, shaded = twofold, white = no overlap. The points stand for the intensity of use in different parts of the overlapping areas based on the grid shown in Fig. 7; smallest points = area used once or twice, largest points = area frequented more than 50 times, *F* = feeding station

regions, the centres lie in the more open mountain woods. However, the activity centres can change from year to year for an animal, as illustrated by hind No. 6 in Fig. $7b_1$ and $b_2$, for two successive years.

### *4.5. Overlap of Home Ranges*

The amount of overlap in the home ranges has a direct relation to, for example, the density of animals that a given area can support. Hence it is of interest to show, to which extent home ranges of different individuals may overlap, especially of such animals belonging not to the same herd. This can be done for four of the radio-marked hinds (Fig. 8).

The calculation of overlap was based on the grids already used in Fig. 7. The degree of overlap between the autumn/spring ranges of the four animals averages 69% (SD = 16%) and between their summer ranges 43% (SD = 15%). For the winter ranges a mean overlap of 83% (SD = 13%) was estimated, the extreme being even 100%. Thus the degree of overlap is highest in winter, less during autumn and spring and smallest in summer.

There appears to be no clear correlation between overlap and intensity of use. As may be seen from the distribution of the larger points in Fig. 8, some parts of the overlapping areas are used more intensively than others. Because of this, the "overlap density" differs within one area of the same degree of overlap. This is true especially for the four-fold overlapped area within the autumn/spring ranges. However, in the summer ranges some parts of the areas used only by two or three individuals seem to be more heavily frequented than the smaller region of four-fold overlap.

Consequently the degree of overlap between different animals' home ranges may be very high but seems to vary seasonally. It should be mentioned, however, that during all seasons the four observed individuals shared their home ranges with other animals and therefore the real overlap may be considerably higher.

## 5. Discussion

This study supports the hypothesis that the original migration behaviour of red deer seems to be expressed in a spatial separation of seasonal home ranges. As Geist (1977) pointed out, this migration is to be expected of an opportunistic ungulate as is the red deer. He suggests that because of its high energy requirements and its teeth which are not fully adapted to grass-forage, red deer must shift to diverse food sources of low fibre content. In the mountains this will be best satisfied by a vertical change of foraging sites as is described here.

Analyses of ground vegetation by Atzler (1978), can also be taken to document this relationship between vegetation conditions and home ranges of female red deer in the study area. Thus the first expansion of winter home ranges in spring has less to do with the receding snow (Phillips et al. 1973; Moen 1973) than with the greening of the valley meadows. Only when the food value of the herbaceous vegetation at elevations about 1,000 m NN is high enough, are the lower parts of the mountains also included in the home ranges. In the case of hind No. 7, at this time a separate spring range was established in medium altitudes. After May/June, the fibre content of the lowland ground vegetation begins already to increase, whereas that of the highland grasses and herbs is still very low due to the delayed plant growth at higher altitudes. This could be the crucial releaser for parts of the population to migrate into the mountaineous summer ranges. The time spent there by many individuals appears to depend on the continuing difference in the food value between the high- and lowland forage described above. Correspondingly the return of the animals down into the valleys coincides with the decrease of the food value in the mountains. It is instructive in this connection that in 1977 hind No. 2 remained longest in its summer home range. At night she was foraging at an alpine meadow which even in late summer was relatively high in nutritional value presumably due to cattle grazing.

In his study on adaptive strategies in the behaviour of elk, Geist (1977) considers these observed space-time differences in nutritional quality and quantity, discussing the implications of the "law of least effort". This law implies that the spatial requirements of herbivores should decline with increasing nutritional density and quality of forage and *vice versa*. It follows then that the home ranges in summer are smaller than in spring or autumn. This expectation is verified not only by the results of Knight (1970, cit. by Geist 1977) and Craighead et al. (1973) both working on elk, but also by the findings of the present work. Thus the open mountain forests providing both cover and browsing areas within short distances and a qualitatively and quantitatively richer vegetation (Wauer 1980) apparently are a more adequate habitat for red deer than the vast managed forests and wide pastures in the valleys. Furthermore, because of the differences between the nutritional value of the high and lowland vegetation, the home ranges of the animals remaining in the valleys even during the summer may be fairly large. The largest home range was that of hind No. 8 which was living in vast and monotonous spruce stands. The only comparable home range size estimates for red deer are found in studies conducted in the Scottish Highlands averaging from 400 (Lowe 1966), up to 6,000 ha (Staines 1970). These values far exceed those found in the Bavarian Alps. Mitchell et al. (1973) consider these to be a consequence of the habitat structure too, that is, a result of the poor cover in Scottish "deer forests". The observed increase of daily range needs still in summer that contrasts to the decrease in home range size (see Figs. 4 and 5) could be induced less by forage quality than by the heightened energy requirements of females due to late pregnancy and the following lactation period. This conclusion is drawn not only because of a concommitant increase in activity at this time (Georgii, in prep.); it is also compatible with the findings of Craighead et al. (1973) on the elk and Phillips et al. (1973) on the moose.

In agreement with the behaviour of several female red deer in the study area, Blankenhorn et al. (1978) report that some 10% of the red deer in the Swiss National Park remain in the valleys all the the year round too. Such behaviour has been also observed in other cervid species (Dasmann and Taber 1956; Sparrowe and Springer 1970; Robin 1975; Drolet et al. 1976). Furthermore Robinette (1966) as well as Bertram and Rempel (1977) report the same "intermediate ranges" or "holding areas" as were observed in two red deer hinds of the study area. In spring this migrational delay may reflect a delay in plant phenology at higher altitudes.

The winter reduction of the home ranges of all the examined red deer hinds appear mainly to be a consequence of the snow restricting mobility of the animals. Studies on many North American cervids document this (Telfer 1970, Wallmo and Gill 1971, Stardom 1975). Using calorimetric analyses, Moen (1973) was able to assess the high energy expenditures for white-tailed deer required for movement in various depths of snow. Kalela (1971) cites the work of Nasimowich (1955) who mentions 50 to 60 cm as being the critical value for red deer. For long periods of the winter these values are exceeded in our study area. Correspondingly, a reduction of activity and food intake accommodates the spatial limitation (Moen 1976; Georgii, in prep.).

How much the observed crowding of animals in a close space, as documented by the high degree of overlap of the winter home ranges, is due to the attractiveness of the feeding stations, is difficult to ascertain. Some other species, which are less social and not fed by man, as, for example, the moose and white-tailed deer, show this "yarding" too. In the present case the remarkably high range overlap during winter is not so much due to a social connection of the four red deer hinds but more to topographic features.

On the other hand, the often poor location of the winter home ranges, both topographically and climatically, suggests that their position is mainly determined by that of the feeding stations, and therefore at least the situation in the valleys is definitely influenced by man. It is difficult to say just how important human influences are for the location of other seasonal ranges. Striking is the constancy with which the deer visit the same winter feeding stations year after year and, from these stations, seek out the same summer ranges. As the studies on red deer in the Swiss National Park by Blankenhorn and co-workers (1978) and on Big horn sheep (*Ovis canadensis*) by Geist (1971) have shown, this is less the result of an active search for suitable summering and wintering sites than of a knowledge of the range position being passed on from generation to generation. This tradition of knowledge about feeding locations appears to contribute highly to the maintenance of home range strategies.

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## References

Atzler R (1978) Schwankungen der Qualität der Bodenvegetation während der Vegetationszeit im Rothirschuntersuchungsgebiet Ammergauer Berge. Diplomarbeit, München, p 155

Bertram RC, Rempel RD (1977) Migration of the North Kings Deer Herd. Calif Fish and Game 63:157–179

Blankenhorn HJ, Buchli Ch, Voser P (1978) Wanderungen und jahreszeitliche Verteilungsmuster der Rothirschpopulationen (*Cervus elaphus L.*) im Engandin, Münstertal und Schweizerischen Nationalpark. Revue Suisse Zool 85:779–789

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Craighead JJ, Craighead FC, Ruff RL, O'Gara BW (1973) Home ranges and activity patterns of nonmigratory elk of the Madison Drainage Herd as determined by biotelemetry. Wildl Monographs 33, p 50

Darling FF (1937) A herd of red deer. Oxford University Press, London, p 226

Dasmann RF, Taber RD (1956) Behavior of Columbian black-tailed deer with reference to population ecology. J Mammal 37:143–164

Drolet ChA (1976) Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. Canadian Field-Naturalist 90:123–136

Feldner R (1978) Waldgesellschaften, Wald- und Forstgeschichte und Schlußfolgerungen für die waldbauliche Planung im Naturschutzgebiet Ammergauer Berge. Dissertation, Wien

Franklin WL, Mossman AS, Dole M (1975) Social organization and home range of Rossevelt Elk. J Mammal 56:102–118

Geist V (1968) Welchen Wert hat die Verhaltensforschung in Wildnisgebieten für eine moderne Verwaltung? Beiträge zur Jagd- und Wildforschung VI:9–16

Geist V (1971) Tradition und Arterhaltung bei Wildschaf und Elch. Naturwissenschaft und Medizin 8:25–35

Geist V (1977) Adaptive strategies in the behaviour of elk. In: The Ecology and Management of the North American Elk, ed JW Thomas. Washington DC: Wildlife Management Institute. In press

Georgii B Activity patterns of female red deer in the alps. Oecologia (Berl) in press

Hayne DW (1949) Calculation of size of home range. J Mammal 30:1–17

Heezen K, Tester JR (1967) Evaluation of radio tracking by triangulation with special reference to deer movements. J Wildl Manage 31:124–141

Hediger H (1950) Wild animals in captivity. London Butterworth, p 152

Jewell PA (1966) The concept of home range in mammals. Symp Zool Soc Lond 18:85–109

Kalela O (1961) Wanderungen. Handbuch der Zoologie 8:27/1–39

Kobell F v (1859) Wildanger. JG Cotta'scher Verlag, Stuttgart, p 491

Lowe VPW (1966) Observations on the dispersal of red deer on Rhum. In: PA Jewell and C Loizos (ed) Play, Exploration and Territory in Mammals. Academic Press, London and New York, 211–228

Miller FL (1970) Distribution patterns of black-tailed deer (*Odocoileus hemionus columbianus*) in relation to environment. J Mammal 51:248–259

Mitchell B, Staines BW, Welch D (1977) Ecology of red deer. Institute of Terrestrial Ecology, Cambridge, p 74

Moen AN (1973) Wildlife Ecology. Freeman and Company, San Francisco, p 458

Moen AN (1976) Energy conservation by white-tailed deer in the winter. Ecology 57:192–198

Nievergelt B (1966) Der Alpensteinbock in seinem Lebensraum. Mammalia depicta 1:p 86

Odum EP, Kuenzler EJ (1955) Measurement of territory and home range size in birds. Auk 72:128–137

Phillips RL, Berg WE, Siniff DB (1973) Moose movement patterns and range use in northwestern Minnesota. J Wildl Manage 37:266–278

Robin K (1975) Räumliche Verschiebungen von markierten Rehen (*Capreolus capreolus L.*) in einem voralpinen Gebiet der Ostschweiz. Z Jagdwiss 21:145–163

Robinette WL (1966) Mule deer home range and dispersal in Utah. J Wildl Manage 30:335–349

Schröder W (1978) Der Rothirsch. Jahrbuch des Vereins zum Schutze der Bergwelt 43:123–150

Sonnenberger H, Georgii B, Schröder W, Freimann D (1977) Ein System zur Funkortung und automatischen Aufzeichnung der Aktivität von wildlebenden Huftieren. Z Jagdwiss 23:137–143

Sparrowe RD, Springer PF (1970) Seasonal activity patterns of white-tailed deer in eastern South Dakota. J Wildl Manage 34:420–431

Staines BW (1970) The management and dispersion of a red deer population in Glen Dye, Kircadineshire. Ph D Thesis University of Aberdeen

Stardom RRP (1975) Woodland caribou and snow conditions in southeast Manitoba. Proc Ist Int Reindeer and Caribou Symp Fairbanks, Alaska

Stevens DR (1970) Winter ecology of moose in the Gallatin Mountains, Montana. J Wildl Manage 34:37–46

Telfer ES (1970) Winter habitat selection by moose and white-tailed deer. J Wildl Manage 34:553–559

Wallmo OC, Gill RB (1971) Snow, winter distribution, and population dynamics of mule deer in the central Rocky Mountains. Snow and Ice Symposium, 1–15. Iowa Cooperative Wildlife Research Unit, Ames, Iowa

Wauer A (1979) Deckung und Nahrung in einem Aktivitätszentrum von Rothirschen in den Ammergauer Bergen. Diplomarbeit, Universität München, p 106

Wiesner H (1977) Narkosepraxis mit dem Blasrohrgewehr. Kleintierpraxis 22:327–330

Winkle W van (1975) Comparison of several probalistic home range models. J Wildl Manage 39:118–123

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