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Effects of air traffic, snow cover and weather on altitudinal short-term and medium-term movements of female Alpine chamois *Rupicapra rupicapra* in winter

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We studied the altitudinal movements of eight radio-collared female Alpine chamois *Rupicapra rupicapra* in the Swiss Alps to investigate how air traffic and environmental factors affect daily movements and medium-term altitudinal displacements in winter. Average altitude was often similar during periods of several days depending mainly on snow cover. Daily altitudinal movements occurred at all altitude levels and seemed to be affected more by local topography and habitat structure than by current environmental conditions. In individuals that were above the timberline in the morning, and thus were potentially exposed to air traffic, the first aircraft of a day could induce a downward movement, and a high intensity of air traffic (i.e. many aircraft during most of the day) affected the altitudinal difference that was covered during the whole day. After a downward movement the chamois returned to higher altitudes within a day and the following night, confirming their preference for the open pastures above the timberline. Two groups of chamois that were exposed to different intensities of air traffic, did not differ in their altitudinal movements, indicating a weak effect of aircraft. The daily energy costs of altitudinal locomotion were not considerably increased. We estimate that, on an average winter day, the energy costs of locomotion were not increased by more than 0.1% of the field metabolic rate (FMR) due to aircraft. However, a combination of deep snow and very intensive air traffic may result in a much higher increase in the energy expenditures on certain days. Further reasons for this ambiguous influence of aircraft are discussed.

Key words: aircraft, Alpine chamois, human disturbance, paragliders, Rupicapra rupicapra, vertical movements, winter conditions

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Three spatio-temporal scales of altitudinal movements can be distinguished in mountain ungulates such as the Alpine chamois *Rupicapra rupicapra*: 1) migration between different seasonal ranges at higher and lower altitudes, 2) medium-term displacements between different altitudes within a seasonal range, and 3) daily altitudinal movements. The altitudinal movements between different seasonal ranges are well documented in Alpine chamois (e.g. Hofmann & Nievergelt 1972, Hamr 1985, Clarke 1986, Bögel 2001), Pyrenean chamois *R. pyrenaica* (Herrero et al. 1996) and other ungulate species (e.g. Hofmann & Nievergelt 1972, Drolet 1976, Francisci et al. 1985, Albon & Langvatn 1992, Mysterud et al. 1997). In contrast to these movements, the altitudinal displacements during a season and the daily altitudinal movements, in particular how they are affected by human activities, have only rarely been investigated in mountain ungulates.

Paragliders and other air traffic have increased in intensity in recent decades in many mountain areas, causing Alpine chamois to leave the open pastures at high altitudes and retreat into the forest (Schnidrig-Petrig 1994, Zeitler 1995, Schnidrig-Petrig & Ingold 2001, Bögel 2001). So far studies have only been carried out in summer. However, it is crucial to investigate the effect of air traffic on chamois movements in winter, at a time when the animals are energy limited. Energetic costs for altitudinal movements are much higher than for horizontal movements, particularly under winter conditions (Parker et al. 1984, Dailey & Hobbs 1989). Increased energetic costs for locomotion caused by air traffic may influence the condition of the chamois, which is of particular concern during times of high mortality in winter (Crampe et al. 2002).

There are indications that medium-term displacements in winter are affected by natural conditions such as snow cover and snow depth (Drolet 1976, Goodson et al. 1991, Pauley et al. 1993, Armleder et al. 1994), because food resources are less accessible under snow cover and energy expenditures for locomotion are much higher in snow (Dailey & Hobbs 1989). Alpine chamois avoid areas with a high proportion of snow cover, but they can use very high altitudes in snow-poor periods during winter (Hofmann & Nievergelt 1972, Hamr 1985, von Elsner-Schack 1985, Berdoucou 1986). It is not known whether other factors are causing these displacements.

The objective of our study was to find out how natural environmental conditions such as snow cover, snow depth or weather and aircraft interacted to affect medium-term altitudinal displacements and daily movements of chamois in winter. Because it takes a few days for snow-free patches to reappear after heavy snowfall, we

expected chamois not to return to higher altitudes within a short time (i.e. a day), but to stay at lower altitudes for some time after heavy snowfall. Accordingly, we hypothesised that the medium-term displacements to lower altitudes in winter are mainly affected by a high proportion of snow cover, and only marginally by other weather factors or by air traffic. We expected no differences in the factors relevant to the altitudinal displacements between two chamois groups which were exposed to different intensities of air traffic.

However, air traffic or other short-term factors (e.g. solar radiation and temperature) could influence the daily altitudinal movements in winter. We expected chamois to return to higher altitudes within a short period of time (i.e. within a day) in order to return to a foraging site as soon as possible (possibly depending on the severity of a disturbance). The result of such downward and upward movements should be a regular pattern of the altitudinal movements during a winter day. We hypothesised that downward movements from the open pastures into the forest are induced, and their extent influenced, by short-term factors such as paragliders and other aircraft, rather than by medium-term natural environmental conditions like snow cover.

We further applied the results of altitudinal movements to models of energy requirements. From this, we estimated the energetic consequences of increased altitudinal movements due to air traffic.

Methods

Study area and animals

Our study was carried out on the southwestern slope of the Männlichen Mountain (2,343 m a.s.l.) in the Bernese Oberland region (Switzerland). The study area covers an area of 3.5 km² situated between the town of Wengen (1,275 m a.s.l.) and the ridge leading south from the Männlichen Mountain (2,200–2,343 m a.s.l.). The topography has a fairly constant gradient of 40°. The vegetation is dominated by subalpine pastures above the timberline, which is at about 1,900–1,950 m a.s.l. (comprising 42% of the study area). The lower part is covered by a forest consisting mainly of spruce *Picea abies* (33%), interrupted by some gullies with screes and small meadow patches (9%). Some of the gullies lead all the way down to Wengen. Larger rocky parts occur along the ridge and in some parts of the pastures and the forest (16%).

Under winter conditions (November–April) the open pastures are often snow-free to a varying extent. The steep slope and the intensive solar radiation result in many snow

slides. As a result, many patches of vegetation become accessible and increase in size with the subsequent melting of snow. Snow lasts longer but the snow depth is often lower in the forest. The lower gullies are snow-free during most of the winter. The whole study area is usually free of snow between the end of May and October, but occasional snowfall is possible also in summer.

Human activities in winter concentrate on the ridge, which separates the study area from the ski area on the northeastern slope (towards the town of Grindelwald). The ridge can be reached by gondolas and some hiking trails lead along the ridge and down the northeastern slope of the mountain. The study area on the southwestern slope is not accessible in winter due to the high risk of avalanches. Therefore, there are no human activities on the ground in winter, but there is some air traffic on most winter days. Paragliders have a starting point on the ridge. Most of them fly away from the mountain immediately after the start, either by flying down the valley towards the city of Interlaken or by soaring into higher altitudes. But some paragliders fly along the slope of Männlichen Mountain, thus above the upper, open parts of the study area. There is also an airfield for helicopters and fixed-winged aircraft near the gondola stations for emergency and sightseeing flights. Most helicopters and aircraft approach and leave the airfield at high altitudes, but some helicopters fly close to the ground when crossing the study area.

The study area is inhabited by approximately 100–150 Alpine chamois of both sexes. Most of the females belong to two large home range groups that occasionally meet in the central part of the study area, whereas the males live solitarily or in small, loose groups. Most of the males stay in the same home ranges all year round, whereas females move to different home ranges in summer (P. Ingold et al., unpubl. data).

Data sampling and preparation

During the winter of 1999/2000, 10 chamois were captured using snare traps and equipped with radio collars of the type TXG (FIWI / Segadat, Vienna, Austria) with sensors for air pressure and air temperature to record altitude (Bögel & Burchard 1992). The radio collars also recorded activity and were used to localise the animals by triangulation (P. Ingold et al., unpubl. data).

Real time measurements of air pressure and temperature were transmitted by modulation of pulse duration and pulse interval during 15 seconds every minute. Data were recorded automatically and continuously by two RX-900 (Televilt, Ramsberg, Sweden) data loggers that were located at the foot of the mountain, with an unob-

structed view to almost the whole study area. The loggers scanned a particular frequency during one minute and then switched to the next frequency. With 10 frequencies scanned overall, this resulted in one value for air pressure and temperature per animal every 10 minutes. The data from two reference transmitters, located at 1,550 and 2,020 m a.s.l. in the study area, were also recorded in the same way. These data were used to compensate for atmospheric variation in air pressure (P. Ingold et al., unpubl. data). Data were recorded continuously between 25 February 2000 and 1 April 2002.

Air pressure and air temperature from the radio collars and the data of the reference transmitters were used to calculate the altitude of an animal with a barometric equation (Bögel & Burchard 1992) using a computer routine written by E. Bächler (unpubl. data). The altitude database consisted of 820,786 measurements of eight female and two male chamois, in intervals of 10 minutes during more than two years. All further analyses were carried out separately for the five female individuals of home range group A and for the three female individuals of group B. Group A stayed in the central part of the study area and was more affected by air traffic (on 43% of the days with a median of three aircraft per day). In contrast, group B had a different home range with slightly different conditions and habitat structure. In particular it was much less exposed to air traffic (on 30% of days with a median of one aircraft per day). The original sample consisted of $N = 2,852$ cases (one case being one individual on one day, $N_A = 1,732$, $N_B = 1,120$).

Environmental parameters such as snow depth, wind speed, air temperature, and short-wave and long-wave radiation were recorded in 10-minute intervals at an automatic weather station near the summit of Männlichen Mountain (data used with the permission of the Swiss Federal Institute for Snow and Avalanche Research, and of the Physical-Meteorological Observatory Davos). The amount of fresh snow was summed up during a day or a night. Wind speed was averaged over a day or night. From short-wave and long-wave radiation, air temperature and several constant parameters of emissivity and absorptivity for the animal, air, snow and grass, we calculated a value of radiation balance per day and per night. We used the equations by Parker & Gillingham (1990) to calculate one value of radiation balance on snow and one on grass, and combined the two values proportionally according to the snow cover in the respective sectors of the study area. Additionally, we recorded snow cover by taking photographs of the mountain twice a day. The distribution of black and white colours on the photographs was analysed digitally using the

colour histogram feature in the Spatial Analyst extension of ArcView 3.2 (ESRI, Redlands, California, USA), resulting in a proportion of the snow-covered area, separately for five different sectors of the study area. We used the measurement in the afternoon in the sector where the animals stayed as the snow cover value of that particular day. The corresponding value for the night was calculated as the average snow cover in the afternoon and the following morning.

All aircraft in the study area were recorded during visual observation sessions of at least three consecutive days (type of aircraft, times of appearance and disappearance, overflowed sectors of the study area). We calculated an index of air traffic intensity, *I*, according to the following equation:

$$I = (\Delta t / dl) * (\Sigma t_i / dl)$$

where Δt is the timespan between the first and the last aircraft of a day, dl is the length of the day between dawn and dusk, and Σt_i is the overall time that all aircraft actually spent in the area.

Data analyses

We only analysed winter data (November–April). All analyses used non-parametrical statistical methods (Mann-Whitney Test with normal approximation; Zar 1999) or general linear regression models (GLM) in the SPSS 10.0 software package (SPSS, Chicago, Illinois, USA).

The average altitude per day or night as parameter representing medium-term altitudinal displacements was analysed using GLMs with the following independent input variables: snow cover, amount of fresh snow, wind speed, radiation balance, intensity of air traffic, as well as several two-way interactions of the variables. Models accounted for the seasonal variation in length of day and night (by including them as a variable in the model) and for individual variation (by coding individuals according to the repeated measure coding method; Pedhazur 1997). Starting with a model incorporating all variables, we stepwise reduced the model by the variable with the smallest influence and calculated the second-order AIC_c (Akaike's Information Criterion). The model with the lowest AIC_c was retained as the best model, explaining most of the variation in the data with the least number of factors. Plausibility of alternative models was calculated as differences in AIC_c (ΔAIC_c) to the best model (Motulsky & Christopoulos 2003). The proportion of variation that is explained by a model is expressed as the likelihood-based coefficient of determination (R^2).

The average altitude per day is compared to the altitudinal range of that day by linear regression.

For the analyses of the daily downward movements we selected cases when an animal started above 2,100 m just after dawn (thus well above the timberline). A relevant daily downward movement was defined as a movement starting above 2,100 m and going below 2,000 m (thus into the forest or at least very close to it) at some time during the day. The extent of the downward and the following upward movements (sum of vertical distances of the 10-minute intervals) was compared during a daylight period and the following night. The effect of environmental factors on the overall extent of the daily downward movement (difference between the first and the lowest measurement for animals starting above 2,100 m in the morning) was analysed using a GLM as described above.

An individual-based spatially-explicit model simulating chamois movements (Fankhauser & Enggist 2004) suggested an influence of local topography and habitat structure on the altitudinal movements in our study area (P. Ingold et al., unpubl. data). To check these patterns with field data, we compared the altitude differences of animals that stayed above 2,000 m throughout the day to animals that stayed below 2,000 m on days without air traffic. Animals foraging at lower altitudes are expected to have a larger altitudinal component in their movements, because the lower part of the study area was much more structured by vertical gullies, ridges and forest patches than the upper part.

The potential trigger of a downward movement by aircraft was analysed by calculating the difference in altitude for two time periods: 1) during the last 30 minutes immediately before the first occurring paraglider or helicopter of the day, and 2) during the first 30 minutes after the first occurring aircraft of the day. For both periods, we compared days with and without air traffic, using daytimes representing the same temporal distribution as the first aircraft on the other days.

Energy costs for altitudinal movements were calculated according to Hüppop (1995) for a chamois of 25 kg in body mass and expressed as percentage of the daily field metabolic rate (FMR). The costs of a downward movement are difficult to estimate. Measurements by Dailey & Hobbs (1989) showed that some individuals expend more energy, others even gain some energy from moving downhill as compared to a horizontal movement. We assumed that on average the costs for moving downward did not exceed those for moving horizontally. Accordingly, we concentrated on the upward movements. We assumed an average snow depth of less than 0.3 m (which was confirmed by many pers. obs. by A.

Table 1. Generalised linear model with coefficient of determination (R^2), Akaike's Information Criterion (AIC_c), sample size (N), regression coefficients (b and t) and P-values for the effects of environmental parameters on the average altitude of female Alpine chamois during daylight hours in the winters of 2000, 2001 and 2002. Group A was regularly and group B rarely exposed to air traffic.

	Group					
	A			B		
R^2	0.677			0.345		
AIC_c	4708.31			2829.59		
N	466			347		
Parameter	b	t	P	b	t	P
Constant	2748.33	52.188	< 0.001	2390.11	50.638	< 0.001
Snow cover	-338.13	-20.151	< 0.001	-77.48	-5.781	< 0.001
Length of the day	-49.72	-10.570	< 0.001	-528.09	-5.093	< 0.001
Wind speed X Radiation balance	-0.003	-3.174	0.002	-0.002	-1.915	0.056

Boldt & E. Bächler), thus no additional costs due to snow was included in the calculations (Dailey & Hobbs 1989).

Accuracy of the data

We evaluated the accuracy of the altitude measurements by comparing them to simultaneous visual observations of the radio collared individuals. The deviation of all comparisons was not different from zero (mean = -0.95 m, N = 151 observations, 95%-confidence interval = -4.62 to +2.72 m, $t = -0.51$, $P = 0.611$). Of all measurements, 90% were within less than ± 24 m of the true altitude, and only three deviations were ≥ 50 m. The mean deviations of the 10 different collars ranged from -12.55 m to +16.75 m.

Results

Medium-term altitudinal displacements in winter

Snow cover was the strongest factor affecting the average altitude during the day in both chamois groups (Table 1). The chamois were significantly lower with a

high proportion of snow cover ($b_A = -338.18 \pm 16.77$, $b_B = -77.48 \pm 13.32$). The interaction of wind speed and radiation balance also affected the average altitude to a small degree ($b_A = -0.003 \pm 0.001$, $b_B = -0.002 \pm 0.001$). The model also indicated a seasonal effect, because day length was a significant factor ($b_A = -49.72 \pm 4.70$, $b_B = -528.09 \pm 101.75$). Alternative models had values with $\Delta AIC_c \geq 7.24$ for group A and ≥ 55.16 for group B and were therefore not supported by the data. Individual differences had no significant effect (F-test: $P_A = 0.176$, $P_B = 0.093$).

The GLM for the average altitude during the night showed very similar results. The factors that remained in the model after the reduction of factors (Table 2) were snow cover as the strongest factor ($b_A = -334.54 \pm 18.32$, $b_B = -94.66 \pm 13.06$), while wind speed and radiation balance contributed only marginally to the model ($b_A = 0.006 \pm 0.003$, $b_B = 0.005 \pm 0.002$). ΔAIC_c was ≥ 12.34 for group A and ≥ 94.75 for group B for all alternative models, and individual differences had no significant effect (F-test: $P_A = 0.236$, $P_B = 0.194$).

As indicated by the models, the average altitude showed some variation in the course of the winter. The chamois often stayed at one altitude level for some time

Table 2. Generalised linear model with coefficient of determination (R^2), Akaike's Information Criterion (AIC_c), sample size (N), regression coefficients (b and t) and P-values for the effects of environmental parameters on the average altitude of female Alpine chamois during the night in the winters of 2000, 2001 and 2002. Group A was regularly and group B rarely exposed to air traffic during the day.

	Group					
	A			B		
R^2	0.579			0.331		
AIC_c	4368.69			2714.98		
N	448			341		
Parameter	b	t	P	b	t	P
Constant	1594.43	37.640	< 0.001	1851.34	54.478	< 0.001
Snow cover	-334.54	-18.286	< 0.001	-94.66	-7.235	< 0.001
Length of the night	51.09	14.345	< 0.001	659.85	10.090	< 0.001
Wind speed X Radiation balance	0.006	2.070	0.039	0.005	2.332	0.020

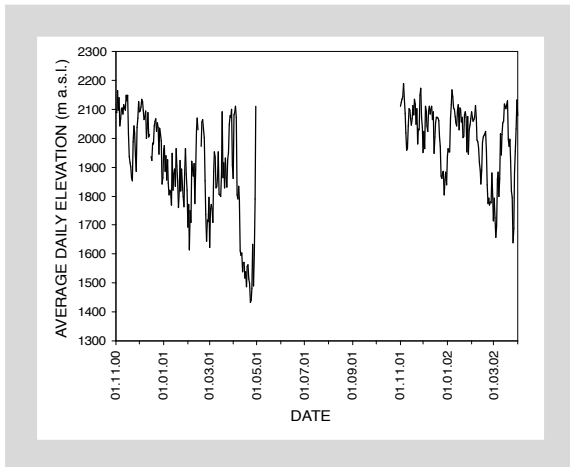


Figure 1. Mean daytime altitude of five female Alpine chamois on Männlichen Mountain between 1 November 2000 and 30 April 2001 and between 1 November 2001 and 31 March 2002.

before moving to a higher or lower altitude level (Fig. 1). Most displacements to lower altitudes occurred when the area was completely snow-covered. For example, the study area received some late and unexpected snow in April 2001, forcing the chamois to stay at very low altitudes for a prolonged time (see Fig. 1). The data of the year 2000 and anecdotal observations in the years 1999 and 2002 confirmed that this was an exceptional situation.

Daily pattern of altitudinal movements in winter

The average daily pattern of altitudinal movements was very similar throughout the whole winter. During the night until the early morning, the chamois were at high altitudes, often well above the timberline at around 1,950 m a.s.l. In the morning they moved downwards, reach-

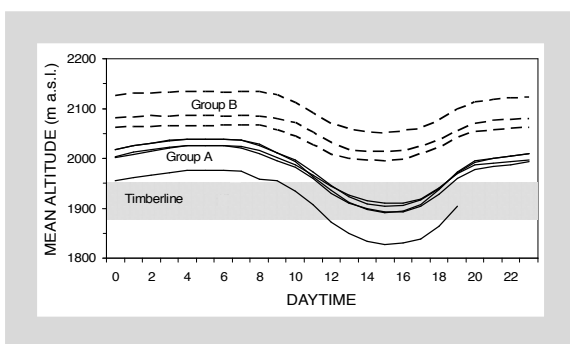


Figure 2. Daily pattern of altitudinal movements of female Alpine chamois on Männlichen Mountain in the winters of 2000, 2001 and 2002 (February-April, November 2000 - April 2001 and November 2001 - March 2002). Mean patterns of five individuals of group A (—) and three individuals of group B (---); $58.7 \leq SD \leq 143.9$; $169 \leq N \leq 171$.

ing the lowest altitude in the early afternoon. From the early evening until dusk, they started to move upwards again. All individuals showed very similar patterns, group B usually being at higher altitudes than group A (Fig. 2).

However, the variation from day to day was quite large. On some days the chamois performed almost no altitudinal movements, or they moved to high altitudes in the afternoon, or they showed no regular altitudinal movements at all. One could often find similar daily altitudinal movements when an animal was at higher altitudes above the timberline or when it was at low altitudes well in the forest. Thus, the range of the daily altitudinal movements was only marginally depending on the average altitude at which these movements occurred (group A: $z_{\text{range}} = 744.63 - 0.30 z_{\text{mean}}$, $N = 1,731$, $R^2 = 0.231$, $P < 0.001$; Fig. 3; group B: $z_{\text{range}} = 852.83 - 0.35 z_{\text{mean}}$, $N = 1,119$, $R^2 = 0.147$, $P < 0.001$).

In 52.7% of all observations of group A (1,732) the chamois were above 2,100 m in the morning. In half of these cases (25.9% overall) they moved below 2,000 m during the day, performing a significant altitudinal movement of more than 100 m. In all other cases, the animals stayed at high altitudes all day long (26.8%), at low altitudes all day long (42.9%), or were at low altitudes in the morning and moved up during the day (4.4%).

The chamois of group A balanced a downward movement and returned to higher altitudes within the same day or the following night. The downward movement was concentrated to the daylight hours ($N_{\text{day}} = 1,732$, $N_{\text{night}} = 1,694$ cases, $Z = -38.56$, $P < 0.001$; Fig. 4 left

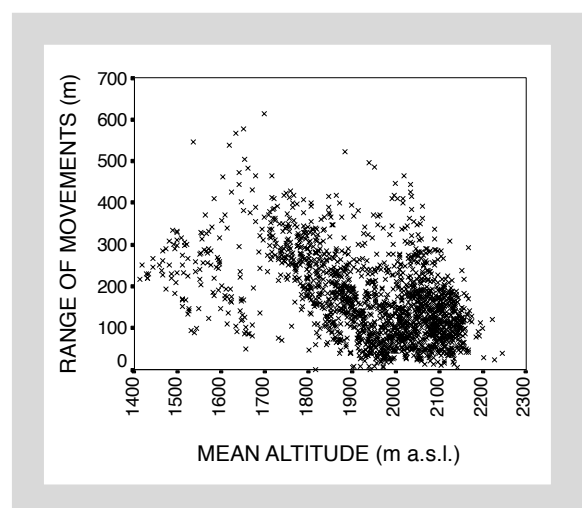


Figure 3. Range of altitudinal movements during the daylight period in relation to the mean daily altitude of five female Alpine chamois on Männlichen Mountain in the winters of 2000, 2001 and 2002.

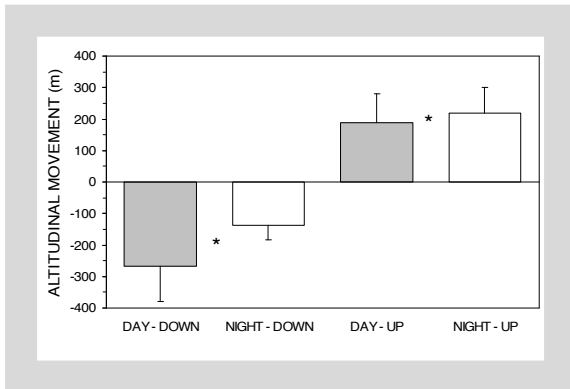


Figure 4. Altitudinal movements and distances (in m) downhill and uphill recorded during daytime and nighttime for five female Alpine chamois on Männlichen Mountain in the winters of 2000, 2001 and 2002. The graph shows mean and SD, and * = $P < 0.001$.

side). The following upward movement already started during the same day, but took place mainly during the following night ($N_{\text{day}} = 1,732$, $N_{\text{night}} = 1,694$ cases, $Z = -13.20$, $P < 0.001$; see Fig. 4 right side). Whatever the vertical distance downward they covered during the day, they moved up again the same altitudinal distance during the next 24 hours ($z_{\text{up}} = 0.976 * z_{\text{down}}$, $N = 1,694$ cases, $R^2 = 0.935$, $P < 0.001$; Fig. 5).

Effect of environmental conditions, local topography and air traffic on daily altitudinal movements

The outcome of a GLM relating the difference between the first and the lowest altitude measurement of a day (limited to individuals starting above 2,100 m in the morning) with several environmental parameters showed that the natural environmental parameters only had a marginal influence. Even the best model did not explain

Table 3. Generalised linear model with coefficient of determination (R^2), Akaike's Information Criterion (AIC_c), sample size (N), regression coefficients (b and t) and P -values for the effects of environmental parameters on the altitudinal difference covered by female Alpine chamois during the daylight period in the winters of 2000, 2001 and 2002. Group A was regularly and group B rarely exposed to air traffic during the day.

	Group					
	A			B		
R^2	0.108			0.013		
AIC_c	1662.7			1031.4		
N	241			201		
Parameter	b	t	P	b	t	P
Constant	31.91	0.665	0.507	115.58	15.885	< 0.001
Intensity of air traffic	1338.16	4.979	< 0.001	884.32	1.912	0.057

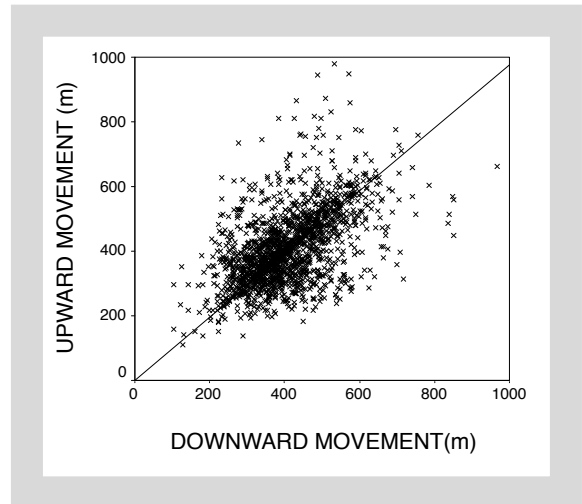


Figure 5. Relation between up- and downward movements (in m) for five female Alpine chamois in the winters of 2000, 2001 and 2002. Linear regression: $y = 0.976x$.

much of the variation (Table 3). The only significant parameter that remained in the model after the stepwise reduction was the intensity of air traffic. Intensive air traffic caused the chamois of group A to perform slightly larger downward movements during the day ($b = 1,338.16 \pm 362.61$). No alternative model was supported by the data ($\Delta AIC_c \geq 83.91$). For the individuals of

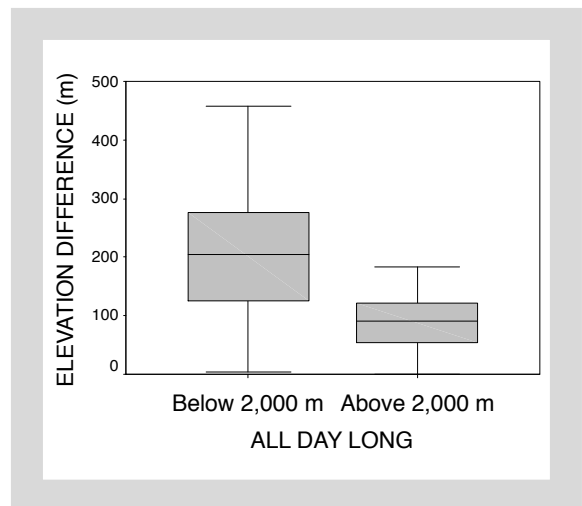


Figure 6. Difference between the highest and lowest altitudes during daytime for five female Alpine chamois on Männlichen Mountain that stayed either below ($N = 165$) or above ($N = 94$) 2,000 m a.s.l. throughout the day in the winters of 2000, 2001 and 2002. The graph shows the median, quartils and range, and one case is one individual on one day; $P < 0.001$.

Table 4. Altitudinal movements (in m; mean \pm SD) of five female Alpine chamois in periods of 30 minutes before and after the appearance of the first aircraft of the day, comparing days with and without air traffic during the winters of 2000, 2001 and 2002. For days without air traffic, daytimes represent the same distribution as the first aircraft.

	Days with air traffic	Days without air traffic
N	138	89
Altitudinal movement before first aircraft (m)	-9.23 \pm 24.64	-8.12 \pm 20.88
Z		-0.726
P		0.468
Altitudinal movement after first aircraft (m)	-12.46 \pm 21.34	-4.93 \pm 17.37
Z		-3.244
P		0.001

group B no model could explain much of the variation and no parameter had any significant effect, although the intensity of air traffic was the strongest of the factors considered ($P = 0.057$).

Animals of group A that stayed in the lower part of the study area throughout the day performed significantly larger altitudinal movements than animals that stayed in the upper part (mean \pm SD; low: 203.0 \pm 110.3 m, $N = 165$ cases; high: 89.2 \pm 49.2 m, $N = 94$ cases; $Z = -8.497$, $P < 0.001$; Fig. 6). A smaller, but significant difference was found in group B, although much fewer individuals stayed at low altitudes (low: 101.5 \pm 69.1 m, $N = 28$ cases; high: 62.6 \pm 53.3 m, $N = 648$ cases; $Z = -3.581$, $P < 0.001$). It seems that animals at lower altitudes are performing larger vertical movements due to the topography and habitat structure in these areas.

Comparing the altitudinal movement in a 30-minute period before the occurrence of the first aircraft of the day with the movement on days without human flying activities, we found no differences (Table 4). In most cases, the animals' movements were already oriented slightly downwards. But during the 30-minute period after the first aircraft, the chamois were significantly more oriented downwards than on the control days (see Table 4). It seemed that the first aircraft of a day could induce or increase a downward movement or reduce an upward movement.

Table 5. Energy costs for altitudinal movements in winter of female Alpine chamois caused by air traffic. Calculations of additional altitude covered due to air traffic (in m) are according to the model analysis (see Table 3, group A). Calculations of additional energy costs due to the movements (in kJ) are based on a mammal of 25 kg in body mass according to Hüpopp (1995; 100 m uphill result in 93 kJ, which equals 1% of the FMR).

	Mean intensity of air traffic	Highest intensity of air traffic
Intensity of air traffic, I	0.00561	0.0913
Additional altitude covered due to air traffic (m)	7.5	122.2
Additional energy costs due to these movements (kJ)	7.0	113.6
Additional energy costs due to these movements (% of the FMR)	0.08	1.22

Energy costs of altitudinal movements due to air traffic

Calculations with our best-fit model (see Table 3) showed that the average intensity of air traffic resulted in an additional altitudinal movement of 7.5 m. On the day with the most intensive air traffic, the altitudinal movement was increased by 122.2 m (Table 5). A chamois of 25 kg body mass spends 93 kJ on an uphill move of 100 m (Hüpopp 1995 after Dailey & Hobbs 1989), which equals 1.0% of its FMR. In our study, the average intensity of air traffic resulted in increased energy costs relative to the FMR of 0.08%. Even on the day with the most intensive air traffic, the FMR was increased only by 1.22% (see Table 5).

Discussion

When discussing the spatial behaviour of chamois, in particular displacements on the vertical axis, it is necessary to distinguish between the temporal levels of the movements: the migrations between seasonal ranges (on a time scale of weeks up to a year), displacements from one area to another during a season (on a time scale of several days), and the altitudinal movements during a day (on a time scale of hours up to a day). The chamois in our study area performed daily altitudinal movements of different patterns and extents in winter which took place at different average altitude levels.

Medium-term altitudinal displacements in winter

The access to food resources is restricted at times of a high proportion of snow cover, but chamois seem to be able to find food on snow-covered pastures, provided the snow is not too deep (A. Boldt, pers. obs.). In the course of winter, the variation in the proportion of snow cover and not snow depth was the most important factor affecting the vertical displacements of the chamois, most pronounced above a threshold of about 60% snow cover. This is in contrast to Goodson et al. (1991), who concluded that even small amounts of snow had a relevant effect on the habitat use of bighorn sheep *Ovis canadensis*. Even with a high proportion of snow cover on > 60% of our study area, the chamois could probably find enough food in the many snow-free patches.

But when the distances between snow-free patches increase with a higher proportion snow cover, the energetic costs of locomotion increase considerably (Dailey & Hobbs 1989). Energetic costs of locomotion on snow can be up to five times higher than those of locomotion on dry ground in mountain goats *Oreamnus americanus* and bighorn sheep, depending on sinking depth (Dailey & Hobbs 1989). Higher energy expenditures can ultimately lead to higher mortality and lower reproduction rates (Mech et al. 1987 for white-tailed deer *Odocoileus virginianus* and moose *Alces alces*, and Crampe et al. 2002 for Pyrenean chamois).

To avoid these costs, the chamois leave the snow-covered pastures and move to lower altitudes after heavy snowfall. Snow is scarcer at lower altitudes and in old-growth or denser forests (Kirchhoff & Schoen 1987), and the structure of the habitat at lower altitudes (i.e. in the forest and particularly in the lower gullies) results in a patchy small-scale distribution of the remaining snow.

Both groups of female chamois showed the same medium-term altitudinal displacements. Because the two groups were exposed to different intensities of air traffic, this result corroborates that air traffic has no significant effect on these displacements.

Daily pattern of altitudinal movements in winter

We showed that altitudinal movements during a day are a common phenomenon in winter, and that the day-to-day variability in altitudinal movements can be quite substantial. The chamois performed considerable altitudinal movements on many days, but they only rarely covered all altitude levels of 1,300–2,300 m in a single day. On some days they stayed at a more or less constant altitude all day long. These different patterns could be observed in animals at higher as well as at lower average altitudes and in both female groups. However, the

mean pattern of altitudinal movements was characterised by a downward movement between dawn and noon and an upward movement in the evening and early night. This is in contrast to Pépin et al. (1996) who concluded that “during winter mountain ungulates usually restrict their movements to horizontal travels”.

The daily pattern of altitudinal movements can obviously differ very much from one area to another. Depending on the small-scale topography and habitat structure, the density of the population, as well as the environmental conditions of a particular area, chamois may perform larger altitudinal movements or not, they may stay at higher or lower altitudes during the day or at night (e.g. Boillot 1980, Hamr 1985, Schnidrig-Petrig 1994, Pépin et al. 1996, Bögel 2001).

A downward movement was almost always followed by a similar-sized upward movement later during the same day or during the following night, irrespective of the altitudinal differences. As a result, at some time in the early night the chamois arrived at the same altitude level, from which they started their downwards movement in the morning (if they moved downwards at all). There were deviations from this regular daily pattern, but most deviations resulted from a medium-term displacement from higher to lower altitudes and not from a different daily altitudinal movement. These findings corroborate the assumption that the daily altitudinal movements are affected by short-term factors (e.g. air traffic) and that the chamois move upwards to their preferred feeding grounds as soon as possible.

Effect of environmental conditions, local topography and air traffic on daily altitudinal movements

In half of the observations the chamois were above the timberline in the early morning and thus potentially exposed to air traffic. The first helicopter or paraglider of the day could trigger a downward movement in these individuals, and the intensity of air traffic was affecting the overall altitudinal difference covered during the day. This indicates a cumulative effect of the aircraft on chamois movements. No such effect was found in the individuals of group B which were less often exposed to air traffic. The results are in accordance with those found in other studies where chamois showed immediate reactions to aircraft, often expressed as flights or slow retreat towards the forest (Schnidrig-Petrig 1994, Zeitler 1995, Schnidrig-Petrig & Ingold 1995, 2001).

Individuals that stayed at altitudes below 2,000 m also performed daily vertical movements of 100 m or more, i.e. even larger movements than the individuals staying above 2,000 m throughout the day. But this could not

be caused by the air traffic, because the lower areas in the forest or close to the forest were rarely frequented by paragliders and other aircraft, and because the individuals of group B showed the same difference. This is an indication that the altitudinal movements in the lower areas were affected by the local small-scale topography and habitat structure and not by the aircraft. Vertical ridges, gullies and forest edges may serve as guiding structures for the movements of chamois. These findings corroborate the simulations with an individual-based spatially-explicit model of chamois behaviour using data on topography and habitat structure from our study area (P. Enggist, unpubl. data).

It is often assumed that mountain ungulates have to seek cover from high solar radiation or temperature (Parker & Robbins 1985). Such cover sites seem to be important to avoid thermal stress in mule deer *Odocoileus hemionus* (Parker 1988, Leckenby & Adams 1986, Parker & Gillingham 1990) and in red deer *Cervus elaphus* (Conradt et al. 2000). In Alpine chamois, the influence of radiation on movements and habitat use has also been suggested (von Elsner-Schack 1985, Bögel 2001). In our study, we found no significant influence of radiation on daily altitudinal movements in winter. We assume that the solar radiation in winter in our study area did usually not reach values high enough to cause the chamois to seek thermal cover. This is confirmed by observations from other areas where chamois can be observed to rest at exposed sites, seemingly unaffected by high radiation or temperature (P. Ingold, pers. obs.).

The accessibility of certain sites or the availability of forage in parts of an area may also affect the movements of chamois. On Männlichen Mountain there may be sufficient food resources on small open meadow patches along the gullies below the timberline. This may enable the chamois to forage at low altitude, too (P. Ingold et al., unpubl. data). On the other hand, the ridge along the top of the mountain was not available as a foraging or resting site for the chamois, because it was used on most days by people (starting point for aircraft, observation viewpoint, restaurant, skiing and hiking area outside our study area). Accordingly, the chamois could not move upwards during the day as they do in some other areas, but had to move downwards. In parts of our study area as well as in other areas, such anthropogenic effects may contribute more to the expression of a relevant downward movement than environmental factors.

Energy costs of altitudinal movements due to air traffic

We calculated that on a winter day with average snow depth an average intensity of air traffic did not increase

the energy costs for altitudinal locomotion by more than 0.1% of the FMR. Deep snow can increase this value considerably by up to five times, but only with sinking depths of more than 0.3 m (Dailey & Hobbs 1989), which rarely occurred in our study area. And when they did occur, the chamois avoided the deep snow by staying at lower elevations. The speed of locomotion also contributes to the energy costs. Fast flights would result in much higher costs (Dailey & Hobbs 1989).

We concluded that during a whole winter season the energetic costs were not considerably increased by aircraft. Daily energy costs, however, depend on the current conditions in an area. Deep snow, very intensive air traffic, a flight style of the aircraft leading to more aircraft-chamois encounters, or a higher sensitivity of the chamois may very well cause additional energy expenditures of 5% or more of the FMR. These conclusions do not include possible indirect effects on energy balance that may arise in displaced chamois foraging in areas of lower food quality.

Conclusions on the effect of air traffic on altitudinal movements

The effect of the air traffic was ambiguous in our study. Relevant altitudinal movements starting above and leading below the timberline also occurred on 38% of days without any air traffic. They were obviously not directly induced by aircraft. The effect of aircraft on the movements of chamois seemed to be highly dependent on the particular circumstances of the encounter, the relative positions of chamois and aircraft to each other, the flight style of the aircraft, and the time of the encounter. Most paragliders did not fly close to the ground as they did in earlier years, when the equipment and experience of the pilots did not allow high soaring flights.

In winter, the chamois on Männlichen Mountain had shorter flight distances compared to the data from other areas in summer (P. Ingold et al., unpubl. data), maybe due to reduced sensitivity in winter or habituation to the air traffic in this area.

The relatively low influence of air traffic on the movements of the chamois may also be due to the low average intensity of air traffic. During our study, aircraft were observed only on some of the days, and air traffic was not very intensive on most days. However, we observed that flight reactions can occur in some cases and that during periods of very intensive air traffic, the altitudinal movements can be considerably affected by human activities.

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