

REACTIONS OF CHAMOIS TO HUMAN DISTURBANCE IN BERCHTESGADEN NATIONAL PARK

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ABSTRACT.— *The objective of this study was to test whether the source and frequency of disturbance result in different behavioural responses of Chamois and if practical management guidelines can be drawn from these findings. The results clearly indicate that type and frequency of the disturbance have a strong influence on the behavioural response and that the disturbance tolerance varies with season, time of the day, sex and group size. Disturbances from flying resulted in a much stronger response than disturbances from the ground, and the response increased with velocity and/or noise level of the disturbance source. In areas with frequent disturbances the behavioural response was reduced when compared with remote areas, indicating habituation effects. While distance at first reaction and flight distance varied with disturbance intensity, the length of the flight path was not influenced by the disturbance type and frequency. Habitat use was also affected by disturbances: post-disturbance habitat types were mainly rocks and forests indicating a shift in habitat selection towards inaccessible habitat types or habitat types with good cover.*

RÉSUMÉ.— *Chez les chamois, nous avons étudié l'influence des différentes perturbations de diverses fréquences sur le comportement et nous nous sommes demandés si les résultats obtenus pouvaient orienter la gestion des populations. En effet, aussi bien le type que la fréquence de la perturbation ont influencé de manière significative le comportement. De plus, la tolérance aux perturbations varie avec la saison, l'heure du jour, le sexe et la taille du groupe. Les perturbations produites par des engins aériens ont provoqué une réponse beaucoup plus forte que celles provenant du terrain; la réponse étant augmentée avec la vitesse ou le degré du bruit de la source de perturbation. Là où les perturbations étaient fréquentes, la réponse se voyait réduite par rapport à des territoires éloignés, cela nous indiquant une habituation certaine. La distance de fuite et la distance de la première réaction ont suivi de près l'intensité de la perturbation; par*

contre, la longueur de la distance de fuite n'est pas influencée par le type de perturbation et la fréquence. L'utilisation de l'habitat était aussi affectée par les perturbations, ainsi les habitats choisis après la perturbation étaient les rochers et les forêts. Il y avait une préférence pour les habitats plus inaccessibles ou avec un meilleur recouvrement.

RESUMEN.— El objetivo del presente estudio es valorar si molestias de diferentes tipos y frecuencias producen diferentes respuestas en el comportamiento del rebeco, y si esto permite extraer recomendaciones en cuanto a su gestión. Los resultados indican claramente que el tipo y frecuencia de las molestias tienen una fuerte influencia en la respuesta y que la tolerancia a las molestias varía con la estación, hora del día, sexo y tamaño grupal. Las molestias producidas por objetos volantes provocan una respuesta mucho mayor que las originadas desde tierra, además la intensidad de la respuesta se incrementa con la velocidad o el nivel de ruido de la molestia. Donde las molestias son frecuentes la respuesta es menor que en áreas remotas, lo que indica un efecto de habituación. Mientras la distancia de reacción y la de huida varía con la intensidad de la molestia, la longitud del recorrido de huida no se vio influida por el tipo o frecuencia de las molestias. Las molestias afectaron también al uso del hábitat: los hábitats seleccionados tras la molestia fueron principalmente rocas y bosques indicando un cambio en el uso hacia hábitats inaccesibles o con abundante cobertura.

Key-words: Disturbance, Chamois, *Rupicapra rupicapra*, European Alps, management.

1. Introduction

More frequently outdoor activities focus on the remoter reserves and protected areas which have been established in order to guarantee refuge areas for wild animals. Such activities may have a strong influence on habitat use, behaviour and condition of Chamois (*Rupicapra rupicapra*) and other wild ungulates (CEDERNA & LOVARI, 1985; COTE, 1996; GANDNER & INGOLD, 1995; HAMR, 1988; PATTERSON, 1988; RAUER-GROSS, 1992; SCHNIDRIG-PETRIG & INGOLD, 1995; STOCKWELL *et al.*, 1991). The Berchtesgaden National Park (BNP) is the only large protected alpine reserve in Germany. Due to intensive wood logging and restocking with coniferous species in the past most of the present forests in the BNP are highly modified in terms of species composition, structure and age distribution. Besides the core area of some 66% without any management activities, permanent and temporal management zones exist for the re-establishment of natural mixed-forests and for population control of wild ungulates. In this context, the role of large ungulates, especially Chamois, on forest degradation is discussed and a study on space use and habitat selection of Chamois was initiated (BÖGEL *et al.*, 1998, 1999 and 2001). As part of this broader research on Chamois ecology, the objective of this study was to test whether different sources and frequencies of disturbance events result in different behaviour-

al responses of chamois and if management guidelines can be drawn from these findings.

2. Study Area

The BNP was established in 1978, it is located in the south-eastern part of Germany (N=47.7°, E=13.0°). It is 210 km² in size and bordered by a buffer zone to the north (260 km² in size) and by remote areas of the Austrian Alps to all other sides. Landscape characteristics are typically high alpine with altitudes ranging from 600 to 2713 m a. s. l. and cliffs of up to 2000 m. The geomorphology is determined by 3 valleys that lie in a north-south direction and by steep and rugged mountains in between mainly comprise limestone. Climate is strongly influenced by altitude with average yearly temperatures ranging from 7.2 °C (542 m a. s. l.) to 2.3 °C (1800 m a. s. l.) and precipitation ranging from 1514 mm (542 m a. s. l.) to 1753 mm (1740 m a. s. l.) with a pronounced peak (39%) during summer (June-August) and a minimum in November (5.5%). Days with total snow coverage vary with altitude and range from some 30 to >170 days. Habitat composition is: 40% forests, 25% rocks, 20% alpine meadows and pastures and 15% krummholz (typical sub-alpine shrub vegetation along the timberline). Three test sites were selected along the eastern mountain ridge of the BNP as actual study area. The test sites were comparable in their geo-morphological characteristics and habitat composition but differed in their infra-structural endowment and thus in their disturbance frequency.

3. Methods

In order to quantify the behavioural response resulting from different disturbance sources, the following parameters were recorded: i) type and amount of the disturbance source (5 classes), ii) distance to the chamois at first reaction ("reaction distance"), iii) distance to the chamois at the onset of flight ("flight distance"), iv) flight path (length, altitude difference covered, flight direction with respect to the relief and the disturbance source, and pre- and post-disturbance habitat types used), v) amount of time spent in vigilance behaviour (frequency and duration of securing activities), and vi) pre-disturbance activity, group size and composition. Weather conditions and estimated visitor frequency (4 classes, average estimate for the day) were also recorded in order to check if these variables had any influence on the behav-

avioural response. All distance measurements were taken with a LEICA VECTOR 1500 DAES geological binoculars from a suitable viewpoint in the research area (observer distance >500 m). This optical instrument has a laser distance meter (range 20-1500 m, 1 m resolution), a compass (0,1° resolution), and an inclinometer (0,1° resolution). By this, horizontal, vertical and true geometric distances can be measured separately. An integrated microprocessor allows relative vector measurements between any two points within the binoculars range. The effects of inclination and tilt on the accuracy of the compass measurements are compensated or, if too big, are indicated in the display. Therefore, relative vector measurements are highly precise and are practically limited by the size of the target area which is indicated in the field of view. To minimize failures associated with parallaxes, observational projections close to 90° were selected. Altitude differences between chamois and disturbance source >10 m were classified as "approach from above" or "below", with respect to relative position; altitude differences of less than 10 m were classified as "along altitude isoline". Distances at first reaction and flight distances were determined for the individual within a group which reacted first while all parameters related to the flight path were determined for the individual which performed the longest flight. By this procedure, results reflect the behavioural response of the most sensitive animals within a social group. From a total of 217 independent disturbance events, 174 and 188 reaction and flight distances, respectively, and 168 flight paths could be determined accurately. As the behavioural response varied greatly with the type of the disturbance source, possible effects of other parameters were tested pooling the data of hikers and ascending skiers, which did not differ significantly in terms of quantitative measurements of the observed flight reaction. By this it was possible to avoid effects related to different disturbance sources to conceal differences in the behavioural response associated with other parameters like season, visitor frequency or social structure of the disturbed group. All statistic tests were performed with SPSS.

4. Results

While reaction and flight distances varied significantly between test sites (Kruskal-Wallis-H-Test, reaction distances: $P < 0.001$; flight distances: $P < 0.001$), no differences in the length of the flight paths were observed (Kruskal-Wallis-H-Test: $P = 0.171$). Reaction distances varied between 43 and 390 m (mean=123 m) during winter and 18 and 1800 m (mean=207 m) during summer. The corresponding values for flight distances were 17-319 m (mean=85 m) during

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winter and 18-1600 m (mean=126 m) during summer. Lengths of flight paths ranged from 15-500 m (mean=112 m) during winter and 15-392 m (mean=126 m) during summer. The disturbance source had a highly significant influence on the behavioural response (Kruskal-Wallis-H-Test: $P < 0.001$, Figure 1). Disturbances from flying (para- and deltagliders, motorized aircrafts and helicopters) resulted in a stronger response than disturbances from ground

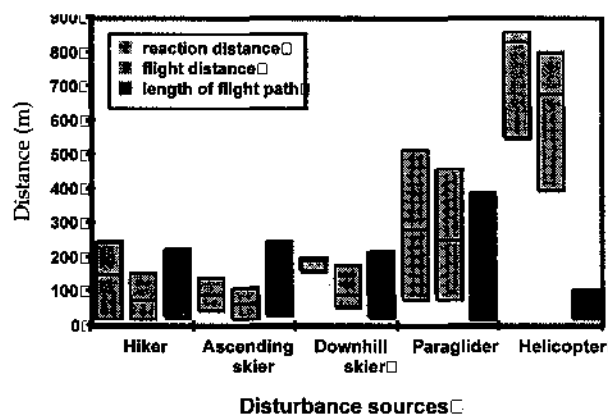


Figure 1. The influence of the disturbance source on the behavioural response (plotted are medians and 95% percentiles).

objects. Furthermore, downhill skiers resulted in a more intensive reaction than ascending cross-country skiers (Mann-Whitney-U-Test, reaction distance: $p < 0.001$, flight distance: $P = 0.007$). Motorized flying objects induced a much stronger response than para- or deltagliders (Mann-Whitney-U-Test, reaction distance: $P < 0.004$, flight distance: $P = 0.001$). In areas with frequent disturbances, the behavioural response (as indicated by all quantified parameters) was significantly reduced when compared with remote areas (Nemenyi and Mann-Whitney-U-Tests, $P = 0.036 \dots 0.001$, Figure 2). The group size of ground disturbance sources influenced the reaction distance (Kruskal-Wallis-H-Test: $P = 0.004$) but not the flight distance or the length of the flight paths (Kruskal-Wallis-H-Test, $P = 0.118$ and $P = 0.334$ respectively). Thus, larger groups resulted in a quicker reaction but not in an earlier flight or longer flight path. The direction of approach did not have any significant effect on the behavioural response as indicated by the quantified parameters (Mann-Whitney-U-Test, reaction distance: $P = 0.078$, flight distance: $P = 0.171$, length of flight path: $P = 0.559$). As to season, flight reactions were more intensive in

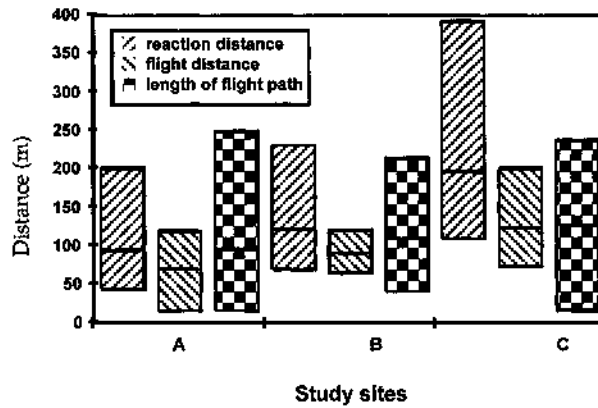


Figure 2. The influence of disturbance frequency on the behavioural response. Sites A, B and C represent test plots with increasing remoteness and thus decreasing disturbance frequency (plotted are medians and 95% percentiles).

summer than in winter (Kruskal-Wallis-H-Test, reaction distance: $P=0.008$, flight distance: $P=0.035$, length of flight path: $P=0.008$, Figure 3). There was no significant influence of snow coverage on flight reactions during the winter season (Kruskal-Wallis-H-Test, reaction distance: $P=0.074$, flight distance: $P=0.301$, length of flight path: $P=0.139$). The measured distances did not decrease with increasing snow coverage as might be expected to minimize energy expenditure (snow coverage refers to percentage of land covered with

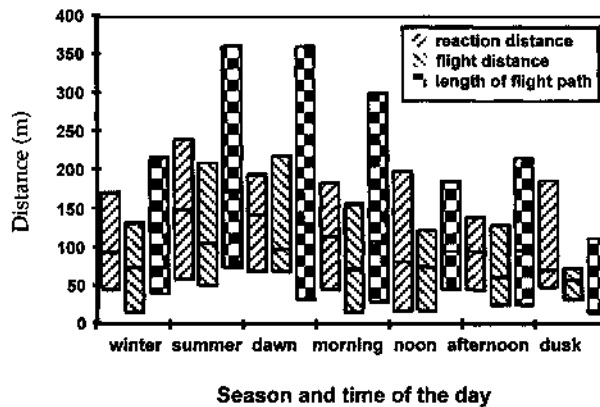


Figure 3. The influence of season and time of the day on flight reaction (plotted are medians and 95% percentiles).

snow as data on snow depth and composition were not available). Disturbance tolerance as indicated by reaction and flight distance was reduced during the early morning when compared to other daytime periods (Kruskal-Wallis-H-Test, reaction distance $P=0.003$, flight distance: $P=0.006$, Figure 3). Generally, males had shorter flight distances than females (Memenyi-Test: $P<0.05$) and the group size was negatively correlated with flight behaviour (Figure 4). Larger groups had reduced reaction and flight distances (Kruskal-Wallis-H-Test, reaction distance $P=0.001$, flight distance: $P=0.006$) and showed longer flight paths (Kruskal-Wallis-H-Test: $P=0.047$).

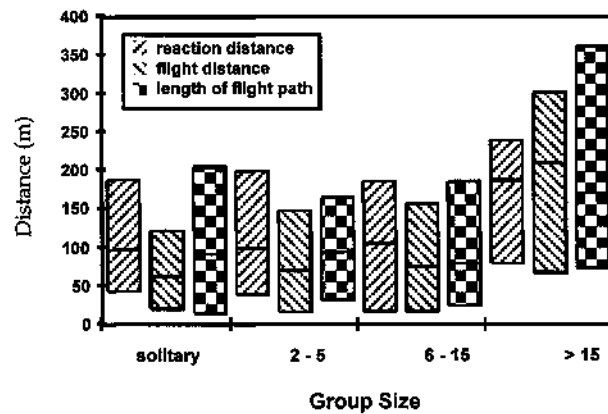


Figure 4. The influence of group size on flight reaction (plotted are medians and 95% percentiles).

Duration of the disturbance effect ranged from 2-30' (mean=5') and varied with sex and social organisation. Disturbances lasted longer in females than in males (Mann-Whitney-U-Test: $P=0.021$), and the duration of the disturbance increased with group size (Kruskal-Wallis-H-Test: $P=0.002$, Figure 5). The investment for vigilance behaviour (duration of securing behaviour) ranged from 0-69'' during a 5 minute period (mean=14'') with a corresponding securing frequency of 0-9 times/5' (mean: 5.2). Both variables were not correlated with remoteness of the test plots (Kruskal-Wallis-H-Test, duration of securing behaviour: $P=0.099$, securing frequency: $P=0.373$) or the daily variation in visitor frequency (Kruskal-Wallis-H-Test, duration of securing behaviour: $P=0.331$, securing frequency: $P=0.174$). There was also no significant difference between seasons (Kruskal-Wallis-H-Test, duration of securing behaviour: $P=0.557$, securing frequency: $P=0.064$). Males invested more time in vigilance behaviour and had a higher securing frequency than females

(Kruskal-Wallis-H-Test, duration of securing behaviour: $P=0.012$, securing frequency: $P=0.037$). The investment in vigilance behaviour was closely correlated with group size (duration of securing behaviour, Kruskal-Wallis-H-Test: $P=0.012$, Spearman rho: $s=-0.171$; securing frequency, Kruskal-Wallis-H-Test: $P<0.001$, Spearman rho: $s=-0.336$, Figure 6).

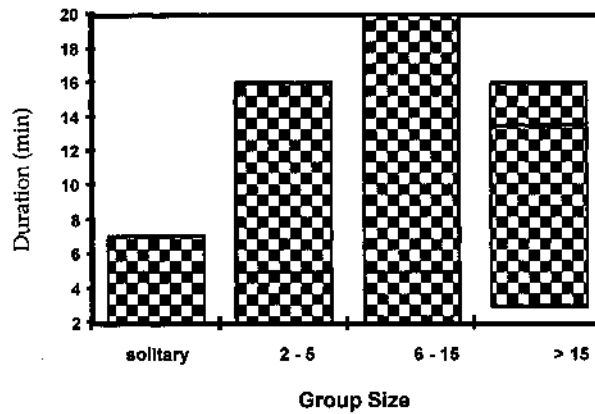


Figure 5. The influence of group size on the duration of disturbance effect (plotted are medians and 95% percentiles).

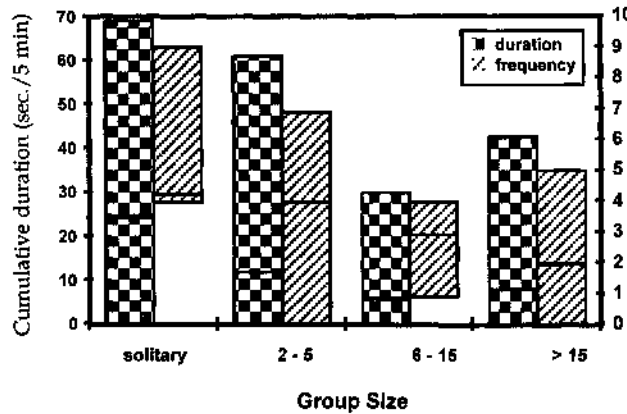


Figure 6. The influence of group size on the investment in vigilance behaviour (plotted are medians and 95% percentiles).

Habitat use was also affected significantly by disturbance events (Figure 7). In contrast to preferred pre-disturbance habitat types, post-disturbance habitat types consisted mainly of rocks and forests, indicating a shift in habitat use towards inaccessible habitat types (rocks) or habitat types with good cover

(krummholz and forests). When comparing open habitat types (alpine meadows, grassland and rocks) with woodlands (all forest types and krummholz), the disturbance-induced shift in habitat use towards woodlands was highly significant (McNemar test: $P < 0.001$). However, only minor differences in disturbance tolerance between various habitat types exist: while flight distances and flight paths did not vary between rocks, alpine meadows / grasslands and forests / krummholz, there were some significant differences in reaction distances between these habitat classes (Kruskal-Wallis H-Test: $P = 0.027$). The distance to the next safe refuge terrain turned out to be the dominant factor for the behavioural response: all measured parameters closely correlated to this distance (Spearman rho, reaction distance: $s = 0.390$, $P < 0.001$, flight distance: $s = 0.323$, $P < 0.001$). Uphill flight paths were significantly preferred (Π^2 test: $P = 0.001$): 47% were oriented uphill while 24% were oriented downhill and 24% of the flights followed the altitude isoline. This holds true even if the approach of the disturbance source was not from below (Π^2 test: $P = 0.029$). The length of the flight path was not influenced by the flight direction (Kruskal-Wallis H-Test: $P = 0.648$).

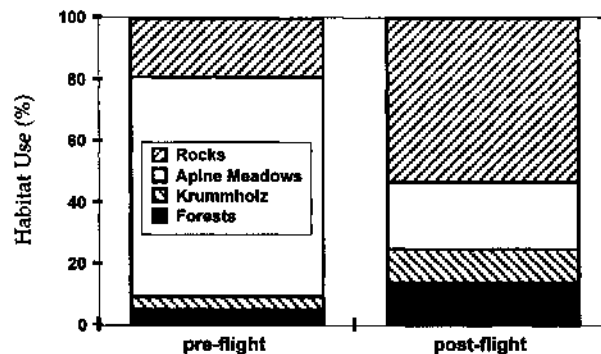


Figure 7. The influence of human disturbances on habitat use (% of habitat use refers to no. of observations).

5. Discussion

Although individual variation in the measured parameters was generally high, the study revealed a clear ranking of the disturbance impact according to the type of disturbance. As disturbances from flying and from downhill skiers were significantly higher when compared to slow moving hikers or ascending cross-country skiers, it can be postulated that the intensity of the

reaction increased with the speed of the disturbance source. This is in conformity with the neural response of specific retinal photosensors of mammals which are selectively sensitive to moving objects. This response is expected to be proportional to the angular velocity of the object, a hypothesis which could not be tested under field conditions as speed, ground distance and geometric perspective were highly variable within the data set, and the measured parameters do not allow for a geometric standardisation of measurements. As the behavioural response dramatically increased for motorized flying and at least helicopters are not characterized by very high air speeds, it can also be concluded that the noise level also has a strong influence on the behavioural response. We do not have sound pressure measurements to test this hypothesis, and it would be difficult to refer such measurements to the animals (and not the observer's) location. The massive behavioural response to helicopters is confirmed by other authors for Chamois (CZAKERT, 1985; GROSS, 1985; HAMR, 1984 and 1988; LEITNER, 1998; MOSLER-BERGER, 1983) and other wild ungulates (COTE, 1996; DAVIS *et al.*, 1985; DE-YOUNG & GUTHERY, 1989; GUNN *et al.*, 1985; GUNN & MILLER, 1980; MOSLER-BERGER, 1983; STOCKWELL *et al.*, 1991; SZEMKUS, 1993). HAMR (1984 and 1988) postulated that this may be due to the airborne threat caused by golden eagles (*Aquila chrysaetos*) as the main predator. However our data and that of other authors did not demonstrate a comparably intensive flight reaction following confrontation with golden eagle (CZAKERT, 1985; GREBENSTEIN, 1997; GROSS, 1985; KAPELARI, 1998), and ZEITLER (1995) reported even stronger reactions in red deer (*Cervus elaphus*), a species which is not preyed upon by golden eagle. In addition to speed and noise level, the predictability of disturbances seems to be of high importance: disturbance sources which are highly predictable like hikers on trails or ascending skiers on traditional routes resulted in the weakest response while highly unpredictable sources like cross-country downhill skiers or flying which are independent from any kind of infrastructure were characterized by the strongest response. However, KAPELARI (1998) and ZEITLER (1995) suggest that Chamois can adapt to some extent to flying by learning, if these activities occur on a regular basis. Our own results did not support this hypothesis. However, we did not have test plots with remarkably different helicopter frequencies to assess this properly. As the behavioural response was generally reduced in the easily accessible test plots (many visitors) when compared to the remote ones (few visitors), it can also be argued that disturbance frequency has a clear effect on the flight reaction, indicating habituation effects. It is important to note, that within the same test plots, the behavioural response was not significantly influenced by daily variations in visitor numbers. Obviously, habituation effects occur on a long but not on a short term basis. It can be hypothesized that

the adaptative value of habituation effects may focus on the limitation of time invested for vigilance behaviour in favour of increased time spent in other types of behaviour, like feeding. Habituation to regular and predictable disturbances were also reported by GREBENSTEIN (1997), GROSS (1985) and PATTERSON (1988) and can also be observed when comparing different intensities of hunting pressure (BÜTTNER, 1994; GUTÖHRL, 1995; LAUDO, 1988; SIMMEN, 1996; VÖLK & GOSSOW, 1997; PATTERSON, 1988; SCHRÖDER *et al.*, 1983; WEBER, 1982).

Reaction distances and flight distances were closely correlated. Individuals or social groups which reacted early also flew at a closer distance. While distance at first reaction and flight distance varied with disturbance intensity, the length of the flight path was not influenced by the disturbance type or frequency. This indicates that the flight path is clearly determined by the location of the closest adequate refuge terrain, and thus cannot be adapted to energetic constraints which may result from disturbance impacts. As the length of the flight path is also independent from flight direction (uphill, downhill or constant-level flights), the energetic cost of flights are obviously highly variable and not adapted in order to minimize energy expenditure. The prolonged flight paths, increased time budgets for vigilance behaviour and longer lasting disturbance impacts in larger social groups are of special concern in this context. However, the significantly reduced length of flight paths during wintertime may indicate limitations in energy budgets and can be interpreted as a biological adaptation to the harsh environmental conditions during this season. However it is difficult to determine whether this is a consequence of physiological exhaustion or a real strategy for minimizing energy expenditure. In conjunction with the decreased reaction and flight distances this reduction in flight paths might be interpreted as an increased stress tolerance during winter. However, this conclusion is questionable because physiologic consequences are likely (KRUCKENBERG *et al.*, 1998; BÖGEL *et al.*, 2001). HERBOLD (1992) and SCHNIEDRIG-PETRIG & INGOLD (1995) also argued that a reduced disturbance impact may not be concluded from shorter flight distances. The same is true concerning the constant length of flight paths regardless the type and frequency of the disturbance. As the reaction and flight distances are affected and other authors reported consequences for time budgets for various activity patterns (GROSS, 1985; GREBENSTEIN, 1997), an increased investment for vigilance behaviour may limit time for feeding and thus have a negative impact on energy budgets. While LEITNER (1988) and GREBENSTEIN (1997) supported our results that no sexual differences occur in vigilance behaviour, GROSS (1985) found an increased investment for females (securing frequency and duration). As group size in females is typically bigger than in males (own results;

GREBENSTEIN, 1997 and GROSS, 1985), it is likely that effects of group size and sex may interact and result in confounding interpretations. Our results on differences in investment for vigilance behaviour have been statistically analysed accounting for differences in group size, and other authors confirmed our findings that female groups have increased reaction and flight distances when compared with males (CZAKERT, 1985; GANDNER & INGOLD, 1995; GREBENSTEIN, 1997; GROSS, 1985; SCHNIEDRIG-PETRIG, 1994; LEITNER, 1998). Concerning correlation with group size, results of different authors are contradictory and suggest that the local situation (geomorphology, habitat patch size, etc.) is important in this context (CEDERNA & LOVARI, 1985; GREBENSTEIN, 1997; RAUER-GROSS, 1992). The same is true for possible preferences of certain flight directions (CEDERNA & LOVARI, 1985; CZAKERT, 1985; GREBENSTEIN, 1997) and underlines the dominant role of the location of the closest suitable refuge terrain (SCHNIEDRIG-PETRIG, 1994). Preferred post-disturbance habitat types were rocks and forests. However, the disturbance source is important in this context: while rocks were preferred in cases of ground disturbances (our results; CEDERNA & LOVARI, 1985; INGOLD *et al.*, 1986), forests were the preferred habitats if disturbances originated from flying objects (our results; SCHNIEDRIG-PETRIG, 1994). When comparing results between different studies, this might be caused by different habitat composition and specifically evolved behavioural responses. However, this was also the case within the same study areas of our own studies. If the preference of forest as escape terrain is the ultimate cause of forest damage and to which extent this is originated by human disturbance cannot be addressed by this study. As the behavioural response to disturbances is also dependent on the habitat type, the daily patterns of reaction and flight distances could be related to a circadian rhythm in habitat use: chamois feed mainly during the early morning and these feeding grounds are far from refuge areas resulting in increased reaction and flight distances. Later, they move into steep terrain and cliffs for rumination, resulting in a decreased behavioural response to disturbances. However, a decreased sensitivity to disturbances cannot be concluded from these findings as disturbance intensity may be decreased in remote areas such as cliffs and forests.

6. Management implications

The results presented above establish a clear ranking of the impact of human disturbance: motorized flying has by far the strongest effect followed by para-/delta-gliders and downhill skiers; ascending skiers and hikers cause

the weakest flight reactions. The spatial and temporal predictability of the activities is important. In order to manage the visitor flow, sporting activities and airborne traffic, our findings suggest that park users should stay on trails and traditional skiing routes, and restrict starting points for paragliders to few spots and implement a minimum flight altitude (above ground). As a practical guideline we suggest a magnitude of 300 m (75% percentile of the observed flight distance for this disturbance type) although the angle of perception of chamois may deviate from the vertical axis. By referring to the 75% percentile, the majority of the observed animals are considered without accounting for the most sensitive individuals. Motorized flying should be restricted to rescue and urgent transport with a flight altitude as high as possible. It may be adequate to discuss restricted-access areas where forest damage is high and may be triggered by disturbance impacts. This is especially valid for high quality habitats during winter and or early spring with their naturally high Chamois densities and group sizes. In this context, we believe that convincing people on a voluntary basis is the better approach rather than a legislative route which is difficult to control. Public education is of critical importance in this context. The significance of the disturbance impact on energy budgets, condition and population dynamics of Chamois is not addressed in this study and clearly place a limit on the assessment of human disturbance impacts. A study addressing physiological consequences of disturbances using heart rate telemetry and faecal cortisol concentrations is currently under ways and will enhance a more complete assessment of disturbance impacts.

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