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Winter ecology of nonmigratory Alpine red deer

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Abstract. In winter, red deer *(Cervus elaphus hippelaphus)* that are not receiving supplementary feeding emphasize and rely on energy-saving strategies. In severe winters with deep snow, they select a home-range habitat – windblown alpine pastures above the timberline – that meets the requirements of this strategy: a much lower sinking depth and good forage availability are due to patchy snow distribution, while the open area provides higher radiation, permits group formation and thus sociobiological wellbeing. The energy costs of thermoregulation are minimized by selecting slopes with south to south-west exposures, seeking thermal shelter from strong winds, while high flight distances and horizontal flight routes reduce the energy costs of fleeing. In years with little winter snowfall non-supplemented red deer prefer the greater security of forested habitats in lower areas and obtain higher food intake from slightly more nutritious meadows in the valley bottom. The food-supplemented herd has much more constant and predictable habitat use, combining an energy-saving strategy – choosing alpine pastures as low-cost winter home range – with high energy income at the feeding station.

Key words: *Cervus elaphus* – Winter ecology – Behavioural adaptations – Habitat use – Winter feeding

Nonmigratory alpine red deer populations *(Cervus elaphus hippelaphus)* may winter in high alpine habitats without supplementary feeding. Little is known of the winter ecology of these populations. Till now, research on winter ecology of alpine red deer has mainly concentrated on the effects of supplementary feeding (e.g. increased antler size, forest damages). Hunters justify the use of feeding stations by the fact that alpine red deer were once known to migrate seasonally between high-elevation alpine summer ranges and low-elevation winter ranges (e.g. Bützler 1972; Georgii 1980; Hofman and Kirsten 1982; Raesfeld and Reulecke 1988). These migrations no longer take place. Human land use occupied the original red deer habitats (riverine lowland forests) and artificial feeding retains populations in alpine ranges. Red deer have become year-round inhabitants of alpine regions. Most studies consider that nutritional needs are the main determinants of migration (Atzler 1984; Morgantini et al. 1989; Ruhle and Looser 1991). The lack of adequate and accessible forage in alpine habitats in winter is thought to be compensated by artificial feeding, which in alpine regions is regarded as a prerequisite for the survival of huntable stocks. But these feeding stations strongly influence natural habitat choice in red deer. Therefore one main objective of this research study was to examine winter habitat choice in a non-supplemented herd and what adaptations to winter severity these red deer have developed.

This paper compares wintering strategies of alpine red deer populations with and without winter food supplementation, wintering in the same area.

Material and methods

Study area

Situated in the eastern part of the Austrian Alps, in the Lower Tauern mountain range (47°17′N, 14°18′E), the study area (Fig. 1) includes the west and east slopes of a valley running north to south, with an altitudinal range from 900 m above sea level (a.s.l.) to the highest elevation of the alpine meadows at 2260 m a.s.l. Boreal vegetation, consisting nearly exclusively of spruce *(Picea abies)* and larch *(Larix decidua)*, reaches 1700–1750 m a.s.l. The timberline is bordered in some areas by alder and dwarf pine.

The dominant rock is mica slate. The vegetation of the alpine brown soil includes *Carex curvula, Nardus stricta, Deschampsia cespitosa, Calluna vulgaris, Loiseleuria procumbens, Vaccinium* spp. *(V. myrtillus, V. vitis-idae, V. uliginosum), Festuca* spp., and various lichens (Klug et al. 1989). Mountain meadows above the timberline cover extensive, moderatly inclined areas which are extensively grazed by cattle in summer and are potential red deer home range in winter.

Study methods

Two herds, with and without supplementary winter feeding, were compared. The winter ranges of the two herds were clearly

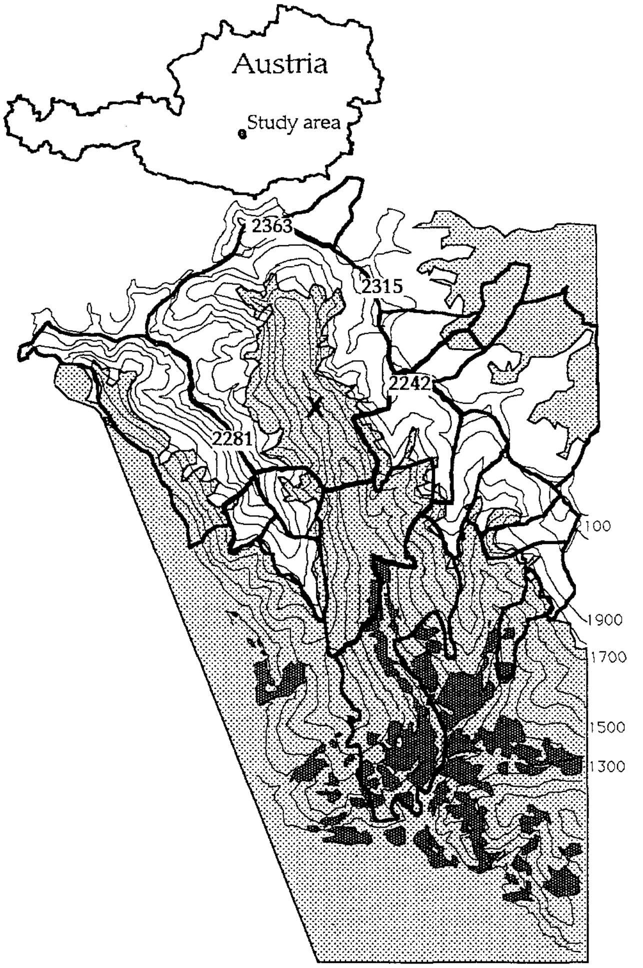

Fig. 1. The *study area* covered the slopes and alpine pastures west and east of the north-south running valley as well as the cultivated meadows at the entrance. *Dark lines* mark the boundaries of the different hunting grounds. Red deer home ranges are shown in Figs. 3 and 4. *Symbols:* ☐ alpine pastures above timberline; ▨ forested areas; ■ cultivated meadows (near farmhouses) in the valley bottom; × Feeding station 1400 m

separated by the bottom of the valley. Tracking and patrolling forestry roads between the two home ranges confirmed that the non-supplemented herd never made use of the feeding station. The feeding station is situated in the bottom of the valley (1400 m a.s.l.) and food (mainly good quality hay, but also small amounts of maize, turnips and grain bran) is put out daily in the afternoon. Due to the different sizes of the various hunting grounds (Fig. 1), the two herds were subjected to different hunting pressures. The alpine winter range of the non-supplemented red deer lay within four different hunting grounds. Hunting activities were not coordinated and red deer were hunted on alpine pastures and at the timberline until the end of the hunting season in mid-January. In severe winters, hunters' access to high areas was restricted by deep snow, reducing hunting pressure on the alpine pastures considerably after the beginning of winter.

Both the home range and the feeding station of the supplemented herd lie within a single, large, actively managed hunting ground. Hunting pressure is kept low in the traditional winter range above the timberline in all years (Schmidt 1992).

Field data were collected from October to the end of May (472 field days from 1985 to 1989).

Climatic parameters (especially snow depth) at the nearest meteorological stations differed considerably from the study area, so weather variables were measured by the author on the spot. Snow depth at various exposures and altitudinal zones and in different timber stands was measured by 26 permanent snow posts. Additional records were obtained by measuring snow depth with a yardstick. Measurements were made as frequently as possible, especially after snowfall or on thaw days. Snow distribution and thawing patterns were recorded by panoramic shots and later analysed by grid squares (250 × 250 m).

Temperature was continuously recorded at three altitudinal zones. For comparison, mean daily minima and maxima were computed.

Three permanent stations were established to record wind speeds in the study area. Measurements were supplemented by hand anemometer sampling.

Observations were carried out using binoculars (10 × 25) and a spotting scope (30 × 57). In spring a night-vision set was used to observe and count red deer in the dark. Mean observational distances were between 1.5 and 2 km, due to the high flight distances, for the non-supplemented herd. The usual observation point was suitable for observing the winter ranges of both herds simultaneously, so mean observational distance for the supplemented herd was between 2 and 3 km.

Direct and indirect observations (frequency and intensity of utilization of tracks and trails, sinking depths, pellets, bark-stripped trees, feeding craters and bedding sites) were noted on a grid-square map (250 × 250 m). Home range size was determined from the number of squares used (evaluating direct observations, tracks, cratering and bedding places). Forestry roads running along the bottom and the slopes of the valley were checked at least weekly for red deer tracks, providing precise data on movements of non-supplemented red deer to lower feeding grounds at beginning of spring.

Individuals were considered to be members of the same group if they exhibited some form of cohesive behaviour (moving, feeding and escaping together). When non-supplemented red deer were using the craggy and uneven terrain of their alpine home range, bias in determination of group size was avoided by observing the animals from the opposite slope. In wooded areas approximate group size was determined by tracking and counting bedding places, preferably after snowfall. To describe the social structure of the group, animals were classified as male, female or calf.

Flight distances were measured by recording the animals' position and the cause of flight (skiing tourists, observer) on the detailed map, which was easy for a trained person using various small-scale topographic features. Afterwards linear distances were measured on the map.

Behavioural records included 10-min continuous records of "focal animals" (vigilance behaviour) and "instantaneous scan" records of group activities every 15 min (Martin and Bateson 1986). Activity data were statistically analysed; correlations were tested by the Student-Newman-Keuls test ($P < 0.05$). Differences in herd size were tested by the Mann-Whitney *U*-test.

Anthropogenic influences – hunting activities, supplementary feeding (what, where, and how often used) and ski tourism – were recorded.

Results

Climatic conditions

Snow. The timing and amount of snowfall differed considerably between winters. The winters of 1985/1986 and 1986/1987 started early and were high in snowfall. Snow depth in the bottom of the valley was over 50 cm throughout the winter. In contrast, in 1987/1988 snowfall did not start until the end of January, and snow depths did not exeed 45 cm. In the winter of 1988/1989, pre-

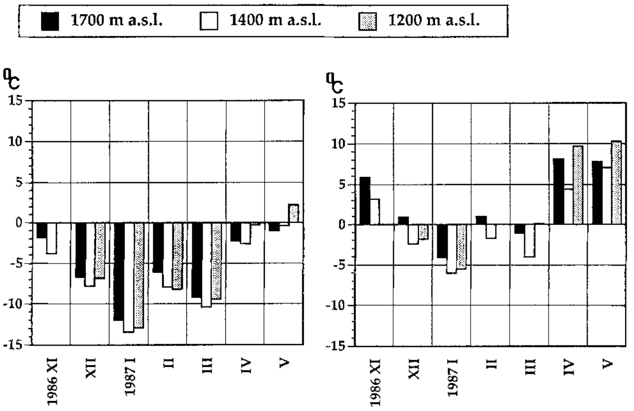

Fig. 2. Mean minimum values *(left)* and mean maximum values *(right)* for temperature measured at three different altitudes

cipitation mainly fell as rain or sleet below the timberline, and above the timberline as snow. Areas in the valley bottom remained completely snow-free; the little snow that did fall never lasted longer than a few days.

A more detailed inspection of the home range areas above the timberline showed an amazing constancy in snow distribution and hardness. Due to low winter temperatures, snow easily forms drifts. The combination of frequent winds and a very structured microtopography creates a characteristic snow distribution and melting pattern, which is reflected in plant sociology and vegetation phenology. Similarly, snow hardness patterns are constant. Regardless of the severity of the winter (in terms of precipitation), a certain amount of the alpine pasture remained permanently free of snow. Due to exposure, these snow-free patches were more frequent and larger on the eastern slope. In contrast, snow distribution in the woodlands and meadows in the valley bottom varies with overall snowfall. In winters with heavy snowfall there is a deep and relatively uniform (in terms of depth and hardness) snow layer. In mild years, snow cover is very thin or absent.

The chance of observing non-supplemented red deer on alpine pastures is related to snow depth in the valley bottom: a deep snow layer in the valley and forested areas resulted in a high probability of observing red deer on pastures above the timberline, and shallow snow in the valley to a low probability. Neither wind nor temperature appeared to influence large-scale home-range selection (i.e. of alpine meadows above the timberline or low-elevation forests).

Temperature. Mean daily temperature minima were less extreme and mean daily maxima were higher above the timberline than in forest stands and areas in the valley bottom (Fig. 2). This is due to winter temperature inversion and unimpeded radiation on the open alpine pastures. Temperature differences were especially pronounced in severe, cold winters.

Wind. Wind velocities and directions did not differ much between winters. Medium wind velocities (20–50 km/h) were most frequent, and there were stormy days with wind speeds above 50 km/h every winter. Winds were mainly from north and west. Wind velocities above the timberline were little affected by different elevations or slope exposure, but were much reduced in wooded areas irrespectively of slope exposure.

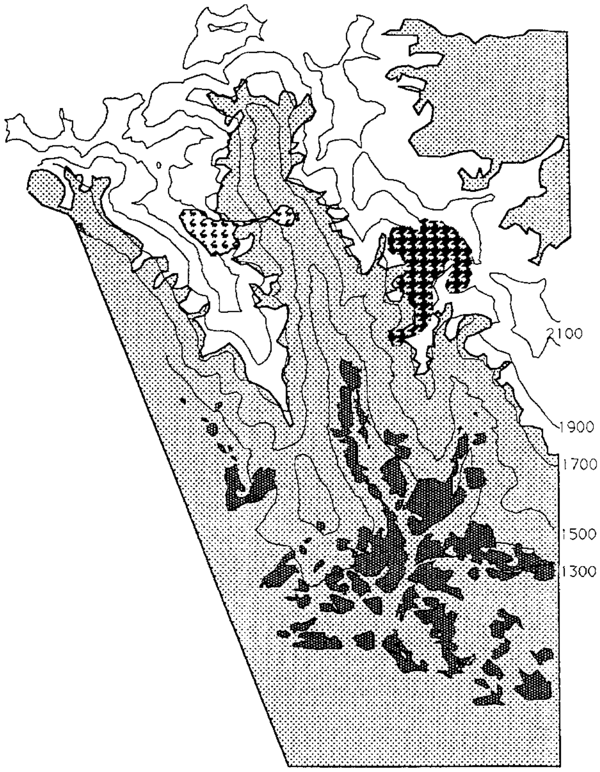

Fig. 3. Home range areas of non-supplemented and food-supplemented red deer herds for severe, snow-rich winters. *Symbols:* ▨ Supplemented red deer winter range; ▩ Non-supplemented red deer winter range; ☐ alpine pastures above timberline; ░ forested areas; ■ cultivated meadows (near farmhouses) in the valley bottom

Location, size and composition of the winter range

The food-supplemented red deer herd showed a remarkable constancy in its habitat use: the winter home range extended over more or less the same alpine area every winter (Figs. 3 and 4). The non-supplemented red deer used high alpine pastures regularly only during severe winters with deep snow (1985/1986 and 1986/1987) (Fig. 3). In mild winters (1987/1988 and 1988/1989) most non-supplemented deer spent the winter in lowland forests, bordering cultivated meadows at the entrance to the valley. Only small groups of non-supplemented red deer could be seen on alpine pastures, preferring areas near the timberline (Fig. 4). Sizes of winter ranges varied with winter severity: range size increased consistently in both groups with decreasing total winter snowfall. In conformity with the different herd size, home range size for non-supplemented red deer was about twice as large as that of supplemented red deer regardless of winter severity (Fig. 5).

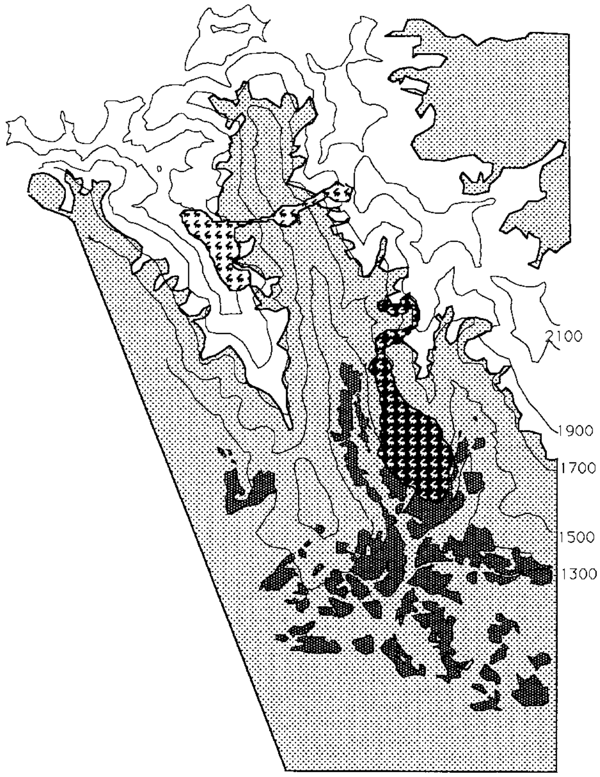

Fig. 4. Home range areas of the same red deer herds (as shown in Fig. 3) for mild winters with little snowfall. Symbols see Fig. 3

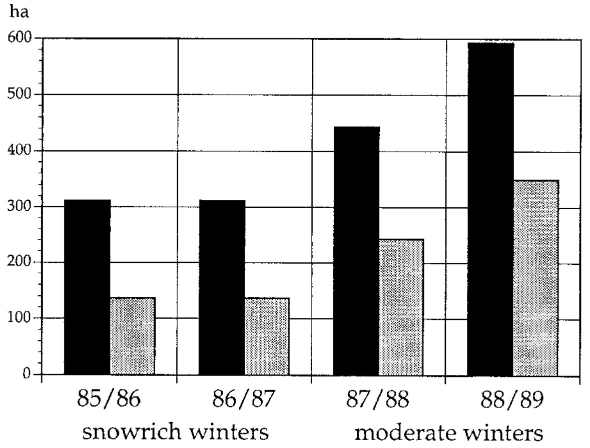

Fig. 5. Winter home range size for non-supplemented and food-supplemented red deer herds (1985/1986 to 1988/1989) based on the number of map grid squares used throughout the winter (direct and indirect observations). *Symbols:* ■ non-supplemented, ▨ supplemented

Thermal environment – use of shelter

Non-supplemented red deer selected southern (from southeast to southwest) exposures every winter. Whenever home range was confined to areas above the timberline, red deer reacted to wind velocities above 45–50 km/h (and temperatures between roughly − 5 and − 20° C) by shifting their range to just below the timberline where wind velocities were considerably lower (Fig. 6). Group and coppice rejuvenations provide bedding sites with favourable thermal microclimates and windchill protection. When wind speeds on alpine pastures were lower the animals sought microtopographic structures such as hummocks as thermal shelter.

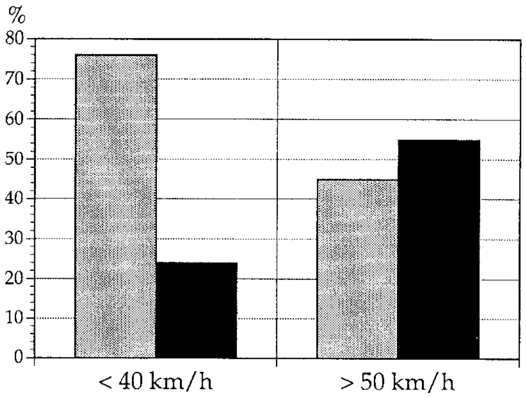

Fig. 6. Percentage of days where non-supplemented red deer were seen in open or windsheltered positions on days with different wind speed conditions (winter 1986/1987) *Symbols:* ▨ open alpine area; ■ windsheltered position

Social structure of the groups

The non-supplemented red deer herd consisted of 25% males, 49% females and 26% calves ($n = 149$). The supplemented herd was composed of 23% males, 48% females and 28% calves ($n = 83$) (data from 1986/1987).

Group formation

For the deer without supplementary feeding maximum (and median and mean) group sizes were larger throughout snow-rich winters when winter ranges were primarily limited to alpine pastures, compared to mild years when home ranges mainly included wooded areas (Fig. 7). Non-supplemented red deer herds were smaller in craggy and broken terrain, compared to open areas above timberline (Fig. 8). This difference was highly significant for 1986/1987 ($P = 0.00001$), but not for 1987/1988 ($P = 0.29$) when sample size in open alpine meadows was low ($n = 8$) (Mann-Whitney *U*-test). The group size of food-supplemented red deer was, like winter range, much more constant over several winters (Fig. 7).

In both herds, group sizes declined in spring, in connection with dispersal after antler casting and movements to spring home range areas.

Flight behaviour

Flight distances from human intruders, mainly skiing tourists, varied from 400 to 1500 m. Flight was frequently elicited by loud voices.

Flight routes ran parallel to the slope contour lines. During winter red deer always took refuge in open alpine terrain, achieving safety by a wide view. In autumn and

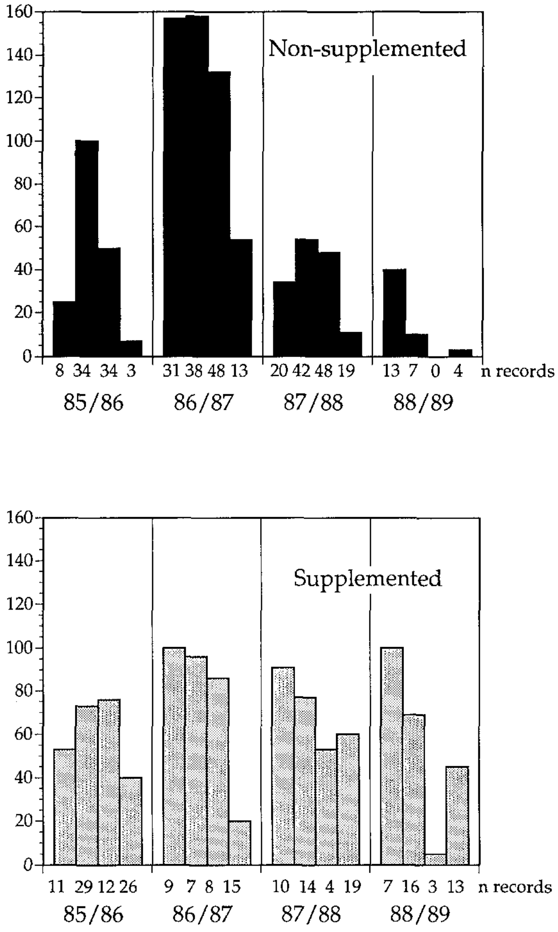

Fig. 7. Maximum group sizes for non-supplemented *(above)* and food-supplemented *(below)* red deer during the course of four winters *(early winter, midwinter, late winter, spring)*. Group size is shown on the vertical axis

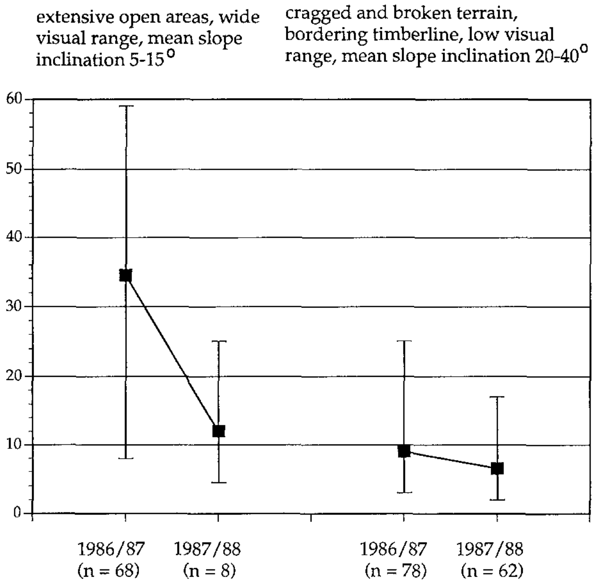

Fig. 8. Group size (median values) in non-supplemented red deer varied with topography and visual range. The graph also shows the preference for open areas in snow-rich winters (1986/1987). Group size is shown on the vertical axis. The bars present 25% iles and 75% iles

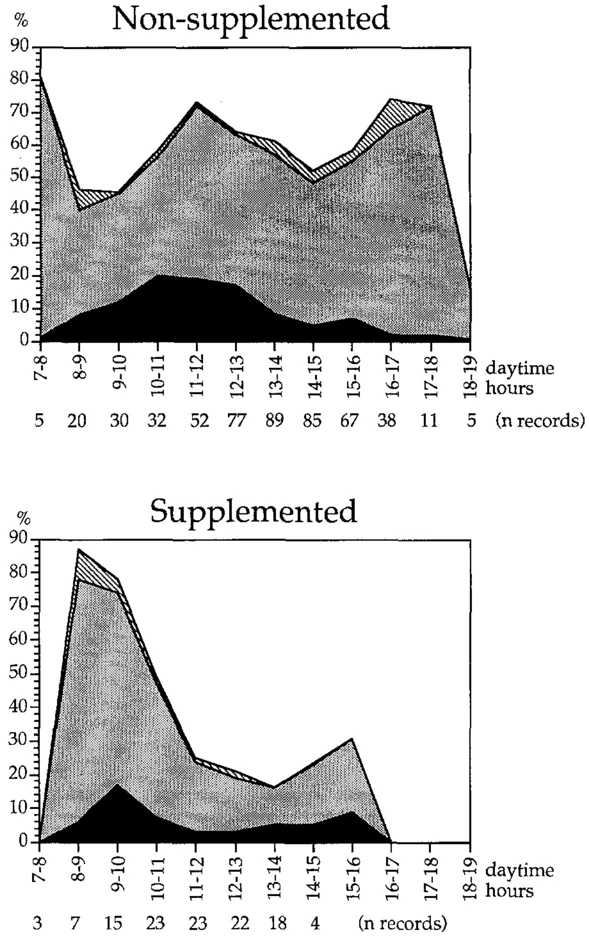

Fig. 9. Significantly differing activity budgets between non-supplemented and food-supplemented red deer (% of animals of the herd) on alpine pastures in winter. Observations of supplemented red deer cease at approximately 1700 hours, as the herd left the open alpine range for the feeding station around sunset. *Symbols:* ▨ Moving while feeding; ▩ Feeding; ■ Standing

spring, however, they fled from alpine pastures downslope to wooded areas, seeking cover to hide in. Because of the patchy snow distribution, ski tourism is low in this area and did not seem to influence large-scale habitat choice (alpine pastures versus forest stands) in either red deer herd.

When taking flight, the animals mostly moved in single file. This behaviour was even more pronounced whenever the herds moved into or out of thermal shelter stands. By using the same path every time, they created a trampled route with low sinking depths even in snow-rich stands.

Activity

The following activities were significantly higher in non-supplemented red deer than in food-supplemented red deer: feeding, moving while feeding, and standing (inactively or ruminating) (Fig. 9; Student-Newman-Keuls test).

Food

Non-supplemented red deer could be observed feeding in all accessible plant communities on the alpine pastures. Available forage on alpine pastures consists largely of wind-tolerant species, mainly *Calluna vulgaris* and *Loiseleuria procumbens;* the latter forms dense carpets, mixed with lichens like *Alectoria ochroleuca* and *Thamnolia vermicularis*. In snow-free areas red deer frequently fed on an area of *Deschampsietum cespitosae*. The crude fat content of *Loiseleuria* is relatively high in autumn and winter. The nutritional quality of other partly accessible plants, like *Carex curvula, Nardus stricta, Calluna vulgaris* and *Vaccinium* spp., is generally low in winter (Klug et al. 1989). In thermal-shelter stands, arboreal lichens and conifers provide a large proportion of the diet.

In mild winters non-supplemented red deer fed on ground and browse vegetation of aged forest stands with low canopy closure, rich in various *Vaccinium* species, predominantly *Vaccinuim uliginosum*. During the night the animals fed on adjacent cultivated meadows, which are also heavily used in spring.

Discussion

The criterion for habitat selection is the relative net energy available (Harestad et al. 1982) and in alpine and boreal winter this is mainly a function of snow depth. Authors agree that snow accumulation in summer home ranges is the primary stimulus for autumn migration (Kelsall and Telfer 1971; Gavin 1972; Bunnell 1978; Adams 1982; Skovlin 1982). The critical snow depth seems to be approximatly 25 cm, depending on snow consistency (Skovlin 1982; Rudd et al. 1983; Fischer and Gossow 1987). Pruitt considers the initial accumulation of 20 cm of snow to mark the true beginning of the winter – "hiemal threshold" as he calls it (quoted in Marchand 1987, p. 10). Deep snow in forested summer habitats, impeding access to food and rendering locomotion difficult and costly, thus triggers a change in home-range use. Red deer move up to alpine pastures.

The use of high-altitude areas as winter home range is not typical of red deer. There are only a few reports of European or North American red deer using high elevation home ranges in winter (e.g. Zecha 1963). This is only possible where atypical snow conditions occur, e.g. in Yellowstone National Park, where thermal areas and warm streams alter winter environment (Craighead et al. 1973; Cayot et al. 1979). Elevation *per se* is not of great importance; it is the snow cover pattern that determines the suitability of a winter habitat for red deer.

The total amount of fallen snow (usually referred to as snow depth) and the duration of snow cover generally increase with increasing elevation and decreasing canopy cover (Bunnell 1978; Harestad et al. 1982). This holds true for the research area also, but the negative effects of snow cover on red deer are moderated and compensated by the action of the wind, which causes a patchy distribution of high, compressed cornices with much lower sinking depths, and bare spots where forage is available. Thus, alpine pastures may be a very constant and predictable winter range in terms of available food supply and energy expenditures. (Lowland areas may be described as changing, unpredictable habitats, varying with the overall winter severity). Features of the wind-blown alpine pastures, or alpine tundra ranges, resemble habitats with little winter precipitation, e.g. Svalbard (Tyler and Øritsland 1989), or Rhum, where winters are mild and snow seldom lies for long (Clutton-Brock et al. 1982).

In snow-rich winters, the advantages of alpine pastures over timber stands are not due only to snow cover patterns, but also to other factors. The thermal environment is favourable due to high solar radiant energy input. It is known that elk, North American red deer, on spring migrations avoid canyon bottoms with nocturnal flows of descending cold air (Skovlin 1982). In this respect, the location of the feeding station at the valley bottom is very unsuitable. The unfavourable thermal environment may be one reason why individuals of the supplemented herd sometimes visit the feeding station only every 2nd or 3rd day and use alpine pastures as their winter home range.

From the energetic point of view "resting in conifer shelter is not always less costy than foraging in open habitats" (Schmitz 1990). This seems to be confirmed by the fact that, whenever home range is confined to alpine pastures, timber stands are used only as wind shelter. Both food-supplemented and non-supplemented red deer react to increasing wind speeds by switching to habitats where cover is available (at temperatures between roughly $-5°$ and $-20°$ C). Various factors contribute to this behaviour. High wind speeds and drifted snow obstruct the animals' vision and hamper olfactorial and acoustic perception. Thus, timber stands might also provide concealment or secure resting sites. The same critical wind speed of approximately 40–50 km/h is also reported for North American red deer (Beall 1974, Quoted in Skovlin 1982) and for Scottish red deer (Clutton-Brock et al. 1982).

Alpine pastures therefore may serve as "cheap" winter habitats, suitable for energy saving adaptations of red deer to winter conditions. Several behavioural traits indicate energy-saving strategies. Group formation, favoured in open areas, agrees with the social demands of red deer, and is known as an antipredator strategy (Bergerud 1974; Jarman and Jarman 1979; Clutton-Brock et al. 1982; Geist 1982; Underwood 1982; Lipetz and Bekoff 1982; La Gory 1986). Since available forage patches are small, widely distributed and fairly predictable, it does not seem likely that large groups here are predominantly due to the patchiness of the forage.

The high visibility meets the security demands of red deer. By having high flight distances, the animals avoid overhastly, costly flights. The quite untypical high flight distances (up to 1.5 km) are caused by high shooting distances during hunting season (June till mid-January).

The horizontal flight routes minimize energy expenditure for hurried locomotion even in deep snow. Likewise, single-file movements on packed trails might be an adaptation to reduce the energetic costs of movement (Fancy and White 1985; Reynolds and Peden 1987). The range of activities is greatly reduced, to standing, feeding, rumination and bedding. "Winter bedding is a means of conserving energy and combating the stress of cold weather and limited food" (Craighead et al. 1973).

During daytime, moving (without feeding) activity does not significantly differ between the two herds. But, unlike non-supplemented red deer, the food-supplemented deer have to shuttle between feeding station and resting site. (As the herd moved to and from the feeding station around dusk and dawn, these activities were not included in the activity budgets.) Therefore, in the course of 24 h, the time spent moving by non-supplemented red deer is probably much less than for food-supplemented red deer. Lack of supplementary fodder presumably results in higher selectivity as well as higher energy costs of searching in non-supplemented red deer, reflected in significantly higher feeding and moving-while-feeding activity in non-supplemented red deer compared to supplemented red deer. The fact that, in winter, food on alpine pastures is unprofitable (low quality), widely dispersed and nearly always accessible, reduces aggressive behaviour. At feeding stations, where food is of relatively high quality and concentrated in time and space, aggressive behaviour is rather pronounced (personal observations, though data are not sufficient for statistical analysis; Linn 1987; Bützler 1972).

The nutritional value of these windblown pastures in mid- and late winter is generally low (Atzler 1984; Klug et al. 1989), but northern ungulates are well adapted to low nutritional values in winter (Silver et al. 1969; Clutton-Brock et al. 1982; Hofman and Kirsten 1982; Nelson and Leege 1982; Bubenik 1984; Arnold 1985; Hawley 1987). Even without anthropogenic subsidy alpine pastures provide sufficient and adaequate forage for a herd of red deer throughout the winter. The similar social group composition suggests that there are no appreciable differences in productivity. Obviously, differences in winter diet do not affect reproduction rates.

Preferred feeding plants (*Vaccinium* spp., *Calluna*, *Deschampsia*) are the same as those of red deer in Northern Scandinavia (Ahlén 1965). Digestibility of *Calluna* is high until late April (Bubenik 1984). At higher altitudes this plant species has a relatively high leaf/stem ratio, increased digestibility and high sugar levels, particularly in winter (Clutton-Brock et al. 1982). Furthermore, even if feeding values are low, it may be the combination diet which is sufficiently nutritious (Craighead et al. 1973; Harestad et al. 1982) or even necessary. The variety of different plant species of the alpine pastures may be a necessary balance and complement to the food at the feeding station. The constant accessibility ensures regular food intake which is necessary for maintenance and stabilization of the environment of microorganisms in the rumen. This ensures maximal digestive efficiency (Clutton-Brock et al. 1982).

Concerning the main aspects of habitat use – food quality and predator avoidance – the supplemented herd could just as well choose a resting site in forested areas near the feeding station (as many food-supplemented herds in other alpine regions do). But alpine pastures obviously more than compensate for the costs of shuttling between these two places: the fact that the food-supplemented herd, consistently every winter, travels 800 m of altitude nearly every (2nd) day to use its alpine home range demonstrates the attractivness of this wintering habitat in severe as well as in mild winters.

Non-supplemented red deer have a different basis for home range selection. The decisive aspect is snow depth in the forested areas, which determines forage accessibility and hunting pressure. As the long hunting season only ends in mid-January, open alpine pastures remain dangerous until midwinter. In winters with early, heavy snowfall, hunters' access to alpine pastures is restricted and hunting pressure is low. In mild winters, when prescribed hunting bags are difficult to ful fill, hunting pressure on alpine pastures and the neighbouring timberline areas is very high and long-lasting (Schmidt 1990, 1992). It is well known, that European red deer (for instance in the Swiss National Park, Blankenhorn et al. 1978) as well as North American elk (Adams 1982; Rudd et al. 1983), tend to stay within protected areas until driven out by increasing snow depth. Moreover, in midwinter the nutritional values (protein and crude fibre content) of the cultivated meadows in the lower areas are slightly higher than those of alpine pastures (Klug et al. 1989). These lowland pastures, accessible in mild winters, and *Vaccinium* species in the forested areas that are then used provide sufficient forage. Non-supplemented red deer choose their winter habitat according to forage availability and hunting pressure, both factors influenced by snow depth. They consequently adjusted their security strategy according to the chosen habitat: security demands are met by high visibility ranges and high flight distances on open alpine pastures and by concealment in forested areas. Considering the balance between gains and costs, alpine pastures prove to be the most suitable habitats in snow-rich winters but the forested slopes of the valley are more suitable in mild winters.

The reactions of red deer without food supplementation are very fine-tuned to even small changes in climatic and anthropogenic influences. They respond to seasonal variations of local conditions by a local shift of their range use and adjust their behaviour correspondingly. Alpine pastures may be considered as their prime winter habitat. However, they are fairly adaptable to a wide range of environmental conditions. Wintering strategy is appearently based on energy conservation and on minimizing expenditures, in both severe and mild winters.

For food-supplemented red deer, home range is more predictable due to supplementary energy input at the feeding station as well as a much more regulated hunting pressure (at least in the study area). Correspondingly, home range selection and behaviour in time and space become more stable. The wintering strategy is based on a combination of high energy input at the feeding station and energy saving in choosing low-cost winter ranges – high alpine pastures – consistently every winter.

A discussion of expediency, efficiency and effects of feeding stations would go beyond the scope of this article. Consequences for feeding and hunting management are discussed elsewhere (see Schmidt 1992; Schmidt and Gossow 1991, 1992; Gossow and Schmidt 1991).

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