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Original article

Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse *Tetrao tetrix* hens: habitat management implications

Natalina Signorell, Sven Wirthner, Patrick Patthey, Rebekka Schranz, Luca Rotelli & Raphaël Arlettaz

Declines of Alpine black grouse *Tetrao tetrix* populations have been linked to increasing disturbance by recreation and degradation of breeding habitat due to changes in land-use, especially abandonment of traditional farming practices. Appropriate forest, shrubland and grassland management may mitigate the negative effects of land abandonment. The habitat associations and trophic requirements of brood-rearing Alpine black grouse hens were appraised to inform effective habitat management policies. We measured the abundance, biomass and phenology of arthropods, a key food source for grouse chicks, in eight timberline habitat categories and performed a habitat selection analysis based on radio-tracking data collected from eight brood-rearing hens in the Swiss and Italian Alps. Arthropod biomass differed significantly between habitat categories and peaked in early summer due to a sharp increase of orthopterans (Saltatoria), an essential food source for Alpine black grouse chicks. Open grassland and grassy shrubland yielded the highest arthropod biomass, with Saltatoria dominating the sample. Yet, brood-rearing hens avoided open grassland, opting for a mosaic of grassy shrubland with scattered trees. Chick-rearing hens apparently traded-off food abundance for reduced predation risk, i.e. habitats offering cover for concealment and escape from predators. These specific black grouse breeding habitat requirements inform about habitat management within Alpine timberline ecosystems. Managers should not restore extensive, homogeneous pasturelands. Instead, a complex heterogeneous habitat mosaic, consisting of patches of grassland and shrubland interspersed with scattered coniferous trees should be promoted.

Key words: Alpine timberline ecosystems, arthropod phenology, black grouse, breeding habitat selection, food abundance, habitat management, species conservation, Tetrao tetrix

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Productivity and juvenile recruitment have been identified as important components of population dynamics in many grouse species (e.g. Moss et al. 2001, Ludwig et al. 2006, Sachot et al. 2006), and mainly depend on weather conditions and predation rate. The first weeks of a chick's life are regarded as the most sensitive phase of grouse life history (e.g. Ellison 1979, Ludwig et al. 2008). During this period, chicks need arthropods, i.e. an easily digestible food rich in protein, for optimal development and survival (Savory 1989, Rumble & Anderson 1996, Hannon & Martin 2006). However,

food abundance may be traded-off against predation risk in habitat selection decisions. This would be especially crucial for precocial, ground-nesting birds such as grouse, whose young chicks are flightless and depend on their mother for thermoregulation during their first weeks of life. Chicks expose themselves to aerial and terrestrial predators when foraging. In boreo-alpine environments, where the time window for reproduction is extremely short, the conjugated effects of high seasonality in arthropod availability and pronounced predation risk might represent real challenges to grouse.

We studied black grouse *Tetrao tetrix*, a declining species of timberline ecosystems in the Alps. Principal threats to Alpine grouse populations are habitat alteration and disturbance through recreation, especially winter outdoor sports (Storch 2007, Arlettaz et al. 2007, Patthey et al. 2008). In Alpine timberline habitats, the area of pastureland continues to decline due to shrub and forest succession following the abandonment of traditional pasture management by farmers. Projects to mitigate the effects of land abandonment have recently been launched by the Swiss Government in the form of subsidies to biodiversity-friendly forestry practices. Black grouse was chosen as a target species for modern timberline ecosystem management in some parts of the Swiss Alps, given its possible role as an indicator, if not umbrella species of this ecosystem (Storch 2007). Yet, key information for sound management recommendations is lacking. So far, there have been no quantitative studies of arthropod abundance, biomass and phenology in different characteristic Alpine black grouse habitats, despite the fact that this information would be essential for understanding the relationship between reproductive performance and habitat selection patterns in brood-rearing hens.

We analysed habitat selection of radio-tracked brood-rearing hens, testing whether their habitat preferences mirrored habitat-specific patterns of arthropod biomass. Our ultimate goal was to identify the habitat requirements of brood-rearing black grouse hens in order to provide guidelines for conservation and restoration management of this emblematic species of Alpine timberline ecosystems.

Methods

Study areas and habitat characterisation

We studied arthropod abundance, biomass and phenology in the Alps of southwestern Switzerland, in the cantons of Valais and Vaud, from June to August 2005. Three different sites were 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 one in the Southern Alps (Simplon, 46°15'N, 8°02'E).

We investigated habitat selection by black grouse females during the summers of 2004-2007 at six different sites in the Central Alps (Valais Canton, 46°12'N, 7°20'E) and at two sites in the Southern Alps (Verbania Province, 46°06'N, 8°18'E). Although a yearly survey of arthropod abundance and biomass at the exact brood location (Baines et al. 1996, Tirpak et al. 2008, Wegge & Kastdalen 2008) would probably have yielded more accurate data, we had to refrain from disturbing the brood-rearing hens while radio-tracking them.

On the above mentioned slopes in the southern Alps (Simplon area in southeastern Valais and northern Italy), the dominant tree species of upper subalpine forests and the adjacent timberline is larch *Larix decidua*, whereas in the other study areas, Norway spruce *Picea abies* and Arolla pine *Pinus cembra* are also present. Dwarf shrubs (e.g. alpenrose *Rhododendron ferrugineum*, bilberry *Vaccinium myrtillus*, northern bilberry *Vaccinium uliginosum*, dwarf juniper *Juniperus communis nana*, heather *Calluna vulgaris*, bearberry *Arctostaphylos uva-ursi* and crowberry *Empetrum nigrum*) and grasses (e.g. matgrass *Nardus stricta*, *Calamagrostis villosa*) represent a characteristic understorey in all areas. The study areas are characterised by a subcontinental to continental climate, with warm, dry summers, and cold, relatively wet winters (Reisigl & Keller 1999).

We defined 19 different habitat types by the vertical and horizontal structure of their vegetation (Table 1). These habitat types were regrouped into eight habitat categories, with respect to habitat structure. Since the horizontal understorey structure plays a greater role than the age of the trees (Signorell 2008), we grouped young and old forests that had the same understorey pattern. All 19 habitat types were present in the summer home ranges of brood-rearing black grouse females (Signorell 2008).

Delineation of home ranges and generation of random points

Some hens were captured from snow burrows during January-March 2003-2006. We used a 2 ×

Table 1. Habitat categories (I-VIII) and habitat types (1-19) with indication of main structural and compositional features used for habitat selection analysis of Alpine black grouse in Switzerland and Italy. Habitat types in which arthropod supply was sampled is indicated by *.

Habitat category		Habitat type	Vertical structure	Horizontal structure	Characteristic
I Bare ground, rock, scree	1	Rocks/scree			> 75% cover
	2	Bare ground			> 75% cover
II Grassland	3*	Open young forest with grass cover	Young trees	Grass cover	> 75% grass
	4*	Open old forest with grass cover	Old mature trees	Grass cover	> 75% grass
	5*	Alpine pasture	Pasture		
III Grassy shrubland	6*	Pasture with *Rhododendron*/*Vaccinium*	Pasture & shrub		> 75% Ericaceae
	7*	Pasture with *Rhododendron*/*Vaccinium*/*Juniperus*	Pasture & shrub		
	8*	Pasture with *Juniperus*	Pasture & shrub		> 75% *Juniperus*
IV Closed shrubland	9*	Mixed *Rhododendron*-*Vaccinium* shrub	Shrub		> 75% Ericaceae
	10*	Mixed *Rhododendron*-*Vaccinium*-*Juniperus* shrub	Shrub		Ericaceae & *Juniperus*
	11*	*Juniperus* shrub	Shrub		> 75% *Juniperus*
V Grassy shrubland with scattered trees	12*	Open young forest with grass/*Ericaceae* cover	Young trees	Grass & Ericaceae	
	13*	Open old forest with grass/*Ericaceae* cover	Old mature trees	Grass & Ericaceae	
VI Closed shrubland with scattered trees	14*	Open young forest with *Ericaceae* cover	Young trees	Ericaceae	> 75% Ericaceae
	15*	Open old forest with *Ericaceae* cover	Old mature trees	Ericaceae	> 75% Ericaceae
VII Dense forest	16*	Dense *Alnus viridis* forest	Dense bush		
	17	Dense forest	Dense forest		> 75% tall trees
VIII Others	18	River/water			> 75% water area
	19	Adenostyle, willow herb, raspberry, etc.			> 75% cover

2.5 m mist net stretched between two ($\leq$ 6 m) telescopic fishing rods. The net was placed on the snow surface above apparently occupied igloos (Marti 1985). We also capture hens at leks from May to June with 1 m high mist nets. Caught birds were tagged with necklace radio-transmitters weighing 12 g (29 × 19 × 15 mm; Holohil Systems Ltd, Carp, Canada, RI-2D).

In July and August, hens were radio-located once a day during 30 consecutive days, starting on the day the chicks hatched. The resulting 30 locations were obtained by triangulation and homing in on the bird (White & Garrott 1990), but without approaching closer than 10-15 m in order to avoid inadvertently flushing it. A pole which indicated the distance and direction to the expected bird position was placed at each location. At the end of the breeding season, the coordinates of 30 bird locations per hen were recorded with a global positioning system. We referred to these locations as visited points.

Individual home ranges were determined using the minimum convex polygon method based on the 30 locations per hen (White & Garrott 1990). We defined two buffer zones of 150 m in altitude above and below each home range, perpendicular to the main slope. We generated 100 random points (non-visited points), uniformly distributed, using the Animal Movement extension (Hooge & Eichenlaub 1997). The buffer zones provide enough contrast to analyse habitat selection, by comparing used with non-used habitats (see below). The lower buffer zone was likely to include more forested habitats, whilst the upper buffer zone tended to enclose more open habitats than the average black grouse habitat. Buffers were restricted to upper and lower altitudes because lateral extension would potentially have overlapped with home ranges occupied by other hens, and thus the habitat selection pattern might have been biased due to intraspecific competition, therefore not representing the actual habitat choice (Angelstam 1984).

After the radio-tracking season, we assigned one of the 19 habitat types to every visited and random point. We characterised the habitats within a circle of 15 m radius around each point (see Table 1).

Arthropod abundance and biomass

A combination of pitfall trapping (epigeal fauna) and sweep-netting (epiphytic fauna) was used to estimate arthropod abundance and biomass (Standen 2000) within 14 of the 19 habitat types (see Table 1). We did not include rocks and scree, bare ground, dense coniferous forest, river and other water bodies, adenostyles *Adenostyles alliariae*, willow *Salix* sp. herb and very dense raspberry *Rubus idaeus*, as they are known to be avoided by the birds (Klaus et al. 1990, Signorell 2008). For each study site, a random station was selected within each habitat type and equipped with three pitfalls installed 5 m apart in a row. The pitfalls consisted of 8 cm deep PVC tubes (diameter of 7 cm), which were buried in the ground. An open plastic cup was placed in each tube, which contained ethylene glycol as a means to attract, kill and preserve the arthropods. A square piece of transparent PVC sheet installed 2-3 cm above the ground covered the pitfall, protecting it from rain. The pitfall traps were emptied every ten days between 20 June and 22 August (N = 6 sampling events). This time window was chosen to be sure that arthropods were sampled during the most critical period ranging from hatching until chicks are four weeks old (Klaus et al. 1990). In addition, at each trap clearance, a sweep-net sample was collected along two 10 m transects situated 1 m from and parallel to the rows of pitfalls traps. The epiphytic sample consisted of 20 sweeps (Oppermann 1999, Di Giulio et al. 2001, Britschgi et al. 2006). Collected arthropods were preserved in small plastic bags containing 70% ethanol.

In the laboratory, the sampled arthropods were dried for 72 hours at 60°C (Southwood 1978). Once dried, the arthropods were identified to order or suborder and categorised into 14 main groups according to Ponce & Magnani (1988): Opiliones, Aranea, Diplopoda, Saltatoria, Dermaptera, Diptera, Hymenoptera without Formicidae, Formicidae, Coleoptera, Lepidoptera imagines (adults), Lepidoptera larvae (caterpillars), Isopoda, Heteroptera and Homoptera. We then counted the number of individuals per group and measured their biomass to the nearest 0.001 g with a precision balance. We calculated the averaged arthropod group dry biomass per station and sampling period.

Statistical analysis

Habitat selection of hens

To analyse habitat selection patterns at the home range level (Johnson 1980), we compared the frequency distribution of used habitats (visited points) with the distribution of non-used habitats (random points) for each hen. As some pre-defined habitat types were not present within individual home-ranges, we regrouped these habitat types into broader habitat categories before performing the analysis (see Table 1). We applied a randomised contingency table procedure (Manly 1997) to estimate the probability of any positive or negative deviation between observed and expected habitat category frequencies (10,000 iterations, program Actus2, Estabrook & Estabrook 1989, Arlettaz 1999).

Arthropod data

We applied linear mixed-effects models with maximum likelihood estimation to test if biomass and diversity of arthropods from pitfalls or sweep-net samples differed between habitat categories and varied among ten-day periods (Crawley 2007). The same habitat categories as for the habitat selection analysis were used here (see Table 1). To account for our repeated and nested design, each station was nested within study site and treated as a random effect. To obtain an estimate of the influence of the fixed effects habitat category and ten-day period, we used ANOVA tests to compare the full model (containing both habitat category and ten-day period) with models containing only habitat category or ten-day period, as suggested by Crawley (2007). *Post hoc* contrast tests were used to compare the arthropod biomass between habitat categories. The analyses were performed with the software R (R 2.4.1, nlme library, R Development Core Team 2006, available at: http://cran.r-project.org). Variables were tested for homogeneity of variance and normality of residuals. All variables had to be log transformed.

Results

We captured 22 hens (16 in winter, six in spring). Only 15 females were still alive at the beginning of

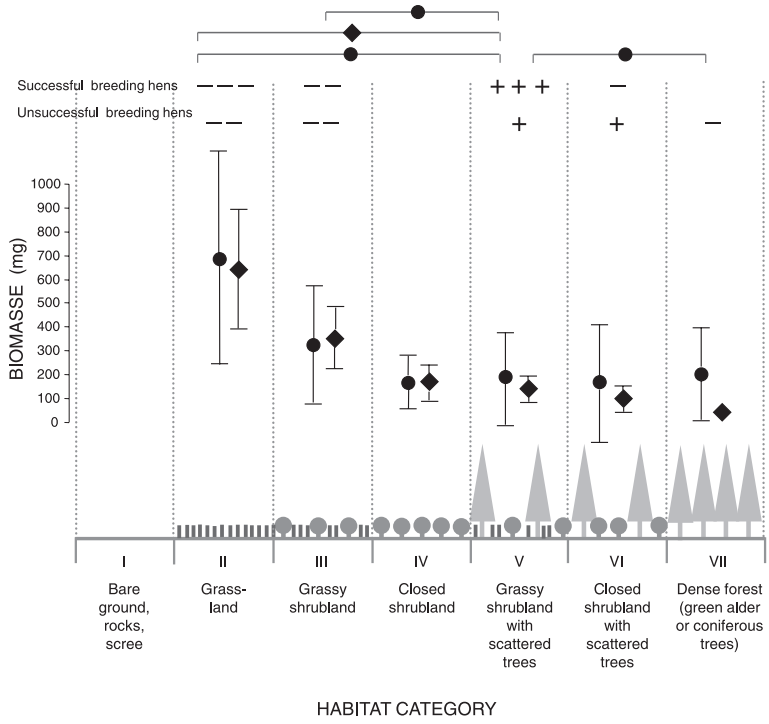

Figure 1. Arthropod biomass averaged (± SD) across the six sampling events, in relation to habitat category (see Table 1) for epigeal fauna (pitfall sampling; ●) and epiphytic fauna (sweep-netting; ♦). Habitat selection pattern (+: selection and -: avoidance) for four successful and four unsuccessful brood-rearing black grouse hens, is indicated at the top of the figure. The number of symbols indicates the number of individuals out of four showing that selection pattern. Differences in arthropod biomass were tested between the selected habitat (habitat V) and all other habitat categories. Significant differences are depicted by the horizontal bars ($P < 0.05$, from *post hoc* contrast tests). Symbols in the centre of the bar refer to the response variables described above.

the next laying period. Of the surviving females, 80% (N = 12) began incubation, and 28.6% (N = 4) of these successfully raised chicks to 30 days of age. Failures were mostly due to nest predation (N = 5) and a high mortality of young chicks during bad weather (N = 3). These percentages are similar to those described by Klaus et al. (1990) and Ludwig et al. (2008). Thus, we were able to radio-track only four successful brood-rearing females. We also considered four unsuccessful brood-rearing hens that had lost their chicks during their first 10 days of life, and that had home ranges close to the four successful brood-rearing hens. In total we collected 120 locations for each group of four females.

The frequency distribution of habitat categories for successful brood-rearing females differed significantly between visited and random points (χ^2, randomised contingency table procedure, all four P-values < 0.05; Fig. 1). This difference was mostly due to a statistically significant selection for grassy shrubland with scattered coniferous trees (habitat category V, N = 3 hens), and an avoidance of both grassland (habitat category II, N = 3 hens) and grassy shrubland (habitat category III, N = 2 hens; see Fig. 1).

Three out of the four unsuccessful brood-rearing females showed significant differences in the frequency distribution of habitat categories between visited and random points (χ^2, $P < 0.05$; see Fig. 1). A habitat avoidance pattern similar to that of the successful brood-rearing females emerged, whilst only one hen showed a significant selection for the same favourite habitat as successful brood-rearing females: grassy shrubland with scattered trees (habitat category V; see Fig. 1).

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

As arthropod number and biomass for pitfall trapping, as well as sweep-netting, were highly correlated (Spearman's rank correlations: $P < 0.05$ for all ten-days period for epigeal and epiphytic samples), we restricted further analyses to biomass only.

Epigeal and epiphytic arthropod dry biomass varied significantly between habitat categories and throughout the season (Table 2 and Fig. 2A,E). Of the different habitat categories, grassland yielded, on average, the highest total biomass for both the epigeal and epiphytic arthropod fauna, followed by grassy shrubland (see Table 2 and Fig. 2A,E). Coleoptera and Orthoptera (mainly Saltatoria)

Table 2. Linear mixed models of the effects of habitat category (see Table 1) and ten-day period on the biomass of arthropods sampled by pitfall-trapping (A-F) and sweep-netting (G-L) in Swiss and Italian Alps. Model comparison was obtained through *a posteriori* ANOVAs between the full and sub-models (see text for more details). df = degrees of freedom, logLik = log Likelihood and LRatio = Likelihood ratio. The second model compares the full model to a model without habitat category, thus estimating the effect of the latter. The third model compares the full model to a model without the factor ten-day period, thus estimating the effect of the latter.

	Source of variation	df	logLik	LRatio	P-value		Source of variation	df	logLik	LRatio	P-value
Pitfall trapping (epigeal fauna)						Sweep-netting (epiphytic fauna)					
A)	Total biomass (all categories)					G)	Total biomass (all categories)				
	Full model	14	-213.99				Full model	14	-30.75		
	Habitat category effect	9	-228.20	28.42	<0.0001		Habitat category effect	9	-40.36	19.21	0.0018
	10-day period effect	9	-303.91	179.85	<0.0001		10-day period effect	9	-90.39	119.28	<0.0001
B)	Biomass of Coleoptera					H)	Biomass of Coleoptera				
	Full model	14	-143.33				Full model	14	-137.83		
	Habitat category effect	9	-150.41	14.16	0.0146		Habitat category effect	9	-148.60	21.53	<0.0001
	10-day period effect	9	-156.83	27.01	<0.0001		10-day period effect	9	-190.18	104.70	<0.0001
C)	Biomass of Orthoptera					I)	Biomass of Orthoptera				
	Full model	14	-306.38				Full model	14	-259.76		
	Habitat category effect	9	-320.95	29.15	<0.0001		Habitat category effect	9	-271.17	22.82	<0.0001
	10-day period effect	9	-349.35	85.95	<0.0001		10-day period effect	9	-274.44	29.34	<0.0001
D)	Biomass of Formicidae					J)	Biomass of Formicidae				
	Full model	14	-79.98				Full model	14	-73.55		
	Habitat category effect	9	-83.54	7.12	0.2119		Habitat category effect	9	-74.29	1.48	0.9152
	10-day period effect	9	-102.80	45.64	<0.0001		10-day period effect	9	-169.06	191.03	<0.0001
E)	Biomass of Lepidoptera larvae					K)	Biomass of Lepidoptera larvae				
	Full model	14	-201.91				Full model	14	-166.87		
	Habitat category effect	9	-206.23	8.64	0.1244		Habitat category effect	9	-171.96	10.17	0.0705
	10-day period effect	9	-217.58	31.34	<0.0001		10-day period effect	9	-186.04	38.33	<0.0001
F)	Biomass of Opiliones and Aranaea					L)	Biomass of Opiliones and Aranaea				
	Full model	14	-181.17				Full model	14	-81.27		
	Habitat category effect	9	-183.30	4.25	0.5142		Habitat category effect	9	-86.85	11.15	0.0484
	10-day period effect	9	-190.61	18.87	0.0020		10-day period effect	9	-185.84	209.15	<0.0001

biomass differed significantly between habitat categories, irrespective of the capture method (see Table 2 and Fig. 2). Biomass of Formicidae was not significantly different between habitats (see Table 2 and Fig. 2D,H). Saltatoria contributed most to the total biomass collected with pitfalls and sweep nets. They were especially abundant in grassland, showing a sharp increase in biomass from late June until late July (see Table 2 and Fig. 2C,G). In contrast, biomass of Coleoptera and Formicidae was largest early in the season and decreased progressively thereafter (see Table 2 and Fig. 2B,D,F,H).

Both epigeal and epiphytic biomass progressively decreased along a gradient from open towards closed habitats (habitat categories II to VII; see Fig. 1). We compared biomass occurring in grassy shrubland with scattered trees (habitat V), the selected habitat by black grouse hens, with biomass from all other habitat categories. For pitfall trapping, significant differences in biomass were found for grassland (habitat category II), a habitat avoided by hens (*post hoc* contrast test, $P < 0.01$, see Fig. 1), and for grassland and grassy shrubland (habitat categories II and III), both habitats avoided by successful chick-rearing hens ($P < 0.05$ and $P < 0.05$, respectively; see Fig. 1), which yielded higher total dry biomass. Green alder *Alnus viridis* forest (Habitat VII) showed significantly lower biomass collected by pitfall trapping ($P < 0.05$; see Fig. 1).

Discussion

In Britain and in Scandinavia, black grouse broods forage in herb-rich heather, mooreland or semi-open boreal forests searching mainly for ants and

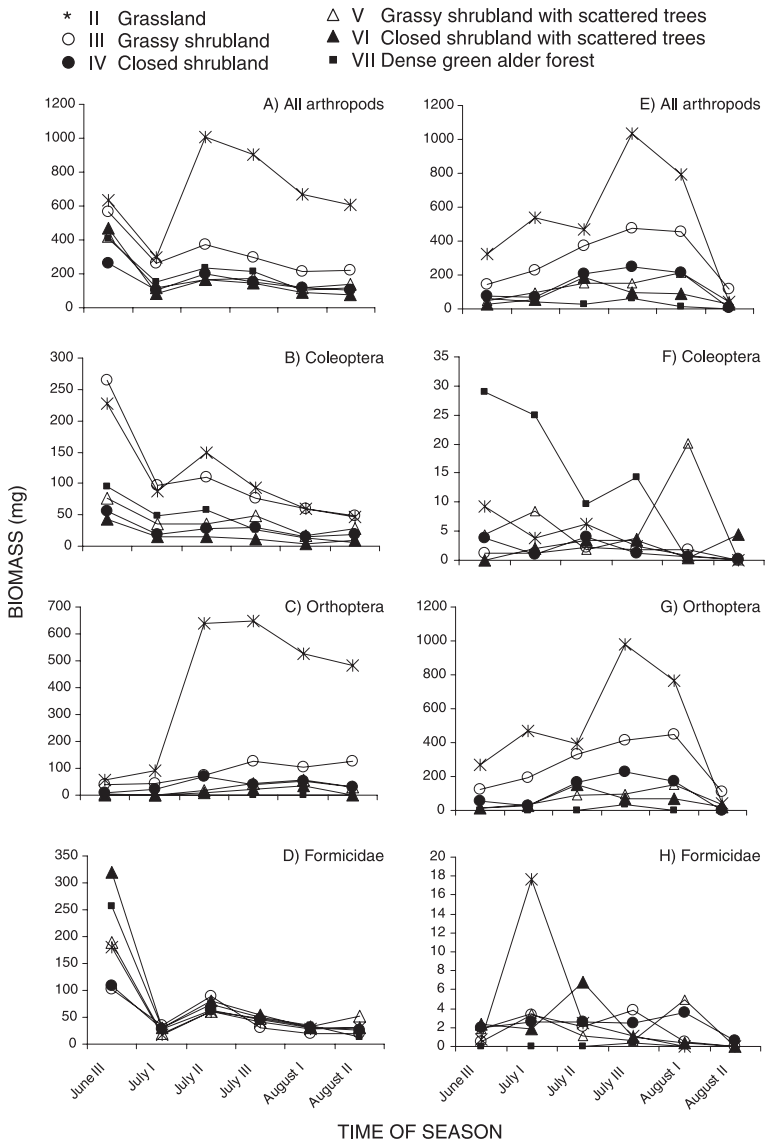

Figure 2. Phenology of mean arthropod dry biomass collected at three Swiss Alpine study sites for different black grouse habitat categories (see Table 1) from pitfall trapping (A-D) and sweep-netting (E-H). Shown are the total biomass (A,E) and the biomass of the three groups contributing most to total biomass (Coleoptera, Orthoptera and Formicidae).

larvae of sawflies and caterpillars (Picozzi & Hepburn 1984, Baines et al. 1996, Starling-Westerberg 2001, Wegge & Kastdalen 2008). Habitats selected by our Alpine hens have similar vegetation structure such as grassy shrubland with scattered trees, but are drier than those in Britain and Scandinavia (Bernard 1982, our study). Within these habitats, Alpine chicks probably prey mainly on orthopteran (Saltatoria) larvae and imagines (Ponce & Magnani 1988, Ponce 1992) whose phenology explains the peak of global arthropod biomass in early summer (our study), when most chicks hatch (Klaus et al. 1990, Signorell 2008). This pattern suggests a close coincidence between timing of reproduction and availability of a rich protein supply (Saltatoria), in line with what is observed in British and Scandinavian black grouse, but for other arthropod groups (Baines et al. 1996, Wegge & Kastdalen 2008).

Our comparison of arthropod biomass in different habitats with the pattern of habitat selection indicates that Alpine brood-rearing hens did not select the habitats providing the best food supplies, but apparently traded-off food biomass for habitat cover (e.g. shrubs and scattered coniferous trees), most likely to reduce predation risk (Tirpak et al. 2008). Predation risk is presumably higher in open grassland and shrubland than in more heteroge-

neous habitats such as grassy shrubland with scattered tress, the selected foraging habitat for reproduction. A grassland and shrubland mosaic offers also Ericaceae leaves and fruit to growing chicks, which progressively integrate more vegetative items into their diet (Ponce 1992, Wegge & Kastdalen 2008). The present findings corroborate a previous fine-grained habitat selection analysis, which demonstrated the relevance of structural and compositional habitat heterogeneity for chick-rearing in Alpine black grouse (Signorell 2008).

Green alder represents an invertebrate-poor, thus unfavourable habitat for black grouse reproduction. Consequently, green alder which is spreading rapidly in many parts of the Alps following land abandonment might present a significant threat to the black grouse (Anthelme et al. 2001).

Implications for habitat management

A heterogeneous landscape matrix, consisting of a mosaic of open Ericaceae shrubland, interspersed with patches of meadow, both associated with scattered young and mature coniferous trees occurring at low density, should be promoted to provide suitable breeding conditions for black grouse. Signorell (2008) provides details about proportions of each component of the mosaic for achieving an optimal habitat configuration.

As mentioned above, in the European Alps this mosaic is threatened due to shrub and forest encroachment after abandonment of traditional land-use by farmers. Incentives for reinstating pastureland within the narrow belt of timberline ecosystems should be promoted, but practitioners should refrain from managing extensive areas of monotonous open grassland and recreate heterogeneity. The reintroduction of traditional livestock grazing by cattle and goats after forestry interventions, to reduce canopy and Ericaceae cover, could be one solution to maintain the mosaic in the long term. If the black grouse actually plays the role of an umbrella species within timberline ecosystems, which still ought to be demonstrated, the promotion of its habitat would likely benefit an entire biocoenosis.

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References

Angelstam, P. 1984: Factors influencing the distribution and abundance of the black grouse - a review. - In: Hudson, P.J. & Lovel, T.W.I. (Eds.); Proceedings of Third International Symposium on Grouse, York. International Council for Game & Wildlife Conservation World Pheasant Association, Paris Reading, UK, pp. 401-433.

Anthelme, F., Grossi, J.L., Brun, J.J. & Didier, L. 2001: Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. - Forest Ecology and Management 145: 57-65.

Arlettaz, R. 1999: Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. - Journal of Animal Ecology 68: 460-471.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R. & Jenni-Eiermann, S. 2007: Spreading free-riding snow sports represent a novel serious threat for wildlife. - Proceedings of the Royal Society, Series B 274: 1219-1224.

Baines, D., Wilson, I.A. & Beeley, G. 1996: Timing of breeding in Black Grouse *Tetrao tetrix* and Capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. - Ibis 138: 181-187.

Bernard, A. 1982: An analysis of black grouse nesting and brood habitats in the French Alps. - In: Lovel, T.W.I. (Ed.); Proceedings of the Second International Symposium on Grouse at Dalhousie Castle, Edinburgh, Scotland. World Pheasant Association, Exning, Suffolk, UK, pp. 156-172.

Britschgi, A., Spaar, R. & Arlettaz, R. 2006: Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. - Biological Conservation 130: 193-205.

Crawley, M.J. 2007: The R Book. - John Wiley & Sons Ltd, Chichester, UK, 942 pp.

Di Giulio, M., Edwards, P.J. & Meister, E. 2001: Enhancing insect diversity in agricultural grasslands: 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.); Woodland Grouse Symposium at Culloden House, Inverness, Scotland. World Pheasant Association, Bures, UK, pp. 64-73.

Estabrook, C.B. & Estabrook, G.F. 1989: ACTUS: A solution to the problem of small samples in the analysis of two-way contingency tables. - Historical Methods 22: 5-8.

Hannon, S.J. & Martin, K. 2006: Ecology of juvenile grouse during the transition to adulthood. - Journal of Zoology 269: 422-433.

Hooge, P.N. & Eichenlaub, B. 1997: Animal movement extension to arcview. - Alaska Biological Science Center, U.S. Geological Survey, Anchorage, USA.

Johnson, D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. - Ecology 61: 65-71.

Klaus, S., Bergmann, H.H., Marti, C., Müller, F., Vitovic, O.A. & Wiesner, J. 1990: Die Birkhühner. - A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany, 288 pp. (In German).

Ludwig, G.X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006: Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. - Proceedings of the Royal Society, Series B 273: 2009-2016.

Ludwig, G.X., Alatalo, R.V., Helle, P., Nissinen, K. & Siitari, H. 2008: Large-scale drainage and breeding success in boreal forest grouse. - Journal of Applied Ecology 45: 325-333.

Manly, B.F.J. 1997: Randomization, Bootstrap and Monte Carlo Methods in Biology. 2nd edition. - Chapman & Hall, London, UK, 399 pp.

Marti, C. 1985: Differences in the winter ecology between cock and hen black grouse *Tetrao tetrix* in the Swiss Alps. - Der Ornithologische Beobachter 82: 31-54.

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*. - Die Vogelwelt 120: 7-25. (In German).

Patthey, P., Wirthner, S., Signorell, N. & Arlettaz, R. 2008: Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. - Journal of Applied Ecology 45: 1704-1711.

Picozzi, N. & Hepburn, L.V. 1984: A study of black grouse in North East Scotland. - In: Hudson, P.J. & Lovel, T.W.I. (Eds.); Proceedings of Third International Symposium on Grouse, York. International Council for Game & Wildlife Conservation, World Pheasant Association, Paris Reading, UK, pp. 462-480.

Ponce, F. 1992: Régime alimentaire du Tétras lyre *Tetrao tetrix* dans les Alpes françaises. - Alauda 60: 260-268. (In French).

Ponce, F. & Magnani, Y. 1988: Régime alimentaire des poussins de Tétras lyre (*Tetrao tetrix*) sur deux zones des Alpes françaises: méthodologie et résultats préliminaires. - In: Office National de la Chasse, Paris (Ed.); Colloque Galliformes de montagne, pp. 225-228. (In French).

Reisigl, H. & Keller, R. 1999: Lebensraum Bergwald. 2nd edition. - Spektrum Akademischer Verlag, Heidelberg, 147 pp. (In German).

Rumble, M.A. & Anderson, S.H. 1996: Feeding ecology of Merriam's turkeys (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota. - American Midland Naturalist 136: 157-171.

Sachot, S., Perrin, N. & Neet, C. 2006: Viability and management of an endangered Capercaillie (*Tetrao urogallus*) metapopulation in the Jura Mountains, Western Switzerland. - Biodiversity and Conservation 15: 2017-2032.

Savory, C.J. 1989: The importance of invertebrate food to chicks of Gallinaceous species. - Proceedings of the Nutrition Society 48: 113-133.

Signorell, N. 2008: Habitat management guidelines for the conservation of an emblematic species of Alpine timberline ecosystems, the Black grouse: from fine-grained habitat selection to large-scale habitat suitability modelling. - PhD thesis, University of Bern, Switzerland, 179 pp.

Southwood, T.R.E. 1978: Ecological methods. 2nd edition. - Chapman & Hall, London, UK, 524 pp.

Standen, V. 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. (Ed.) 2007: Grouse: Status Survey and Conservation Action Plan 2006-2010. - IUCN, The World Pheasant Association, Gland, Switzerland, 114 pp.

Tirpak, J.M., Giuliano, W.M. & Miller, C.A. 2008: Ruffed grouse brood habitat selection at multiple scales in Pennsylvania: implications for survival. - Canadian Journal of Zoology-Revue Canadienne De Zoologie 86: 329-337.

Wegge, P. & Kastdalen, L. 2008: Habitat and diet of young grouse broods: resource partitioning between Capercaillie (*Tetrao urogallus*) and Black Grouse (*Tetrao tetrix*) in boreal forests. - Journal of Ornithology 149: 237-244.

White, G.C. & Garrott, R.A. 1990: Analysis of Wildlife Radio-Tracking Data. - Academic Press, Inc., San Diego, USA, 383 pp.