

Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*

Stefano GRIGNOLIO^{1,3}, Francesca PARRINI², Bruno BASSANO¹, Siriano LUCCARINI³ and Marco APOLLONIO^{3*}

¹ Alpine Wildlife Research Centre, Gran Paradiso National Park, Via della Rocca 47, I-10123 Torino, Italy; e-mail: scientifico@pngp.it

² Centre for African Ecology, School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa; e-mail: frances@gecko.biol.wits.ac.za

³ Università di Sassari, Dipartimento di Zoologia e Antropologia Biologica, via Muroni 25, I-07100 Sassari, Italy; e-mail: marcoapo@discau.unipi.it

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Abstract. Habitat use and selection of 14 Alpine ibex males were studied in the Gran Paradiso National Park. Alpine meadows were always overused and positively selected, because this habitat constituted an important food resource for the ibex. Even if rocks (30%) and stone ravines (22%) were the most frequented habitats in the study area, their use was lower than their availability because they offered few trophic resources. Pastures were used only in spring when the ibexes were looking for those sites just free from snow and with fresh vegetation. Stone ravines, where the ibexes rested in the hottest days, were most used in summer. Rocks were most used in winter: rock-faces are the only sites where the risk of avalanches is low and where it is still possible to find snow-free patches. Larch woods were especially used in winter and spring when it was still possible to find snow-free patches. The home range sizes proved to be influenced by the amount of Alpine meadows and rocks.

Key words: radio-tracking, alpine meadows, rocks, snowfall

Introduction

While in ungulates habitat use can be determined by a combination of several causes such as food availability, cover availability, female distribution, and population density (C r o o k et al. 1976), many studies have shown a flexibility of their social systems related to environmental conditions (L e u t h o l d 1970, W a l t h e r 1972, P e e k et al. 1975, L e u t h o l d & L e u t h o l d 1975, H i r t h 1977, G e o r g i i 1980, S c h a a l 1982, 1987, U n d e r w o o d 1982, M a u b l a n c et al. 1987). Mountain ranges, for instance, are characterized by marked spatio-temporal heterogeneity of habitat types due both to climatic and topographical conditions (P e p i n et al. 1996). Animals should therefore opt for those areas that improve survival and reproductive success, and when different ranges have different seasonal suitability, a seasonal pattern of range utilisation may be established so as to obtain the maximum benefit (B e r g e r u d 1974). Seasonal range use may be affected by specific requirements: for example, F o x et al. (1992) reported that habitat use in *Capra ibex sibirica* is related with predation, winter snowpack, forage availability, and human activities; in moose and white-tailed deer snow fall has an important influence on habitat selection (T e l f e r 1970), while in mule deer, as well, A r m l e d e r & W a t e r h o u s e (1994) reported that winter habitat use is related with snow. Habitat use is said to be selective if habitat types are used disproportionately to their availability; in fact, J o h n s o n (1980) defined a habitat as being “preferred” when its use is significantly greater than its availability in the environment.

*Corresponding author

Alpine ibex (*Capra ibex ibex*) are large grazing mountain ungulates living in the European Alps. Their habitat use has been studied in reintroduced populations in the central and eastern European Alps (Nievergelt 1966, Hofmann & Nievergelt 1972, Schaerer 1977, HoutedeLange 1978, Kofler 1981) and in France (Wiersema 1984), but never in an autochthonous population. Alpine ibex almost became extinct all over Europe at the beginning of the XIX century, surviving only in the area around the Mt Grivola within what nowadays is the Gran Paradiso National Park (GPNP, north-western Italian Alps). The GPNP population was saved from extinction and recovered thanks to the setting up of the royal hunting reserve in 1856, later transformed into the GPNP in 1922. All other Alpine ibex populations existing nowadays in the European Alps originated from reintroduction projects or natural emigrations, but reintroduced populations might have an anomalous behaviour compared with autochthonous ones (Pedrotti et al. 1995).

The present study used radiotracking techniques to observe spatial behaviour and habitat use in adult male Alpine ibex within the autochthonous GPNP population. The results regarding adult male space use will be published elsewhere (Parrini et al. in press), but since, in our study area, this parameter presented important differences from that of reintroduced populations (Terrier & Polaert 1987, Michallet 1994, Terrier et al. 1994, Terrier & Rossi 1994, Tron et al. 1994, Pedrotti et al. 1995), we aimed to investigate whether this was the case also with habitat use and selection. Thus, we analysed the data regarding habitat selection in Alpine ibex adult males in the GPNP and compared our results with those from previous studies conducted on reintroduced populations. Alpine ibex have a large rumen and are thus expected to graze for long periods of time. Furthermore, they lose weight during the harsh Alpine winters (Giacometti et al. 1997), and therefore during the growth season they have to accumulate as much fat as possible for the winter. We thus predicted that during the growth season, adult male Alpine ibex would particularly select Alpine meadows, in which they can find the large amounts of food resources they need.

Study Area

The study was carried out from December 1995 to January 1998 in the Cogne Valley, in the northern part of the Gran Paradiso National Park (45°26'N, 7°08'E). The study area (13 000 ha) lies between 1450 m and 3969 m a.s.l. and the main axis is the Valnontey Valley running N–S. Secondary pastures are present in the bottom of the valley. Between 1500 and 1900 m a.s.l., the slopes are covered by larch *Larix decidua*, spruce *Picea abies*, and pine *Pinus cembra*. Instead, between 1900 and 2400 m a.s.l., the area is characterised by bushes (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Juniperus communis*), while above 2400 m, Alpine meadows of *Festuca varia*, rock cliffs, and stone ravines are present. The permafrost limit is at 3200 m a.s.l.. Temperatures ranged from a minimum of –23 °C in winter 1996 to a maximum of +25 °C in summer 1997. Mean precipitation was 40 mm per month.

Methods

In November 1995, ten adult (7–11 years old) Alpine ibex males were live-captured and individually marked with radio collars (Televilt). Four males died from starvation during the first winter and were replaced by four other adult males (8–11 years old) captured in May 1996. The transmitters worked on a 151 MHz waveband and included an activity sensor. The ibexes were radio-tracked from December 1995 to January 1998. At least ten fixes per month per individual

were recorded, evenly distributed over the daylight hours. During the rutting period one fix per day per individual was collected. Most fixes (70%) were obtained using the homing technique, by direct observation of the animal (C r a i g h e a d et al. 1973, T e r r i e r & P o l a e r t 1987, H a r r i s et al. 1990), while the remainder were obtained by triangulation using at least three bearings (W h i t e & G a r r o t 1990). The position of each radio-tagged male was plotted into a 1:10,000 scale map. Fixes and home range were overlapped on the land use map of the area using MAPINFO 5.0 (Microsoft). Additional data were recorded: date, hour, activity, and weather conditions. The meteorological station of the Paradisia Botanical Garden (Valnontey, 1700 m a.s.l.) provided temperature and precipitation data in the two years of the study (Fig. 1).

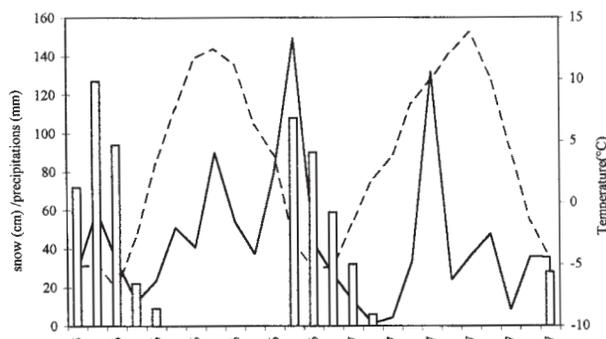


Fig. 1. Mean monthly temperature (broken line), total monthly precipitation (continuous line), and total monthly snow-cover (column) during the two years of study. Cogne Valley (Italy) 1996–1997.

Home ranges were calculated with the Kernel method (W o r t o n 1989, H a r r i s et al. 1990, K e r n o h a n et al. 1998) using the RANGES V software (K e n w a r d & H o d d e r 1996). Ninety-five-percent of fixes (Kernel method) was used for statistical analysis. Annual, seasonal, and rut period home ranges were calculated. Seasons were defined using the following subdivision: winter (December–February); spring (March–May); summer (June–August); autumn (September–November). The rut period (1st December–10th of January) was determined through observations of ibex behaviour. The utilisation of one habitat type was calculated for each animal as the frequency of active localisations in that habitat type, while the study area was defined as the area that included all the localisations of all marked animals. Study area availability (SAA) was defined as the proportion of that habitat within the study area (T h o m a s & T a y l o r 1990), and home range availability (HRA) as that within the home range (T h o m a s & T a y l o r 1990). Habitat selection was analysed using the Jacobs selection index (J a c o b s 1974), in which values range from -1 (an available habitat is not used) to +1 (an available habitat is highly used). An index of 0 indicates that an available habitat is used in proportion to availability. For each habitat, the mean index of all animals was then calculated. When possible, the chi-square goodness-of-fit test was used to compare habitat use to availability (A l l r e d g e & R a t t i 1986, 1992). When a significant difference was detected ($p < 0.05$), Bonferroni z statistics were used to determine which habitat types were used more or less frequently than expected (N e u et al. 1974). To determine changes in habitat use among seasons, Friedman’s ANOVA was used and, if significant ($p < 0.05$), we tested which season differed significantly from the others (S i e g e l & C a s t e l l a n 1992). The Spearman correlation coefficient (S o k a l & R o h l f 1995) was used to analyse correlations between home range size and the percentage of each habitat in it. Eight habitat types were defined in the study area

(Fig. 2), but in the analysis “glaciers” and “others” were not taken into account because they were never present in the ibex home ranges. “Alpine meadows” were defined as high altitude natural meadows, and “Pastures” as valley bottom fields and agricultural areas.

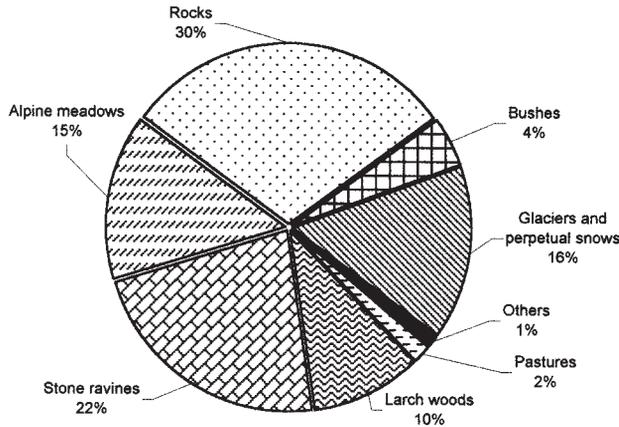


Fig. 2. Percentage of each habitat type present in the Alpine ibex study area. Cogne Valley (Italy) 1996–1997.

Results

The mean annual size of home range in 1996 was 430 ± 52.4 ha (Kernel 95%), while in 1997 it was 486 ± 78.7 ha (Kernel 95%) (Parrini et al., in press).

The proportion of active fixes in each annual habitat was compared with the SAA (Table 1). Alpine meadows were always positively selected, while bushes were always negatively selected, and often never used. The proportion of active fixes in each habitat of the annual home range was compared with the annual HRA (Table 1). Bushes were overused in 1997 and in 1996–1997 by those animals captured in May 1996, while they were never used or used less than their availability, in 1996. The preference for the other habitat types varied from animal to animal and from year to year. The chi-square test and Bonferroni intervals could be used in only five cases: two for the SAA (ibex 45, year 1996, $\chi^2=185.11$, d.f.=5, $p<0.001$, ibex 45, year 1997, $\chi^2=123.16$, d.f.=5, $p<0.001$); three for the HRA (ibex 45, year 1996, $\chi^2=28.22$, d.f.=5, $p<0.001$, ibex 44, year 1997, $\chi^2=10.43$, d.f.=4, $p<0.05$, ibex 41b, year 1996, $\chi^2=15.71$, d.f.=4, $p<0.001$). Alpine meadows were the only habitat significantly positively selected, while rocks were always negatively selected, and stone ravines were negatively selected in two cases and positively in one. The number of active fixes was compared with the availability of each

Table 1. Habitat selection by adult male Alpine ibex in Cogne Valley (Italy) 1996–1997. Analysis relative annual habitat selection. a) Study area availability. b) Annual home range availability. MJI mean Jacobs index calculated for all individuals. Column 1996–97 = values for animals captured in May 1996. For more details, see the text.

	1996a)		1996b)		1997a)		1997b)		1996–1997a)		1996–1997b)	
	MJI	sd	MJI	sd	MJI	sd	MJI	sd	MJI	sd	MJI	sd
Pastures	-0.56	0.52	-0.44	0.08	-0.17	0.96	-0.15	0.51	-1.00	0.00	/	/
Larch woods	0.10	0.21	0.11	0.16	-0.33	0.48	-0.51	0.47	-0.15	0.45	-0.14	0.37
Stone ravines	-0.46	0.14	-0.03	0.26	-0.22	0.29	0.14	0.18	-0.39	0.15	-0.06	0.17
Alpine meadows	0.77	0.08	0.09	0.19	0.71	0.09	0.20	0.54	0.73	0.08	0.07	0.21
Rocks	-0.36	0.38	-0.25	0.36	-0.32	0.24	0.14	0.61	-0.19	0.21	-0.11	0.28
Bushes	-0.77	0.46	-0.67	0.67	-0.39	0.42	0.47	0.30	-0.24	0.20	0.41	0.17

habitat type in the seasonal home ranges (seasonal HRA) (Table 2). In winter, the pastures in the bottom of the valley, snow covered throughout the winter, were never present in the home range. Also the bushes were not used except in a few cases, and only in one of these they were overused. Stone ravines were present in the home range but were never used. The other habitat types were used differently from one animal to another. Spring was the only season in which home ranges included pastures: underused in 1996, used in proportion to their availability or just a little more in 1997. Pastures, bushes and larch woods in 1996 were always excluded from summer home ranges; in 1997 larch woods were underused, as were rocks in both years. There was often a preference towards Alpine meadows, and sometimes towards stone ravines. In autumn, pastures and bushes were not included in the home ranges except in a few cases, there being a great variability between animals in their use of all other habitats.

Table 2. Habitat selection by adult male Alpine ibex in Cogne Valley (Italy) 1996–1997. Analysis relative to seasonal habitat selection. MJI mean Jacobs index calculated for all individuals. Positive values indicate preference, while negative ones indicate avoidance. For more details, see the text.

		Pastures	Larch woods	Stone ravines	Alpine meadows	Rocks	Bushes
winter	MJI	/	-0.04	-0.80	0.01	-0.09	0.42
1995–96	sd	/	0.03	0.49	0.03	0.42	0.59
spring	MJI	-0.37	0.04	-0.57	0.11	-0.24	0.40
1996	sd	0.18	0.08	0.74	0.23	0.33	/
summer	MJI	/	/	-0.09	0.15	-0.82	/
1996	sd	/	/	0.34	0.32	0.47	/
autumn	MJI	/	-0.27	0.18	-0.001	-0.26	0.69
1996	sd	/	0.62	0.24	0.29	0.42	/
winter	MJI	/	-0.09	-1.00	-0.06	-0.10	-0.48
1996–97	sd	/	0.25	0.00	0.28	0.62	0.74
spring	MJI	0.03	-0.36	-0.27	0.09	0.09	0.28
1997	sd	0.04	0.39	0.59	0.25	0.31	0.39
summer	MJI	/	-0.89	-0.13	0.30	0.75	0.02
1997	sd	/	0.30	0.35	0.30	0.38	/
autumn	MJI	/	-0.38	-0.10	-0.01	-0.34	0.80
1997	sd	/	0.73	0.31	0.56	0.49	/

During the rut period (Table 3) ibexes never included pastures in their home ranges, preferring small stone ravines and bushes, although in some cases these were overused. Larch woods were used in proportion to their availability in the rut period in the first and

Table 3. Degree of habitat selection by adult male Alpine ibex in Cogne Valley (Italy) 1996–1997. Analysis relative to rut habitat selection. MJI mean Jacobs index calculated all for individuals. Positive values indicate preference, while negative ones indicate avoidance. For more details, see the text.

	rut 1995–96		rut 1996–97		rut 1997–98	
	MJI	sd	MJI	sd	MJI	sd
Pastures	/	/	/	/	/	/
Larch woods	-0.04	0.29	-0.40	0.55	0.02	0.56
Stone ravines	-0.71	0.59	-0.64	0.81	-0.69	0.59
Alpine meadows	-0.04	0.29	-0.08	0.43	-0.09	0.29
Rocks	0.04	0.23	0.09	0.33	0.12	0.37
Bushes	0.89	0.00	-0.20	0.74	-0.42	0.59

third years, while in the second year they were negatively selected. Rocks were positively selected in all three rut periods. Friedman's ANOVA was calculated only in 1997 because of the insufficient data available for 1996. There were significant differences in habitat use among seasons: stone ravines (Friedman's ANOVA, $n=5$, $p=0.026$), rocks (Friedman's ANOVA, $n=5$, $p=0.007$), and larch woods (Friedman's ANOVA, $n=5$, $p=0.012$) were used differently in the course of the year and the difference in use between summer and winter was significant ($z=2.638$, $n=5$, $p<0.05$, Siegel & Castellan 1992).

Ibex home ranges seemed to be influenced by the proportions of Alpine meadows in winter and in summer 1996 and by the proportion of rocks in summer 1996 (Table 4), whereas the percentage of Alpine meadows was negatively correlated with the percentage of rocks and stone ravines in almost all seasons (Table 4).

Table 4. Spearman correlation coefficient used to analyse a possible correlation between Alpine ibex home range dimensions and percentage of habitats in Cogne Valley (Italy), and between one habitat and another, in cases where it was significant.

		P	Rs
winter 1996	Home range – Alpine meadows	0.006	-0.612
	Alpine meadows – Rocks	0.004	-0.818
summer 1996	Home range – Alpine meadows	0.036	-0.786
	Home range – Rocks	0.014	-0.857
	Stone ravines – Alpine meadows	0.023	-0.821
	Alpine meadows – Rocks	0.03	-0.929
autumn 1996	Stone ravines – Alpine meadows	0.003	-0.929
rut 1995–96	Alpine meadows – Rocks	0.006	-0.794

Discussion

Rocks (30%) and stone ravines (22%) were the habitats most frequented in the study area, but they offered few food resources and their use was consequently lower than their availability. Alpine meadows were always overused and positively selected, because this habitat constituted an important food resource for the ibex almost all year long. In fact, a negative correlation was found between Alpine meadow percentages and home range sizes. The amount of this habitat therefore was decisive in the foraging strategy of individuals: a home range poor in Alpine meadows should be enlarged to include a sufficient amount of this habitat.

The snow cover was very important for habitat selection; rocks were positively selected in winter, confirming what was found also for Asiatic ibexes in India (Fox et al. 1992). In 1996, the use of rocks was greater than in 1997. During the first winter, snow cover was present for a longer time, while in 1995–1996 it forced ibexes to stay longer on the rock-faces, where small patches of vegetation were available (Geist & Petrocz 1977). Instead stone ravines were not used because of the high risk of avalanches, the vast amount of snow, and the scanty vegetation available. In March, and partially in April, climatic conditions were very similar to those in winter, and consequently habitat use was similar to that of the previous season.

In general, however, in spring there was great variability in the use of the different habitats. The ibexes exploited all kinds of fresh vegetation to satisfy their energetic requirements, and low altitude pastures were used only in this season. In summer, ibexes stayed at a higher altitude (Parrini et al., in press), above the timberline (Nievergelt 1966), and seemed to prefer Alpine meadows and stone ravines. In the

hottest hours of the day males alternated resting and foraging activities in stone ravines and in meadows, provided with good quality forage. In autumn 1996, larch woods and stone ravines were the two most used habitats, unlike autumn 1997.

The different habitat use in the two years could be due to the different climatic conditions. In September 1996, the temperature values were lower than summer ones, and at high altitude it had already snowed. On the contrary, in September 1997 the mean temperature was similar to that of summer, so the males stayed longer on the Alpine meadows. During the rut, ibexes used larch woods and rocky slopes, probably to minimize the risk of avalanches. In the 1996 rut period, there was a wider use of all habitats, caused by a limited snow cover that allowed the use of Alpine meadows, too.

Finally, it seems clear that ibexes selected the sites in relation to environmental conditions, as happens with other mountain ungulates (Koubek & Hrabě 1996) and in relation to climatic factors, particularly snow cover.

LITERATURE

- ALLREDGE J.R. & RATTI J.T. 1986: Comparison of some statistical techniques for analysis of resource selection. *J. Wildlife Manage.* 50: 1050–1053.
- ALLREDGE J.R. & RATTI J.T. 1992: Further comparison of some statistical techniques for analysis of resource selection. *J. Wildlife Manage.* 56: 1–9.
- ARMLEDER H.M. & WATERHOUSE M.J. 1994: Winter habitat use by mule deer in the central interior of British Columbia. *Can. J. Zool.* 72: 1721–1725.
- BERGERUD A.T. 1974: The role of the environment in the aggregation, movement and disturbance behaviour of caribou. In: Geist V. & Wather F. IUCN (eds), The behaviour of ungulates and its relation to management. *Canadian Arctic Gas Study, Morges, New series No 24: 552–584.*
- CRAIGHEAD J.J., CRAIGHEAD F.G. & O'HARA B.W. 1973: Non-migratory Elk in Madison Drainage. *Wildlife Monogr.* 33: 1–50.
- CROOK J. H., ELLIS J. E. & GOSS-CUSTARD J.D. 1976: Mammalian social system: structure and function. *Anim. Behav.* 24: 261–274.
- FOX J.L., SINHA S.P. & CHUNDAWAT R.S. 1992: Activity patterns and habitat use of ibex in the Himalayan mountains of India. *J. Mammal.* 73: 527–534.
- GEIST V. & PETOCZ R.G. 1977: Bighorn sheep in winter: do rams maximise reproductive fitness by spatial and habitat segregation from ewes? *Can. J. Zool.* 55: 1802–1810.
- GEORGII B. 1980: Type d'activité du Cerf (*Cervus elaphus*) en fonction de la structure du biotope. *Ciconia* 4: 35–41.
- GIACOMETTI M., BASSANO B., PERACINO V. & RATTI P. 1997: Die Konstitution des Alpensteinbockes (*Capra ibex*) in Abhängigkeit von Geschlecht, Alter, Herkunft und Jahreszeit in Graubünden (Schweiz) und in Parco Nazionale Gran Paradiso (Italien). *Z. Jagdwiss.* 34: 24–34.
- HARRIS S., CRESSWELL W.J., FORDE P.G., TREWHELLE W.J., WOLLARD T. & WRAY S. 1990: Home range analysis using radio-tracking data. A review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* 20: 97–123.
- HIRTH D. 1977: Social behaviour of white tailed deer in relation to habitat. *Wildlife Monogr.* 53: 1–55.
- HOFMANN A. & NIEVERGELT B. 1972: Das jahreszeitliche Verteilungsmuster und der Äsungsdruck von Alpensteinbock, Gemüse, Rothirsch und Reh in einem begrenzten Gebiet im Oberengadin. *Z. Jagdwiss.* 18: 185–212.
- HOUTE DE LANGE S.M. 1978: Zur Futterwahl des Alpensteinbockes (*Capra ibex*). *Z. Jagdwiss.* 24: 113–138.
- JACOBS J. 1974: Quantitative measurement of food selection. *Oecologia* 14: 413–417.
- JOHNSON D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- KENWARD R. & HODDER K.H. 1996: Ranges V 2.01. An analysis system for biological location data. *Institute of Terrestrial Ecology, Wareham, U.K.*
- KERNOHAN B.J., MILLSPAUGH J.J., JENKS J.A. & NAUGLE D.E. 1998: Use of an adaptative kernel home-range estimator in a GIS environment to calculate habitat use. *J. Environ. Manage.* 53: 83–89.

- KOFLER H. 1981: Ökologisch-vegetationsmündliche Untersuchungen zur Nahrungswahl und Konkurrenz von Gams (*Rupicapra rupicapra* L.) und Steinbock (*Capra ibex ibex* L.) im Hochlatschstock, Steiermark. *Ph.D. Thesis, Graz*.
- KOUBEK P. & HRABĚ V. 1996: Home range dynamics in the red deer (*Cervus elaphus*) in a mountain forest in central Europe. *Folia Zool.* 45: 219–222.
- LEUTHOLD W. 1970: Observations on the social organisation of impala (*Aepyceros melampus*). *Z. Tierpsychol.* 27: 639–721.
- LEUTHOLD W. & LEUTHOLD B. 1975: Pattern of social grouping in ungulates in Tsavo National Park, Kenya. *J. Zool.* 175: 405–420.
- MAUBLANC M. L., BIDEAU E. & VINCENT J.P. 1987: Flexibilité de l'organisation sociale du Chevreuil (*Capreolus capreolus* L.) en fonction des caractéristiques de l'environnement. *Rev. Ecol. – Terre Vie* 42: 109–133.
- MICHALLET J. 1994: Domaines vitaux et déplacements de Bouquetins des Alpes (*Capra ibex* L.) dans le massif de Belledonne-Sept-Laux: bilan de deux années de suivi télémétrique. *Travaux Scientifiques du Parc National de la Vanoise* 18: 239–248.
- NEU C.W., BYERS C.R. & PEEK J.R. 1974: A technique for analysis of utilisation-availability data. *J. Wildlife Manag.* 38: 541–545.
- NIEVERGELT B. 1966: Der Alpensteinbock (*Capra ibex* L.) in seinem Lebensraum. Ein ökologischer Vergleich. *Parey, Hamburg*.
- PEDROTTI L., TOSI G., FACOETTI R. & PICCININI S. 1995: Organization of a study using radio-tracking and analysis of home ranges: application to Alpine ungulates. *Supplemento Ricerche Biologia Selvaggina* 23: 3–100.
- PEEK J., LERESCHE R. & STEVENS D. 1975: Dynamics of moose aggregations in Alaska, Minnesota and Montana. *J. Mammal.* 55: 126–137.
- PEPIN D., JOACHIM J. & FERRIÉ E. 1996: Variability of spring selection by isards (*Rupicapra pyrenaica*). *Can. J. Zool.* 75: 1955–1965.
- SCHAAL A. 1982: Influence de l'environnement sur le composante du groupe social chez le Daim (*Dama dama* L.). *R. Ecol. – Terre Vie* 36: 161–174.
- SCHAAL A. 1987: Le polymorphisme du comportement reproducteur du Daim d'Europe (*Dama dama dama*). Contribution à la socioécologie des Cervidés. *Ph. D. thesis, Strasbourg*.
- SCHAERER O. 1977: Standortwahl, Tagesaktivität und Verbandstruktur in einem Bockrudel des Alpensteinbocks (*Capra ibex* L.). *M.Sc. Thesis, Zürich*.
- SIEGEL S. & CASTELLAN N.J.JR. 1992: Non parametric statistics for behavioural sciences (II edition). *New York, McGraw-Hill*.
- SOKAL R.R. & ROHLF F.J. 1995: Biometry, 3rd edition. *W.H. Freeman & Co., San Francisco*.
- TELFER E.S. 1970: Winter habitat selection by moose and white-tailed deer. *J. Wildlife Manage.* 34: 553–559.
- TERRIER G., CHOISY J.P., GAUTHIER D., MICHALLET J. & VILLARET J.C. 1994: Approche comparative des modalités d'occupation de l'espace par les populations de Bouquetin des Alpes françaises (*Capra ibex* L.). *Travaux Scientifiques du Parc National de la Vanoise* 18: 249–270.
- TERRIER G. & POLAERT F. 1987: Occupation de l'espace par le Bouquetin des Alpes (*Capra ibex* L.): une approche par différentes méthodes de suivi individuel. Premiers résultats obtenus dans le Parc national du Mercantour. *Atti del convegno internazionale "Lo Stambecco delle alpi: realtà attuale e prospettive", Valdieri 17–19/IX/87*: 39–51.
- TERRIER G. & ROSSI P. 1994: Le Bouquetin (*Capra ibex ibex*) dans les Alpes maritimes franco-italiennes: occupation de l'espace, colonisation et régulation naturelles. *Travaux Scientifique du Parc National de la Vanoise* 18: 271–288.
- THOMAS D.L. & TAYLOR E.J. 1990: Study designs and tests for comparing resource use and availability. *J. Wildlife Manage.* 54: 322–330.
- TRON L., TERRIER G., COLOMBINI P. & BRET E. 1994: Déplacements de Bouquetins des Alpes au cours des douze premiers mois après leur lâcher dans les parcs des Ecrins, du Mercantour et du Vercors. *Travaux Scientifiques du Parc National de la Vanoise* 18: 291–320.
- UNDERWOOD R. 1982: Vigilance behaviour in grazing African antelopes. *Behaviour* 79: 81–107.
- WALTHER F. 1972: Social grouping in Grant's Gazelle (*Gazella granti* Brooke, 1827) in the Serengeti National Park. *Z. Tierpsychol.* 31: 347–403.
- WHITE G.C. & GARROT R.A. 1990: Effects of bio telemetry triangulation error on detecting habitat selection. *J. Wildlife Manage.* 50: 509–513.
- WIERSEMA G. 1984: Seasonal use and quality assessment of ibex habitat. *Acta Zool. Fenn.* 172: 89–90.
- WORTON B.J. 1989: Kernel methods for estimating the utilisation distribution in home-range studies. *Ecology* 70: 164–168.