Conservation ecology of the Alpine Black grouse (*Tetrao tetrix*): 1) modelling the impact of snow sports on local density; 2) arthropod food supply in different habitat types

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Does human disturbance by spreading snow sports impact on local abundance of Alpine wildlife: a case study of the Black grouse (*Tetrao tetrix*)

Part 1

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Abstract

1. Tourism and leisure activities in remote areas have increased continuously over the last decades, exerting a growing pressure upon wildlife. Increasing disturbance by winter snow sports affects animal species which are already threatened otherwise. It could be a reason for the reported decline in many Black grouse populations in the Alps.

2. The aim of this study was to evaluate the relative impact of the main factors thought to affect the local density of Black grouse populations in the Alps: habitat characteristics (plant association), presence of ski resorts and hunting pressure.

3. Our results show that ski resorts have a strong negative impact on Black grouse abundance, with plant association also playing a role. Hunting pressure, however, has a marginal adverse influence on local density.

4. Conservation action plans for Black grouse should aim at reducing the multiple negative effects generated by ski resorts (habitat alteration, disturbance by snow sports, etc.). Wintering preserves where human penetration is banned should be promoted. Further alteration of optimal habitats must be limited, and management integrating land-use practices respecting Black grouse requirements should be implemented. Specific game reserves in areas with declining populations would contribute to the protection of this emblematic species of the Alps.

Key words: Ski resorts, habitat quality, hunting, *Tetrao tetrix,* species conservation

1. Introduction

On a global scale, tourism and other public recreational activities, even in remote areas, have been continuously increasing over the last decades (Wüthrich, 2001). The effects of these activities on wildlife are complex, highly variable and remain largely ill-understood. Behavioural studies of the impact of human outdoor activities have been shown to potentially disturb wildlife, resulting in partial abandonment of suitable habitats (Ingold, 2005). Yet, there is a lack of information about the "area of influence" of different forms of recreation (Taylor & Knight, 2003). It is in most cases unknown over which area such activities can exert their impact, i.e. within which radius individuals or populations are displaced from suitable habitat due to human pressure. The increasing human use (habitat alteration, disturbance etc.) of fragile Alpine ecosystems affects numerous threatened and vulnerable species. An example is the Black grouse (*Tetrao tetrix*), an emblematic game bird with economic and cultural value. The Black grouse has the greatest range among all Tetraonidae (Potapov, 1985). Even so, Black grouse populations are declining in several parts of their geographic distribution, especially in Western and Central Europe. Many lowland populations have disappeared, with the remaining ones being mostly small (Klaus et al., 1990; Loneux and Ruwet, 1997; Storch, 2000a). Most populations in the Alps seem now to be stable, although local dramatic declines have been reported over the last decades (Klaus et al., 1990, Hess, 2000). Several potential reasons have been proposed. Fragmentation, degradation and total loss of habitats due to increased use of space by humans seem to represent the major factors at low elevations (Niewold, 1990; Storch, 1990; Kurki et al., 2000; Sun et al., 2003). In the mountainous regions, ski resorts have profoundly modified the landscape (Ingold, 2005; Zbinden et al., 2001). Moreover, the progressive abandonment of traditional farming practices, such as cattle grazing and meadow mowing can also be considered as a possible threat in some Alpine regions (Storch, 2000).

A further series of factors could be the steady increase of tourism and related leisure activities, which exert a continuously rising pressure on wildlife, this

especially in the Alpine regions. Wintering habitats of Black grouse are particularly at risk because they overlap with popular ski resorts (Meile, 1982; Ménoni and Magnani, 1998; Zeitler and Glänzer, 1998). Outside ski resorts, rapidly developing off-piste skiing, snowboarding, snowshoeing or mountaineering skiing pose new additional threats to Black grouse populations. Repeated flushings, especially of birds resting in snow burrows, induce first extra energetic costs during the physiologically critical cold season (Baltic et al., 2005), which may constrain Black grouse to occupy suboptimal habitats (Marti, 1986a). They also induce stress (Baltic, 2005), which may decrease fitness and survival. Ski infrastructures influence Black grouse populations not only indirectly by transporting people to the wintering habitats, they also cause additive mortality through cable collisions especially during foggy days (Meile, 1982). It has also been shown that ski resorts lead to higher densities of some predators, possibly due to the availability of new garbage food sources (Storch, 2000). Last but not least direct exploitation by hunting could seriously reduce Black grouse density (Baines & Linden, 1991). In Central Europe, trophy-hunting remains the major motivation of Black grouse hunters. When hunting takes place on leks in autumn it may disturb the whole mating system, and lead to reduced reproductive success. Regardless of the ongoing discussion about compensatory or additive mortality, hunting may have contributed to a rapid decline of low-density Black grouse populations in some areas (Storch, 2000).

The aim of this research was to quantify precisely the main threats affecting Black grouse populations in the Swiss Alps, namely to assess the relative influence of snow sport infrastructures, human winter activity and hunting pressure on Black grouse abundance, while controlling for the effect of habitat type (plant association).

2. Methods

2.1 Study area

The study was conducted in the Alps of Valais and Vaud (south-western Switzerland, 46°10' N, 7°20' E). The study area is an inner Alpine valley along the Rhone River and extends from the Lake of Geneva to the Rhone glacier (Appendix 1). The climate is characterized by warm and dry summers and cold, relatively wet winters.

2.2 Estimation of Black grouse cocks abundance

Fifteen anthropized study sites (≥ one skilift each) and 15 natural study sites (outside ski resort, no skilift) were chosen (Table 1 & Appendix 1). The criterion for selecting these 30 sites was the possibility to observe cocks along a 1.5 km transect above timberline (altitude range of 1900 - 2300 m) from the opposite side of the valley (maximum distance of 3.5 km between observer and study site). This way, disturbance by the observer was null. A single person per site was needed for a proper census.

Black grouse abundance was estimated from the spring density of lekking males between mid April and the end of May 2005 (Zbinden, 1985). Each study site was censused 3 times (n = 90 censuses in total), at the beginning, in the middle and at the end of the courtship season, respectively. The visit sequence to the sites was randomized pairwisely, for each season, i.e. ensuring an even temporal distribution to anthropogenic and natural sites, respectively. All Black grouse cocks present in a habitat belt along the 1.5 km transect (100 m below and 200 m above the timberline) were located from the opposite side of the valley with telescopes or binoculars (x 20-40), beginning at dawn. Every transect survey consisted of 3 periods of 15 minutes observation, with a gap of 15 minutes in between. The break between successive periods was used to fill in the forms (number of birds, date and time). The maximum number of simultaneously observed cocks in one of the three daily surveys per transect in the three seasons was our estimate of Black grouse local abundance.

2.3 Habitat typology

We distinguished 13 different habitat types (Table 2), encompassing all extant habitats in the study area. In summer, a contour «line» in situ was stepped out into the polygon transect (see methods 2.2), at the mean altitude of the censused cocks. Along the transect we took GPS coordinates at each habitat type boundary (Table 2). On that basis, the proportions of each habitat type were estimated. We obtained 13 values per transect, namely one for each habitat type.

To reduce both the number of variables and variable interdependency (and therefore to get more statistical power in the models), a principal component analysis (PCA) was performed on the raw variables. The resulting factors of this PCA (named HABITAT) were then included as new synthetic variables in the models. To determine the number of factors to consider, the broken-stick method was applied (Jackson, 1993).

2.4 Hunting pressure

To calculate a hunting pressure index for each study site, we referred to a vectorial map containing all game reserves of Vaud and Valais as polygons, which was rasterized (pixel size = 50 x 50 m). Because we ignore up to which distance game reserves can influence Black grouse abundance, buffered game reserve effects were estimated for each pixel at the 250, 500, 750, 1000 and 1500 m radius, respectively. For each study site transect a mean value per radius increment (5 resulting variables) was calculated as the average game reserve density among pixels within that radius. Using a similar procedure, a mean distance to game reserves was calculated for each transect. A PCA was run with the six resulting variables (named HUNT).

2.5 Skilift index

A raster map was prepared using a GIS vectorial map including all skilifts of Valais and Vaud, which yielded a skilift presence index for each pixel. Similar

variables as mentioned above for hunting pressure were then calculated for each transect based on the above mentioned radius increments. Likewise we performed a PCA and included the resulting factors in models (SKI).

2.6 Statistical analysis

For all the calculations based on raster maps we used a geographical information systems (GIS) application (ArcView version 3.2 and ArcView Spatial Analyst, Environmental Systems Research Institute, California). In order to test for the relative contribution (to cocks abundance) of habitat typology, hunting pressure and skilift index we developed Poisson linear models with the corresponding variables. Black grouse abundance was the response variable, whereas the PCA factors HABITAT, HUNT and SKI were the independent variables. The competing models were ranked according to the "small sample unbiased" Akaike Information Criterion (AIC_c). AIC_c weights enabled the selection of the best model among the candidate set of models (Johnson, 2004). This technique utilizes log-likelihood scores as measures of fit and includes a term that, in effect, penalizes models for greater complexity.

Stepwise backward and forward elimination procedures were applied to drop out insignificant variables (Program R, Version 2.2.0, Gentleman, R. & Ihaka, R., Statistics Department of the University of Auckland, 1994). All variables were tested for homogeneity of variances and normality prior to running the models.

3. Results

3.1 Model selection

Regarding habitat typology the first five factors of the PCA HABITAT explained together 63.1% of variance (Table 4). For hunting pressure (HUNT) the first two factors explained 98.8% of the variance (Table 4), whereas the two first factors for skilift index (SKI) explained 97.9% of the variance (Table 4).

The best model among the set of candidate models took into account all three factor groups, namely SKI, HABITAT and HUNT (AIC_c weight = 0.543; Table 3; see 3.2.1). The second best model included only SKI and HABITAT (AIC_c weight = 0.446; Table 3; see 3.2.2). Models with other combinations of factors as well as all other models containing one single factor group had a higher AIC_c-value and considerably lower probabilities to be the best model among the candidates (AIC_c weights < 0.006, Table 3).

Among the models with only one factor group, the model «skilift index» (SKI) was the most «powerful» (Delta AIC_c = 12.9; AIC_c weight= 0.001, Table 3). The model HABITAT had very little power (Delta AIC_c = 14.81; AIC_c weight< 0.0001, Table 3), whereas the lowest ranked of all competing models was HUNT (Delta AIC_c = 20.73; AIC_c weight< 0.0001, Table 3).

3.2 Effect of different variables

3.2.1 Best model

In the best model above (SKI, HABITAT, HUNT) the factor HABITAT_PC 5 had the strongest effect of all integrated variables. The influence of this factor on Black grouse abundance (response variable) was negative (p< 0.001; Table 5). Since the factor HABITAT_PC 5 is per se negatively correlated with the variable «mixed *Rhododendron-Vaccinium* shrubs» (habitat type 8; Table 4), the latter habitat type had a positive effect on Black grouse abundance. As another example, the variable «rocks and scree» (habitat type 13; Table 4) is positively correlated to the factor HABITAT_PC 5, establishing a negative association between «rocks and scree» and Black grouse abundance.

The factor «skilift index» (SKI_PC 1) had the second strongest effect (Table 5). The relation to the Black grouse abundance is also negative and highly significant (p< 0.002). The factor SKI_PC 1 is negatively correlated with the variable «mean distance to skilift», resulting in a positive association between «mean distance to skilift» and Black grouse abundance. This means the greater the distance to the skilifts the higher the Black grouse abundance. The factor SKI_PC 1 is positively correlated with the variables «skilift density radius 250-1500 m», resulting in a negative correlation among skilift presence and Black grouse abundance. The second «habitat typology» factor (HABITAT_PC 2) had a negative influence on Black grouse abundance, which was nearly significant (p = 0.08; Table 5). That factor was negatively correlated with the habitat type «open old forest with grass/Ericaceae groundcover» (habitat type 6), which means a positive effect of that habitat on Black grouse abundance.

The factor HUNT_PC 1 had the smallest impact (positive, but not significant, p= 0.08) on the Black grouse abundance. This factor is negatively correlated to the variable «game reserve distance». In other terms the greater the distance to game reserves the smaller the Black grouse abundance.

3.2.2 Second best model

The second best model above (HABITAT, SKI) includes the factors HABITAT_PC 5, HABITAT_PC 2 and SKI_PC 1 (Table 5). The only difference with the best model is the elimination of the HUNT factor, which was not significant in the best model. Regarding the coefficients of these two best models, they go all in the same direction and have moreover almost identical values. Consequently the effects of the specific variables on the Black grouse abundance are the same as mentioned above for the best model (3.2.1).

3.2.3 Black grouse abundance

Regarding the best model and including the factors for HABITAT and HUNT as constants, the factor «skilift index» (SKI_PC 1) shows a negative correlation with Black grouse abundance (Fig. 1; Table 5). In other terms the higher the skilift index the smaller the Black grouse abundance, with a mean transect density of 6.3 cocks in natural habitats compared to 4.2 in anthropized habitats.

4. Discussion

This study establishes that ski resort presence is likely to be the main regulator of Black grouse abundance in Alpine ecosystems: density was 50% higher in natural than in anthropized habitats, other factors being equal. This may be due to habitat destruction (Ingold, 2005), habitat fragmentation, increase of disturbance by humans or predators (Storch & Leidenberger, 2003), higher stress (Baltic, 2005), if not direct mortality due to cable collisions (Storch, 2000a). Which among these factors contribute more to lowering density remains to be shown. Habitat type played a secondary role in population density, but this study confirms that «open young and old forest structures» (Storch, 2000) favour Black grouse abundance, whilst unproductive habitats like «rocks and scree» have a negative effect.

Regarding the model selection analysis, hunting had only a small negative impact on our Black grouse populations. Therefore hunting in our study area seems to be more likely a compensatory mortality trigger: the loss of Black grouse through hunting could induce higher survival of the remaining cocks due to diminished intraspecific competition (Zbinden & Salvioni, 2001a). This contrasts with other findings elsewhere, that additive mortality through hunting is likely to operate (Baines & Linden, 1991). We actually think that hunting can lead to local population reductions of cocks (only males are hunted in Switzerland) but that it would probably not affect overall demography in the study area. A remedy would be to implement spatially explicit models for developing adequate Black grouse hunting plans. Regarding the impact of hunting in general, more concerning might be the effect of shooting on the social and mating system of Black grouse, with possible long term consequences regarding reproductive success (Baines & Linden, 1991; Alatola et al., 1996).

Although our study yielded clear results regarding spatial abundance in relation to several series of factors, there is certainly room for improvement. In order to better identify what could be the «key factor» hidden in our «skilift index» effect (habitat alteration, disturbance, higher predation and hunting risk, etc.), disturbance intensity should be quantified by appropriate measurements of actual winter sport activity rather than by a mere skilift index.

To get also a better estimate of the hunting pressure, it would be necessary to take into account local hunting bags. Unfortunately this data was not delivered by the game and hunting service of Valais.

Implications for conservation

One main conclusion of this study is that regions where all the three potential threats (ski resort presence, unsuitable habitat typology and hunting pressure) can operate concomitantly may experience severe decreases of their Black grouse populations. Corrective conservation measures could be the creation of specific Black grouse wintering preserves, which would prohibit human pressure during the critical winter period. Public awareness campaigns should accompany this. The main goal would be to reduce human disturbance, especially that due to snow sports like skiing, snow boarding, mountaineering skiing or snowshoeing in fragile wintering populations.

More generally, further alteration and/or destruction of otherwise suitable Black grouse habitat (e.g. extension of ski resorts and infrastructures, ski pistes or roads) must be contained. Habitat management respecting species habitat requirements must be implemented. Open forest structures with Ericaceae/grass groundcover should be conserved, and, if necessary, restored. Closure of vegetation cover and bush encroachment caused by the abandonment of Alpine summer pastures could be hampered by thinning of trees and bushes.

Specific Black grouse game reserves could be created, especially in areas with relict or declining populations, such as ski resort zones, which are most of the time easily accessible to hunters thanks to a dense road network. In order to define protected zones, a spatially explicit habitat suitability map should be drawn; our results could contribute to its elaboration. Since displaying birds at leks are relatively easy targets and leks may be extirpated with little effort, at minimum the core area of leks should be protected. Last but not least, it should be reminded that any conservation of this threatened umbrella species of Alpine ecosystem would improve life conditions of many other sympatric species.

Acknowledgements

References

Alatalo, R.V., Hoglund, J., Lundberg, A., Rintamaki, P.T., Silverin, B. (1996) Testosterone and male mating success on the black grouse leks. Proceedings: Biological Sciences, 263 (1377), 1697- 1702.

Baines, D. & Linden, H. (1991) The impact of hunting on grouse population dynamics. Ornis Scandinavica, 22, 245-246.

Baltic, M. (2005) Impact of human disturbance on Alpine wildlife in winter: stress, activity and energetics in the endangered Black grouse *Tetrao tetrix*, PhD work, division of Conservation Biology, University of Bern.

Baltic, M., Jenni-Eiermann, S., Arlettaz, R., Palme, R. (2005) A Noninvasive Technique to Evaluate Human-Generated Stress in the Black grouse. Ann.N.Y.Acad.Sci, 1046, 1-15.

Gentleman, R., Ihaka, R. (1994) Statistics Departement of the University of Auckland.

Hess, R. (2000) Bestandesrückgang und räumliches Rückgangsmuster des Birkhuhns (Tetrao tetrix) am Rand des Verbreitungsgebietes (Schwyzer Voralpen, 1977-1999). Ornithologischer Beobachter, 97, 147-152.

Ingold, P. (2005) Freizeitaktivitäten im Lebensraum der Alpentiere. Haupt Verlag, Bern.

Jackson, D.A. (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology, 74 (8), 2204-2214.

Johnson, J. B. (2004) Model selection in ecology and evolution. Trends in Ecology and Evolution, 19 (2), 101-108.

Klaus, S., Bergmann, H.-H., Marti, C., Müller, F., Vitovic, O. A., Wiesner, J. (1990) Die Birkhühner. Die Neue Brehm-Bücherei, Wittenberg.

Kurki, S., Nikula, A., Helle, P., Linden, H. (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology, 81 (7), 1985-1997.

Loneux, M., Ruwet, J.C. (1997) Evolution des populations du Tétras lyre en Europe. Cahiers d'Ethologie, 17, 287-343.

Marti, C. (1986a) Situation énergétique du Tétras-Lyre en période d'hivernage. In Journées d'étude „Tétras-Lyre et ski", Champagny-en-Vanoise (1985); Offl. Natl. Chasse, 12-15

Meile, P. (1982) Zur Platzkonkurrenz von Balzplätzen und Wintersportanlagen. Beih. Veröff. Naturschutz Landschaftspflege Bad. - Württ., 16, 51-58.

Ménoni, E., Magnani, Y. (1998) Human disturbance of grouse in France. Grouse News, 15, 4-8.

Niewold, F.J.J. (1990) Hypothesis on the cause of the decline in the Black grouse population in the Netherlands. Ecology, 46, 107-116.

Potapov, R.L. (1985) Otrjad kuroobraznye (Galliformes). Fauna SSSR, Pticy Tom III, Vyl. 1. Leningrad.

Storch, I. (1990) Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie. Ornis Scand., 22, 213-217.

Storch, I. (2000) *Tetrao tetrix* Linnaeus, from Grouse Action Plan 2000- 2004.

Storch, I. (2000a) Conservation status and threats to grouse worldwide an overview. Wildlife Biology, 6, 195-204.

Storch, I., Leidenberger, C. (2003) Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. Wildlife Biology, 9, 301-308.

Sun, Y.-H., Swenson, J. E., Fang, Y., Klaus, S., Scherzinger, W. (2003) Population ecology of the Chinese grouse, *Bonasa sewerzowi*, in a fragmented landscape. Biological Conservation, 110, 177-184.

Taylor, A. R., Knight, R. L. (2003) Wildlife responses to recreation and associated visitor perceptions. Ecological Applications, 13 (4), 951-963.

Wüthrich, F. (2001) Lebenswelt Alpen. Sehen – kennen – verstehen. Sauerländer, Aarau.

Zbinden, N. (1985) Zur Verbreitung, Siedlungsdichte und Balzgruppengrösse des Birkhuhns *Tetrao tetrix* im Tessin. Der orithologische Beobachter, 82, 107-115.

Zbinden, N., Salvioni, M. (2001a) Einfluss der Jagd auf den Bestand, das Geschlechterverhältnis und den Fortpflanzungserfolg des Birkhuhn Tetrao tetrix im Tessin, Südschweiz. Aus der Schweizerischen Vogelwarte Sempach und dem Ufficio caccia e pesca del Cantone Ticino.

Zbinden, N., Salvioni, M. (2001) Das Birkhuhn *Tetrao tetrix* als Verlierer bei der Entwicklung der ehemals alpwirtschaftlich genutzten Kulturlandschaft zur Naturlandschaft in der Südschweiz. Repubblica Ticino Dipartimento del territorio e Schweizerische Vogelwarte Sempach.

Zeitler, A. & Glänzer, U. (1998) Skiing and grouse in the Bavarian Alps. Grouse News, 15, 8–12.

Table 1. Abundance of lekking Black grouse males in 15 natural and 15 anthropized sites in the Alps of Vaud and Valais. Mean = average number of cocks present during each of three seasonal surveys; SD = standard deviation; max = maximum number of cocks simultaneously present at census with peak count.

№	Study site	Location		mean	SD	max
1	Belalp	Alpe Bäll	natural	14.7	2.9	20
2	Simplon Sud	Nideralp	natural	4.0	1.5	5
3	Montana	Bevron	natural	3.6	1.2	7
4	Arolla	La Tsa	natural	5.4	2.9	9
5	Binntal	Eggerhorn	natural	15.0	1.2	17
6	Bourg St-Pierre	les Arpalles	natural	3.1	1.5	5
7	Bourg St-Pierre	Tsanlotset	natural	7.2	1.2	10
8	Bourg St-Pierre	Azerin	natural	3.4	0.6	6
9	Visperterminen	Gebidum	natural	5.2	0.6	7
10	Gryon	Les Planards	natural	3.9	2.5	7
11	Val d' Hérémence	Les Barmettes	natural	1.8	0.6	3
12	Ovronnaz	Fratier	natural	3.1	0.6	6
13	Hérens	Vendes	natural	2.2	1.7	5
14	Hérens	Eison	natural	3.8	1.2	6
15	St-Luc	Montagne du Touno	natural	2.0	1.0	3
16	Bürchen	Moosalp	anthropized	2.3	0.0	3
17	Champoussin	Pertuis	anthropized	2.8	0.6	4
18	Thyon	Thyon east	anthropized	1.3	0.6	2
19	Thyon	La Combire	anthropized	1.4	1.2	3
20	Torgon	Les Fontanettes	anthropized	0.6	0.0	2
21	Rosswald	Abewed	anthropized	1.2	0.6	2
22	Siviez	Les Marenda	anthropized	2.7	0.6	6
23	Ovronnaz	Bougnone	anthropized	1.0	0.6	3
24	Verbier	Les Attelas	anthropized	4.1	0.6	7
25	Nendaz	Dent de Nendaz	anthropized	0.9	0.0	2
26	Hérens	Combetta	anthropized	0.9	1.5	3
27	St-Luc	Prarion	anthropized	1.9	1.7	4
28	Grimentz	Bendolla	anthropized	1.3	0.0	2
29	Anniviers	Alpage Chandolin	anthropized	5.6	2.3	9
30	Verbier	Le Vacheret	anthropized	1.0	0.0	1

Table 2. Typology of Black grouse habitats found in the study area along our census transects.

#	Habitat type
1	*Alnus* forest
2	Open young forest with grass cover
3	Open young forest with grass/Ericaceae cover
4	Open young forest with Ericacea cover
5	Open old forest with grass cover
6	Open old forest with grass/Ericaceae cover
7	Open old forest with Ericacea cover
8	Mixed *Rhododendron-Vaccinium* shrubs
9	*Juniperus* shrubs
10	*Rhododenron/Vaccinium* and pasture
11	*Juniperus* and pasture
12	Typical alpine pasture
13	Rocks and scree

Table 3. Model selection summary and ranking (best model on top) of the candidate set of competing Poisson models to estimate the abundance (A) of Black grouse cocks along our transects. SKI = factors expressing skilift index; HUNT = hunting pressure; HABITAT = habitat typology. AICc Weights are a measure of relative support for each competing model, i.e. the proportion to be the best model of the various candidate set of models.

#	Model description	Retained factors	Delta AICc	AICc Weights
1	A (SKI + HUNT + HABITAT)	4	0.00	0.543
2	A (SKI + HABITAT)	3	0.39	0.446
3	A (HUNT + HABITAT)	3	9.42	0.005
4	A (SKI + HUNT)	2	9.83	0.004
5	A (SKI)	2	12.90	0.001
6	A (HABITAT)	2	14.81	0.000
7	A (HUNT)	2	20.73	0.000

Table 4. Eigenvectors of the principal component analyses (PCA) run for reducing variable number in model selection procedures. HABITAT= habitat typology; HUNT = hunting pressure; SKI = skilift index. The retained factors were selected via the broken-stick method.

	PC factor 1	PC factor 2	PC factor 3	PC factor 4	PC factor 5
HABITAT					
Explained variance	16.25%	14.63%	13.11%	9.79%	9.29%
1 *Alnus* forest	0.40887	0.26862	0.11431	-0.03022	-0.41746
2 Open young forest with grass cover	0.36160	0.15982	-0.09286	0.43675	0.22545
3 Open young forest with grass/Ericaceae cover	-0.05277	-0.39013	-0.15454	-0.41514	-0.02808
4 Open young forest with Ericacea cover	-0.40764	0.22684	-0.22864	-0.07314	0.07536
5 Open old forest with grass groundcover	0.03580	-0.36684	0.23094	0.51284	0.05100
6 Open old forest with grass/Ericaceae cover	-0.11235	-0.54853	0.28840	0.08774	0.13510
7 Open old forest with Ericacea cover	-0.35485	0.28245	0.43001	0.11588	-0.05070
8 Mixed *Rhododendron-Vaccinium* shrubs	-0.03867	-0.05171	-0.29971	0.19547	-0.59429
9 *Juniperus* shrubs	-0.32597	0.37193	0.24823	0.05830	0.03101
10 *Rhododenron/Vaccinium* and pasture	0.05155	0.11247	-0.50400	0.34369	0.33967
11 *Juniperus* and pasture	-0.18320	0.02717	-0.25842	-0.18383	0.34908
12 Typical alpine pasture	0.45286	0.10042	0.09708	-0.38406	0.15892
13 Rocks and scree	0.21034	0.13756	0.31475	-0.07409	0.35829
HUNT					
Explained variance	88.54%	10.30%			
Mean distance to game reserve	-0.30572	0.94851			
Game reserve density radius 250 m	0.43000	0.21000			
Game reserve density radius 500 m	0.42753	0.16374			
Game reserve density radius 750 m	0.42952	0.14409			
Game reserve density radius 1000 m	0.43003	0.12130			
Game reserve density radius 1500 m	0.42002	0.06895			
SKI					
Explained variance	88.65%	9.30%			
Mean distance to ski lift	-0.29228	0.93789			
Ski lift density radius 250 m	0.42068	0.24686			
Ski lift density radius 500 m	0.42766	0.18724			
Ski lift density radius 750 m	0.43118	0.13293			
Ski lift density radius 1000 m	0.43117	0.08162			
Ski lift density radius 1500 m	0.42764	-0.00538			

Table 5. Coefficients of the factors that best contributed to models estimating Black grouse male abundance. Only the final models are shown, after removal of the non-significant factors and interactions dropped in the backward and forward elimination procedure (a = best model; b = second best model). As an example, HABITAT_PC 5 = factor 5 of the principal component analysis (PCA; Table 4 Habitat). The same nomenclature applies to SKI and HUNT. . p < 0.1   * p < 0.05   ** p < 0.01   *** p < 0.001

a) SKI + HUNT + HABITAT

	estimate	p	
HABITAT_PC 5	-0.22702	0.000421	***
SKI_PC 1	-0.15142	0.002013	**
Habitat_PC 2	-0.09923	0.080764	.
HUNT_PC 1	0.06158	0.076276	.

b) SKI + HABITAT

	estimate	p	
HABITAT_PC 5	-0.22674	0.000488	***
SKI_PC 1	-0.16931	0.000412	***
Habitat_PC 2	-0.13043	0.015322	*

Figure captions

Fig. 1. Correlation between the number of Black grouse males and the factor «skilift index» (SKI_PC 1; Table 4) predicted from the best model with the HUNT and HABITAT factors fixed.
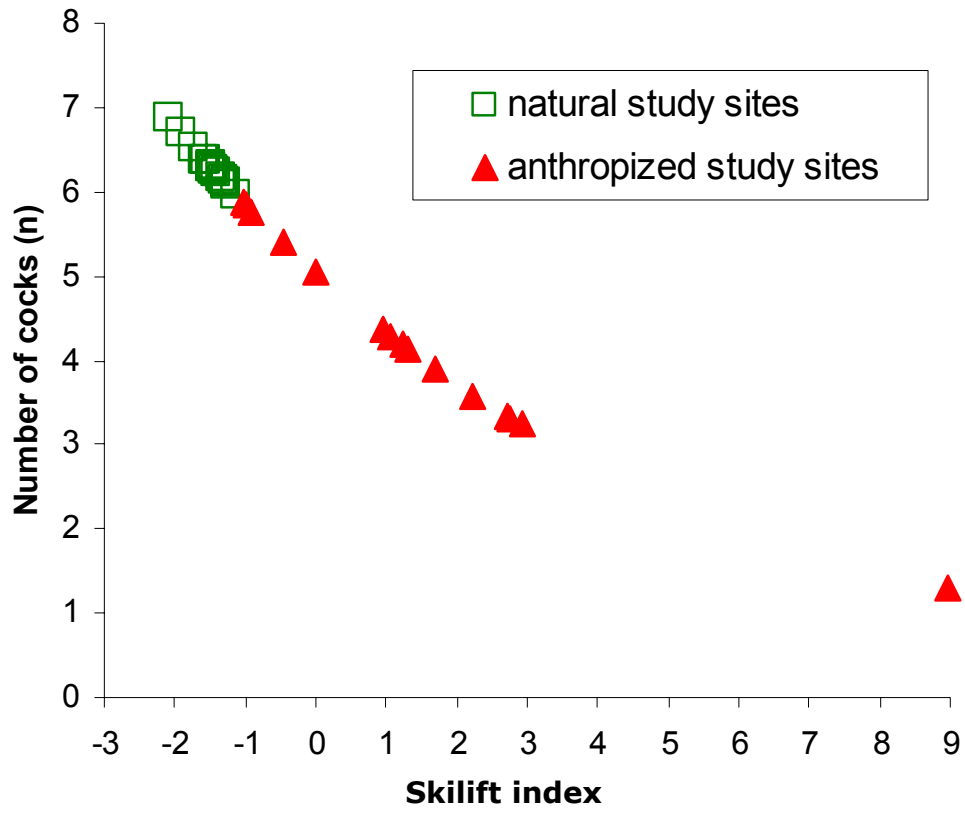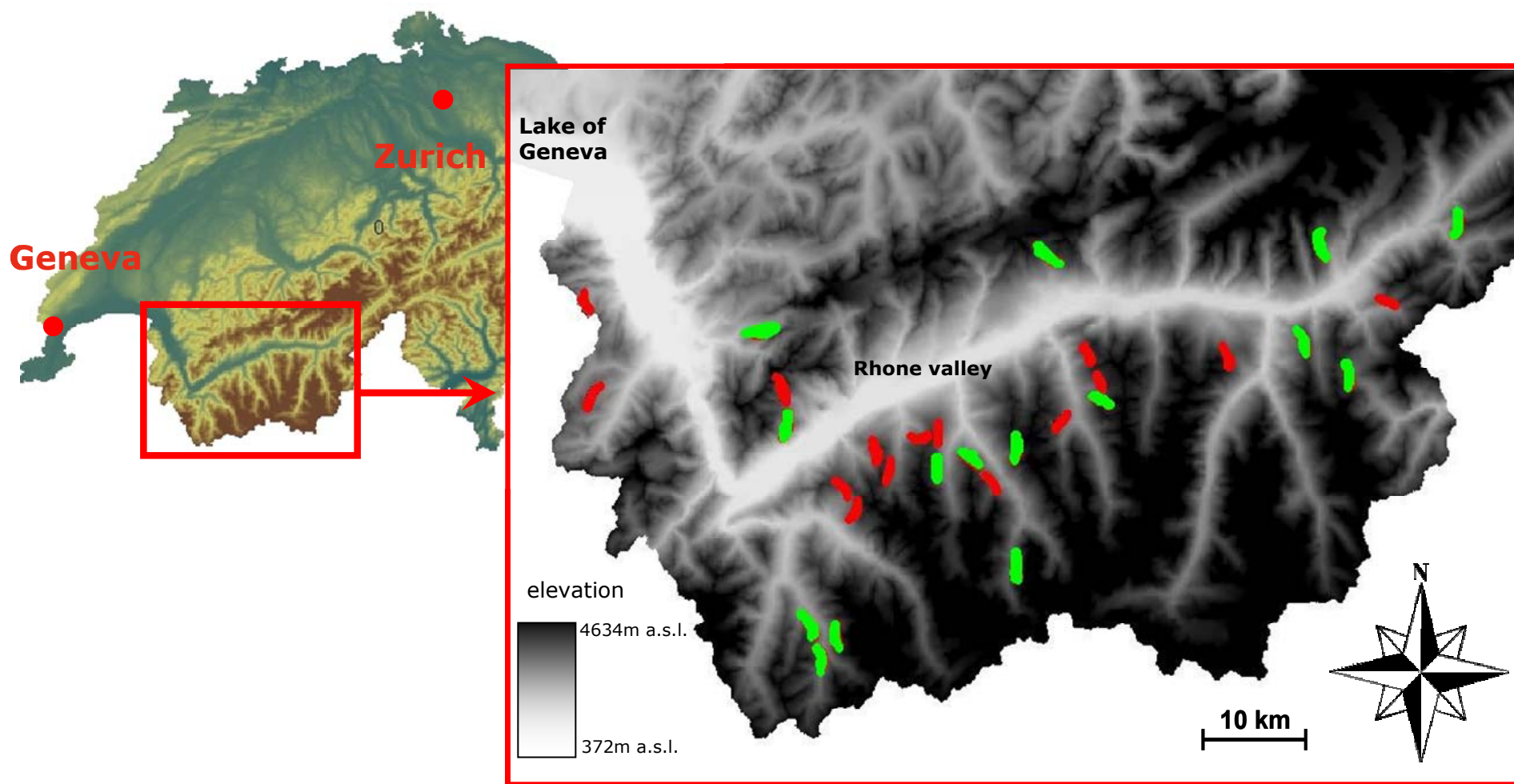
Appendix 1. Study sites for lek counting (green = natural sites; red = anthropized sites).

Comparison of arthropod abundance in different characteristic habitats
of the Alpine Black grouse: towards an understanding of habitat selection pattern by chick-rearing hens

Part 2

Table of contents

Abstract

1. Many European grouse populations have declined continuously over the past decades. Black grouse (*Tetrao tetrix*) have also decreased in some parts of the Alps, particularly since 1970. Breeding success has been claimed to be a major factor of decline.

2. During their crucial first 3– 4 weeks of life chicks are depending on protein-rich arthropod food. We tested the hypothesis that arthropod abundance differs markedly among different habitat types, predicting higher prey availability in the habitats selected by chick-rearing hens.

3. Arthropod abundance differed significantly between habitat types and varied with respect to season. Alpine pastures and open forest habitats yielded the highest arthropod biomasses, as estimated through two sampling techniques (pitfall trapping and sweep-netting). Different arthropod categories showed different phenologies as well as unequal habitat dependences. Grasshoppers (Saltatoria), beetles (Coleoptera) and ants (Formicidae) represented the most abundant categories.

4. Conservation measures aiming at improving habitat quality must focus in priority on the arthropod productive and predator safe habitats which are favoured by chick-rearing hens, especially open forest structures with a patchy grass and Ericacae groundcover.

Key words: Alps, *Tetrao tetrix*, breeding success, arthropod abundance, habitat types, seasonal trends, species conservation

1. Introduction

Black grouse (*Tetrao tetrix*) populations have been continuously declining during the last decades, especially at low elevation in Western and Central Europe. A decline of marginal populations has also been reported in the Alps (Klaus et al., 1990; Hess, 2000). Principal threats have been claimed to be habitat alteration and fragmentation, human disturbance and exploitation (Storch, 2000). Breeding success has been identified as an important component of population dynamics in many grouse species (e.g. Moss et al., 2001). Particularly crucial is chick development and survival during the first weeks after hatching. The former affects the future social rank of the individual, whilst the latter determines overall demographic trends (Rajala, 1974; Ellison, 1979). The fact that chicks are not able to control their body temperature (i.e. to thermoregulate) in their first weeks of life render them very vulnerable (Zbinden, 1987). Chick mortality varies thus greatly from year to year, as it is liable to fluctuations in weather and food offer. In cold and wet weather chicks have less time available for feeding because they must warm up under the plumage of their mother (Zbinden, 1987). Additionally, adverse weather conditions reduce dramatically the activity and therefore availability of arthropods to chicks. Making up the bulk of chicks' diet (≥ 80%), arthropods represent an essential source of protein-rich and easily-digested food that boosts their growth (Ponce, 1992a; Gregersen & Olstad, 2002, Starling-Westerberg, 2001). The arthropod diet of chicks can be quite diverse. In Black grouse forested habitats, ants (*Formicidae*) seem to predominate (Picozzi & Hepbrun, 1984; Ponce & Magnani, 1987), whereas beetles (*Coleoptera*), grasshoppers (*Acrididae* and *Tettigonidae*), spiders (*Aranae*), *Opiliones* and larvae of different orders can play a considerable role in other habitats (Klaus, 1990). Many studies have addressed the issue of habitat selection by Black grouse at different stages of their biological cycle, including the reproductive season (Ponce, 1992a; for the Red Grouse: Park et al., 2001; for Capercaillie: Gregerson & Olstad, 2002; Pauli, 1974, 1978; Zbinden, 1980; Marti, 1985; Marti & Pauli, 1985; Ponce, 1992a; Starling-Westerberg, 2001). However, there exists so far no study which could actually demonstrate that habitat selection by chick-

rearing hens is tightly linked with arthropod abundance and/or availability in different habitat types. In parallel to a fine-grained comparative radiotracking investigation of habitat selection by males, non-reproducing and breeding females (Signorell et al., unpublished), we therefore assessed quantitatively arthropod abundance and phenology in different characteristic Alpine habitats of the Black grouse.

2. Methods

2.1 Research area and study sites

The study was conducted in the Alps of Valais and Vaud (south-western Switzerland) from June to August 2005. Three different sites where chosen, one site in the Central Alps (Aletsch 46°22'N, 8°01'E), one in the Prealps (Les Diablerets 46°19'N, 7°05'E) and another in the Southern Alps (Simplon 46°15'N, 8°02'E; Appendix 1). Altogether 14 different characteristic Black grouse habitat types were recognized (Table 1). The determination of these habitat types was based on vertical and horizontal habitat features, as well as on degree of xericity of the vegetations. Collectively, these 14 habitat types represent all potential habitats for male, non-breeding and breeding female Black grouse summer range in the Alps.

2.2 Arthropod abundance

In order to estimate arthropod abundance, a combination of pitfall trapping (epigeal fauna) and sweep-net sampling (epiphytic fauna) was used (Standen, 2000): in every habitat type 3 pitfalls were installed 5 meter apart in a row (n = 126 sampling plots in total). The pitfalls were composed of 8 cm deep PVC tubes (diameter of 7 cm), which were buried in the ground. A plastic yogurt cup was placed in each tube; it contained ethylene glycol both as preservative and to attract and kill the arthropods. A quadratic piece of transparent PVC installed 2-3 cm above the ground covered the pitfall to protect it from rain. The pitfall traps were set continuously and emptied every ten days from 20th June to 22nd August (i.e. 6 sampling events). Additionally, two sweep-net subsamples were collected at the time of trap clearance, this along the pitfall trap row (10 m long transect forth and back), one metre on each side of the transect. One sweep-net subsample was defined as 10 strokes performed at equal intensity along the 10 m long pitfall trap alignment trough the sward (standardized sweep-net method according to Oppermann, 1999; Di Giulio et al., 2001; Britschgi et al., 2006).This sampling design thus resulted in 4 samples (3 pitfall trap samples and one

sweep-net sample) per habitat and sampling event. The collected arthropods were conserved in small vacuum plastic bags in 70% Ethanol.

In the laboratory, the sampled arthropods were dried for 72 h in an oven at 60°C according to Southwood (1978). After drying, plant parts were separated from the arthropods. Then the arthropods were identified down to order or suborder and categorized into 14 main taxonomic groups (according to Ponce, 1987: Opiliones, Aranea, Diplopoda, Saltatoria, Dermaptera, Diptera, Hymenoptera without Formicidae, Formicidae, Coleoptera, Lepidoptera, Larvae spp., Isopoda, Heteroptera, Homoptera). We used identification guides (Chinery, 1993) and a binocular microscope when necessary. Finally, we counted the number of individuals per group and determined biomass to the nearest 0.001 g with a precision balance (Mettler Toledo PB303-L Delta Range, Greifensee, Switzerland).

2.3 Weather data

An average ambient temperature and precipitation per sampling period was calculated on the basis of daily averages obtained from the weather station in Evolène-Villaz (46°7'N, 7°30'E; Federal Office of Meteorology and Climatology, MeteoSwiss 2005). This station is located in the core of the study area.

2.4 Statistical analysis

For pitfall data we calculated the arthropod mean number and mean biomass (mean from 3 pitfalls) per habitat type and sampling period with respect to the 14 categories above. Finally we calculated a value per habitat type and sampling period, averaging between the three study sites. For sweep-netting we summed up the two collected subsamples per habitat type and sampling event.

Dry biomass and number of arthropods were the response variables, whereas habitat type was the independent variable. As dry biomass and item number were sampled continuously throughout the season, the six consecutive sampling events were considered as repeated measures, providing information about seasonal trends. In the analysis of pitfall trapping data we ran separate analyses

for total biomass and number of arthropods (sum of all categories), as well as for ants (*Formicidae*), beetles (*Coleoptera*) and grasshoppers (*Saltatoria*), the latter three representing typical chick diet. Additionally, we calculated a Shannon index of diversity (Shannon and Weaver, 1949) averaged for each habitat type and sampling period using the 14 prey groups mentioned above. Sweep-netting data were analysed only for total dry biomass. All variables were tested for homogeneity of variance and normality prior to running MANOVAs. Some variables (dry biomass and number of arthropods) had to be log transformed ($\log_{10}(x+1)$). After conducting the MANOVAs the residual distributions were also checked for normality. All statistical analyses were performed with the program JMP 4 (SAS Institute Inc. 2001, Cary, NC, USA). All values reported are means and standard errors of the means; P-values are two-tailed with rejection levels set at 5%.

3. Results

A total number of 33 276 arthropods (298.7 g dry biomass) were collected with pitfall traps and sweep net during the six sampling periods. The composition was dominated by the categories Saltatoria (29.5% of dry biomass, 8.7% of number), Coleoptera (23.1% and 9.5%, respectively) and Formicidae (18.4% and 53.2%, respectively).

Regarding pitfall trapping, total arthropod dry biomass varied significantly between habitat types (F_{13} = 2.62, P = 0.016) and throughout the season (F_5 = 22.10, P < 0.0001; Table 2 and Fig. 1). There was a sharp fall of total dry biomass between the last decade of June and the first decade of July due to a cold spell (Fig. 3). Concerning the different habitat types, when considering the mean of all sampling events across the season, Alpine pastureland yielded the highest total biomass, followed by open old forest with Ericaceae cover, open old forest with grass/Ericaceae cover and *Rhododendron*/*Vaccinium* & pasture, respectively. All the other habitat types showed distinctly lower biomasses (Table 3). Regarding mid July (which coincides with the peak of the chick-rearing period) Alpine pastureland also showed the highest value of biomass, followed by open old forest with Ericaceae cover, *Rhododendron*/*Vaccinium* & pasture and open old forest with grass/Ericaceae cover, respectively (Table 3).
Total number of arthropods differed almost significantly (F_{13} = 2.03, P = 0.058) between the different habitat types (Fig. 1). There was a significant seasonal variation (P < 0.0001, Table 2). Given that arthropod number and biomass were highly correlated (matched pairs t-test; df = 83, P = 0.006) we eventually restricted further analyses to biomass.
Beetles (Coleoptera) dry biomass resulted in significant differences between habitat types (P = 0.0003), with a significant seasonal effect (P < 0.0001, Table 2 and Fig. 1). The total dry biomass of grasshoppers (Acrididae and Tettigonidae) differed almost significantly between habitat types (P = 0.057), with a significant seasonal effect (P = 0.0002, Table 2). Alpine pasture yielded the highest grasshopper biomass among all habitat types (Fig. 1).

Ant (Formicidae) biomass showed non-significant differences between habitat types (P = 0.8707), but again a significant seasonal variation (P < 0.0001, Table 2), with highest values in late June and a second peak around mid July (Fig. 1). The Shannon indices of diversity of arthropods collected with pitfall trapping showed a trend between the habitat types (P = 0.085), with a significant seasonal effect (P < 0.0001, Table 2 and Fig. 2).

Concerning sweep-netting, total dry biomass differed highly significantly between habitat types (P = 0.0054), with a distinct seasonal pattern (P < 0.0001; Table 2 and Fig. 1). Saltatoria (Acrididae and Tettigonidae) were dominating this sample with 82.3% biomass occurrence. Alpine pasture again yielded the highest dry biomass at every sampling event, followed by open young forest with grass cover (Fig. 1).

4. Discussion

Our results highlight first that grasshoppers (Saltatoria, i.e. Acrididae and Tettigonidae, 29.5% of dry biomass , 8.7% of number), beetles (Coleoptera, 23.1% and 9.5%, respectively) and ants (Formicidae, 18.4% and 53.2%, respectively) are the three most abundant categories, representing all together 71% of biomass (71.4% of number) of arthropod food present in Black grouse characteristic habitats. It is thus not surprising if this prey makes up the bulk of the diet of young Black grouse chicks (Picozzi & Hepbrun, 1984; Ponce & Magnani, 1987; Klaus, 1990).

Secondly, our results establish that epigeal as well as epiphytic arthropods vary significantly among different characteristic Black grouse habitat types. Similar results or trends were evidenced for beetles (Coleoptera) and grasshoppers (Saltatoria). It is thus confirmed that arthropod abundance depends heavily upon habitat type. Alpine pastures yielded the highest arthropod biomass (pitfalls), followed by open old forest with Ericaceae cover, *Rhododendron/Vaccinium* & pasture and open old forest with grass/Ericaceae cover. The sweep-net sampling led also to highest biomass values for Alpine pastureland. This habitat selection pattern confirms former findings (Kurki et al., 2000) that a mosaic of grassland interspersed with shrubland and isolated tall trees constitutes the optimal habitat of female Black grouse during the breeding season.

For chick-rearing Black grouse hens, however, there must be a trade-off between arthropod abundance/availability and predation risk, and this risk is clearly habitat dependent. This would suggest that the arthropod-rich open habitats such as pastureland, despite high food supply, are comparatively more avoided by hens due to a higher predation risk. In this respect, old forests with grass or shrub cover would probably provide more suitable foraging habitats (Kurki et al., 2000). This hypothesis is currently tested in an ongoing fine-grained habitat selection analysis in our research programme. Concerning those crucial first weeks for chick development (around mid-July in the Alps, Pauli, 1974), it is striking that they match exactly the period of peak arthropod abundance in this study. No doubt that natural selection has prompted a finely-timed phenology of

Black grouse breeding coinciding precisely with that of availability of a nutrient rich food supply (Zbinden, 1987). Accessibility of animal food for Black grouse chicks depends on ambient temperature, given that arthropods are less active in adverse weather conditions. This occurred in our case in early July, with a sharp fall of the biomass. At that time persistent low temperatures and even casual snow falls were recorded.

There are discrepancies, however, between prey categories. Whereas biomasses of beetles and ants are steadily decreasing from June to August, the biomass of grasshoppers in contrast increases continuously. This is largely due to the successive instars to reach adult size. The peak of grasshoppers in mid July in habitats dominated by grassland may play a key role for hatching takes place at that time.

Implications for conservation

Open forests offer the highest arthropod fauna and smaller predation risks. They should be conserved in priority. The construction of new infrastructures should be avoided in those important habitats, e.g. pistes for skiing, snowboarding, trails for mountain bikes and quads, hiking trails and roads. A traditional management of these habitats with livestock must be ensured in the long-term so as to avoid progressive encroachment and forest closure, and to keep some vegetation patchiness, in particular the persistence of insect-rich grassland. Where cattle pressure becomes insufficient, tree thinning and grazing (e.g. by goats) might be implemented for restoring Black grouse habitat.

The conservation of the habitat of this emblematic umbrella species of Alpine ecosystems requests management efforts, but those are worthwhile: the presence of dense grouse populations would be an indication that an entire biocenosis has persisted.

Acknowledgements

References

Britschgi, A., Spaar, R., Arlettaz, R. (in press) Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Conservation Biology.

Chinery, M. (1993) Pareys Buch der Insekten, 2. Auflage, Hamburg, Berlin.

Di Giulio, M., Edwards, P.G., Meister, E. (2001) Enhancing insect diversity in agricultural grassland: the roles of management and landscape structure. Journal of Applied Ecology, 38, 310-319.

Ellison, L.N. (1979) Black grouse population characteristics on a hunted and three unhunted areas in the French Alps. In Lovel, T.W.I. (ed.) Proceedings of International Symposium on Grouse, 2, 64-73.

Gregersen, H., Olstad, T. (2002) Habitat use and movement of Capercaillie *Tetrao urogallus* broods in a forest reserve in NW Russia during summer. Cand. Scient. Thesis, Department of Biology and Nature Conservation Agriculture University of Norway.

Hess, R. (2000) Bestandesrückgang und räumliches Rückgangsmuster des Birkhuhns (Tetrao tetrix) am Rand des Verbreitungsgebietes (Schwyzer Voralpen, 1977-1999). Ornithol. Beobachter, 97, 147-152.

Klaus, H., Bergmann, H.-H., Marti, C., Müller, F., Vitovic, O. A., Wiesner, J. (1990) Die Birkhühner. Die Neue Brehm-Bücherei, Wittenberg.

Kurki, S., Nikula, A., Helle, P., Linden, H. (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology, 81 (7), 1985-1997.

Marti, C. (1985) Unterschiede in der Winterökologie von Hahn und Henne des Birkhuhns *Tetrao tetrix* im Aletschgebiet (Zentralalpen). Der ornithologische Beobachter, 82, 1-30.

Marti, C., Pauli, H.-R. (1985) Wintergewicht, Masse und Altersbestimmung in einer alpinen Population des Birkhuhns *Tetrao tetrix.* Der ornithologische Beobachter, 82, 231-241.

Moss, R., Oswald, J., Baines, D. (2001) Climate change and breeding success: decline of the Capercaillie in Scotland. Journal of Animal Ecology, 70, 47-61.

Oppermann, R. (1999) Nahrungsökologische Grundlagen und Habitatansprüche des Braunkehlchens *Saxicola rubetra.* Vogelwelt, 120, 7-25.

Park, K.J., Robertson, P.A., Campbell, S.T., Foster, R., Russel, Z.M., Newborn, D., Hudson, P.J. (2001) The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. J. Zool. Lond., 254, 137-145.

Pauli, H.-R. (1974) Zur Winterökologie des Birkhuhns *Tetrao tetrix* in den Schweizer Alpen. Der ornithologische Beobachter, 71, 247-278.

Pauli, H.-R. (1978) Zur Bedeutung von Nährstoffgehalt und Verdaulichkeit der wichtigsten Nahrungspflanzen des Birkhuhns *Tetrao tetrix* in den Schweizer Alpen. Der ornithologische Beobachter, 75, 57-84.

Picozzi, N., Hepbrun, L.V. (1984) A study of Black grouse in north east Scotland. Proc. 3rd Int. Grouse Symposium, York 1984, 462-480.

Ponce, F., Magnani, Y. (1987) Régime alimentaires des poussins de tetras lyre (*tetrao tetrix*) sur deux zones des Alpes françaises: méthodolgie et résultats préliminaires. Actes Coll. Galliform. Mont., 225-228.

Ponce, F. (1992a) Régime et selection alimentaires des poussins de tetras lyre (*tetrao tetrix*) dans les Alpes françaises. Gibier Faune Sauvage, 9, 27-51.

Rajala, P. (1974) The structure and reproduction of Finnish populations of Capercaillie, *Tetrao urogallus*, and Black grouse*, Lyrurus tetrix*, on the basis of late summer census data from 1963-1966. Finn. Game Res., 35, 5-51.

Shannon, C.E., Weaver, W. (1949) The Mathematical Theory of Communication, Urbana.

Southwood, T.R.E. (1978) Ecological Methods. Chapman and Hall, London.

Standen, S. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. Journal of Applied Ecology, 37, 884-893.

Starling-Westerberg, A. (2001) The habitat use and diet of Black grouse *Tetrao tetrix* in the Pennine hills of northern England. Bird Study, 48, 76-89.

Storch, I. (2000) Conservation status and threats to grouse worldwide: an overview. Wildlife Biology, 6, 195-204.

Zbinden, N. (1980) Zur Verdaulichkeit und umsetzbaren Energie von Tetraoniden-Winternahrung und zum Erhaltungsbedarf des Birkhuhns (*tetrao tetrix)* in Gefangenschaft mit Hinweisen auf Verdauungsversuche. Sonderdruck aus : Vogelwelt, 101, 1-18.

Zbinden, N. (1987) Zum Aufzuchterfolg des Birkhuhns *Tetrao tetrix* im Tessin. Der Ornithologische Beobachter, 84, 49-61.

Table 1. The 14 habitat types distinguished for arthropod sampling.

№	Habitat type	vertical structure	horizontal structure	characteristics	humidity
1	*Alnus* forest	dense bush			
2	Open young forest with grass cover	young trees	grass cover	> 75% grass	
3	Open young forest with grass/Ericaceae cover		grass & Ericaceae		
4	Open young forest with Ericaceae cover		Ericacae	> 75% Ericaceae	
5	Open old forest with grass cover	old mature trees	grass cover	> 75% grass	
6	Open old forest with grass/Ericaceae cover		grass & Ericaceae		
7	Open old forest with Ericaceae cover		Ericaceae	> 75% Ericaceae	
8	Mixed *Rhododendron-Vaccinium* shrub	shrub		> 75% Ericaceae	wet
9	Mixed *Rhododendron-Vaccinium-Juniperus* shrub			Ericaceae & *Juniperus*	medium
10	*Juniperus* shrub			> 75% *Juniperus*	dry
11	Pasture with *Rhododendron/Vaccinium*	Mix pasture & shrub		> 75% Ericaceae	wet
12	Pasture with *Rhododendron/Vaccinium/Juniperus*				medium
13	Pasture with *Juniperus*			> 75% *Juniperus*	dry
14	Alpine pasture	pasture			

Table 2. Effect of the factors «habitat» (see Table 1) and «season» on the biomass, number and Shannon index of diversity of arthropods caught by pitfall-trapping (a-f) and sweep-netting (g). MANOVA: df = degrees of freedom, F = F statistic P = probability: * < 0.05   ** < 0.01   *** < 0.001

Source of variation	df	F ratio	P
a) Total biomass (all categories)			
habitat	13	2.62	0.0159 *
season	5	22.1	< 0.0001 ***
b) Total number (all categories)			
habitat	13	2.03	0.058
season	5	110.81	< 0.0001 ***
c) Biomass of grasshoppers			
habitat	13	2.03	0.0575
season	5	7.58	0.0002 ***
d) Biomass of beetles			
habitat	13	4.64	0.0003 ***
season	5	42.51	< 0.0001 ***
e) Biomass of ants			
habitat	13	0.55	0.8707
season	5	63.69	< 0.0001 ***
f) Shannon index of diversity			
habitat	13	1.85	0.085
season	5	8.61	< 0.0001 ***
g) Total biomass (all categories) with sweep-netting			
habitat	13	3.15	0.0054 **
season	5	8.68	< 0.0001 ***

Table 3. Mean total dry arthropod biomass (averaged across the three study sites) sampled by pitfall trapping (last decade of June to second decade of August) in 14 habitat types (see Table 1). SD = standard deviation.

Habitat type	Total dry arthropod biomass (mg)							
	June III	July I	July II	July III	August I	August II	Mean	SD
1	576.9	156.2	215.3	136.0	148.2	91.7	220.7	179.0
2	602.2	123.7	182.2	82.9	62.3	38.6	182.0	212.0
3	612.9	452.8	391.9	314.8	353.4	225.6	391.9	132.4
4	523.3	125.7	310.8	276.6	176.9	253.8	277.8	138.0
5	804.7	177.2	397.6	217.9	194.0	355.1	357.7	236.8
6	1114.9	269.0	673.3	573.2	476.7	517.4	604.1	283.8
7	1000.0	476.3	1030.4	740.8	353.9	343.7	699.2	376.9
8	1250.0	101.4	189.6	259.6	103.2	154.4	229.1	175.4
9	453.3	87.9	199.7	124.1	92.9	93.2	175.2	142.6
10	442.0	84.1	208.1	218.6	60.6	88.1	183.6	143.4
11	603.7	353.6	726.6	756.3	476.0	315.8	538.6	187.0
12	291.8	144.0	227.8	336.7	146.2	317.6	244.0	85.0
13	233.3	156.0	151.8	129.8	134.1	140.0	157.5	38.5
14	586.7	333.7	1603.6	1647.8	1284.4	1125.7	1097.0	536.5
Mean	649.7	217.3	464.9	415.3	290.2	290.0		
SD	295.8	135.0	417.9	416.8	320.1	275.5		

Figure captions

Fig. 1. Phenology of the mean arthropod dry biomass and mean item number collected at the three study sites (Les Diablerets, Aletsch, Simplon) in 14 different habitat types. a) total biomass; b) total number; c) biomass of beetles; d) biomass of grasshoppers; e) biomass of ants; f) Shannon index of diversity (a-f from pitfall-trapping); g) total biomass from sweep-netting.

Fig. 2. Seasonal trends in the mean Shannon index of diversity of arthropods collected with pitfall trapping at the three study sites (Les Diablerets, Aletsch, Simplon) in 14 different habitat types (habitat symbols, see Fig. 1).

Fig. 3. Mean daily ambient temperature and precipitation per sampling period (averaged across the 10 d time interval) at the station Evolène-Villaz (last decade of June to second decade of August).
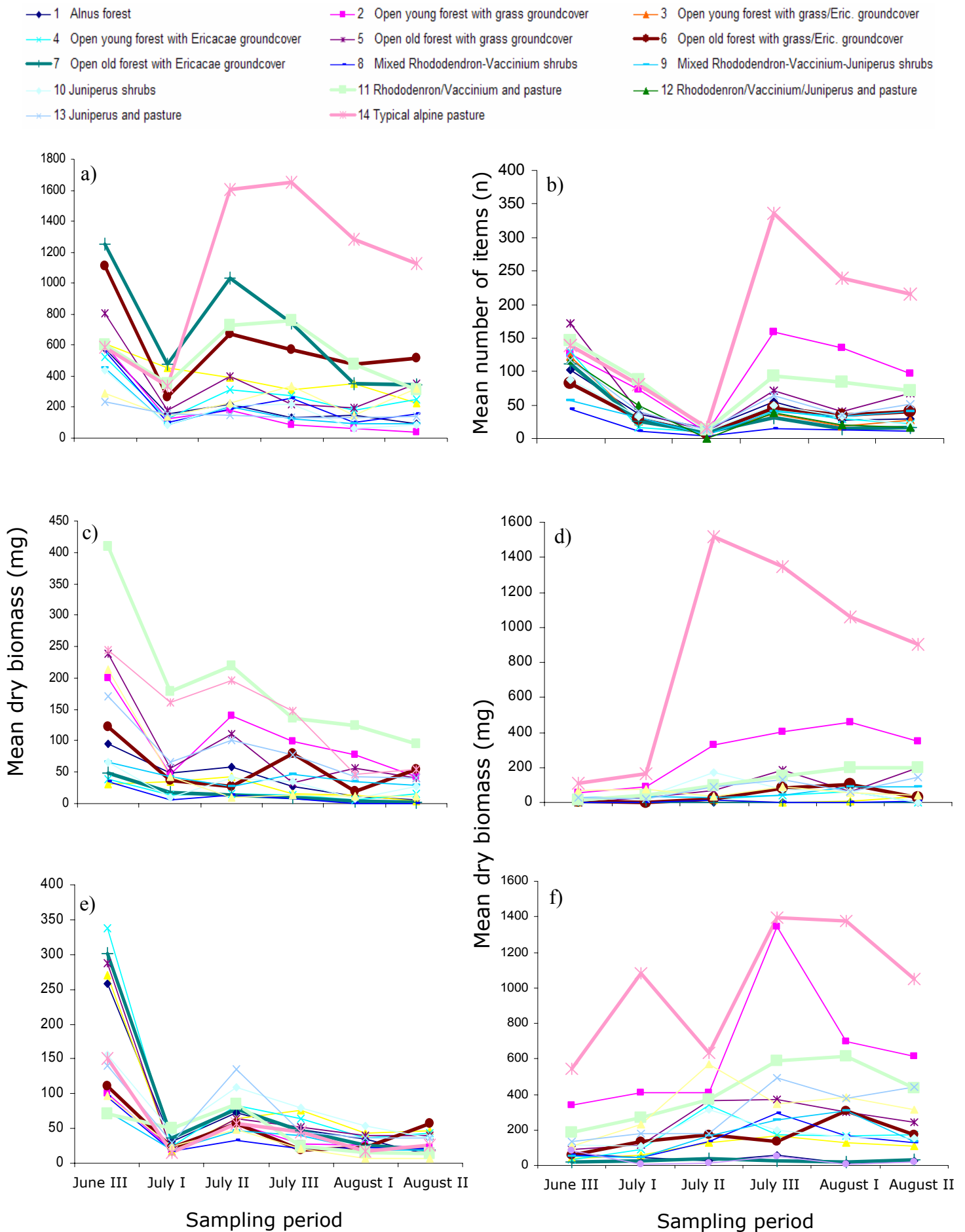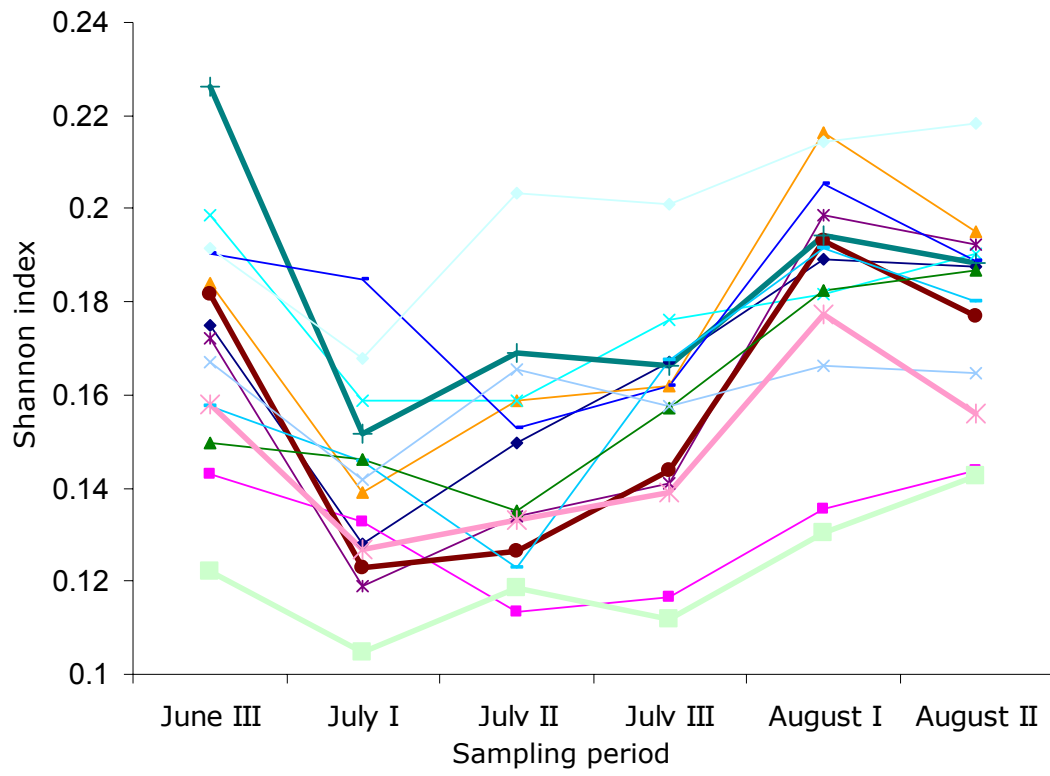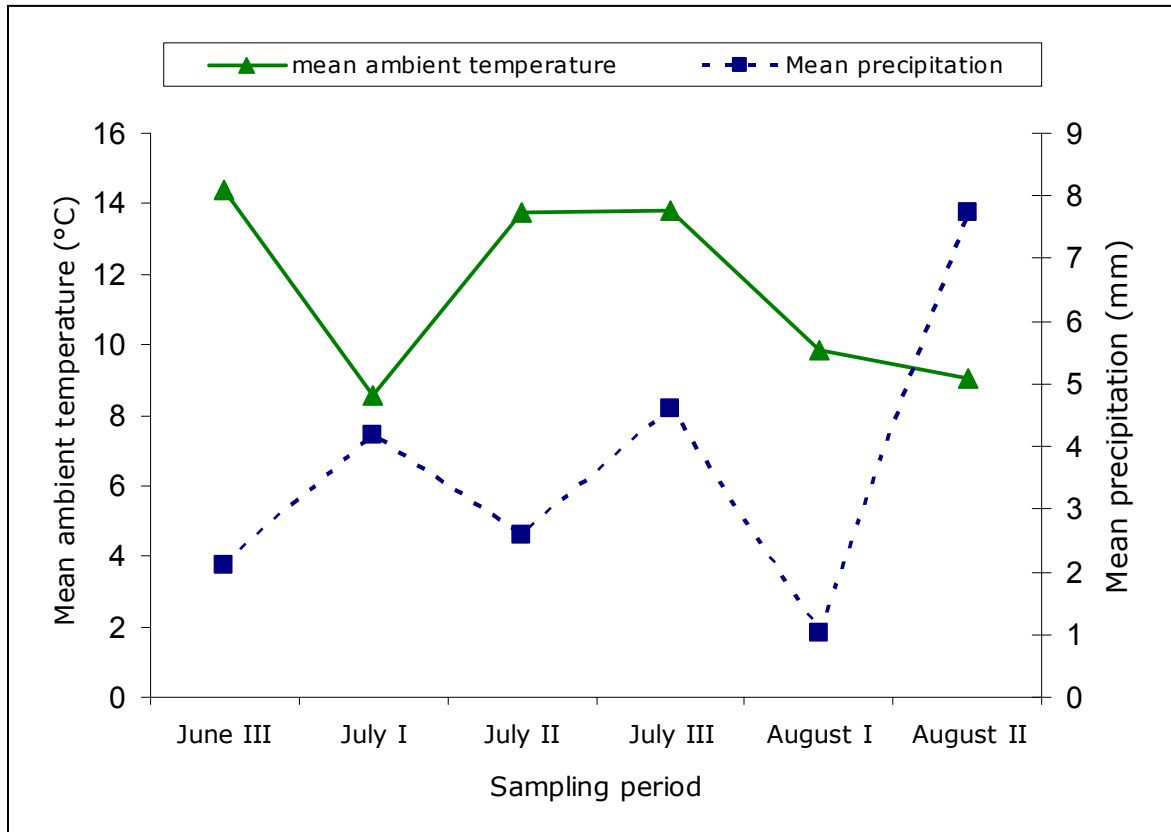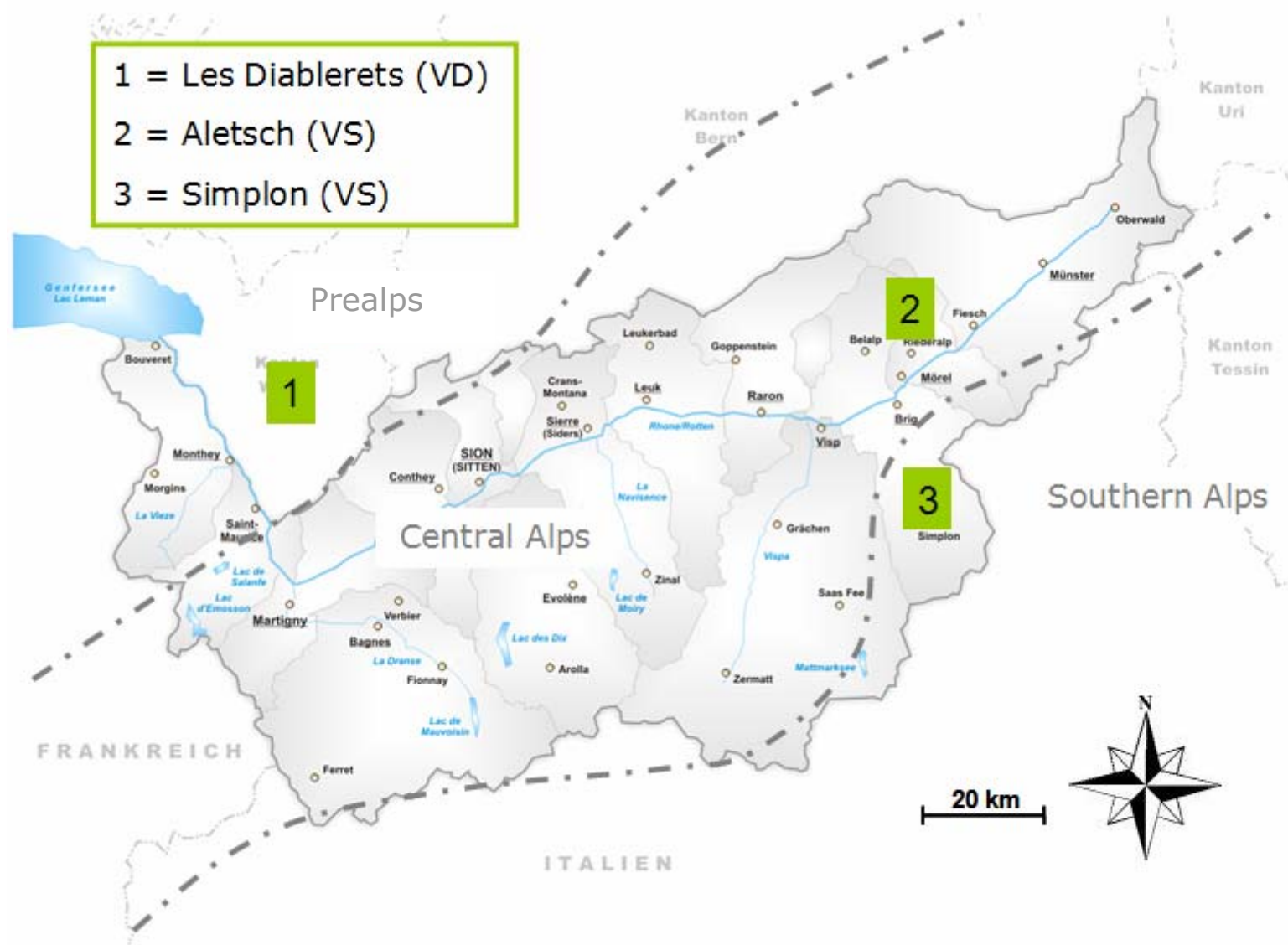
Fig. 1

Fig. 2

Fig. 3

Appendix 1. Our three main study sites in the Alps of Valais (VS) and Vaud (VD)