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Authors: Enggist-Diiblin, Peter, and Ingold, Paul

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Modelling the impact of different forms of wildlife harassment, exemplified by a quantitative comparison of the effects of hikers and paragliders on feeding and space use of chamois *Rupicapra rupicapra*

Peter Enggist-Düblin & Paul Ingold

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We developed a mathematical model to quantify and compare the impact of different forms of wildlife harassment, and applied it to compare the effects of hikers and paragliders on the feeding time and area of chamois *Rupicapra rupicapra*, considering differences between hikers and paragliders in terms of their prevalence and behaviour. Although many more hikers than paragliders visited the study area, the impact of paragliders was much stronger. With increasing paraglider traffic, the effects would steeply increase, whereas the effects of hikers approached an asymptote. With modification of input values and/or parameters, the model can be applied to other species, to compare the effects of other forms of wildlife harassment, and to simulate effects of changing conditions such as habituation of the animals or changes in the daily or spatial pattern of occurrence of tourism.

Key words: hikers, human disturbance assessment, modelling, paragliders, Rupicapra

Peter Enggist-Düblin & Paul Ingold, University of Bern, Zoology Department, Ethology and Nature Conservation, Länggassstrasse 27, CH-3012 Bern, Switzerland - e-mail addresses: peter.enggist@gmx.net (Peter Enggist-Düblin); paul.ingold@aen.unibe.ch (Paul Ingold)*

**Present address: Rohrmatt 24, CH-3126 Kaufdorf, Switzerland*

Corresponding author: Peter Enggist-Düblin

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It is well established that outdoor activities affect wildlife. Effects of hikers, skiers, hunters, snowmobiles, aeroplanes and paragliders have been investigated (Cassirer, Freddy & Ables 1992, Cederna & Lovari 1983, Colescott & Gillingham 1998, Ericsson & Wallin 1996, Harrington & Veitch 1991, 1992, Ingold, Schnidrig-Petrig, Marbacher, Pfister & Zeller 1996, Patterson 1988, Pépin, Lamerenx, Chadelaud & Recarte 1996, Schnidrig-Petrig & Ingold 2001). With increasing development of formerly unused areas and the appearance of new sports such as paragliding and mountain-biking, animals are increasingly exposed to outdoor activities. Some types of outdoor recreation may have more severe effects on wildlife than others and may therefore require stricter regulations. Several studies compared the effects of different human activities, e.g. hikers, joggers and mountainbikers (Gander & Ingold 1997), hikers and snowmobiles (Freddy, Bronaugh & Fowler 1986) ori-

enteering and hunting (Jeppesen 1987) recreational and hunting activities (Maublanc, Dubois, Teillaud & Cugnasse 1992), paragliding and other air traffic (Szemkus, Ingold & Pfister 1998). In most cases animals reacted differently to different human activities (but see Gander & Ingold 1997). Nevertheless, no quantitative tool is available to decide which activity has the greatest impact on the animals. It is important not only to study the reaction of the animals, but also to consider aspects of the occurrence of outdoor activities. In general, it is not the single disturbance event, but its repeated occurrence that affects the animals the most. To quantify wildlife harassment we therefore need quantities which sum up with repeated incidences of disturbing events. For example, the distance to an approaching hiker at which a chamois *Rupicapra rupicapra* stops feeding and eventually begins to move away, i.e. the flight distance, is not such a quantity, although it is a good indicator of the sensitivity of chamois to hikers. However, how long feeding is interrupted, or the distance covered by escaping chamois, can be added over repeated encounters with hikers. We developed a mathematical model to calculate such additive effects and thereby became able to compare different forms of harassment in relation to possible differences in their impact and varying relationships with its extent.

We used the model to compare the influence of hikers and paragliders on chamois. Earlier studies have shown that chamois react strongly to paragliders at great distances and usually escape into the forest (Schnidrig-Petrig 1994, Schnidrig-Petrig & Ingold 2001). They are also affected by hikers, but reactions are less severe than to paragliders as animals react at shorter distances and remain in open habitat (Ingold et al. 1996, Gander & Ingold 1997). In our study area, hikers are much more numerous than paragliders. Therefore, overall hikers might be expected to affect chamois more than paragliders. We tried to answer the question, which one of these activities has the highest impact, by comparing the amount of feeding time and feeding area chamois lose due to encounters with hikers and paragliders. We simulated the effect of additional paragliders on chamois behaviour, and investigated how changes in the reaction of chamois would affect their feeding time and the feeding area available.

Model parameters

To apply the model, we obtained information about 1) characteristics of the area, 2) the daily feeding patterns of chamois, 3) their reactions towards hikers and paragliders, and 4) about the occurrence of hikers and paragliders in the study area. The area from which we obtained our data and to which we applied the model is the same.

The national game reserve Augstmatthorn in the Swiss Alps (46°45'N, 7°56'E) offers species-rich alpine pastures that are important feeding grounds for chamois. The pastures are located between 1,500 and 2,100 m a.s.l., primarily on northwest and southeast facing steep slopes interspersed with rocky cliffs. Lower elevations are dominated by subalpine coniferous forest. The model was applied to the part of the game reserve which was traversed by the main walking trails covering approximately 7.5 km in length and in which paraglider flights occurred. It covers an area of 6.4 km^2, of which 4.9 km^2 are feeding grounds; the rest of the area consists of forests and cliffs. Although hunting is prohibited, sick or injured animals may be shot by the game warden.

Zeller (1991) investigated the daily feeding activity and determined every 15 minutes the proportion of feeding chamois during the daytime hours 05:30-21:30 on eight different days. We used the mean proportions as an estimate of the probability that an individual would be feeding during the respective time interval. To smoothen the temporal pattern we used moving averages over five successive recording intervals. The probability that an animal will be feeding varies during the day, being high in the morning and evening and low during mid-day hours.

From several studies within the same area, we obtained measures of the reactions of chamois to hikers (Gander 1994, Gander & Ingold 1997, Vallan 1992, Zeller 1991) and paragliders (Schnidrig-Petrig 1994, Schnidrig-Petrig & Ingold 2001). The flight distance was defined as the distance between an approaching person or paraglider and a chamois when the chamois moved away. The distance fled was the distance from the point of flight to the place where the chamois resumed feeding. Accordingly, the reaction time was the time from fleeing until the chamois resumed feeding. We pooled the median values from these studies and calculated the mean.

The following parameter values were applied in the model: flight distance from hikers and paragliders were 120 (range: 57-300 m; N = 63) and 780 m (range: 640-900 m; N = 10), respectively, with reaction times of 5 (range: 1.2-7.7 minutes; N = 53) to 150 minutes (range: 20-240 minutes; N = 15). Distance fled after encounters with hikers was 130 m (range: 40 - >1,500 m; N = 63). On encounters with paragliders (N = 15), all chamois left the feeding area and escaped mostly into forests, sometimes to cliffs. In the model, this resulted in a total loss of feeding area for the duration of a reaction to paragliders. Consequently, the proportions of feeding time loss are identical to the proportions of feeding area loss.

From June to early October 1994 we investigated the occurrence of hikers and paragliders in our study area on 13 randomly chosen weekdays and in 14 weekends. An observer on the ridge with a 360° view of all walking trails counted at intervals of 20 minutes the number of hikers on each trail from early morning to late evening and scanned the sky for approaching paragliders.

For each trail, we calculated the approximate walking time using an empirical formula which was developed to calculate walking times of hikers in groups in mountainous areas (Fuchs & Hasenkopf 1988). Two time values were calculated: one for the horizontal part and one for the vertical part. Time for the horizontal part was horizontal distance (m) divided by 4,000 m/hour, and for the vertical part its distance divided by 400 m/hour for rising slopes and 500 m/hour for falling slopes, respectively. Walking time was then the larger of these two values plus half the smaller value. A mean velocity was calculated for ascending and descending walk for each trail.

The air space over the study area was divided into four rectangular sectors, two on both sides of the ridge with the observer located in the intersection of the four sectors. Each occurrence of a paraglider in a sector was noted, together with the flight route and height. For calculations, we assumed that the sectors were passed along a flight-path with the length of the mean of the side lengths of the rectangle; for two sectors 1,000 m and for the others 800 m.

As a measure of the duration of the presence of hikers or paragliders in the study area, we calculated hiker-hours and paraglider-hours as their number in each time interval multiplied by the interval length in hours and summed.

To simulate the effect of additional paragliders, we included the additional occurrence of delta-gliders in the study area. We have no indication of any difference in the reactions of the chamois towards paragliders and delta-gliders. However, because we have no data to compare the reactions quantitatively, we restricted our analysis to paragliders and took the observed delta-gliders as a simulation for the occurrence of additional paragliders. Consequently, the range of paraglider-hours was doubled to two paraglider-hours per day.

Effects of changing values of the reaction parameters

We ran simulations with different values separately for flight distances, distances fled and reaction times and compared their effects on daily losses of feeding time and feeding area. The simulations were based on an 'average day' for the occurrence of hikers in the area. We took the rounded mean of the number of hikers on each trail at each time interval observed on 27 days. Simulations were conducted in the range between half and twice the mean values obtained from our studies on chamois behaviour in the study area. The values of the other parameters remained the same as given in the previous sections. The curves were fitted by linear or polynomial functions. Regression coefficients were in every case >0.9.

Model description

On encountering hikers or paragliders, a chamois stops feeding and eventually moves away, resulting in reduced time and space for feeding. Loss of feeding time and area was the quantity we calculated. Both factors depend on the reaction of the animals and the characteristics of human activities. On the one hand, loss of feeding time and area depend on whether animals are feeding at the time of the encounter, their reaction distance, how far they move and how long it takes for them to resume feeding. On the other hand, loss in feeding time and area depends on the number of encounters with humans, on when and where they occur and how many humans are in the area. The important question is: what is the mean proportion of feeding time and feeding area lost due to encounters, and what proportion of these losses is caused by encounters with hikers and paragliders, respectively?

The model is based on the probabilities of encounters, on the reaction parameters (flight distance, distance fled and reaction time), and on the daily feeding patterns of the chamois. The probability of encounters depends on the number of hikers and paragliders, on previous encounters, on the reaction parameters of the chamois and on the size of the feeding area. It was assumed that a chamois could be anywhere in the area. The resulting proportions of feeding time and area lost due to human activities are therefore to be interpreted as mean values for all individuals inhabiting the area, regardless of the distribution of home ranges.

The probabilities of loss of feeding time and area were calculated for discrete time intervals of 10 minutes over a whole day. First, we calculated the probability of an encounter between a chamois and hikers or paragliders. An encounter occurred when the distance between chamois and hiker or paraglider fell below the flight distance, defined as an area around the hiker or paraglider within which a chamois will react. Calculated for time intervals, this area increases, depending on the velocity of the hiker or the paraglider and the interval duration. Then, the probability of an encounter during a certain time interval is this area as a proportion of the entire area

where a chamois can be. Because we are interested in the losses of feeding time and area, we only considered the open meadows, the feeding areas of chamois. In summary, the probabilities of encounters were calculated as the proportion of the area where an encounter could potentially occur to the area where a chamois could potentially be, and these areas change over the course of time, depending on the number of hikers and paragliders. Therefore, our model accounts for the effects of possible previous encounters with either hikers or paragliders. Previous encounters entail a reduction in both the usable area and the area of possible encounters.

We also took into consideration that hikers in our study area almost exclusively use trails. Above a certain number, additional hikers may not have any additional effect on chamois, as the area of possible encounters around a trail will become zero; the chamois have already left this area due to encounters with previous hikers. Additionally, hikers often walk in groups. We assumed a mean group size of two (therefore the number of hikers observed was divided by two, except when only one hiker was recorded) and we assumed that groups were evenly spaced along a trail. For each trail of specific length we then calculated the maximum number of hikers required to 'fill up' the trail. Additional hikers accordingly had no additional effect on loss of feeding time and area.

It is also possible that additional paragliders will have no additional effect on losses of feeding time and areas if they fly the same routes at intervals shorter than the chamois' reaction time. However, this has never been observed in our study area. Therefore, in our calculations each paraglider contributed to losses in feeding time and feeding area. For paragliders, we assumed a straight-line flight over the feeding area at an altitude of 300 m.

The probability of a loss of feeding time and area additionally depends on the probability that a chamois is actually feeding when an encounter occurs. This probability was calculated for each 10-minute interval over the day. The probability of a loss of feeding time and area is then the product of the probability of encounter and the probability of feeding, and therefore varies over time according to the daily pattern of feeding and the occurrence of hikers and paragliders.

For the loss of feeding time, we multiplied the probability of loss of feeding time by the reaction time. Similarly, we calculated the loss of feeding area by multiplying the probability of losing it with the area lost. This area is composed of the area of possible encounters and the area resulting from the reacting animal moving away from the place of encounter for a certain distance (according to the distance fled). These losses were calculated as proportions of the total available feeding time and area, respectively.

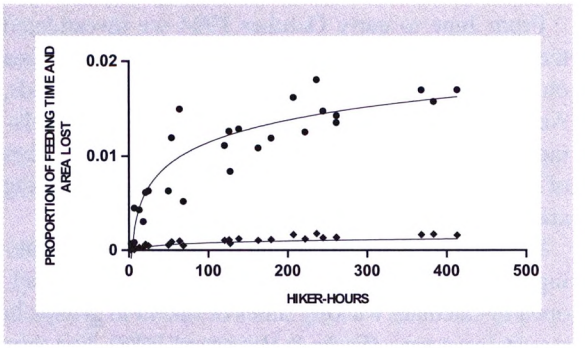

Figure 1. Relationship between the number of hiker-hours per day and the proportion of feeding time (V(t); •, upper curve) and feeding area (V(at); ♦, lower curve) chamois loose due to encounters with hikers. N = 26 days. The lines represent curve fitting by V(t) = 0.0034*ln(Hh) - 0.0042 and V(at) = 0.0003*ln(Hh) - 0.0006

To compare the losses caused by hikers and paragliders, we calculated the losses resulting from encounters with hikers and paragliders separately. The sum of these losses is generally lower than the total loss, because the effects of simultaneous occurrences of hikers and paragliders were excluded from this calculation. The equations for the model are given in Appendix I.

Results

Comparing effects of hikers and paragliders

Hikers were observed in the study area on 26 out of 27 days. The calculated mean daily loss in feeding time ranged between fractions of 1% and a maximum of about 1.8% (median = 1.2%). The maximum loss of feeding area was less than 0.2% (median = 0.1%). The amount of loss was dependent on the number of hikers (Fig. 1) and thereby on hiker-hours, which ranged from a few to 400 per day (median = 126.7 hiker-hours). At lower frequencies of hikers the losses increase much faster than at higher frequencies, until additional hikers only had a marginal effect on the increase in losses.

Paragliders flew over the area on six of 27 days. Whereas the numbers of paraglider-hours ranged from 0.08 to 1 per day (median = 0.17), the losses in both feeding time and area were between 2.2 and 26.5% (median = 7.8%), increasing steeply with the number of paraglider-hours (Fig. 2).

For the six days on which paragliders and hikers occurred simultaneously in the study area, we calculated their relative influence on the loss in feeding time and area. Although the numbers of hiker-hours were much greater than those of paragliders, and moreover, hikers

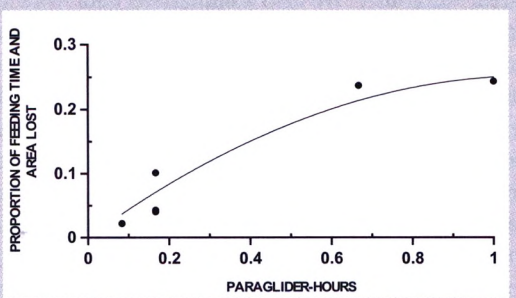

Figure 2. Relationship between the number of paraglider-hours (Ph) per day and the proportions of feeding time (V(t)) and feeding area (V(at)) chamois loose due to encounters with paragliders. N = 6 days. The line represents curve fitting by $V(t) = V(at) = -0.21*Ph^2 + 0.46*Ph$.

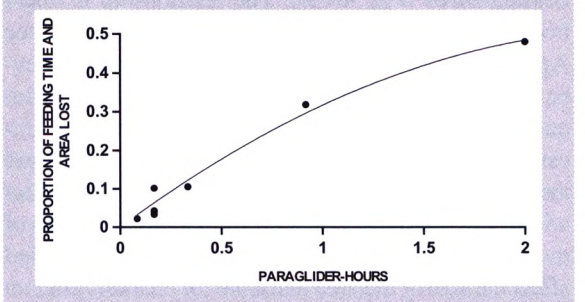

Figure 3. Simulation of the occurrence of additional paragliders expressing the relationship between the number of paraglider-hours (Ph) per day and the proportions of feeding time (V(t)) and feeding area (V(at)) chamois loose due to encounters with paragliders. N = 8 days. The line represents curve fitting by $V(t) = V(at) = -0.075*Ph^2 + 0.392*Ph$.

appeared earlier than paragliders, i.e. during the morning peak of feeding, the daily effects on the losses due to encounters with paragliders were much greater. On days when both hikers and paragliders were present, losses of feeding time due to encounters with paragliders were about 5.5 times greater (medians = 7.8 and 1.4%) and losses of feeding area 75 times greater (medians = 7.8 and 0.1%) than losses due to encounters with hikers.

Effect of additional paragliders

We doubled the range of paraglider-hours by including the observed occurrence of delta-gliders in the study area. Our results suggest that the higher frequency of flights would reduce the feeding time and feeding area by about half (Fig. 3).

Effects of changing parameter values of the reaction towards hikers

We simulated changes of the parameters in the range between half and twice the values used in the previous sections to compare their effects on loss of feeding time and area. Changes in the reaction time had marked

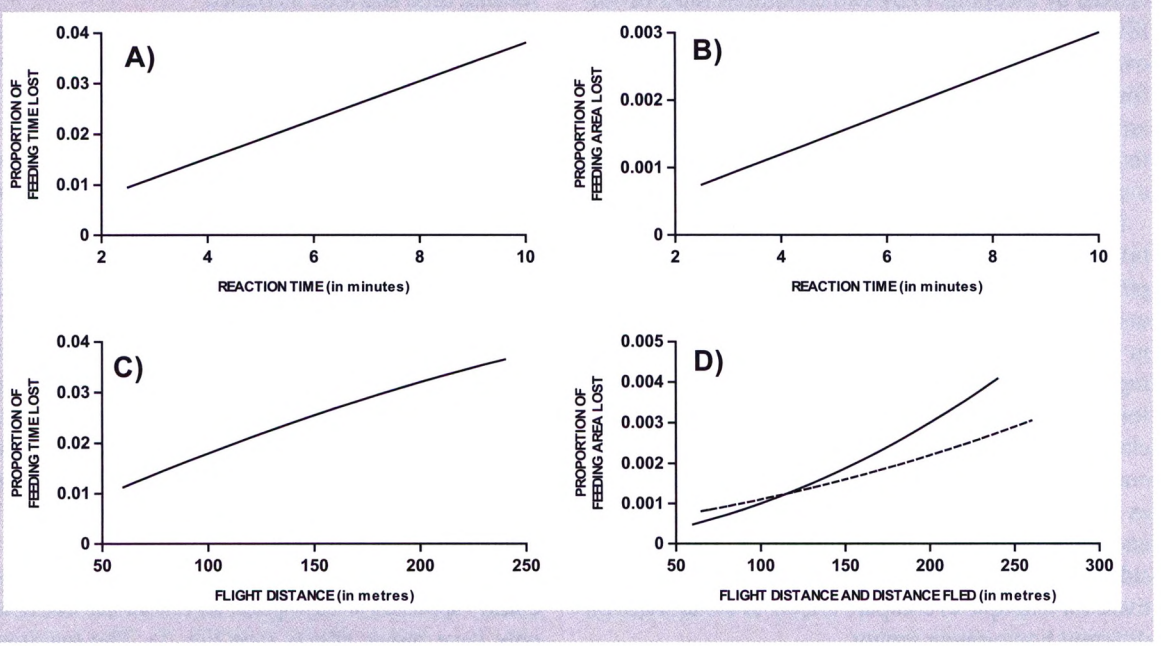

Figure 4. Daily proportions of feeding time (V(t)) and feeding area (V(at)) lost by chamois disturbed by hikers in relation to changing values of the reaction parameters of chamois, i.e. reaction time (A,B; in minutes), flight distance (C,D; in metres) and distance fled (D----; in metres). Simulations were run with changing values for each reaction parameter separately. The values of the other parameters remained constant and the same as given in the model parameter section. Calculations are based on a 'mean day' for the occurrence of hikers.

consequences (Fig. 4A,B). The relationship is linear because the reaction time acts as a multiplier (see Appendix I, formulas 6 & 9). Flight distance, however, affected the probability of encounter, and consequently the loss of feeding time, resulting in a non-linear relationship, although within the range considered the relationship was nearly linear (see Fig. 4C). The effect within the simulated range is comparable with that of the reaction time. Flight distance and distance fled affect the size of the area unusable for chamois after an encounter. As mentioned above, flight distance affects the probability of encounter. With increasing flight distance, the probability of encounter increases as well. This leads to a steeper increase in the loss of feeding area with increasing flight distance compared to distance fled (see Fig. 4D). Distance fled and reaction time have comparable effects within the ranges considered.

Discussion

We developed a model to quantify the effects of disturbance by recreationists on chamois, and used it to calculate the proportion of feeding time and area chamois lost when they fled from approaching hikers or paragliders. The model could also be applied using other parameters, such as the total distance covered by escaping chamois or the amount of additional energy expenditure caused by escaping. Only two conditions must be fulfilled by the dependent variables: they must be additive over repeated encounters, and they should be relevant for the animal. The time and area available for feeding are certainly relevant for the chamois because feeding time is closely related to energy intake, and feeding area available has consequences on habitat use.

Loss of feeding time and area depend on the probability of encounter with hikers and/or paragliders. This probability is the proportion of the area in which an encounter could happen as a proportion of the whole area in which the chamois could be. The size of the total feeding area considered in the model therefore is important for the interpretation of the results. In our study, it included the home ranges of two female groups and of several males. Therefore, the losses have to be understood as mean values for all the chamois inhabiting the area, and not as the loss by individual animals. The area considered may be modified according to a study's objectives, for example to compare effects of disturbance on different home-range groups.

We further have to interpret the results as mean values because we used mean values of the reaction parameters of the chamois, and therefore did not consider individual variability. We also summarised data from several studies conducted during 1991-1994 on the reactions of chamois towards hikers. The reactions were comparable, also between the sexes (median flight distances obtained in four studies were 90, 120 and 160 m for males and 120 m for females). In addition, no difference in flight reactions according to sex or age class was found in Apennine chamois *Rupicapra pyrenaica ornata* (Patterson 1988). However, we did not consider additional factors, which may have affected the reactions of chamois. Distance to refuge sites could influence flight reactions (Pepin et al. 1996, Schnidrig-Petrig & Ingold 2001). Flight distances were greater when hikers approached the chamois from above than from below (Zeller 1991). Flight reactions to hikers were inversely correlated to group size in Apennine chamois, and flight distances changed with the season for groups with kids (Cederna & Lovari 1983). These considerations, however, are highly unlikely to affect our main result that a few paragliders affected the chamois much more than the far more numerous hikers.

We have shown that reaction time strongly affects loss of feeding time. Therefore, much of the difference between hikers and paragliders resulted from the dramatic difference in reaction time, five minutes to hikers vs 150 minutes to paragliders. In addition, the large differences in the other parameters considerably contributed to the losses. With increasing flight distance, loss of both feeding time and area increased.

We made several assumptions concerning the occurrence of hikers and paragliders. Our assumption that paragliders flew straight over the area at an altitude of 300 m likely underestimated their effects. Four of 13 paragliders that we observed in the study area were circling, and five even took off within the core study area. It is unlikely that such an underestimation also applies to hikers, although we assumed that they remained on trails. It was rare for hikers to leave the trail, because the slopes are very steep and mostly rocky. By assuming a mean group size of two hikers moving evenly spaced on a trail, their effects were more likely to have been overestimated. Most groups of hikers included more than two people, and hikers were clustered rather than evenly spaced. If hikers were clustered, the resulting area of potential encounters and hence losses would be smaller than we assumed.

As long as hikers stay on trails, their effects will quickly approach an asymptote, and additional hikers will only have minor effects (see Fig. 1). The maximum loss in feeding time and area will then depend on the density of the network of trails in an area. Such 'trails' do not exist for paragliders in our study area. Therefore, each

additional paraglider contributed to an increase in the losses. The estimated relationship between paraglider-hours and losses is based on a narrow range with few data points, which limits its predictive power. Nevertheless, we can assume that even a few more paragliders would have a considerable effect, as shown by our simulations. In other areas, the situation may be different. Where standard flight routes are used by the paraglider pilots (Schnidrig-Petrig & Ingold 2001), their effects could stabilise as well, although at a higher level than with hikers. On the other hand, if additional trails were built, and/or if hikers would go off the trails, their effects would increase. With some modifications of the model, such effects could be simulated.

The chamois is not an endangered species in Switzerland, but could potentially alter or even abandon substantial parts of its habitat with increasing human pressure. If chamois were to increasingly seek refuge in the alpine forests and thereby browse on trees, the protective function of the forests against avalanches might deteriorate. It is therefore important to identify the main human activities causing disturbances well before permanent damage is done. Our model helps to detect such problems, and is therefore a useful tool for wildlife management and human disturbance assessments. It can easily be applied to other locations as well as to other species, whenever the required parameters are known or can be estimated. Furthermore, we can also simulate changes in effects under varying conditions. Consequences of habituation of the animals to recreational activities (effects of reduced reaction time and flight distance) as well as the impact of land development (e.g. by constructing additional walking trails) could be simulated.

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Appendix I

The probabilities of encounters between chamois and hikers (p(H)), or paragliders (p(P)), considering possible previous encounters with hikers or paragliders, equals

$$p(H) = \frac{n_{Ht} * F(x)_H}{F(a) - n_{Ht-1} * F(x)_H - n_{Pt-1} F(\times)_P} * (1 - \frac{n_{Ht-1} * F(x)_H}{F(ed)_H}) \qquad (1)$$

$$p(P) = \frac{n_{Pt} * F(x)_P}{F(a) - n_{Ht-1} * F(x)_H - n_{Pt-1} F(\times)_P} \qquad (2)$$

respectively, where F(a) = the total feeding area, n_{Ht} = the number of hikers in the time interval t, n_{Ht-1} = the number of hikers in the previous time interval t-1, n_{Pt}, n_{Pt-1} = the number of paragliders in this and in the previous time interval, $F(x)_H$ = the area where an encounter with a hiker in the time interval Δt can occur, depending on the flight distance *f*d and the mean velocity of the hikers v:

$$F(x)_H = \pi f d^2 + 2f d * v * \Delta t.$$

Correspondingly for paragliders $F(x)_P = 2 * \sqrt{fd^2 - h^2} * l * r$ with h = the flight level above ground, l = the length of the flight path and r = the proportion of open pastures on the whole study area. We assumed a flight time of Δt.

$F(ed)_H$ = the maximum area along a trail with length, l, where an encounter with hikers is possible:

$$F(ed)_H = (2f d * l) + \pi f d^2.$$

In the case of paragliders, the second term corresponding to p(H) is missing, because paragliders do not fly on identical routes, whereas hikers move on trails.

The relative loss of feeding time is calculated as:

$$Vt = \frac{\sum_{t=1}^{n} \{ \sum_{a=1}^{m} p(n) * p(a) * t_r \}}{\sum_{t=1}^{n} \{ p(a) * \Delta t \}} \qquad (3)$$

which is a sum over all time intervals t = 1...n and over all trails or flight paths, respectively, a = 1...m. p(n) is the probability of encounter according to the above calculation (either for hikers (formula 1) or paragliders (formula 2), p(a) is the probability that a chamois is feeding in that time interval, according to the daily feeding rhythm of the chamois, and t_r is the reaction time. The denominator is the feeding time without encounters.

For the losses due to encounters with either hikers ($p(H \wedge \neg P)$) or paragliders alone ($p(P \wedge \neg H)$), the respective probabilities of encounters are:

$$p(H \wedge \neg P) = p(H) * (1-p(P)) \qquad (4)$$

and

$$p(P \wedge \neg H) = p(P) * (1-p(H)) \qquad (5).$$

Total loss of feeding time (V_t (tot)) due to encounters with hikers and paragliders was calculated as follows:

$$V_t\,(tot) = \frac{V_t\,(H \wedge \neg P) + V_t(P \wedge \neg H) + \sum_{t=1}^{n}\left\{\sum_{a=1}^{m} p(H) * \sum_{a=1}^{m} p(P) * p(a) * t_{rp}\right\}}{\sum_{t=1}^{n}\left\{p(a) * \Delta t\right\}} \qquad (6).$$

V_t(tot) is the total loss of feeding time caused by encounters with hikers and paragliders as a proportion of the total feeding time without encounters in a specified time interval t = 1-n. It is composed of the losses due to encounters with hikers alone, $V_t(H \wedge \neg P)$, to read as loss of feeding time due to encounters with hikers and not with paragliders, with paragliders alone, $V_t(P \wedge \neg H)$ and with possible simultaneous encounters with hikers and paragliders. For simultaneous encounters we applied the longer of the reaction times, i.e. that of paragliders, t_{rp}.

The relative contributions of hikers (v_t(H) and paragliders (v_t(P) to loss of feeding time are then

$$v_t(H) = V_t(H \wedge \neg P) / V_t(tot) \qquad (7)$$

and

$$v_t(P) = V_t(P \wedge \neg H) / V_t(tot) \qquad (8).$$

Accordingly, the total loss of feeding area is calculated as:

$$V_{at}(tot) = \frac{V_{at}\,(H \wedge \neg P) + V_{at}(P \wedge \neg H) + \sum_{t=1}^{n}\left\{\sum_{a=1}^{m} p(H) * \sum_{a=1}^{m} p(P) * p(a) * F(v)_P * t_{rp}\right\}}{\sum_{t=1}^{n}\left\{p(a) * \Delta t\right\} * F(a)} \qquad (9)$$

with F(v), the area not usable for the chamois after an encounter, as:

$$F(v) = \pi(fd + df)^2 + 2(fd + df) * v * \Delta t * n,$$

with df = the distance fled, i.e. the distance which the chamois moved away after an encounter.
Again, the relative contributions of hikers (v_t(H)) and paragliders (v_t(P) are then

$$v_{at}(H) = V_{at}(H \wedge \neg P) / V_{at}(tot) \qquad (10)$$

and

$$v_{at}(P) = V_{at}(P \wedge \neg H) / V_{at}(tot) \qquad (11).$$