Abstract: 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.
Effects of paragliding on alpine chamois *Rupicapra rupicapra*

Reinhard Schmidrig-Petrig & Paul Ingold


We studied the influence of paragliding flying activity on female chamois *Rupi- capra r. rupicapra* behaviour and distribution in four areas in the Swiss Alps. We observed chamois as they were overflown by co-operative pilots on con- trolled 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 mead- ows 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 distance, habitat use, paragliding, *Rupicapra rupicapra* rupicapra, ungulates

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In Central Europe there are few places left where un- touched wilderness can still be found. The Alps may be regarded as one of these places as they still have val- leys and mountain ranges with very moderate human influence. However, increasing tourism in the Alps, which continually takes on new facets, is advancing fur- ther and further into the natural habitats of wildlife (Ingold, Schmidrig-Petrig, Marbachter, Pfister & Zeiller 1996). In particular, the touristic conquest of the air has been very successful in the last two decades. The num- ber of licensed aircraft in Switzerland has increased within-

in this time period by about 70% for motor- and sul- planes, 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 >4,000 licensed pilots in Switzerland (SiHV 1999). Paragliders turn easily and can be flown close to mountains slopes. Due to better equipment, longer flights have become pos- sible and more pilots are moving into new, previously unflown areas, which include prime wildlife habitat.
How do paragliders affect animals such as mountain gazelles? The chamois, Eupotes nasua, is a suitable species for examining this question due to its Alp-wide distribution (Kastel & Schrögl 1983, Stigsnes & Knapp 1985), its feeding activity above the timberline (Cottier 1983, Schröder 1972), Hofmeier & Nöhring 1972, Pucholé 1980, Römer von des Malbarg 1981, Pucholé & Nöhring 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 (Grima 1990.a), March (1984). Kids are born in May or June and are tended until November (Ruckstuhl & Ingold 1994).

The effect of paragliding on chamois in the open pastures above alpine forests produced 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 ignoring the unpredictable appearance of paragliders flying off normal routes? Do they avoid them by flight over long distances or by retiring 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 sites, 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 bases for management decisions.

Study areas

Our study was conducted at four locations in the Swiss Alps. Each location consisted of extended alpine pastures, huge 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 (30-400 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, in the Augustmatthorn, where paragliders first appeared in 1989 and could only be seen specifically, and in the Zöllberg, where no paragliders have been observed to fly. In the Kandersteg, Niesen and Zöllberg areas, chamois were limited every year during two weeks in September. The Augustmatthorn study area lies within a game reserve. All study areas were regularly visited by the FFG (Fore and goldennaug aubej private areas, 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 between 1,300-2,300 m a.s.l. and encompasses approximately 550 ha of alpine pastures and fairly steep, bare rocks in the upper part facing southeast. Below the tree line (1,350 m a.s.l.), pine and fir forests and for About about 500 ha face with sparse vegetation are on the ground are interpreted with rockslabs. 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 treatment season in July and August and on sunny weekends, 20-25 paragliders started at the Alpental. Most pilot flow 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 three paragliders as off-course paragliders. Paragliding mostly occurred from 07:40 to 17:00. The off route paragliding began depend on the thermal conditions.

The Niesen, a 2,365 m high mountain peak of the Bernese Alps rising up below Lake Thun. The study area contained the southeast facing slopes of the Niesen and the northeast-facing slope of the adjoining 2,394 m high mountain Kronberg on the same mountain range and covered approximately 450 ha. The cliffs below the peaks pass into some fields and vast alpine pastures and below ca 1,600 m a.s.l. spruce fir forest are interspersed withadows. During sunny summers the study area was inhabited by about 30-40 female chamois and their kids. The first paraglider pilots appeared at the Niesen in 1965. Because of its unpredictable wind conditions, the Niesen was not as popular among paraglider pilots as the Kandersteg region with its predictable wind and thermal 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 Augustmatthorn 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 Augustmatthorn. It is dominated by steep alpine pastures, rock cliffs and steep fields, which give way to

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small forests at lower elevations. The area encompassed of the summer home range of 100-120 females with kig, of which about 30 individuals were marked with yellow homestripes. The first paragliders appeared in this area in 1989. From 1960 to 1992 paragliding has increased during the spring and summer; in 1992 at least one paraglider could be observed at Augustmatthorn on approximately 15% of days. Compared to the flying intensity in Kandersteg and at the Niesen, paragliding at the Augustmatthorn 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 snow fields, and during summer and autumn, chamois lived within the zone dominated by spine 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 Augustmatthorn 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 Augustmatthorn. 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. 1a-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 corresponding 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 fair from air traffic on days with varying flying intensities on and off

Figure 1. Schematic representation of the basis for calculation of alert and escape distance (s X). Of = observation point; r can be measured on the map; h can be estimated by counting the contour lines with an equal distance of 10 m; m = 90°; G = m∠OEF = 90°-a ≈ 90°-a ≈ 90°; G can be measured on the map; G can be estimated by counting the contour lines with an equal distance of 10 m; G can be estimated with an inclinometer; sin G = (sin 90°) sin (90° - α); X = G/4+G/2 = 2·c·c+cos α.

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the normal route, and at Augustmatt on days with and without paraglider flights. We also made observa
tions at the Doldenhorn, as a control. At Kandersteg ob-
servations were carried out from dawn to dusk, where-
by 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 possi-
ble because of the excellent observation conditions.
Furthermore, the following data were recorded: 1) the
take-off site, start time and flight path of every paraglid-
er, and 2) hourly weather conditions and air tempera-
ture at one observation point. At Augustmatt, 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 surround-
ings were scanned to measure the duration of their
stay within the forest cover. At Doldenhorn, the dis-
tribution of the female chamois was observed on ran-
donlly 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 quanti-
fied as relative height between the paraglider and the
chamois (see Fig. 1-e), colour of paraglider (discrete
variable), proximity of the observed chamois to forest
cover, chamois group size, area (Kandersteg, Niesen,
Augustmatt; 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).

The variables included in this analysis were: 1) the time when the first paragliden
took off, 2) the number of paragliders starting within the first 30 minutes on the
normal route, 3) the number of paragliders starting within the first 30 minutes on the
route, and 4) the distance to the forest cover. For assessing the effect of leaving
the forest cover, we used a jackknife method. All 23 whole-day observations (13 summer/10 sum-
tums) with sunny weather were included in the anal-
ysis of the duration of staying within forest cover close
to paragliding traffic (Altme-Griben) in Kandersteg.

The method used for estimating the time of leaving the
feeding grounds and retreating into the forest is indi-
cated above. The time of leaving the forest and return-
ing to the feeding grounds in the afternoon or evening
was defined as the time when 34 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 cov-
er. 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 passengerlight between first and last passenger- 
), 3) duration of the air traffic on the normal route, 4) intensity of off-route paragliding, 5) temperature at 12:00, and 6) season (summers or winters). The air traffic intensity values on and off the normal route were log- 
transformed after adding 1, i.e. \ln(1+x+1); on seven days ne paragliders occurred, so x was 0.

During 1990 and 1991, the distribution of the chamois at the Augustnathorn 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 north-
west facing slope on 11 days. The frequency at which chamois retreated to forest cover (days when >95% 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. Haltsuit use by the Dold-

enhorn chamois was recorded on seven sunny days. 

Results

Reactions of female chamois to paragliders

Female chamois showed strong reactions to paragl 
iders 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 
folded 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 presence of the 
refuge sites relative to the animal's 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 (8.9); 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.

About 60% of the variation among alert distances was 
explained by a reduced regression model containing the 
variables relative height between the paraglider and the 
chamois (RH) and the distance to the observed chamois in 
forest cover (PC; F(2,17) = 18.81, P < 0.001; F = 0.425, N = 54). Relative heights between paragliders and 
chamois affected the alert distance significantly (reduced 
model: F(1,52) = 5.562, df = 52, P = 0.001; F = 1.646, df 
= 52, P = 0.149), chamois reacted at larger distances with 
alert behaviour when paragliders appeared at greater rel-
ative heights. Alert reactions were independent of the 
paragliders' colour (CO), their closeness to forest cov-
er, the focal animal's group size (GS) and of the area 
(A); full model: F(2,50) = 0.226, df = 2,51, P = 0.687; F(1, 
1,114, df = 1,52, P = 0.297; F(1,1,77, df = 1,52, P = 0.286; 
F(1,1,662, df = 2,51, P = 0.302).

More than 75% of the variation among escape dis-
tances was explained by the chosen regression model 
(F = 0.756, N = 47). The relative heights between para-
glider and chamois, the proximity to forest cover, and 
the area affected the escape distances (reduced model: 
F(1,57,742, df = 1,61, P < 0.001; F(1,707, df = 1,41, P = 0.011; F(1,0,077, df = 2,41, P = 0.005). The 
female chamois reacted by fleeing at larger distances 
when the paragliders appeared above (P < 0.001) and when 
they were going far away from forest cover, than they 
did with passing paragliders and when they were standing 
at the forest edge. Escape distances were inde-
pendent of the paragliders' colour and the focal animal's 
group size (full model: F(1,50) = 3.282, df = 2,44, P = 0.990; 
F(1,0,022, df = 1,45, P = 0.883).

Comparisons of the mean escape distances between 
areas indicate, that female chamois at the Augustnathorn 
escaped at larger distances than the females in Kandersteg 
(P = 0.002) and at the Niesen (P = 0.008). On the other hand, the escape distances in the areas Kan-
dersteg and Niesen did not differ (P = 0.677).

Distribution of female chamois exposed to inten-
sive 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 scatter-

Table 1. Median, 1st and 3rd quartile and minimum/maximum values of alert and flight distances (in meters) of female chamois to paragliders in the three areas in the Swiss Alps during 1990-1992.

<table>
<thead>
<tr>
<th>Area</th>
<th>Median</th>
<th>1st Quartile</th>
<th>3rd Quartile</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kandersteg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alert distance</td>
<td>530</td>
<td>240-1090</td>
<td>190-920</td>
<td>20</td>
<td>30</td>
</tr>
<tr>
<td>Escape distance</td>
<td>410</td>
<td>370-750</td>
<td>470-850</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>Niesen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alert distance</td>
<td>406</td>
<td>350-600</td>
<td>320-280</td>
<td>14</td>
<td>18</td>
</tr>
<tr>
<td>Escape distance</td>
<td>410</td>
<td>370-750</td>
<td>470-850</td>
<td>10</td>
<td>14</td>
</tr>
</tbody>
</table>

* VILDSENI SCIENCE 7-4 (2011)
ed all over the area before paragliding started. After paragliding started, they moved away from the flying activity to continue gliding 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 (X) = 430 m, and after (X) = 710 m paragliding started, P < 0.001; section 2: before (X) = 1,210 m, and after (X) = 1,170 m, P > 0.05). Friedman two-way ANOVA.

In the morning, the female chameleons in section 1 left the feeding grounds at an average of about four hours after sunrise, approximately 1.5 hours earlier than the female chameleons in section 2 (Wilcoxon matched-pairs signed rank test, one-sided, P < 0.05). In section 1, the chameleons retreated to the forest on all 15 days. After their extended feeding period, the chameleons in section 2 moved down into the forest on two days, up into the trees 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 chameleons 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 air traffic paragliders flew over section 2, the chameleons also retreated into forest cover. On five of 16 observation evenings, the female chameleons 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 = 5.758, df = 2, P = 0.05), irrespective of the beginning of the air traffic (F = 1.232, df = 2, P = 0.318) and the temperature (F = 0.279, df = 2, P = 0.279); values of the reduced regression model: F = 12.065, P < 0.01, r² = 0.653 (Fig. 2).

On all 13 whole-day observations in summer and on eight of 10 days in autumn, there was intense flying on and off the normal route. On these days, the female chameleons stayed within the forest for several hours each day (2.5-8 hours). When off-route paragliding was encountered for >3.5 hours the chameleons wanted 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 = 15.869, df = 2, P = 0.002), but not by the intensity of paragliding on (F = 0.788, df = 2, P = 0.398) and off the normal route (F = 1.614, df = 2, P = 0.222); the duration of paragliding on the normal route (F = 1.603, df = 2, P = 0.224), tempera-

\[
p(\text{t}) = 0.017, df = 2.20, P = 0.899\] and 
\[
\text{swaass}(F = 0.726, df = 2.20, P = 0.407; \text{values of the reduced regression model: } F = 38.473, P < 0.001, r^2 = 0.647; \text{Fig. 3}).
\]

**Distribution of female chameleons at the Augustusmatt and the Diederikhorn**

On many days in summer and autumn the female chameleons of the southwestern slope of the Augustusmatt normally grazed on the open scree fields and pastures until about noon, when most of the chameleons lay down; in the late afternoon they usually started feeding again. On nine times, after a paraglider appeared, all chameleons 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 Augustusmatt.

![Figure 2](image-url)  
**Figure 2.** Relationship between the intensity of the air traffic on the north slope expressed as a of the number of paragliders starting within the first 30 minutes and the time the female chameleons leave the feeding grounds and retreat into the forest expressed as time after sunrise. The regression is described by: \( y = 2.30 - 1.109 \ln x \).
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 notion 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 threats 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 elicit an alert 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 Surselva Alps and Prealps quantified by Mosler-Berger (1996) 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 (Cederroth & Lovari 1983, Zeller 1991, Vallian 1992, Ingeld et al. 1996). These behaviours seem to be adaptive to avoid predators. Because of their inability to climb, ground-based predators such as wolves 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. Zeller (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 height-of-bird risk sheep Ovis caamadris. According to the predator-prey interaction optimality model of Ydenberg & Eml (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 (Szabo, 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 dfeaflying loud military jets (Ingold et al. 1996). Harrington & Veitch (1991), Murphy, White, Kugler, Kilcullen, Smith & Barber (1993) and Weiseberger, Kresimir, Wallace, De Young & Maugham (1996) have reported similar observations for other ungulate species. But Maier, Murphy, White & Smith (1998) showed that carbon monoxide 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 roar reaches the ears. On the other hand, propel-
ler planes and helicopters often announce themselves acoustically long before they can be seen.

The comparison of the vegetation in different areas reveals that the female chimpanzees at the Augustmuthen take flight at greater distances than the female chimpanzees in Kandertal 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 Augustmuthen chimpanzees so far did not face many paragliders, whereas in Kandertal and at the Niesen fairly intensive paragliding has occurred for several years and chimpanzees definitely have had many encounters. Habituation can be expected sooner with increasing predictability of a stimulus in space and time. Locality-limited and regular air traffic can only be found in areas which are used by paragliding schools (like Kandertal-Altenalmen). Experienced pilots prefer to fly off those normal routes whenever thermic conditions allow them to do so. Off-route flights are very unpredictable and it is not surprising that chimpanzees continue to show strong reactions, even in areas like Kandertal. Sensibility of the animals, or 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 Augustmuthen chimpanzees would be expected to have the shortest escape distances, contrary to the Kandertal and Niesen chimpanzees, 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 Kandertal gamekeeper, approximately half of the chimpanzees population left the Altenalmen 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 Kandertal kept the female chimpanzees 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 chimpanzees in Kandertal 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 chimpanzees, as indicated by the observations at Augustmuthen. Chimpanzees ran downhill and disappeared into the forest at about 1.400 m a.s.l., sometimes covering distances of 500 m in a single paraglider flight along the whole mountain range from Augustmuthen to Brienz Rothorn (about 10 km distance), he might drive hundreds of chimpanzees and ibex into the forest. The Augustmuthen 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, chimpanzees and ibex will alter their habitat use and stay closer to forest cover. The forest seems to be a key factor to the chimpanzees when trying to avoid paragliders. It is surprising how small the forests providing refuge to chimpanzees can be. In Kandertal, large groups of chimpanzees 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 chimpanzees in the Augustmuthen and Niesen areas tended to run out of small forests after a paraglider flew over their refuge again. On one occasion at the Augustmuthen, a herd of about 70 chimpanzees 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 chimpanzees mainly feed during the morning and evening hours in meadows and pastures above the tree line. Chimpanzees staying within the forest for 8-8 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, chimpanzees will browse on trees. Large numbers of chimpanzees regularly staying within mountain forests for long periods of time will play an important role in decreasing rejuvination and viability of bushes and trees (Onderdonk 1990, Reimoser 1993, Meier, Engesser, Forster, Jässen & 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 chimpanzees and other wildlife species throughout the Alps should not be tolerated. Furthermore, measures like paragliding 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 Harzer (near interlaken) to the Brienz Rothorn, including the region of the Augustmartihorn. Paragliders no longer overfly the area from the beginning of April to the end of June (for time of late pregnancy and birth of young).

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References
ZAGL (Bundesamt für Zivilflächen) 1995: Die schweizerische Zivilflächenfotografie Drucksachen und Material- werkzeuge EMAZ, 3003 Bern, Switzerland, 10 pp. (in German).
Mammalia doppia 15, Paul Pury Verlag, Haselberg, Germany, 62 pp.
Kraemer, A. 1969b: Lebensbedürfnisse und Größenvordrängungen 293


