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Effects of paragliding on alpine chamois *Rupicapra rupicapra rupicapra*

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We studied the influence of paragliding flying activity on female chamois *Rupicapra r. rupicapra* behaviour and distribution in four areas in the Swiss Alps. We observed chamois as they were overflown by co-operative pilots on controlled routes. Female chamois fled at great distances (up to a maximum of 900 m) in all areas and sought refuge within forest cover after paragliders appeared. Escape distances were larger when paragliders appeared over the animals than when they appeared at about the same heights, and were shorter when chamois were closer to forest cover than when they were in open alpine meadows above the timberline. Colour of the paragliders, distance to rocks, and group size did not affect the reactions of the chamois. In areas with regular paragliding, chamois moved away from the air traffic and eventually disappeared into the forest, and did so earlier with increasing flying activity. The chamois stayed within forest cover longer with increased duration of paragliding off the normal flight path. In an area with only sporadic paragliding, chamois sought refuge within the forest for up to four hours after single paraglider fly-overs. In an area with no paragliding, chamois stayed in the pastures and rocks above the treeline all day. This study provides a basis for the development of control measures for paragliding in certain areas.

Key words: Alps, chamois, disturbance, escape distances, habitat use, paragliding, Rupicapra rupicapra rupicapra, ungulates

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In Central Europe there are few places left where untouched wilderness can still be found. The Alps may be regarded as one of these places as they still have valleys and mountain ranges with very moderate human influence. However, increasing tourism in the Alps, which continually takes on new facets, is advancing further and further into the natural habitats of wildlife (Ingold, Schnidrig-Petrig, Marbacher, Pfister & Zeller 1996). In particular, the touristic conquest of the air has been very successful in the last two decades. The number of licensed aircraft in Switzerland has increased within this time period by about 70% for motor- and sailplanes, and by approximately 450% for helicopters (BAZL 1995). In the mid-1970s hanggliders appeared, and by 1992 there were >6,000 hangglider-pilots in Switzerland. Around 1985, the first paragliders could be observed in the Alps. By 1998, there were >14,000 licensed pilots in Switzerland (SHV 1999). Paragliders turn easily and can be flown close to mountain slopes. Due to better equipment, longer flights have become possible and more pilots are moving into new, previously unflown areas, which include prime wildlife habitat.

How do paragliders affect animals such as mountain ungulates? The chamois *Rupicapra r. rupicapra* is a suitable species for examining this question due to its Alp-wide distribution (Knaus & Schröder 1983, Sägesser & Krapp 1986), its feeding activity above the timberline (Couturier 1938, Schröder 1971a,b, Hofmann & Nievergelt 1972, Pachlatko 1980, Elsner von der Malsburg 1981, Pachlatko & Nievergelt 1985), its ease of observation, and its ready contact with paragliders in the Alps. Chamois live in groups of varying number and composition and segregate spatially with respect to sex except during the rut in November (Krämer 1969a,b, Marbacher 1989). Kids are born in May or June and are nursed until November (Ruckstuhl & Ingold 1994).

The effect of paragliders on chamois in the open pastures above alpine forests, preferred habitat for female chamois in many parts of the Alps, has not been investigated. Our preliminary observations indicated that in areas where flying activity is rare, female chamois react to paragliders with intense flight behaviour. But how do they behave in areas with regular and intense paragliding on locally limited routes? Do they ignore paragliders or do they alter their habitat use, so that they do not have to take flight anymore? Are chamois capable of adjusting to the unpredictable appearance of paragliders flying off normal routes? Do they avoid them by flight over long distances or by retreating to places offering some hiding? Such behaviour could lead to pronounced changes in the distribution of female chamois.

Our specific objectives were to: 1) determine the distances at which chamois detect and escape from paragliders; 2) describe refuge sites of chamois; 3) evaluate the effect of flight path, paraglider colour, proximity to the preferred refuge site, and chamois group size on the reaction of the chamois; 4) determine the effect of flight activity on chamois distribution. All these aspects were studied on female chamois. The results of our study should provide an insight into the relationship between paragliding and chamois, and provide a basis for management decisions.

Study areas

Our study was conducted at four locations in the Swiss Alps. Each location consisted of extended alpine pastures, scree fields and rocks above the tree line, providing open chamois habitat and thus excellent observation possibilities. The main investigations were carried out in Kandersteg (Allmenalp), where intense paragliding (30-200 take-offs per day) has occurred since 1985. Additional observations were made at the Niesen, an area with regular but less intense paragliding than Kandersteg, at the Augstmatthorn, where paragliders first appeared in 1989 and could only be seen sporadically, and at the Doldenhorn where no paragliders have been observed so far. In the Kandersteg, Niesen and Doldenhorn areas, chamois were hunted every year during two weeks in September. The Augstmatthorn study area lay within a game reserve. All study areas were regularly visited by lynx *Lynx lynx* and golden eagles *Aquila chrysaetos*, which are natural predators of chamois.

The Kandersteg study area lies west of the village of Kandersteg in the Bernese Alps. It ranges in altitude within 1,300-2,500 m a.s.l. and encompasses approximately 550 ha of alpine pastures and fairly steep, bare rocks in the upper parts facing southeast. Below the tree line (1,850 m a.s.l.) spruce *Picea abies* and fir *Abies alba* forests with sparse vegetation on the ground are interspersed with rockcliffs. During the spring and summer months, about 70-90 female chamois with kids inhabited the study area. From May until October, paragliding occurred on almost every clear and calm day. During the vacation season in July and August and on sunny weekends, >200 paragliders started on the Allmenalp. Most pilots flew more or less straight down to the village on the 'normal route'. Some paragliders left the normal route to soar across the slopes. We categorised these paragliders as 'off-route paragliders'. Paragliding mostly occurred from 07:00 to 17:00. The time off-route paragliding began depended on the thermic conditions.

The Niesen is a 2,362 m high mountain peak of the Bernese Alps rising up behind Lake Thun. The study area contained the southeast facing slope of the Niesen and the northeast-facing slope of the neighbouring 2,394 m high mountain Fromberghorn along the same mountain range and covered approximately 400 ha. The cliffs below the peaks pass into scree fields and vast alpine pastures and below ca 1,600 m a.s.l. spruce-fir forests are interspersed with meadows. During summer the study area was inhabited by about 30-40 female chamois and their kids. The first paraglider pilots appeared at the Niesen in 1985. Because of its unpredictable wind conditions, the Niesen was not as popular among paraglider pilots as the Kandersteg region with its predictable wind and thermic conditions. Paragliding usually occurred from 09:00 to 17:00; on sunny, calm days up to 40 paraglider pilots were flying at the Niesen.

The 2,137 m high Augstmatthorn is one of several peaks of a northeast to southwest running mountain ridge of the Bernese Alps near Interlaken. The 500-ha study area is situated on the steep northwest slopes of the Augstmatthorn. It is dominated by steep alpine pastures, rock cliffs and scree fields, which give way to small forests at lower elevations. The area encompassed the summer home range of 100-120 females with kids, of which about 30 individuals were marked with yellow hornstrips. The first paragliders appeared in this area in 1989. From 1990 to 1992 paragliding has increased during the spring and summer; in 1992 at least one paraglider could be observed at the Augstmatthorn on approximately 15% of days. Compared to the flying intensity in Kandersteg and at the Niesen, paragliding at the Augstmatthorn was 'sporadic air-traffic' (<5/week).

Additional observations on the habitat use of female chamois were carried out at the Doldenhorn, a remote area southeast of the village of Kandersteg. The south-facing slope of the 3,643 m high Doldenhorn did not experience any paragliding at all. Above approximately 2,800 m a.s.l., there are only bare rocks, glaciers and scree fields, and during summer and autumn, chamois lived within the zone dominated by alpine pastures (2,000-2,800 m a.s.l.). Below 2,000 m a.s.l. spruce-fir forest dominates. We observed a herd of approximately 40 females and juveniles in this area.

Methods

Chamois reactions and distribution

We observed female chamois being overflown by controlled paragliders from June to October at Augstmatthorn in 1990, at Kandersteg in 1991 and at Niesen and Doldenhorn in 1992.

We documented the response of female chamois to paragliders and measured the escape distance in Kandersteg, Niesen and Augstmatthorn. Alert distance was determined as the distance between chamois and the paraglider at the moment when the chamois raised its head and looked towards the paraglider. Escape distance was determined as the distance between chamois and paraglider at the moment when the chamois ran away. We also marked the positions of the chamois on a map (1:5,000) and recorded the places where they sought refuge, as well as variables such as the paragliders' flight path relative to the observed chamois (Fig.1e-b), the colour of the paraglider, and the group size of the chamois. We observed chamois as they were overflown by paragliders on prearranged routes (controlled paraglider flights). But we also registered the chamois' reactions as they were overflown by paragliders that were not 'controlled', but flew approximately the same routes. We made observations of females in groups with kids.

Before a pilot started, he was told the preferred route to fly. All pilots performed straight flights, were visible at distances of >1.5 km, and kept approximately 150 m away from the slopes of the respective study area. The chamois were observed from two different points that provided coverage of the whole area. The two observers were in radio contact with each other. About half an hour before the arranged starting time of the paraglider, both observers selected a grazing female chamois, if possible one with a kid, which thereafter was observed as a focal animal. There had to be a distance of >500 m between the two chamois under observation (to exclude social influences). Locations of the focal animals were marked on a map. The composition and the number of individuals in the focal animal's groups were recorded, too. After the start of the paraglider flight we dictated our observations to a tape recorder. To be able to estimate the 'alert distance' and 'escape distance' it was necessary to know the position and the absolute height of the paraglider at the time when the focal animals reacted with alert and flight behaviour. To achieve this, the observers drew a line on the area-map connecting the paragliders position with their own location by using the irregularities of the skyline as landmarks; furthermore, one observer estimated the paragliders angle of inclination using a simple inclinometer (see Fig. 1). After a little practice, this whole procedure lasted no more than five seconds.

We studied effects of paragliding on the distribution of female chamois in Kandersteg near and far from air traffic on days with varying flying intensities on and off

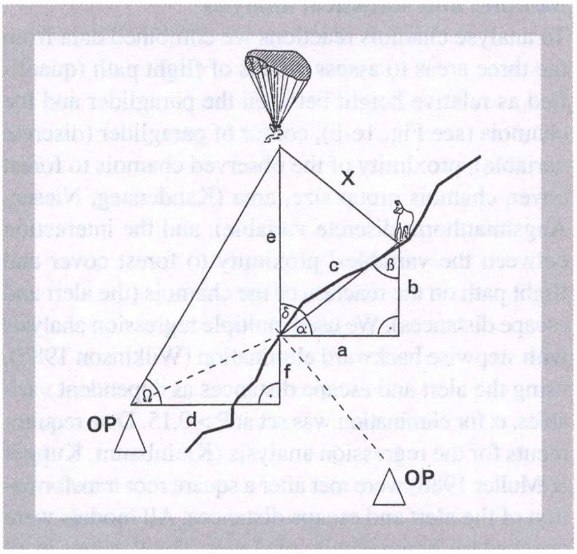

Figure 1. Schematic presentation of the basis for calculation of alert and escape distances (= X). OP = observation points; a can be measured on the map; b can be estimated by counting the contour lines with an equidistances of 10 m; $c = \sqrt{a^2+b^2}$; $\tan\alpha = b/a \Rightarrow 90° - \alpha = ß = \delta$; d can be measured on the map; f can be estimated by counting the contour lines with an equidistances of 10 m; Ω is estimated with an inclinometer; $\tan \Omega = (e+f)/d \Rightarrow e = (d \cdot \tan)-f$; $X = \sqrt{c^2+e^2 - 2 \cdot c \cdot e \cdot \cos\delta}$.

the normal route, and at Augstmatthorn on days with and without paraglider flights. We also made observations at the Doldenhorn, as a control. At Kandersteg observations were carried out from dawn to dusk, whereby the study area was scanned every 15 minutes and the locations of all visible female chamois were marked on a map. The time when a chamois or a group of chamois disappeared into a forest was recorded, and so was the time of reappearance of the chamois. This was possible because of the excellent observation conditions. Furthermore, the following data were recorded: 1) the take-off site, start time and flight path of every paraglider, and 2) hourly weather conditions and air temperature at one observation point. At Augstmatthorn, on the one hand, locations of individually marked female chamois (Bauman 1993, Ruckstuhl & Ingold 1994) were registered continuously from dawn to dusk. On the other hand, the locations of all chamois were marked on a map every hour, registering the individually marked chamois separately. Whenever the individually known chamois retreated into the forest, the forest surroundings were scanned to measure the duration of their stay within the forest cover. At Doldenhorn, the distribution of the female chamois was observed on randomly selected sunny days in the summer of 1992. The locations of the chamois were registered using the scan sampling method at 15-minute intervals from dawn until early afternoon.

Samples and statistical analysis

To analyse chamois reactions we combined data from the three areas to assess effects of flight path (quantified as relative height between the paraglider and the chamois (see Fig. 1e-b), colour of paraglider (discrete variable), proximity of the observed chamois to forest cover, chamois group size, area (Kandersteg, Niesen, Augstmatthorn; discrete variable), and the interaction between the variables' proximity to forest cover and flight path on the reaction of the chamois (the alert and escape distances). We used multiple regression analysis with stepwise backward elimination (Wilkinson 1987), using the alert and escape distances as dependent variables. α for elimination was set at $P > 0{,}15$. Data requirements for the regression analysis (Kleinbaum, Kupper & Muller 1988) were met after a square root transformation of the alert and escape distances. All models were checked for homogeneity of slopes. The P values in all ANOVA tables of this study are two-tailed. Mean flight distances in the different areas were tested pairwise using the Scheffé-test.

For the analysis of chamois distribution we gathered data in Kandersteg from July to October from 23 whole-day (sunrise until sunset) and six half-day (sunrise until noon) observations. Observation days were arranged with regard to season, time of leaving the feeding grounds, and type of paragliding air traffic on and off the normal route.

To assess the effect of paragliding on the distribution of female chamois, the area between the paraglider take-off point and the northern border of the study area was divided into two sections (near the normal route: <800 m; far from the normal route: >1.000 m). Normal-route paragliders could be seen by the chamois in the first section, but not in the second section. Lateral movements of the chamois were analysed by measuring on the map the distance to the normal route within which 3/4 of the maximum number of chamois observed in the morning were grazing 60 minutes before and 30 minutes after the first paraglider started. The time of leaving the feeding grounds was defined as the time after sunrise, when 3/4 of the maximum number of chamois observed in the morning lay down in the cliffs or retreated to the forest. This analysis included data from 15 days with air traffic on the normal route, and no off-route flying before 12:00.

To investigate how different variables affected the time of retreating into the forest, data from all days in summer ($N = 9$) when the female chamois retreated to the forest after normal-route flying began, but before the first paraglider flew cross-country, were analysed using a multiple regression analysis with stepwise backward elimination (Wilkinson 1987). The variables included in this analysis were: 1) the time when the first paraglider started (in minutes after sunrise), 2) the number of paragliders starting within the first 30 minutes on the normal route air traffic as a measurement for the flying intensity (transformed using the natural logarithm function), and 3) the temperature three hours after sunrise. Because of the small sample size, the data were checked for extreme values using the jack-knifing method.

All 23 whole-day observations (13 summer/10 autumn) with sunny weather were included in the analysis of the duration of staying within forest cover close to paragliding air traffic (Allme-Gräben) in Kandersteg. The method used for estimating the time of leaving the feeding grounds and retreating into the forest is indicated above. The time of leaving the forest and returning to the feeding grounds in the afternoon or evening was defined as the 'time when 1/4 of the maximum number of female chamois observed in the morning had left the forest again'. The time between these two points was defined as the 'duration of stay within forest cover'. To investigate how the different variables affected the duration of stay within forest cover, the data were analysed as described above. The variables included in the analysis were: 1) duration of the air traffic on the normal route, 2) intensity of normal route air traffic (number of paragliders/time between first and last paraglider), 3) duration of the air traffic off the normal route, 4) intensity of off-route paragliding, 5) temperature at 12:00, and 6) season (summer/autumn). The air traffic intensity values on and off the normal route were log-transformed after adding 1, i.e. $\ln[(x+1)]$; on two days no paragliders occurred, so x was 0!

During 1990 and 1991, the distribution of the chamois at the Augstmatthorn was observed on 23 sunny days with no paraglider flights. During 1989-1992, it was possible to document the distribution of female chamois before and after a paraglider appeared over the northwest facing slope on 11 days. The frequency at which chamois retreated to forest cover (days when >3/4 of the maximum number of chamois observed in the morning left the feeding grounds and rocks and retreated to forest cover) with and without a paraglider were compared using the Fisher's exact test. Habitat use by the Doldenhorn chamois was recorded on seven sunny days.

Results

Reactions of female chamois to paragliders

Female chamois showed strong reactions to paragliders in all study areas, becoming alert at distances of up to 1,280 m and taking flight at distances of up to 900 m (Table 1). Chamois took flight in 47 of 54 cases; they fled into forests (N = 35), towards forested areas, but remained within their feeding grounds (N = 7), and climbed into steep rocks (N = 5). Their choice to flee into forest cover did not seem to depend on the distance to the nearest forest or rocks, nor on the positions of the refuge sites relative to the animals' location; in 22 cases, the chamois were standing closer to the chosen refuge site. Of 18 cases where rocks were accessible at the same or at a shorter distance, chamois took refuge in forest cover in 16 (16:2; binomial test: $P < 0.001$). In 20 observed cases, chamois fled into the forest in 18, although rocks were accessible at the same elevation as the forest cover (18:2; binomial test: $P < 0.001$). Hence, chamois clearly preferred forest cover to rocks as a refuge site.

Table 1. Median, first/third quartile and minima/maxima of alert and flight distances (in metres) of female chamois to paragliders in the three areas in the Swiss Alps during 1990-1992.

Area	Median	First/third quartile	Minima/Maxima	N
Kandersteg				
Alert distance	530	380/680	190/1020	30
Escape distance	450	280/660	190/870	27
Niesen				
Alert distance	460	300/610	230/1280	14
Escape distance	410	270/540	130/800	10
Augstmatthorn				
Alert distance	780	750/820	640/970	10
Escape distance	780	670/820	640/900	10

About 42% of the variation among alert distances was explained by a reduced regression model containing the variables relative height between the paragliders and the chamois (RH) and proximity of the observed chamois to forest cover (FC; $F_{2,51} = 18.811$, $P < 0.001$, $r^2 = 0.425$, N = 54). Relative heights between paragliders and chamois affected the alert distance significantly (reduced model: $t^{RH} = 5.562$, df = 52, $P < 0.001$; $t^{FC} = 1.464$, df = 52, $P = 0.149$); chamois reacted at larger distances with alert behaviour when paragliders appeared at greater relative heights. Alert reactions were independent of the paragliders' colour (CO), their closeness to forest cover, the focal animal's group size (GS) and of the area (AR; full model: $F^{CO} = 0.328$, df = 2,51, $P = 0.857$; $F^{FC} = 1.114$, df = 1,52, $P = 0.297$; $F^{GS} = 1.177$, df = 1,52, $P = 0.284$; $F^{AR} = 1.662$, df = 2,51, $P = 0.202$).

More than 75% of the variation among escape distances was explained by the chosen regression model ($r^2 = 0.758$, N = 47). The relative heights between paraglider and chamois, the proximity to forest cover, and the area affected the escape distances (reduced model: $F^{RH} = 57.742$, df = 1,41, $P < 0.001$; $F^{FC} = 7.007$, df = 1,41, $P = 0.011$; $F^{AR} = 6.077$, df = 2,41, $P = 0.005$). The female chamois reacted by fleeing at larger distances when the paragliders appeared above them and when they were grazing far away from forest cover, than they did with passing paragliders and when they were standing at the forest edge. Escape distances were independent of the paragliders' colour and the focal animal's group size (full model: $F^{CO} = 0.262$, df = 2,44, $P = 0.900$; $F^{GS} = 0.022$, df = 1,45, $P = 0.883$).

Comparisons of the mean escape distances between areas indicate, that female chamois at the Augstmatthorn escaped at larger distances than the female chamois in Kandersteg ($P = 0.022$) and at the Niesen ($P = 0.008$). On the other hand, the escape distances in the areas Kandersteg and Niesen did not differ ($P = 0.677$).

Distribution of female chamois exposed to intensive paragliding in Kandersteg

In the morning, female chamois in the sections exposed to intense paragliding (section 1) and far from paragliding (section 2) were feeding in small groups in pastures above the tree line. On the 15 observation days with air traffic on the normal route, and no flying off-route until noon, the chamois within section 1 were scattered all over the area before paragliding started. After paragliding started, they moved away from the flying activity to continue grazing at a significantly larger median distance. In the neighbouring section 2 no such movement could be observed (section 1: median distance to normal route before ($\tilde{x}$) = 420 m, and after ($\tilde{x}$) = 710 m paragliding started, $P < 0.001$; section 2: before ($\tilde{x}$) = 1,210 m, and after ($\tilde{x}$) = 1,170 m, $P > 0.05$; Friedman two-way ANOVA).

In the morning, the female chamois in section 1 left the feeding grounds at an average of about four hours after sunrise, approximately 1.5 hours earlier than the female chamois in section 2 (Wilcoxon matched-pairs signed rank test, one-tailed: $P < 0.05$). In section 1, the chamois retreated to the forest on all 15 days. After their extended feeding period, the chamois in section 2 moved down into the forest on two days, up into the steep rocks on nine days, and on four days they lay down in the pastures towards noon and stayed there the whole day. Hence, in the section far from paragliding air traffic (2), the chamois stayed in the open more frequently than in the section closer to the air traffic (1) (Fisher-exact-test: $P < 0.001$). However, on all days when off-route paragliders flew over section 2, the chamois there also retreated into forest cover.

On five of 16 observation mornings, the female chamois in section 1 disappeared into the forest shortly after the first paraglider left the normal route. On these days, the first off-route paraglider appeared earlier than on most days. On 11 days, they retreated into forest cover after paragliding started on the normal route, but before the first off-route paraglider appeared. In this latter case, they left the feeding grounds earlier with more intensive paragliding on the normal route ($F = 7.578$, df = 2,6, $P = 0.04$), irrespective of the beginning of the air traffic ($F = 1.232$, df = 2,6, $P = 0.318$) and the temperature ($F = 0.279$, df = 2,6, $P = 0.279$; values of the reduced regression model: $F_{1,7} = 12.065$, $P < 0.01$, $r^2 = 0.633$; Fig. 2).

On all 13 whole-day observations in summer and on eight of 10 days in autumn, there was intensive flying on and off the normal route. On these days, the female chamois stayed within the forest for several hours each day (2.5-8 hours). When off-route paragliding was interrupted for >1.5 hours the chamois started to return to the pastures to feed, only to retreat to forest cover after the next paraglider appeared. The duration of stay within the forest was affected by the duration of air traffic off the normal route ($F = 13.869$, df = 2,20, $P = 0.002$), but not by the intensity of paragliding on ($F = 0.788$, df = 2,20, $P = 0.388$) and off the normal route ($F = 1.614$, df = 2,20, $P = 0.222$), the duration of paragliding on the normal route ($F = 1.603$, df = 2,20, $P = 0.224$), temperature ($F = 0.017$, df = 2,20, $P = 0.899$) and season ($F = 0.726$, df = 2,20, $P = 0.407$; values of the reduced regression model: $F_{1,21} = 38.473$, $P < 0.001$, $r^2 = 0.647$; Fig. 3).

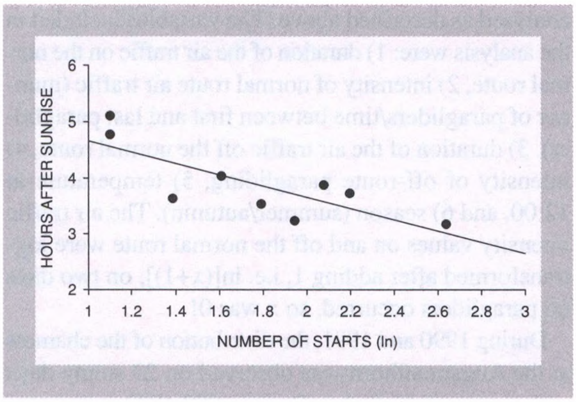

Figure 2. Relationship between the intensity of the air traffic on the normal-route expressed as ln of the number of paragliders starting within the first 30 minutes and the time the female chamois leave the feeding grounds and retreat into the forest expressed as hours after sunrise. The regression is described by: y = 5.700 - 1.009 (ln x).

Distribution of female chamois at the Augstmatthorn and the Doldenhorn

On sunny days in summer and autumn the female chamois of the northwestern slope of the Augstmatthorn normally grazed on the open scree fields and pastures until about noon, when most of the chamois lay down; in the late afternoon they usually started feeding again. On nine days, after a paraglider appeared, all chamois retreated into forest cover, on two days they climbed into the rocks above the feeding grounds and moved over the ridge into the southeastern slope of the Augstmatthorn

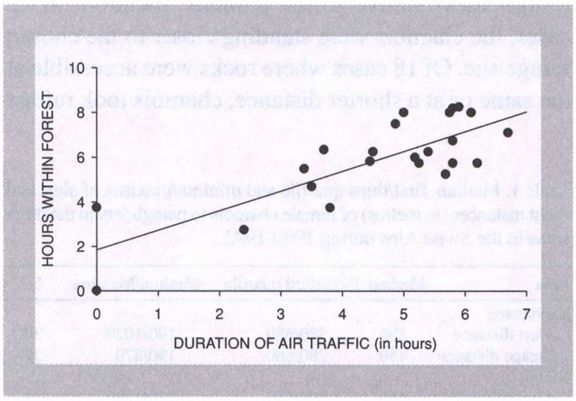

Figure 3. Relationship between the duration of the air traffic off the normal-route and the duration of the time during which the female chamois stayed within forest. The linear regression line is described by: y = 1.842 + 0.884 x.

(remaining in the open without/with paragliders 22:1; retreating into the forest without/with paragliders 2:9; binomial test: $P < 0.001$). Some of the animals that disappeared into the forest reappeared after about 20 minutes to graze again at the edge of the forest, but most of the chamois stayed within the forest for 2-3 hours, some for up to four hours.

On all seven observation days at the Doldenhorn the female chamois spent the morning in the alpine pastures at about 2,300 m a.s.l., above the mountain forest. The chamois grazed until about noon, then climbed up into the steep rocks above the pastures and lay down well hidden; around 15:00 the chamois climbed back down to their feeding grounds and stayed there until dusk.

Discussion

Immediate reactions of female chamois to paragliders and other air-based vehicles

Female chamois reacted to paragliders with alert and flight behaviour at great distances, even in areas with intensive flying activity. Alert distance is thought to indicate when animals take notice of something; escape distance, on the other hand, is an indicator of how threatening something is to the animals. The fact that female chamois seem to feel very threatened when paragliders appear above them is interesting. The reasons behind this phenomenon are untested. Perhaps it is easier for ungulates, having adopted flight as the most important predator avoidance strategy, to escape by running uphill; so anything approaching the animals from below is less disturbing than anything appearing from above. It may also be that a larger proportion of things appear suddenly and threateningly from above and this therefore alarms the animals to a greater extent. Paragliders appearing above female chamois feeding in the open pastures above the tree line elicited early flight at high speed over long distances (several hundred metres). Sporadic observations at other areas with paraglider flying activity in central Switzerland confirm this. Furthermore, most of the gamekeepers of the Swiss Alps and Prealps questioned by Mosler-Berger (1994) reported similar observations among chamois. Chamois react to low-flying air-based vehicles such as paragliders, hanggliders, sailplanes, helicopters, motorplanes or hot-air balloons characteristically with flight downhill towards or into forest cover (Ingold et al. 1996). With hikers, dogs or ground-based vehicles, chamois typically flee uphill to inaccessible rocks (Cederna & Lovari 1983, Zeller 1991, Vallan 1992, Ingold et al. 1996). These behaviours seem to be adaptive to avoid predators. Because of their inability to climb, ground-based predators such as wolf *Canis lupus* and lynx can hardly follow the chamois into the rocks, but they could easily overwhelm the chamois in the forest (Haller 1992). On the other hand, to avoid predators from the air, the best thing to do is to hide in dense cover. Being close to forest cover, their preferred refuge site from air-based vehicles, seems to appease the chamois, as indicated by the shorter escape distances of chamois standing close to forest cover. Zeitler (1995) observed small flight distances among chamois at the Hochgrat and the Nebelhorn in the Bavarian Alps, where chamois live in a more or less forested habitat and hence are never far away from their preferred refuge site. Clearly, staying close to places offering good cover should make the animals feel much more 'secure'. Geist, Stemp & Johnston (1985) found, that distance from escape terrain is a very important factor in affecting heart-rate of bighorn sheep *Ovis canadensis*. According to the predator-prey interaction optimality model of Ydenberg & Dill (1987), the optimal flight distance of a prey-animal reflects a trade-off between the costs of remaining when a predator is at a particular distance (being directly proportional to the risk of capture) and the costs of flight, which reflects the benefits of remaining. When approached by a predator, a prey animal feeding on a high-quality resource should take flight at a shorter distance than an animal feeding on a low quality resource. Basically, all air-based vehicles flying relatively close to the ground, appearing suddenly or hovering for some time over the same spot can elicit flight behaviour among chamois as well as other mountain ungulates such as Alpine ibex *Capra ibex ibex* (Szemkus, Ingold & Pfister 1998). But paragliders, especially, combine the qualities that seem to elicit strong reactions: flying close to mountain slopes, more or less noiselessly, slowly, and staying in the air above the same area for long periods of time, as a raptor-like stimulus. Conversely, chamois hardly react to fast-flying and deafeningly loud military jets (Ingold et al. 1996). Harrington & Veitch (1991), Murphy, White, Kugler, Kitchens, Smith & Barber (1993) and Weisenberger, Krausman, Wallace, De Young & Maugham (1996) have reported similar observations for other ungulate species. But Maier, Murphy, White & Smith (1998) showed that caribou *Rangifer tarandus* increased activity and distance moved in response to jet aircraft during physiologically sensitive periods such as post-calving. Nevertheless, with jet aircraft the optical stimulus does not occur at the same time as the acoustic stimulus: the jet is out of sight by the time the loud roaring reaches the ear. On the other hand, propeller planes and helicopters often announce themselves acoustically long before they can be seen.

The comparison of the reactions in different areas reveals that the female chamois at the Augstmatthorn take flight at greater distances than the female chamois in Kandersteg or at the Niesen. Possible explanations for these differences in escape distances could be habituation (which we regard as a stimulus-specific decrease of response among individuals in the course of time), difference in the reaction sensibility of the animals fixed on a genetic basis, or population dynamic phenomena such as emigration of certain individuals. Habituation could account for the observed difference, since at Augstmatthorn chamois so far did not face many paragliders, whereas in Kandersteg and at Niesen fairly intensive paragliding has occurred for several years and chamois definitely have had many encounters. Habituation can be expected sooner with increasing predictability of a stimulus in space and time. Locally-limited and regular air traffic can only be found in areas which are used by paragliding schools (like Kandersteg-Allmenalp). Experienced pilots prefer to fly off these normal routes whenever thermic conditions allow them to do so. Off-route flights are very unpredictable and it is not surprising that chamois continue to show strong reactions, even in areas like Kandersteg. Sensibility of the animals, on the other hand, must be expected to differ depending on the level of hunting in the past or on the degree to which populations have had contact with different forms of tourism before paragliding started. The latter is not likely to account for the observed differences here, because hiking has taken place in all the study areas for many years (pers. comm. with gamekeepers). If, on the other hand, hunting played an important role, the Augstmatthorn chamois would be expected to have the shortest escape distances because, contrary to the Kandersteg and Niesen chamois, they have not been hunted for the last few decades. Another possible explanation for the different escape distances in the three areas is a population segregation according to timidity. According to observations of the Kandersteg gamekeeper, approximately half of the chamois population left the Allmenalp area after the beginning of the flying activity in 1985 (H. Aegerter, pers. comm.). Possibly, individuals that did not manage to deal with the altered conditions left the area and only the less timid individuals remained. This might result in a selection against timidity.

Altered habitat use and distribution

Paragliding in Kandersteg kept the female chamois away from their preferred feeding grounds and forced them to stay in the forest for up to eight hours. This distribution pattern has been apparent since the onset of paragliding. Moreover, female chamois in Kandersteg today have become resident in the mountain forest zone where they had never been observed previously. Even a single paraglider has a strong effect on the habitat use of female chamois, as indicated by the observations at Augstmatthorn. Chamois ran downhill and disappeared into the forest at about 1,400 m a.s.l., sometimes covering distances of >500 m. If a paraglider flew along the whole mountain range from Augstmatthorn to Brienzer Rothorn (about 10 km distance), he might drive hundreds of chamois and ibex into the forest. The Augstmatthorn mountain range is typical of many other ranges in the Swiss Alps in its exposure and wildlife. It is expected that, with increased flying activity in such areas, chamois and ibex will alter their habitat use and stay closer to forest cover. The forest seems to be a key factor to the chamois when trying to avoid paragliders. It is surprising how small the forests providing refuge to chamois can be. In Kandersteg, large groups of chamois frequently stayed in forests covering approximately 1-2 ha for up to eight hours. Even with very intensive paragliding, they did not leave forest cover. In contrast, the chamois in the Augstmatthorn and Niesen areas tended to run out of small forests after a paraglider flew over their refuge again. On one occasion at the Augstmatthorn, a herd of about 70 chamois ran out of the forest only to flee back in after a few minutes. There does not seem to be a better alternative than retreating into forest cover. Female chamois mainly feed during the morning and evening hours in meadows and pastures above the tree line. Chamois staying within the forest for >8 hours during the day have to feed there, too. Physiological rhythms drive them to feed about every three hours (R. Hofmann, pers. comm.). Depending on the quantity and quality of the grass and herb vegetation within the forest, chamois will browse on trees. Large numbers of chamois regularly staying within mountain forests for long periods of time will play an important role in decreasing rejuvenation and variability of bushes and trees (Onderscheka 1990, Reimoser 1990, Meier, Engesser, Forster, Jansen & Odermatt 1993).

Conclusions

The purpose of nature conservation is to protect intact habitats as a basis for diverse species communities. Losses of important habitat for chamois and other wildlife species throughout the Alps should not be tolerated. Furthermore, ungulates like chamois and ibex may damage the very forests that offer them sanctuary. Thus, paragliding should be controlled in certain areas. This study provides a basis to develop concrete measures for doing this.

Paraglider pilots should be educated about their effects on wildlife. Information about the ecology of alpine wildlife (e.g. chamois, ibex, golden eagle) and the possible effects of paragliding on the animals should be integrated into the normal curriculum of the pilots' education. Also, a broad information campaign targeting paraglider pilots should be designed to draw attention to the negative effects of this sport. However, as the history of nature conservation has shown, the strategy of informing people and asking them to behave in a certain manner is not successful without further action. Precise protection measures referring to a defined space must be developed. Concerning paragliding, 'no-fly-zones' should be designated, standard flight paths drawn up and the number of take-off points across the Alps limited. This structuring should be carried out by regional working-groups, where local people represent different interests (wildlife protection, forestry, hang gliding, tourism) and try to find their own solutions in areas where problems occur. Based on these results, such a working-group has carried out a pilot project along the mountain ridge from the Harder (near Interlaken) to the Brienzer Rothorn, including the region of the Augstmatthorn. Paragliders no longer overfly the area from the beginning of April to the end of June (the time of late pregnancy and birth of young).

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