

Human Disturbance, Behaviour and spatial Distribution of Black Grouse in skiing Areas in the Bavarian Alps^(*)

by
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SUMMARY

Although black grouse (*Tetrao tetrix* L.) are considered as highly susceptible to «human disturbance», they still occasionally can be observed next to even the busiest ski runs. To illustrate that this is no contradiction, but a result of the ecological and ethological plasticity of the species, observations of black grouse in popular skiing areas in the Bavarian Alps, Germany, are presented and discussed. Over a period of 11 years, the behaviour and spacing of black grouse during the winter and the display season were studied in relation to disturbances in an intensively used downhill skiing area. For comparison, observations of black grouse display sites are reported from a ski-touring area adjacent to another downhill ski resort and from an undeveloped ski-touring area. Dependent variable was the temporal and spatial pattern of habitat use by the black grouse, explanatory variables included the temporal and spatial distribution of skiers and snow-boarders on and off pistes, ski-run maintenance activities, snow-conditions and weather. Responses of black grouse to encounters with people or machines within distances of ≥ 10 m ranged from escape flights over interruptions of feeding, resting, or display behaviour to a continuation of the previous activity. Over the years, shifts became obvious in the use of winter feeding and resting sites and the numbers of wintering birds declined. At times and in areas with intensive disturbances, traditional lek sites were abandoned, and the cocks displayed solitarily and dispersed over large areas at temporary sites. The observations indicate that the fewer undisturbed patches with good habitat suitability remain in an area, the more critical human disturbance of black grouse has to be seen. The study resulted in recommendations to the relevant agencies, private organisations, and ski resort operators to establish undisturbed protection zones for black grouse within skiing areas.

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Introduction

Disturbances by human outdoor activities are considered one of the most serious threats to grouse in central Europe (STORCH 2000). With black grouse in the Alps, disturbances during winter are regarded as particularly critical: snow layers several m high restrict suitable habitats to a few patches, food and cover are scarce, and escape flights are energy-consuming. The presence of humans in black grouse winter habitat may result in a negative energy budget; the birds die from starvation or, once weakened, are an easy prey to predators. In addition, disturbance at the traditional leks, which are often located at sites such as ridges, hilltops, or flats also attractive for winter sports, can negatively the social system of the birds and thus their reproductive success (e.g. MÉNONI and MAGNANI 1997, ZEITLER and GLÄNZER 1997).

The potential consequences of human presence in black grouse habitats range from short-term changes in individual behaviour over longer-term shifts in habitat use and spacing patterns to the decline and extinction of local populations. However, because "disturbance" is only one among a variety of interrelated factors (e.g. climate, predation, habitat) that influence a population, causal relationships between the presence of humans and the dynamics of wildlife are difficult if not impossible to prove analytically. For the black grouse, studies in Switzerland and France (MEILE 1982, MIQUET 1988, MIQUET 1990, MÉNONI and MAGNANI 1997) as well as this study demonstrate that the development of ski resorts can lead to serious declines of local populations.

The Bavarian Alps, Germany, are among the most heavily frequented recreational landscapes of Europe. At a regional scale, there is not a single mountain range or black grouse area not used for ski touring, snow-boarding, downhill skiing, or snow-shoeing (ZEITLER and GLÄNZER 1997). To limit the negative consequences of winter sports and leisure activities for black grouse and other wildlife is an important concern of Bavarian conservationists. The Bavarian State Ministry of the Environment has initiated a project to identify and to improve conflict areas between skiing and grouse by spatial and temporal separation of ski routes and important winter habitats; measures are implemented in cooperation between the agencies and all relevant private organisations, particularly the German Alpine Club (Deutscher Alpenverein) (ZEITLER 1996, ZEITLER and GLÄNZER 1997). For operators of ski resorts, governmental regulations require measures to reduce disturbances or other negative effects on the environment as mandatory part of any renovation or development of resort infrastructure.

Thus, the problem of human disturbance of grouse is taken seriously. On the other hand, observations such as black grouse resting on ski-lift masts, feeding next to snow grooming vehicles, or tolerating downhill skiers at even short distances, seem to question the supposed sensitivity of the birds and thus the sense of the measures and regulations mentioned above. To allow for a

differentiated interpretation of the many contradictory anecdotes about «susceptibility» versus «adaptability», it is important to document the behaviour of black grouse according to standard methods and over longer periods in at least a few skiing areas, and to relate the results to the ecology and ethology of the species. Therefore, in this article, observations of the behaviour and spacing of black grouse during the winter and the display season over a period of 11 years in a ski resort in the Bavarian Alps, Germany, are reported. For comparison, observations of black grouse display sites from two further areas are presented.

Study areas and methods

Area 1: Fellhorn

Observations of black grouse in the Fellhorn (2038 m) area near Oberstdorf, Allgäu, Bavarian Alps, which is part of the largest German downhill-skiing area, have been continued for 11 years since 1989/1990. Up to 5000 people per day were transported into the skiing area via cable car. From mid December to late April, lifts were operating from 8:45 a.m. to 4:45 p.m. daily. Since 1999, snow-generators operated along the prepared ski runs up to the summit ridge according to temperatures. Ski-slope maintenance by eight (1999/2000) snow-grooming vehicles continued for several hours after the closing of the lifts, and sometimes until after midnight. After nights with snowfall, pistes were prepared also in the early morning. The Fellhorn area is covered by an extended network of pistes and off-piste runs. In snow-rich winters and before the establishment of a protected area closed for skiers, the criss-cross of skiing tracks became so dense that no quadrat of a 10-m grid remained untouched within three days after snowfall.

Within the Bavarian Alps, Fellhorn is one of the areas with the best structural habitat quality for black grouse. The area is characterized by acidic soils, east to south-eastern aspect, a pronounced relief with gullies, hill-tops, ridges, and crests, extended slopes covered by ericaceous shrubs such as *Rhododendron* and *Vaccinium*, alder (*Alnus viridis*), or dwarf-pine (*Pinus mugo*), and scattered dense rows of spruce trees (*Picea abies*). These features provide a great variety of feeding and resting places for black grouse, including snow conditions suitable for snow-burrows to roost. Snow layers of up to several m high cover the area from at least December through April. Thus, the availability of food and cover in winter is closely related to the amount and distribution of snow. The structurally best winter habitats for black grouse coincided with the areas most heavily frequented by skiers.

Within an area of c. 500 ha that could be overseen from the cable car stations, black grouse were observed for at least 24 hrs several times per year in the winters and springs 1989/90 to 1998/99, and at least once per week in the winter and spring 1999/2000. In 1999/2000, a total of 6844 black grouse observations were collected. One «observation» was the sighting of one

individual during a 15 min interval (e.g. 3 cocks seen for 25 min = 3 individuals x 2 intervals = 6 observation units). The behavioural categories distinguished were feeding, resting, locomotion, and male display. During encounters of black grouse with people or machines, the birds' behaviour and the distances between birds and disturbances were noted continuously; for this paper responses were classified as remaining (birds did not move away from source of disturbance), retreating (birds moved away short distances, mostly slowly walking into cover), and escaping (birds hurriedly moved away, mostly flights over longer distances). The availability of food was measured in relation to the height of the snow-cover. With each observation, locations used by black grouse were described as ground layer, ericaceous shrubs, shrub layer, and tree layer. If possible from the distance, important plant species such as *Alnus viridis*, *Pinus mugo*, *Sorbus aucuparia*, and *Picea abies* were noted. In addition, all structures within a 15 m radius around the observed bird were described in relation to the bird's behaviour (e.g. feeding on plants of the ground layer next to a patch of ericaceous shrubs with single spruce trees).

To exclude biases due to the presence of observers in the behaviour of black grouse or their interactions with other species such as red fox *Vulpes vulpes* or golden eagle *Aquila chrysaetos*, outdoor observations were restricted to the times skiers were present in the area; at other times, observations were exclusively made from existing buildings.

Area 2 : Bolsterlang

Several days each May between 1990 and 2000, displaying black grouse were recorded by several observers within a c. 600 ha area of alpine pasture in 1500-1800 m altitude, Allgäu, Bavarian Alps, Germany. Of a total of 48 observation days, 30 were without and 18 with human disturbances. Disturbances during the morning display or the evening before were recorded either by direct sightings of people, or by fresh footprints or ski-tracks on the lek.

Area 3 : Oberstaufen/Immenstadt

Several times each May between 1990 and 2000, displaying black grouse were recorded by several observers within a c. 300 ha area of alpine pasture in 1350-1800 m altitude, Allgäu, Bavarian Alps, Germany. Of a total of 45 observation days, 20 were without human disturbances. On 25 days, disturbances by herdsmen, cabin visitors, or hikers were observed. In May 2000, a hybrid between a male black grouse and a female capercaillie (*Tetrao urogallus*) caused disturbances of black grouse males at the lek, which resulted in similar dispersion patterns as human disturbances. Red foxes were regularly observed within the surroundings of the lekking area, but they affected the display of the black grouse only on rare occasions.

Results

Response to disturbances

On Fellhorn, black grouse used major parts of the 440 ha study area in winter. At intervals of one or several days to two weeks, the birds moved between 31 different locations that offered food and cover, or snow suitable for snow-burrows. Exogenous factors such as weather, snow cover, snow conditions, and disturbances appeared to trigger movements. However, black grouse also seemed to change between sites independently of noticeable external factors (**Fig. 1**).

In total, the responses of 3856 black grouse to human disturbances were observed (**Tab. I**). Observations comprised one to maximally 17 black grouse; the mean number of simultaneously observed birds was seven. In total, 496 interactions between one or several birds and disturbances were observed. Frequently, two or several simultaneous stimuli were recorded, e.g. skier and snow generator or skier and snow-groomer and snow-scooter.

The behaviour of the black grouse varied with distances and situations (compare **Tab. I**). The birds tolerated a tangential passing of skiers or snow-groomers on pistes and on regularly used off-piste runs while feeding or resting in trees (mostly spruce), and while moving on the ground. When in good cover, they continued their behaviour until the person or machine approached to distances of <10 to 30 m. In the open, however, response distances increased to >30 to 100 m. Closer approaches were either followed by slowly walking aside and hiding, or, most often, by escape flights over distances of 50 m to >1.5 km. Frontal approaches to 5 to >100 m usually led to escape flights into the nearest cover or over long distances. The birds frequently first perched on a spruce top for orientation after an initial, short escape flight, and continued shortly afterwards over distances of up to 3 km.

To unusual events, such as touring skiers climbing uphill after the operating hours of the ski-lifts, the birds responded already at distances of with >150 m with hurried and long escape flights. The receptional conditions for the black grouse were always the same, i.e., the birds used familiar feeding and resting sites, which almost always offered food and cover within short distances, which they usually covered on foot or in short flights between ground and trees. Motionless «freezing» for up to one hour, as repeatedly observed as a response to disturbances during the snow-free season, was never observed in winter. Also, behavioural differences between males and females were not observed in winter.

In contrast to the behaviour of rock ptarmigan in the area, black grouse did not use tree-less sites in winter; their habitat use depended on the presence of at least single dense spruce trees or groups of dwarf pines. Except during

flights between feeding or resting sites or during display in spring, black grouse never used locations without cover-providing spruce or dwarf pines. On a few occasions, black grouse used alder or rowan for daytime resting; in most cases, however, they perched on spruces. Overnight roosting on deciduous trees was never observed. Once, three black cocks were recorded to spend the night perched on a ski-lift support mast.

Black grouse did not keep any distance from non-operating technical structures such as snow-grooming vehicles or snow generators. Males regularly used ski-lift masts for display in spring; however, females were never seen sitting on masts. During the first winter after their installation, 1999/2000, black grouse kept distances of at least 150 m to operating snow generators. Further observations regarding the responses to snow makers were not possible during this winter, as generators next to actual feeding and resting sites of black grouse were not operated to avoid disturbances. At some particularly sensitive locations, snow makers were generally stopped between 06:00 and 09:00 a.m.

Table I. Responses of black grouse to different anthropogenous disturbance stimuli in the Fellhorn skiing area, Germany. Frontal approaches by humans or machines caused escape flights from distances of 5 to >100m in all cases; therefore, stimuli considered here are tangential passings only. Results are based on a total of 496 interactions of 1 to 17 black grouse (3856 observation units) between 1990 and 2000, and are structured in relation to behavioural context (behaviour), kind of disturbance (stimulus), response of the birds (S= total number; remain, retreat, escape as defined above; n= number of observations, m= number of males, f=females) and distance between bird and stimulus. Many interactions involved several stimuli, e.g. skiers and snow-groomers, which were recorded separately.

Réactions des Tétrasyes à différents stimuli perturbateurs d'origine humaine dans l'aire de ski de Fellhorn, en Allemagne. Des approches frontales par des hommes ou des machines à des distances de 5 à plus de 100 m ont provoqué dans tous les cas l'envol et la fuite des oiseaux. Dès lors, les stimuli considérés ici sont uniquement les passages tangentiels. Les résultats reposent sur un total de 496 interactions avec de 1 à 17 Tétrasyes (3856 unités d'observation) entre 1990 et 2000, et sont organisés en fonction du contexte comportemental (nature du comportement), du type du dérangement (stimulus), de la nature de la réaction des oiseaux (S = nombre total ; reste sur place, se retire, s'enfuit en vol ; n = nombre d'observations, m= nombre de mâles, f= femelles) et distance séparant l'oiseau et le stimulus. De nombreuses interactions impliquaient plusieurs stimuli, par exemple des skieurs et du personnel d'entretien, qui ont été répertoriés séparément.

Verhalten von Birkhühnern auf verschiedene anthropogene Störreize im Skigebiet Fellhorn. Frontalannäherungen von Menschen oder Maschinen auf Birkhühner führten immer zur Flucht aus Entfernungen von 5 bis >100m; daher sind als Störreize hier nur Passagen berücksichtigt. Die Ergebnisse basieren auf 496 Interaktionen von 1 bis 17 Birkhühnern (3856 Einzelbeobachtungen) von 1990 bis 2000 und sind gegliedert nach Kontext (Verhalten), Art des Störreizes (Reiz), Reaktion des Birkhühner (Reaktion; S= Gesamtzahl, V=Verbleiben, A=Ausweichen, F=Flüchten, n=Anzahl, m=Hähne, w=Hennen) und Entfernung. Bei vielen Interaktionen waren mehrere Reize, z.B. Skifahrer und Pistenraupen beteiligt, die aber getrennt aufgenommen wurden.

Behaviour	Stimulus	Response	Distance <10 – 30 m	Distance >30 – 100m	Distance >100 m
Feeding	Skiers downhill on and <30 m off piste _s	S	m = 87 f = 68	m = 242 f = 183	m = 212 f = 240
		Remain	m = 50 f = 44	m = 136 f = 106	m = 212 f = 240
		Retreat	m = 12 f = 8	m = 25 f = 17	n = 0
		Escape	m = 25 f = 16	m = 81 f = 60	n = 0
Feeding	Snow grooming vehicles on pistes	S	m = 92 f = 35	m = 65 f = 28	m = 81 f = 39
		Remain	m = 65 f = 26	m = 55 f = 23	m = 81 f = 39
		Retreat	m = 20 f = 5	m = 6 f = 3	n = 0
		Escape	m = 7 f = 4	m = 4 f = 2	n = 0
Feeding	Snow generators operating since 1999	S			m = 18 f = 10
		Remain	no observations	no observations	m = 18 f = 10
		Retreat			n = 0
		Escape			n = 0
Feeding	Touring skiers uphill outside lift operating hours; skiers downhill >30m of pistes	S	m = 28 f = 12	m = 39 f = 16	m = 14 f = 8
		Remain	n = 0	n = 0	n = 0
		Retreat	n = 0	m = 2 f = 1	m = 0 f = 2
		Escape	m = 28 f = 12	m = 37 f = 15	m = 14 f = 6
Resting on trees (daytime and morning) and resting in snow-roosts	Skiers downhill on and <30 m off pistes; 8 near-collisions at escape from snow-burrows; 1 collision fatal for blackcock	S	m = 244 f = 78	m = 209 f = 71	m = 280 f = 192
		Remain	m = 132 f = 48	m = 135 f = 45	m = 280 f = 192
		Retreat	m = 50 f = 22	m = 16 f = 14	n = 0
		Escape	m = 62 f = 8	m = 58 f = 12	n = 0
Resting on trees (daytime and evening) and resting in snow-roosts	Snow groomers; risk of birds being run over, 4 close escapes observed.	S	m = 67 f = 32	m = 252 f = 108	m = 478 f = 194
		Remain	m = 40 f = 18	m = 189 f = 83	m = 461 f = 174
		Retreat	m = 15 f = 6	m = 63 f = 25	m = 8 f = 12
		Escape	m = 12 f = 8	n = 0	m = 9 f = 4
Resting on trees (daytime and evening)	Snow generators operating since 1999	S			m = 44 f = 17
		Remain	no observations	no observations	m = 44 f = 17
		Retreat			m = 0 f = 0
		Escape			m = 0 f = 0
Resting on trees (evening)	Touring skiers, uphill or downhill off usual routes or times; skiers downhill > 30m off pistes	S	m = 23 f = 10	m = 17 f = 11	m = 4 f = 2
		Remain	n = 0	m = f =	m = 1 f = 1
		Retreat	n = 0	m = 2 f = 1	n = 0
		Escape	m = 23 f = 10	m = 15 f = 10	m = 3 w n = 1

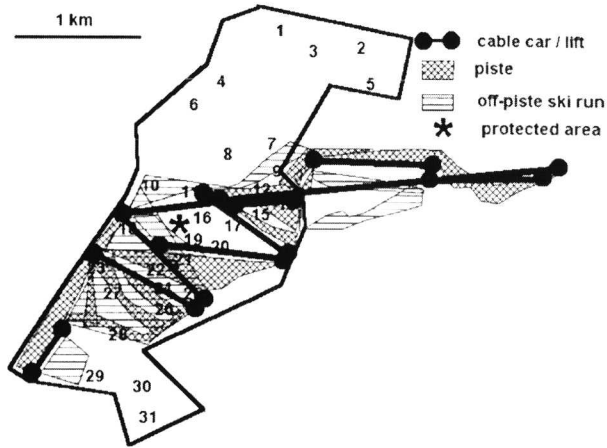


Fig. 1. Black grouse used 31 different locations (see numbers) within the 440 ha study area in the Fellhorn ski resort, Allgäu, Germany, from November 1999 to May 2000. - The surrounding line delineates the study area, bold lines indicate cable car (longest line) and ski-lifts. Cross-hatched areas are prepared pistes, hatched areas off-piste slopes used by skiers, blank areas are undisturbed by skiing activities, including a 50 ha reserve closed for skiers (Schutzgebiet).

Entre novembre 1999 et mai 2000, les Tétrax lyres ont utilisé 31 postes différents (localisables par les chiffres) au sein des 440 ha de l'aire d'étude (délimitée par la ligne brisée externe) du site de la station de ski de Fellhorn, Allgäu en Allemagne. Les lignes épaisses joignant les cercles noirs localisent les remonte-pentes pour cabines (la plus longue) ou skieurs. Les espaces quadrillés correspondent aux pistes préparées, les espaces hachurés à des pentes hors-pistes utilisées par les skieurs, les zones blanches enfin à des espaces non perturbés par les activités de sports de neige, en ce compris une réserve interdite aux skieurs.

Birrkühner nutzen zwischen November 1999 und Mai 2000 31 verschiedene Teilgebiete inner halb des 440 ha großen Untersuchungsgebiets im Skigebiet Fellhorn, Allgäu, Deutschland, zwischen denen sie in täglichen, mehrtägigen bis zweiwöchigen Abständen wechselten. - Die Umrisslinie begrenzt das 440 ha große Untersuchungsgebiet, fette Linien bedeuten die Seilbahn (längste Linie) und Skilifte, Kreuzschraffur bezeichnet die präparierten Pisten, Schraffur Variantenabfahrten, offene Flächen blieben von regelmäßigen Wintersport-Aktivitäten unberührt

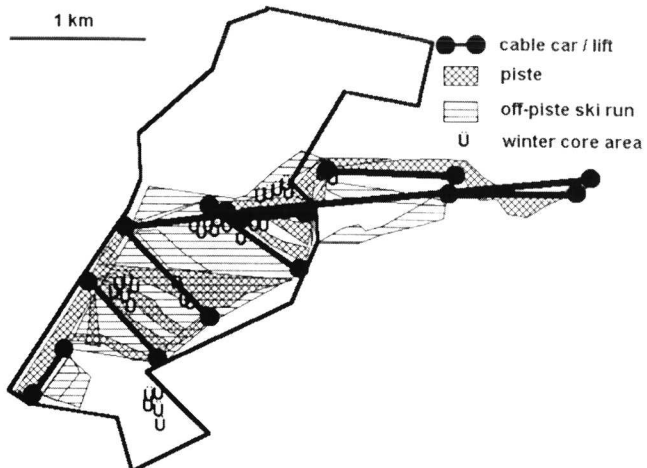


fig. 2. Winter core areas (Ü) within the Fellhorn skiing area, Allgäu, Germany, regularly used by black grouse during the 1989/90. Observed winter population size was 16 males and

13 females. For map symbols see Fig. 1.

Répartition des sites hivernaux (Ü) régulièrement fréquentés par les Tétrasyres en 1998/1999 à la station de sports de neige de Fellhorn en Allemagne. La population hivernale comptait 16 mâles et 13 femelles. Voir les symboles de la carte à la figure 1. Schwerpunkte in der Winternutzung (Ü) von Birkhuhn-Gruppen im Skigebiet Fellhorn im Winter 1989/90. Insgesamt wurden 16 Hähne und 13 Hennen gezählt. Signaturen siehe Abb. 1.

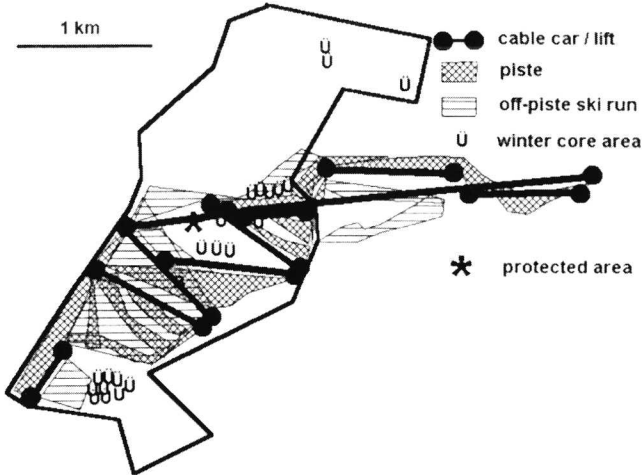


Fig 3. Winter core areas (Ü) within the Fellhorn skiing area regularly used by black grouse during the 1999/00. Observed winter population size was 13 males and 9 females. A 50 ha black grouse protection area closed for skiing activities had been established in 1996 (Schutzgebiet). The replacement of one of the lifts in the south-western part of the area with a chair-lift with doubled capacity (compare Fig. 2) and the installation of snowmakers coincided with the desertion of one of the most regularly used feeding places by black grouse.

Répartition des sites hivernaux (Ü) régulièrement fréquentés par les Tétrasyres durant l'hiver 1999/2000. La population comptait 13 mâles et 9 femelles. Une zone refuge pour les tétras de 50 ha et fermée aux activités de ski avait été créée en 1996. Le remplacement d'un des remontes-pentes dans la zone sud-ouest par un autre de double capacité (cf fig. 2) et l'installation de canons à neige a coïncidé avec l'abandon d'une des zones de nourrissage les plus régulièrement utilisées par les Tétrasyres.

Schwerpunkte in der Winternutzung (Ü) von Birkhuhn-Gruppen im Skigebiet Fellhorn im Winter 1999/2000. Insgesamt wurden 13 Hähne und 9 Hennen festgestellt. Ein 50 ha großes, für Wintersportler gesperrtes Schutzgebiet wurde 1996 eingerichtet. Nach dem Ersetzen eines Schlepplifts im Südwestern des Gebietes durch eine Sesselbahn mit verdoppelter Kapazität (vgl. Abb. 2) und dem Bau einer Beschneigungsanlage wurde eines der am regelmäßigsten genutzten Nahrungsgebiete nach Beginn des Skibetriebes von den Birkhühnern aufgegeben. Signaturen siehe Abb. 1.

Chances in winter spacing and population size

In all winters between 1989/90 and 1999/2000, black grouse on Fellhorn used some locations particularly often and regularly. In the following, such areas were termed winter core areas. Some of these cores remained stable over years, others shifted, partly with and partly without obvious relation to skiing activities. The locations of black grouse winter core areas in the Fellhorn skiing area in 1989/90 are shown in **Fig. 2**. Around one of these core areas, a 50 ha reserve closed for all skiing activities was established in 1996 (**Fig. 3**). After the replacement of a ski-lift in the southwestern part of the area with a chair-lift with doubled capacity (2200 persons/h) (**Fig. 3**, compare **Fig. 2**), one of the core areas most regularly used for feeding and resting was deserted by black grouse. The observed number of wintering black grouse on Fellhorn decreased from 16 males and 13 females in 1990 to 11 males and 9 females in 2000. As a major single cause of this decline an insufficient number of undisturbed feeding and resting sites is hypothesised.

Changes in the use of display areas

On Fellhorn, the skiing season ends variably between late March and late April. The longer the skiing season in spring, the more significant become disturbances of the display season. Compared to experience from other black grouse areas and with descriptions in the literature, the distribution of displaying males at Fellhorn appeared to be more variable and related to disturbances.

In May 1990, 17 black grouse males displayed in the 440 ha the Fellhorn study area. As the ski season ended particularly early that year, the black grouse display remained largely undisturbed. Three leks already known from previous years were regularly used by several males, and one site by a solitary male. In addition, two further sites were occasionally used by solitarily displaying males (**Fig. 4**). Over the following years, the ski seasons extended into the display period, disturbances became more frequent, and the use of the traditional leks decreased continuously. In May 2000, 11 displaying males were observed in the study area (**Fig. 5**). None of the former lek sites was still used. Only one site in the undisturbed north of the area was regularly used by 1-2 displaying males. All other males displayed at various temporary sites among which they switched between and even during mornings.

The impression of a causal relationship between the frequency of disturbances and the stability of leks was supported by observations in the two other study areas. In the Bolsterlang area, a 600 ha ski-touring area adjacent to a downhill ski resort, up to 18 males displayed collectively at the largest and 4 males each at two smaller leks; in addition, two sites were regularly used by solitary males. In 1990-1994, after rare disturbances by skiers, males dispersed over a large number of temporary display sites; however, they returned to their

traditional leks within hours or days. After the construction of a chair-lift in close vicinity in 1995, the frequency of disturbances multiplied. The total number of displaying males decreased to 12 to 14. The number of males displaying at the traditional leks varied between 0 and 6; only on exceptional occasions up to 12 males could still be observed. The remaining 8-10 males displayed solitarily or in small groups at temporary sites distributed over 560 ha (see **Fig. 6**). A causal relation between human disturbances, the population decline and the instability of display sites appears to be likely.

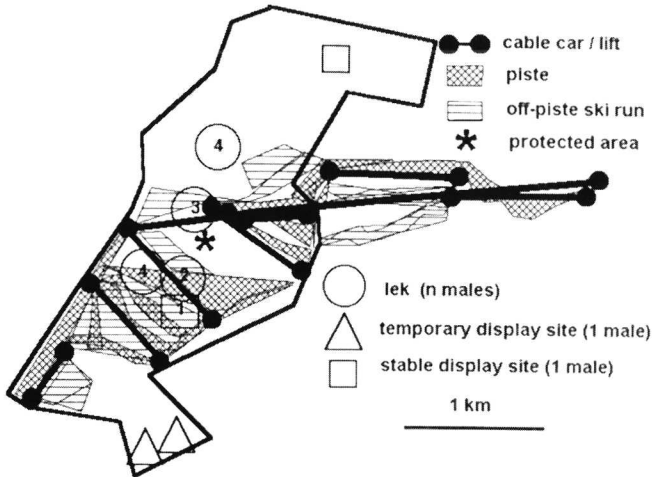


Fig. 4. Distribution of the 17 black grouse males displaying in a 440 ha part of the Fellhorn skiing area in May, 1990. Three locations were regularly used as leks by several males (circles), and two sites by solitary males (squares). In addition, two sites were used temporarily by solitary males (triangles). For further map symbols see Fig. 1.

Répartition des 17 Tétrax lyres mâles paradant sur l'aire de 440 ha du site de la station de ski de Fellhorn en mai 1999. Trois sites étaient régulièrement fréquentés par plusieurs coqs organisés en arène (cercles), et deux par des coqs solitaires (carrés). De plus, deux sites étaient utilisés temporairement par des coqs solitaires (triangles). Les autres symboles sont présentés à la figure 1.

Verteilung von 17 balzenden Birkhähnen in dem 440 ha großen Untersuchungsgebiet im Skigebiet Fellhorn, Mai 1990. Durch das frühe Ende der Skisaison war das Balzgeschehen 1990 weitestgehend störungsfrei. Drei traditionelle Balzplätze wurden von mehreren Hähnen (Kreise) und ein Platz von einem einzelnen Hahn (Quadrat) regelmäßig genutzt. Zudem balzten einzelne Hähne an zwei temporären Balzplätzen (Dreiecke). Weitere Signaturen siehe Abb. 1.

Experience from the Oberstaufen study area confirmed the impressions from Fellhorn and Bolsterlang. In undisturbed situations during the black grouse display seasons in May 1990-2000, up to nine males displayed collectively on a traditional lek of 0.4 ha; in addition, one site was regularly used by a solitary male. After disturbances, males were distributed over 180 ha and varying temporary display sites. From 1997 to Mai 2000, no more than 7 males were simultaneously seen at the lek (**Fig. 7**). In 2000, a hybrid *Tetrao tetrix* x *Tetrao urogallus* attended the lek and had similar effects on the spatial distribution of displaying black grouse males as had human disturbances: black grouse used temporary display sites and returned to the traditional lek within hours or days.

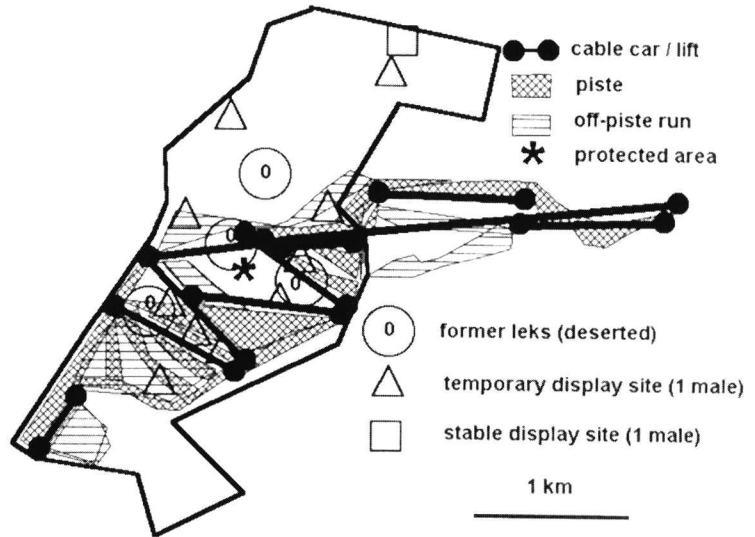


Fig. 5. Distribution of the 11 black grouse males displaying in a 440 ha part of the Fellhorn skiing area in May, 2000. None of the former arena sites (circles; see Figure 4) was still used. Only one site in the north of the area was regularly used by 1-2 displaying males (square). All other males displayed at various temporary sites (triangles) among which they switched between and even within mornings. For map symbols see Fig. 1.

Répartition des 11 Tétrasyes mâles paradant sur l'aire de 440 ha du site de la station de ski de Fellhorn en mai 2000. Aucun des sites des arènes fréquentés l'année précédente (cercles, fig. 4) n'était encore utilisé. Un seul site dans la partie nord de l'aire étudiée était encore utilisé régulièrement par un ou deux coqs (carré). Tous les autres mâles permutaient d'un jour à l'autre ou en cours d'une même matinée entre divers sites temporaires de parade (triangles). Pour les autres symboles, voir la fig. 1.

Verteilung von 11 balzenden Birkhähnen in dem 440 ha großen Untersuchungsgebiet im Skigebiet Fellhorn, Mai 2000. Keiner der traditionellen Balzplätze (Kreise, s. Abb. 4) wurde noch genutzt. Nur an einem störungsfreien Balzplatz im Norden des Gebiets wurden regelmäßig 1-2 Hähne beobachtet (Quadrat). Alle anderen Hähne balzten meist einzeln an temporären Balzplätzen (Dreiecke), zwischen welchen sie von Tag zu Tag und auch während eines Balzmorgens wechselten. Weitere Signaturen siehe Abb. 1.

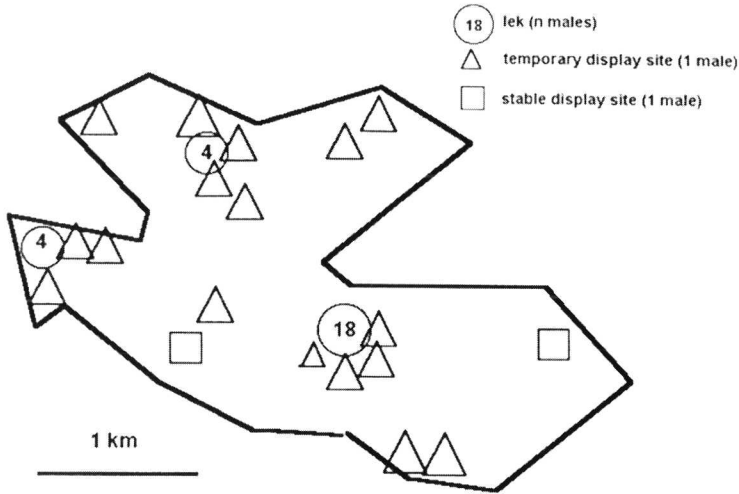


Fig. 6. Distribution of black grouse males displaying within 560 ha adjacent to skiing resort Bolsterlang in the Allgäu Alps, Germany. From 1990 and 1994, up to 18 males displayed collectively on the largest traditional lek (1 ha), two other leks were each used by 4 males (circles), and two sites were regularly used by solitary males (squares). After the construction of a chair-lift in 1995 in close vicinity, the frequency of disturbances by skiers multiplied. On undisturbed days in 1997-2000, the largest lek was used by up to 4-6, and in rare cases up to 12 males, and 8-10 males displayed solitarily or in pairs at temporary sites (triangles). After disturbances, the traditional leks were deserted, and up to 14 displaying males were dispersed over a large number of temporary display sites within a 560 ha area; however, they returned to the traditional display sites within hours or days.

Répartition des Tétras lyres mâles paradant dans une aire adjacente de 560 ha de la station de ski de Bolsterlang dans le secteur alpestre de l'Allgäu en Allemagne. De 1990 à 1994, jusqu'à 18 coqs paradaient collectivement sur une large arène traditionnelle (1 ha), deux autres arènes accueillait 4 mâles (cercles), et deux sites étaient régulièrement utilisés par des coqs solitaires. Après la construction à proximité d'un télésiège en 1995, les perturbations induites par les skieurs se sont multipliées. Pendant les jours de tranquillité de 1997 à 2000, la plus grande arène était utilisée par 4 à 6 coqs, et en de rares occasions par un maximum de 12 coqs, tandis que 8-10 autres paradaient en solitaire ou en duo sur des sites temporaires (triangles). Lors des perturbations, les arènes traditionnelles étaient abandonnées et jusqu'à 10 mâles se dispersaient sur un grand nombre de sites temporaires dans les limites de l'aire considérée de 560 ha ; toutefois, ils regagnaient les sites habituels après quelques heures ou jours.

Verteilung der balzenden Birkhähne in dem 560 ha großen, an ein Pistenskigebiet angrenzende Skitourengebiet Bolsterlang, Allgäuer Alpen, Deutschland. Von 1990 bis 1994 balzten bis zu 18 Hähne auf dem größten traditionellen Balzplatz (1ha), je 4 Hähne balzten auf zwei weiteren Balzplätze (Kreise), außerdem gab es zwei regelmäßige Einzel-Balzplätze (Quadrat). Nach dem Bau einer Sesselbahn 1995 in unmittelbarer Nachbarschaft vervielfachte sich die Frequenz der Störungen. An störungsfreien Tagen in 1997-2000 wurde der größte Balzplatz von 4-6, und in seltenen Fällen von bis zu 12 Hähnen genutzt; 8-10 Hähne balzten einzeln oder zu zweit an wechselnden temporären Plätzen (Dreiecke). Nach Störungen wurden die traditionellen Balzplätzen verlassen und bis zu 14 Hähne balzten einzeln oder in kleinen Gruppen an wechselnden temporären Plätzen, verstreut über eine Fläche von 560 ha.

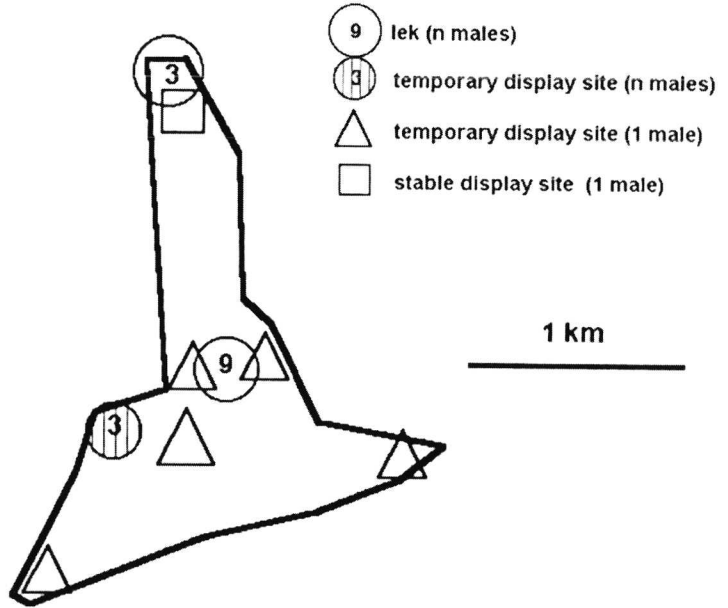


Fig. 7. Distribution of black grouse males displaying within a 180 ha part of ski touring area Oberstaufen in the Allgäu Alps, Germany, 1990-2000. Between 1990 and 1996, on days without disturbances, nine and three males, respectively, displayed on two traditional leks (0.4 ha and 0.2 ha; circles). After disturbances, males left the leks and displayed distributed over varying temporary display sites (triangles); they returned to the traditional leks within hours or days. From 1997 through 2000, the traditional leks remained deserted. Only one site was regularly used by a solitary male (square). Males displayed at varying temporary sites and mostly solitarily (triangles). Only one site was temporarily used by three males (hatched circle).

Répartition en 1990-2000 des Tétrax lyres mâles paradant dans une aire de 180 ha du site de ski de l'Oberstaufen dans le secteur alpestre de l'Allgäu en Allemagne. Entre 1990 et 1996, et pendant les jours de tranquillité, 9 et 3 coqs paradaient respectivement sur deux arènes traditionnelles (0,4 et 0,2 ha ; cercles). Lors des dérangements, les mâles quittaient les arènes et se répartissaient sur une variété de sites temporaires de parade (triangles) ; ils rejoignaient leurs sites favoris dans les heures ou jours suivants. De 1997 à 2000, les arènes traditionnelles restèrent désertes. Un seul site fut encore fréquemment régulièrement par un coq solitaire (carré) ; les autres mâles paradaient sur une variété de sites temporaires, le plus souvent en solitaire (triangles) ; un seul site (cercle hachuré) fut encore utilisé, occasionnellement, par 3 mâles.

Verteilung von balzenden Birkhähnen in einem 180 ha großen Teil des Skitourengebiets Oberstaufen in den allgäuer Alpen, Deutschland, 1990-2000. Von 1990 bis 1996 balzten an Ragen ohne Störeinflüsse neun bzw drei Hähne auf zwei traditionellen Balzplätzen und verteilten sich über wechselnde temporäre Plätze (Dreieck). Von 1997 bis 2000 blieben die beiden traditionellen Balzplätze verlassen. Ansonsten balzten die Hähne an wechselnden Plätzen und meistens einzeln, lediglich ein Platz wurde gelegentlich von drei Hähnen genutzt (schraffierter Kreis).

Discussion

Response to disturbances

The observed responses in this study illustrated the breadth and the limitations of the adaptation of black grouse to «disturbance stimuli» typical for skiing areas. The characteristics of the area, such as its orography and vegetation structure (A. ZEITLER unpubl. data), and the spatial and temporal frequency and regularity of the stimuli appear to be the determinants of the birds' behaviour. In safe cover, black grouse tolerate disturbances that occur within the normal spatial and temporal patterns. Black grouse roosting on spruce trees next to a ski run may tolerate uphill heading touring skiers among hundreds of downhill skiers; a single touring skier, however, climbing uphill the same run after the closing of the ski-lifts in the evening, i.e., outside the normal temporal pattern, will most likely cause an escape.

The relatively short response- and escape distances of black grouse towards passing skiers or snow-groomers were observed only as long as disturbances remained restricted to one side of the birds. Stimuli from two or more directions, e.g. from the front and the back, inevitably led to long (≥ 200 m) escape flights. For the interpretation of the behavioural responses reported here, one should also keep in mind that the hunting of grouse has been banned in Germany, and thus also in the study areas, since the early 1970s; in hunted populations, longer escape distances towards humans should be expected.

The response- and escape distances observed in this study should not be regarded as generally suitable guidelines for the establishment of black grouse protection areas within ski resorts. However, they point to possibilities to develop regulations that allow to maintain black grouse populations and to minimize further habitat losses even in intensively used skiing areas. The most important approach is a strict spatial and temporal separation of skiing activities and the feeding and resting sites of black grouse. This is of particular significance in the Bavarian Alps: at a regional scale, there is not a single mountain range or black grouse area without downhill ski resorts or popular ski touring route networks (ZEITLER and GLÄNZER 1997). Success of regulations implemented to reduce disturbances of black grouse can only be evaluated in the course of the skiing season. Factors influencing black grouse during display, incubation, or chick rearing will affect the population in addition to disturbances in winter; also, larger-scale factors operating at the metapopulation level may significantly affect local population dynamics.

Chances in winter spacing and population size

As elsewhere, black grouse populations in the Alps may show pronounced fluctuations between years (e.g. BOSSERT 1996, BOSSERT *et al.*

1999, HESS 2000). The study areas at the northern slope of the Alps are rich in precipitation, and chick survival may strongly depend on the weather during the first 2-3 weeks after hatching. Also, a late snow-melt may cause poor physical condition in females during the pre-breeding period, and may thus contribute to poor reproductive success (e.g. BOSSERT *et al.* 1999). In downhill skiing areas, cleaning-up activities related to the resort's closing for the summer, as well as an early start of the summer hiking season may cause disturbances of black grouse during incubation and brood rearing. Also, livestock, herdsman and their activities may threaten clutches and broods.

There is the risk that skiing areas that offer habitat structures attractive for incubation and brood rearing such as Fellhorn develop into "ecological traps" (GATES and GYSEL 1978, s. auch BERGMANN *et al.* 1996): The period between the closing of the ski runs in late spring and the onset of livestock pasturing and mass hiking (FELLHORN: some hiking routes continuously used by up to 700 persons per km) in early summer are relatively quiet, and coincide with the periods of mating, egg laying, and early incubation of black grouse. Thus, conditions that seem favourable for breeding, good habitat structure and few disturbances, may attract females to invest in clutches, of which the majority will get lost later. Disturbances may also cause losses among chicks: the time available for feeding and for brooding of the chicks by the female is reduced; in cold and wet weather this may lead to the death of chicks.

In this context, Fellhorn might have developed from a former source population into a sink area; as no juveniles have been observed in summer or autumn for years (A. ZEITLER, unpubl. data), mortality is likely to exceed reproduction. The fluctuations in the numbers of birds observed over the eleven years of study indicate an overall negative population trend. Perhaps the decline of the Fellhorn population is to some degree buffered by immigration of birds from neighbouring areas, which, compared to Fellhorn, are all structurally suboptimal habitats.

Changes in the use of display areas

The interpretation of the observations during the display season is based on the following assumptions: in general, many males at large leks and few solitarily displaying males indicate good populations (BOSSERT 1996), and accordingly, an increase in the proportion of solitary males and small leks is a symptom of declining or low-density populations. The results of this study support this hypothesis.

Within the 11-year study period, the observed changes in the use of leks versus temporary display sites appeared to be reversible. Longer undisturbed periods in the course of the lekking season were associated with a temporary increase in the number of males at the traditional leks in the Bolsterlang and Oberstaufen study areas, whereas disturbances were followed by considerable

shifts in the spatial distribution of males. Of anecdotic nature, but nevertheless worth mentioning, is the observation that a male black grouse x capercaillie hybrid at a black grouse lek caused changes in the spatial distribution of displaying black grouse males similar to those caused by human disturbances. Three of seven black grouse males retreated opportunistically to a dense patch of alder in 400 m distance, where the aggressive attacks of the hybrid male were less effective than on the open lek. The remaining four cocks of the lek displayed solitarily on hill tops in up to 1 km distance (three observation days in May 2000).

HÖGLUND and STOHR (1997) discuss the hypothesis of genetic differences between solitarily and collectively (i.e. lekking) displaying black grouse males. Although these authors favour other factors (age structure, habitat, low population density) as the most likely explanations of a population of non-lekking black grouse observed in Sweden, the genetic hypothesis is interesting with regard to developments in frequently disturbed black grouse habitats. Although during the eleven years of observation at Fellhorn, Bolsterlang, and Oberstaufen, shifts between lekking and solitary display appeared to be reversible, there was an overall tendency towards an increasing proportion of solitarily displaying males. Apparently, the mating system shifted from hens visiting males at leks towards males individually searching for and displaying in habitats used by females. If females avoid open leks in areas with frequent disturbances, and as a consequence, solitary males achieve greater reproductive success than do lekking males, a genetic disposition for solitary display would lead to a decline in the proportion of traditionalistic lekking males and an increase in the numbers of opportunistic solitary males within populations in disturbed areas. It should be stressed, however, that these considerations are speculative and could not be tested within the framework of the present study.

Conclusions for conservation concepts and criteria of success

In an applied conservation context, this study indicates that even intensive use of skiing areas can be compatible with black grouse conservation as long as sufficient undisturbed time and space is secured, and if skiing activities can be strictly and reliably excluded from a sufficient number of feeding and resting areas.

On Fellhorn, black grouse apparently shifted between a variety of preferred winter feeding and resting places also independently of disturbances. This «rotation» of winter groups took place within a 500 ha area; exchange with birds from neighbouring areas can be anticipated within much larger areas of c. 3,000 to 20,000 ha. Thus, to effectively provide for the requirements of a local black grouse population, more than just a few reliably undisturbed habitat

patches must be secured within the surroundings of at least a few thousand hectares. The only presently existing protected area on Fellhorn, which was established as a result of this study in 1996, measured 50 ha. At least 10 further areas within the Fellhorn study area urgently require the exclusion of all skiing activities in order to allow the black grouse to maintain their movements between different feeding and resting locations.

Recent trends in winter sports indicate, however, that equipment will be developed and promoted for all terrains and all interest groups. As a result, the physical limitations to human accessibility of black grouse winter habitats decline rapidly. Snowboards as „fun equipment“ can be used in even the most difficult terrain inaccessible on conventional skis, and with almost all kinds of snow conditions; on the other hand, snowshoes are presently becoming popular in the Alps and lead to a pronounced increase of winter hiking in the quietest and least disturbed areas (see MÈNONI and MAGNANI 1997).

In an applied conservation context, the following criteria of success are suggested:

A sufficient number and size of undisturbed patches to allow for local-scale movements of black grouse between different feeding and resting habitats of high quality,

The reliable closing of these patches for humans and a general acceptance of protected areas by skiers, and, as a longer-term effect, an increasing proportion of lekking males and the stabilisation of lek traditions.

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ZUSAMENFASSUNG : Menschliche Störungen, Verhalten und Raumnutzung von Birkhühnern in Skigebieten der Allgäuer Alpen*

Birkhühner (*Tetrao tetrix* L.) gelten als «störungsempfindlich», andererseits können sie gelegentlich unmittelbar am Rand stark befahrener Skipisten beobachtet werden. Um aufzuzeigen, dass dies kein Widerspruch ist, sondern in der ökologischen und ethologischen Plastizität der Art begründet ist, werden in diesem Artikel Beobachtungen in Skigebieten der Allgäuer Alpen, Deutschland, dargestellt und diskutiert. Das Verhalten und die Raumnutzung von Birkhühnern im Winter und während der Balz in Abhängigkeit des Auftretens von Störungen wurden in einem intensiv genutzten Pisten-Skigebiet über einen Zeitraum von elf Jahren untersucht. Zum Vergleich werden Balzzeit-Beobachtungen aus einem Skitourengebiet am Rand eines Pisten-Skigebiets und aus einem unerschlossenen Skitouren-Gebiet der Allgäuer Alpen berichtet. Abhängige Variable war das Raum-Zeit-Muster der Tiere, unabhängige Variablen waren die konkurrierenden Raum-Zeit-Muster des Skibetriebs auf und abseits der präparierten Pisten, Pistenpflege und Skifahren sowie Schneeverhältnisse und Wetter. Beim Kontakt mit Menschen und Maschinen wurde eine Verhaltensspanne beobachtet, die von Unterbrechungen des aktuellen Verhaltens und Fluchtflügen bis zu einem Beibehalten des aktuellen Verhaltens bei einer Entfernung der Tiere von >10 m von Menschen oder Maschinen reichte. Längerfristig zeigte sich eine Verschiebung der winterlichen Raumwahl in Abhängigkeit vom Skibetrieb bei gleichzeitig abnehmender Populationsgröße. Zu Zeiten und in Gebieten mit starker Belastung durch Störungen wurden traditionelle Balzplätze aufgegeben, die Hähne balzten einzeln und über große Flächen verstreut an wechselnden Orten. Nach den Beobachtungen sind Störereignisse um so kritischer zu bewerten, je weniger Ausweichräume mit guten Habitateigenschaften vorhanden bleiben. Die Ergebnisse führten zu Empfehlungen an die relevanten Behörden, privaten Organisationen und Betreiber, in Skigebieten Ruhezeiten für Birkhühner einzurichten.

* Eine vollständige deutsche Fassung des Artikels kann vom Autor bezogen werden (albinzeitlerwildbiologie@hotmail.com).

Schlüsselwörter: Alpen, Balzplatz, Birkhuhn, menschliche Störung, Schutzmaßnahmen, Ski, *Tetrao tetrix*, Winter.

RESUME : Dérangements d'origine humaine, comportement et répartition spatiale des tétras lyres (*Tetrao tetrix*) dans les zones skiabiles des Alpes bavaroises.

Bien que les tétras lyres soient considérés comme très susceptibles aux dérangements d'origine humaine, ils sont occasionnellement observés près de pistes de ski parmi les plus fréquentées. Pour montrer que ceci n'est pas une contradiction, mais le résultat de la plasticité comportementale et écologique de l'espèce, nous présentons et discutons les résultats d'observations de ces oiseaux dans des sites populaires des sports de glisse dans les Alpes bavaroises, en Allemagne. Le comportement et la répartition des tétras lyres y ont été étudiés pendant 11 ans, durant la saison hivernale et la période des parades, en relation avec les dérangements liés à l'activité d'une piste de descente à skis intensivement fréquentée. Ces données sont comparées aux observations faites sur des sites de parade dans une autre station touristique proche d'une autre piste de descente à skis d'une part, et dans une zone où les sports de neige sont peu développés d'autre part.

La variable dépendante était le patron temporel et spatial de l'utilisation de l'habitat, tandis que les variables explicatives comprenaient la répartition temporelle et spatiale des skieurs et autres utilisateurs de neige, sur les pistes préparées ou hors-piste, les activités d'entretien des pistes, les conditions climatiques et l'abondance de neige. Les réactions des tétras à des rencontres avec des gens ou des machines à des distances supérieures ou égales à 10 m allaient de la continuation de l'activité en cours — repos, alimentation, parade — à l'interruption de celle-ci et ce pour une durée de maximum une heure, et à des fuites en vol vers un point situé à des distances variant de 50 m à 3 km.

Au fil des années, des changements devinrent perceptibles quant à l'utilisation des zones hivernales d'alimentation, et les sites de repos et les effectifs des oiseaux hivernant déclinèrent. À des moments et en des lieux de fortes perturbations, les arènes traditionnelles furent abandonnées, et les coqs paradèrent en solitaire sur des sites temporaires. Il se dégage de l'étude que moins il subsiste dans une zone donnée de petits espaces d'habitats convenables et non perturbés, plus critiques et dommageables pour les coqs sont les perturbations occasionnées par les dérangements d'origine humaine. L'étude a abouti à la formulation de recommandations aux agences, administrations, organisations privées et opérateurs touristiques concernés, en vue de la préservation et de l'aménagement de zones de protection non perturbées en faveur des tétras lyres dans les zones skiées des stations de sports d'hiver.

Mots-clés : Alpes, Tétracidés, *Tetrao tetrix*, Conservation, Dérangements anthropiques, Hiver, Parades, Sports de neige.