Selection of Night Roosts in Winter by Capercaillie Tetrao urogallus in Central Europe

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To survive in harsh winter conditions, animals must make behavioural and physiological adaptations. The selection of good habitats may prevent a negative energy budget and reduce predation risk. The capercaillie *Tetrao urogallus*, the largest of all grouse, feeds in winter on conifer needles, a superabundant but low-energy food resource. We hypothesised that capercaillie should select nocturnal roosting trees that simultaneously provide food, minimise predation risk and reduce energy expenditure. Using paired logistic regression, we studied night roost selection in winter in the Black Forest (Germany), the Swiss Jura, the Swiss Alps and the Thuringia Forest (Germany) by comparing 508 pairs of roosting trees and matched control trees. The most important factors discriminating roosting trees from random trees were tree species and number of forest aisles leading away from the roost tree. Trees with more than one nearby forest aisle for escape by flight were preferred over those with only one aisle or none. Capercaillie strongly selected pine trees *Pinus* spp for nocturnal roosting, and avoided Norway spruce *Picea abies*. At sites without pine trees, deciduous trees were preferred. Compared to females, males preferred larger trees in more open forest stands. Our results suggest that the selection of night roosts is determined by predator avoidance, energy-saving strategies aimed at reducing flight activity and feeding possibilities. Microclimate does not seem to influence selection of night roosts.

Key words: habitat selection, nocturnal roosting tree, paired logistic regression, predator avoidance, Tetrao urogallus

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In northern and temperate areas, winter is a challenging time for most bird species, often causing high mortality (Wegge et al. 1987, Peach et al. 1999, Bro et al. 2000). Climatic conditions are typically harsh, food availability is reduced and predation level high. Particular physiological and behavioural adaptations are required to survive under such conditions. One adaptation is the selection of

a winter habitat that favours energy-saving strategies and reduces predation risk.

The capercaillie *Tetrao urogallus* is a sedentary grouse species that is listed in the national red data books of central and western European (Storch 2000). Capercaillie inhabit a large variety of boreal and mountainous coniferous forests in the Palaearctic, and owing to their great body mass, ≤ 4 kg, they need large amounts of food in winter. During winter, capercaillie feed almost exclusively on conifer (Pulliainen 1970, Storch et al. 1991). Needles are a superabundant food resource, but are low in energy and difficult to digest because of their high content of cellulose and secondary plant compounds (Lindén 1984, Andreev 1988). Capercaillie partly overcome these problems by selecting needles with a high energy and a low resin content (Lindén 1984, Annila et al. 2003). Cellulose is decomposed and digested with the aid of bacteria in specially adapted caeca during a long-lasting process (Moss & Hansson 1980). Because of the particular characteristics of their food and digestion, capercaillie are severely constrained in their rate of energy intake and therefore need to minimise energy expenditure to prevent a negative energy balance (Rintamäki et al. 1984, Andreev & Lindén 1994).

Therefore, optimal selection of winter habitat by capercaillie should result in a reduction of energy expenditure and predation risk, rather than in increased food availability like in many other species (Rolando & Carisio, 1999). Energy expenditure can be reduced by minimising the distance or the frequency of flights between foraging and roost sites, and by choosing favourable microclimatic conditions for roosting. Predation risk can be reduced by choosing habitats with few predators or by adapting a behaviour during foraging and roosting that enables escape flights or hiding.

Habitat requirements may differ between day and night. For example, many species such as ravens *Corvus corax* and Savannah sparrows *Passerculus sandwichensis* feed at particular sites and fly up to many kilometres to attain their roosts (Wright et al. 2003, Ginter & Desmond 2005). In the case of the capercaillie, such flights should be kept at a minimum to minimise energy expenditure and predation risk. Capercaillie roost in both trees and in snow burrows, burrows being used mainly by more northern populations (Seiskari 1962). In the populations that we studied, birds roosted only in trees and therefore it would be advantageous if day and night tree roosts were close together or even in the foraging trees. However, to our knowledge, characteristics of night roosts have not been analysed in capercaillie.

In our study, we examined the following four hypotheses:

1) Capercaillie should choose night roosts to save energy by minimising flight distance between trees used for foraging and night roosts. Furthermore, capercaillie should select favourable microclimatic conditions with wind protection to reduce heat loss at exposed roosts (Walsberg 1986). Therefore, we would expect capercaillie to roost in dense stands of conifers offering food and a favourable microclimate;

2) Night roosts should be inaccessible to most predators, offer escape routes and enable capercaillie to detect approaching predators. Therefore, we would expect night roosts in trees rather than on the ground, to avoid red foxes *Vulpes vulpes*, an abundant predator in Central Europe (Storch et al. 2005). For protection against tree-climbing predators (e.g. martens *Martes* spp.), we would expect capercaillie to select open forest stands that allow detection of approaching predators and that also offer forest aisles or proximity to forest edges for escape flights;

3) These two hypotheses are in conflict, because the minimisation of energy expenditure requires dense stands with a favourable microclimate (Thompson & Fritzell 1988), whereas the detection of predators requires open stands of trees. Therefore, we would expect capercaillie to favour pine trees *Pinus* spp whenever available, because they offer the preferred needle forage (Schroth et al. 2005), and usually grow in relatively open forest stands enabling predator detection and escape flights. In areas without pines, capercaillie should roost in other relatively open conifer stands. To investigate this hypothesis, we examined roosting sites in two study sites with pines and two sites without;

4) Energy expenditure, predation risk and escape behaviour vary between the sexes because body mass of males is nearly twice that of females. We predict that, compared with females, the larger males with their lower mass-specific energy requirements and heat loss, and their much lower critical temperature (Rintamäki et al. 1984) should choose night roosts with a less favourable microclimate. In addition, males should
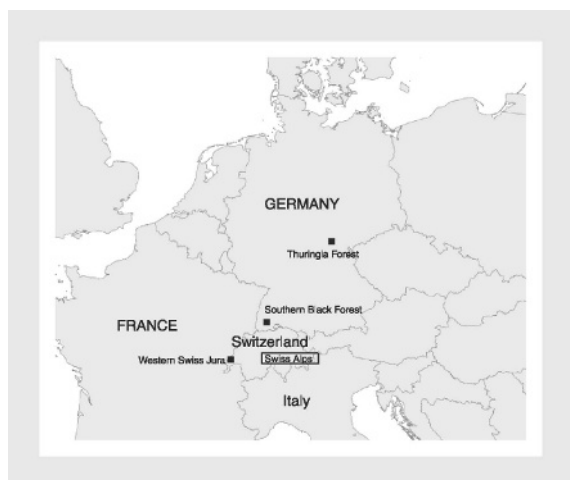
Figure 1. Location of the four study sites in central Europe where we studied night roost selection of capercaillie during 2003-2005 (© Institut für Kartographie ETH Zürich). The study site in the Swiss Alps consisted of 36 independent plots located within the frame.

prefer larger roosting trees in forest stands with more space for escape flight.

Methods

Study sites
Our study was carried out during the winters (November-March) of 2003/04 and 2004/05 in four different study sites in central Europe (Fig. 1): the southern Black Forest, Germany (47°51'N, 8°00'E), western Swiss Jura (46°33'N, 6°15'E), Swiss Alps (46°45'N, 9°04'E) and Thuringia Forest, Germany (50°30'N, 11°08'E). In the Black Forest study site (11 km^2), elevations ranged within 1,000-1,400 m a.s.l., and forests were intensively used for forestry and tourism. Forests were dominated by dense nutrient-rich forest stands containing Norway spruce *Picea abies* (49%) and European silver fir *Abies alba* (19%; Suchant et al. 2003). Common beech *Fagus sylvatica* (22%) was the most abundant deciduous tree. The study site in the western Swiss Jura (4 km^2) encompassed forests ranging within 1,300-1,500 m a.s.l. and dominated by Norway spruce (73%) mixed with common beech (10%), sycamore maple *Acer pseudoplatanus* (4%) and European silver fir (12%; U. Ulmer, unpubl. data). Pines were absent in the Black Forest and in the western Swiss Jura sites. The study site in the Swiss Alps consisted of 36 independent plots

ranging within 14-200 ha, with a mean size of 89 ha, and totalling 32 km^2. The plots consisted of a large variety of different forest types, forest sizes, forest management regimes and altitudes ranging within 1,300-2,200 m a.s.l. Tree composition varied from pure to mixed coniferous forests with different tree species dominating (Swiss mountain pine *Pinus mugo*, Norway spruce, Swiss stone pine *Pinus cembra*, European larch *Larix decidua* or European silver fir). Deciduous trees were absent from nearly all the Swiss Alp plots. Tree composition in the dense productive Thuringia Forest, with a prospected area of about 70 km^2 and elevations ranging within 600-850 m a.s.l., was dominated by Norway spruce (> 80%), with only small proportions of other species (Scots pine *Pinus sylvestris*: 5-10% and common beech *Fagus sylvatica*: < 1%) present. All four forests were subjected to forest management and tourism.

Estimated population size in the Black Forest study site is > 60 capercaillie (Braunisch & Suchant 2006), about 56 in the Swiss Jura study site (S. Sachot, pers. comm.), at least 290 in all Swiss Alp plots combined (K. Bollmann & P. Mollet, pers. comm.), and about 25 in the Thuringia Forest (S. Klaus, pers. comm.). These numbers probably underestimate the number of individuals for which we sampled roosting trees, because we sampled data over two years and because the reproductive success of capercaillie in 2003 increased populations to levels higher than the figures stated above.

During our study, snow covered the ground vegetation completely at all study sites. Snow depth ranged from 10 cm in the Swiss Jura in early winter to at least 200 cm in late winter in the Black Forest and in the Swiss Alps. The top layer of the snow cover varied. It was a hard frozen crust when temperatures were above 0°C at daytime and below 0°C at night. After fresh snow falls with temperatures far below 0°C, the snow was loose and dry. In all study sites, daily mean temperatures between November and March in the winter of 2004/05 (measured 2 m above ground) were < 0°C.

Data collection
In all four study sites, night roosts were found by walking along contour lines crossing forests within mapped capercaillie areas, and by visually searching for faeces on the snow surface. The probability of detecting a capercaillie snow roost is probably lower than that of finding a night roost in a tree. However, during our studies we found several snow

burrows of hazel grouse *Bonasa bonasia* and black grouse *Tetrao tetrix*, but none of capercaillie. Therefore, we believe that snow burrows of capercaillie were rare, but detectable. Each forest was visited once in early winter (November-December) and once in late winter (February-March). In addition, in the Black Forest and Thuringia Forest sites, we also found several night roosts while tracking radio-equipped capercaillie. Our data may contain a certain amount of pseudo-replication, because forests were visited twice. However, the number of capercaillie in the Swiss Alps and in the Black Forest study site was quite high, thus reducing pseudo-replication.

The conspicuous faeces on snow under night roost trees make them easy to detect. Night roosts were distinguished from day roosts by the presence of both caecal faeces and a concentrated heap of long, cylindrical intestinal faeces. Because capercaillie excrete one intestinal faeces every 12 minutes (Klaus et al. 1989), and night roosts are used from dusk to dawn in winter, large heaps of intestinal faeces are a distinct characteristic of a night roost. For each roosting tree located, we chose one currently unoccupied control tree by walking 50 m from the night roost in a random direction. The tree closest to this point and with a circumference at breast-height of at least 20 cm was selected as the control tree. From past experience, we knew that capercaillie always roosted on trees with a circumference of > 20 cm, and this was confirmed by the present study. In total, we analysed 508 pairs of trees.

We investigated predictor variables known to be important for capercaillie winter habitat selection (Klaus et al. 1989, Storch 1993b). To test our hypotheses, we selected variables that could vary within the investigated spatial scale of the tree pairs, and which characterise the appearance of forest stands as perceived by a capercaillie sitting in a tree. For each roost and control tree, we recorded study site (SITE: Black Forest, Swiss Alps, Swiss Jura and Thuringia Forest), circumference at breast-height of the tree (CBH), and tree species (TREESPEC: Norway spruce, European silver fir, pines, European larch, deciduous trees). Pine trees included Swiss stone pine, Swiss mountain pine and Scots pine. Within a 20-m radius of the trees, we estimated canopy cover as the vertical projection on the forest floor (CANOPY: in %), and recorded forest aisles (AISLE: none, 1 or > 1), and steepness of the slope (SLOPE: in °). A forest aisle was defined as a canopy

opening at least 5 m wide and 20 m long leading away from the roost or control tree. In addition, we measured the distance to the nearest edge (EDGE: forest edge, habitat edge or other disrupting element such as a forest road).

For 61 pairs of roost and control trees in the Black Forest in winter 2003/04, we recorded CBH and species of all trees within a radius of 20 m (1,257 m²). Based on these measurements, we computed the deciduous and the conifer tree stocking values (Bickford 1957) by establishing the sum of the cross-section areas of all stems at breast-height. Because the two values for deciduous and conifer tree stocking were highly negatively correlated, only the deciduous tree stocking (DTS) was used in the analysis.

For all night roosts, we determined the sex of the capercaillie from the size of the intestinal faeces, i.e. faeces diameter of males > 10 mm, and those of females < 8 mm (K. Bollmann, unpubl. data). Determination of sex of capercaillie in winter from the size of nocturnal faeces is a reliable method (Gjerde 1990), because faeces do not swell at ambient temperatures below 0°C, and are of comparable consistency due to the unique food source of conifer needles. Night roosts with faeces in the overlapping zone of 8-10 mm were excluded from sampling (N = ~12). We recorded the position of the bird in the tree by measuring the distance between the tree trunk and the centre of the faeces. We noted the orientation of the roosting branch relative to the slope (downhill, uphill, sidewards, or flat for trees in non-sloping forest stands).

Statistical analyses

We used a matched-pairs (also called paired) logistic regression analysis to identify factors related to the choice of roosting trees in capercaillie. In studies of rare events, such as the use of a tree for roosting by a capercaillie, the only realistic sampling design may be to take a sample of roosting trees (cases) and compare each roosting tree to a nearby matched unused (control) tree. In this situation, standard logistic regression is inappropriate and instead paired logistic regression should be used to analyse the determinants of the rare event (Hosmer & Lemeshow 1989, Keating & Cherry 2004). Paired logistic regression is more powerful, since it exploits the information about the pairing of cases and controls, but seems to have been discovered only recently by biologists (see examples in Rocke & Samuel 1999, Weller & Zabel 2001, Compton et

al. 2002).The parameter estimates of the paired logistic regression model are interpreted in terms of the relative risk (odds ratio) of the event, i.e. a tree being used for roosting. The procedure is similar to a paired t-test, where the difference between each pair is a single observation.

To test which tree and habitat variables were most important in distinguishing roosting trees from non-roosting trees, we conducted two different paired logistic regression analyses. In analysis A, we included data from all 508 tree pairs from all four study sites (129 tree pairs in the Black Forest, 213 in the Swiss Alps, 46 in the Swiss Jura, and 120 in the Thuringia Forest), and six explanatory variables without the variable SITE. To test for differences in the preference of tree and habitat characteristics between sites, we included eight biologically relevant interaction terms. Obviously, there is no main effect of SITE, since in our paired design, both trees of a pair always shared the same SITE. Instead, effects of SITE were tested in interaction terms with the other explanatory variables CBH, CANOPY, EDGE, SLOPE and AISLE. The interaction between SITE and TREESPEC could not be included in the model, since some tree species did not occur in all sites. This produced empty cells in the design matrix of the model and prevented computation (see Hosmer & Lemeshow 1989). Furthermore, we included the interactions between AISLE and EDGE and CANOPY, respectively, as well as between EDGE and CANOPY, because we expected them to be biologically relevant. Exploratory analysis showed that no substantial correlation of two continuous predictor variables for roosting trees existed ($R^2 < 0.10$).

Analysis B was similar to analysis A but applied to the data from the 61 tree pairs in the Black Forest, where the additional explanatory variable DTS had been recorded. Obviously, SITE and all interactions with SITE were not included in the analyses, because all trees were in the Black Forest. Because of the small sample size and the absence of pine and larch trees, the TREESPEC factor was reduced to two levels (conifer trees and deciduous trees), and no interaction effects were tested.

In analysis C, we tested for sex differences in the use of 508 night roosting trees, 312 trees being used by males and 196 by females. We applied standard logistic regression analysis to compare sex differences, rather than discriminant function analysis, because it permits inclusion of categorical predictors (North & Reynolds 1996). The response variable was set at 1 for males and 0 for females. The explanatory variable AISLE had only two levels, because there were no cases of hens using trees with no forest aisles. Therefore, we lumped 'no' and 'one' forest aisle into category 1 and '> 1' forest aisle into category 2. In contrast to analyses A and B, standard logistic regression analysis could be used to test the effects of the main factor SITE and its interaction with TREESPEC.

Akaike's Information Criterion AIC (Akaike 1974) was used to select the best model for all three analyses (A, B and C). First, we developed a list of candidate models *a priori* based on our hypotheses. For analysis A, this list included 14 candidate models, including the range from the simplest model, with one main effect, to the most complex model with six main effects (without SITE) and eight interaction terms. For analysis B, seven candidate models were built, including the range from the simplest model with one main effect, to the largest model with all seven main effects without any interaction terms. The list for analysis C contained 15 candidate models including the range from the simplest model with one main effect, to the most complex model with all seven main effects and eight interaction terms. Secondly, models within each analysis (A-C) were ranked using AIC_c (Hurvich & Tsai 1989), and the final model of each of the three analyses (A-C) with the minimum AIC_c was selected to fit to the data. We used GenStat for Windows version 7.3 (Payne 2003) for all analyses.

Results

Nocturnal roosting tree selection

All the night roosts we found were in trees. In 188 out of 508 cases, roosting trees were in flat forest stands ($< 5°$ slope). In sloping forest stands, capercaillie mostly roosted on tree branches which pointed downhill (50% for males and 43% for females), followed by branches pointing uphill (31% for males and 44% for females), and sidewards (19% for males and 14% for females); differences between sexes were not significant ($\chi^2 = 5.34$, df = 2, P = 0.07). Birds roosted at a mean distance of 171 cm (SE $\pm$ 6 cm, range: 15-560 cm, N = 501) from the trunk. There was no significant difference between sexes (ANOVA: df = 500, F = 1.36, P = 0.24).

In analysis A, the best model selected by AIC_c was the second most complex model contain-

Table 1. Model selection results (Analysis A; N = 508) of paired logistic regression models for night roost selection of capercaillie showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AIC$_c$), simple differences (ΔAIC$_c$), and Akaike weights (ωi). Models were numbered according to the number of variables and interaction terms included, the variables being: cbh = circumference at breast-height of the tree, ca = CANOPY, ai = AISLE, e = EDGE, sl = SLOPE, t = TREESPEC, si = SITE.

Model	Variables	Log L	K	AIC$_c$	ΔAIC$_c$	ωi
13	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*ai+ca*si	185.22	32	-302.00	0.00	0.80
14	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*ai+ca*si+sl*si	187.30	35	-299.27	2.73	0.20
12	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*si	162.43	29	-263.22	38.78	0.00
8	cbh+ca+ai+e+sl+t+e*ai+ca*ai	123.82	16	-214.53	87.47	0.00
9	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca	123.82	17	-212.39	89.61	0.00
6	cbh+ca+ai+e+sl+t	117.39	12	-210.15	91.85	0.00
11	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai	132.09	26	-209.27	92.73	0.00
10	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si	124.63	20	-207.54	94.45	0.00
7	cbh+ca+ai+e+sl+t+e*ai	118.18	14	-207.52	94.48	0.00
4	cbh+ca+ai+e	13.34	7	-12.46	289.53	0.00
5	cbh+ca+ai+e+sl	13.87	8	-11.46	290.54	0.00
3	cbh+ca+ai	5.56	6	1.05	303.05	0.00
2	cbh+ca	-44.81	4	97.69	399.69	0.00
1	cbh	-66.49	3	139.02	441.02	0.00

ing all six main effects and seven interaction terms (Table 1). The second best model included one more interaction term. All other models had negligible support. The selection of the two most complex models was probably caused by the fact that study site (SITE) was not included as a main effect, but rather as an interaction term. This indicates that all our variables, and especially the predictor variable SITE, made an important contribution to the model. According to the odds ratios of the main effects and the interaction terms, roosting trees differed from randomly chosen paired control trees mainly by tree species and the presence of flight aisles (Table 2). The effect of the latter mainly depends on study site (see large odds ratios of the in-

teraction terms SITES*AISLE in Table 2). Independent of study site, Norway spruce was always avoided for nocturnal roosting, and the preferred trees were deciduous species (common beech and sycamore maple), pines, silver fir and larch (see Table 2). Many night roosts were in pines (45%), whereas the most common control tree was Norway spruce (67%). In the Black Forest and Swiss Jura study sites, where pines were absent, deciduous trees were strongly preferred for nocturnal roosting. In the Swiss Alps and in the Thuringia Forest where deciduous trees were absent (Fig. 2), pines were strongly preferred for night roosts.

Also tree size (CBH), canopy cover, edge distance and slope contributed to roosting tree selection.
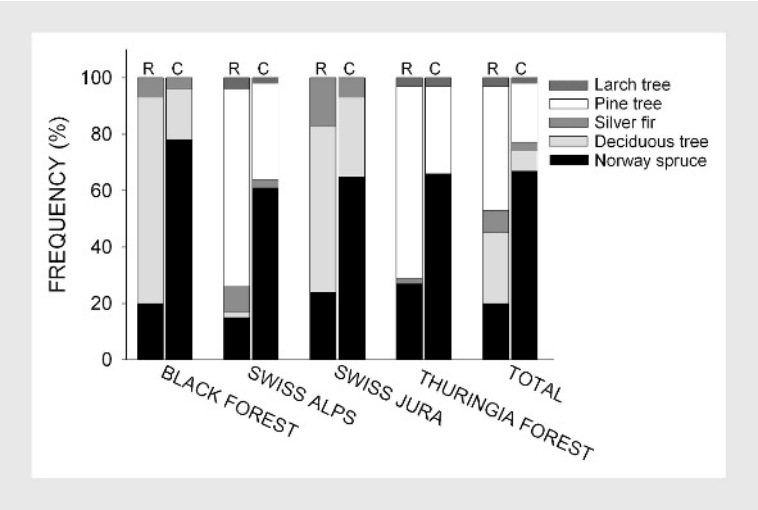

Figure 2. Percentages of tree species of the 508 roost and matched control trees in the four study sites. The percentages sum up to 100% separately for roost (R) and control (C) trees.

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Table 2. Results of the paired logistic regression (analysis A) comparing the characteristics of 508 roost trees with those of 508 paired control trees (see Methods for details). Because tree pairs were from the same sites, SITE was not included as a main factor, but as interaction terms. The first category of categorical variables was set at zero and is not shown (AISLE_no and Norway spruce in the category TREESPEC). SITE1: Black Forest, SITE2: Swiss Alps, SITE3: Swiss Jura, and SITE4: Thuringia Forest. For all variables and interaction terms df = 1.

Variable	Mean deviance	Parameter estimate	Odds ratio	SE
Main factors				
DBH	44.04	0.02	1.02	0.01
CANOPY	54.50	-0.08	0.92	0.05
AISLE_one	13.65	-3.88	0.02	2.53
AISLE_several	95.31	-1.72	0.18	2.65
EDGE	14.79	-0.03	0.97	0.03
SLOPE	1.18	-0.01	0.99	0.02
TREESPEC_deciduous	70.51	3.69	40.00	0.74
TREESPEC_silverfir	26.11	2.04	7.71	0.56
TREESPEC_pine	45.00	2.81	16.56	0.54
TREESPEC_larch	18.84	3.39	29.52	0.83
Interaction terms				
AISLE_one*EDGE	0.58	0.02	1.02	0.02
AISLE_several*EDGE	1.03	0.03	1.03	0.02
AISLE_one*CANOPY	0.71	0.06	1.06	0.04
AISLE_several*CANOPY	5.71	0.06	1.07	0.04
CANOPY*EDGE	0.16	0.00	1.00	0.00
SITE2*DBH	0.45	0.00	1.00	0.01
SITE3*DBH	0.33	-0.01	0.99	0.02
SITE4*DBH	0.35	0.00	1.00	0.03
SITE2*AISLE2	1.92	1.21	3.35	1.59
SITE3*AISLE2	0.81	5.00	148.41	101.00
SITE4*AISLE2	4.73	6.70	812.41	11.10
SITE2*AISLE3	0.60	-0.35	0.70	1.76
SITE3*AISLE3	0.00	6.00	403.43	101.00
SITE4*AISLE3	0.99	4.50	90.02	11.20
SITE2*EDGE	2.45	-0.02	0.98	0.01
SITE3*EDGE	6.43	0.01	1.01	0.02
SITE4*EDGE	24.70	-0.09	0.92	0.03
SITE2*CANOPY	8.45	0.07	1.08	0.03
SITE3*CANOPY	5.75	0.14	1.15	0.09
SITE4*CANOPY	9.04	-0.22	0.80	0.09
SITE2*SLOPE	0.97	0.05	1.06	0.04
SITE3*SLOPE	1.06	0.08	1.08	0.08
SITE4*SLOPE	0.06	-0.04	0.96	0.18

Roosting trees had larger CBH than control trees, 15 cm on average (Fig. 3A). Only in the Black Forest was CBH of roosting trees slightly smaller than in control trees (see Fig. 3A). The difference in CBH medians between roost and control trees for Norway spruce was 13 cm. The corresponding difference for deciduous trees was 23 cm, 30 cm for silver fir, 21 cm for pines, and 29 cm for larch trees. Canopy cover around roosting trees was less than around control trees at two study sites (see Fig. 3B). In all sites, trees with more than one forest aisle were highly preferred for nocturnal roosting, and those with no or one forest aisle were avoided (Fig. 4, see Table 2). The large odds ratios and errors of the interaction terms of SITE3 and SITE4 with AISLE2 (one flight aisle) are due to the fact,

that in the Swiss Jura and in the Thuringia Forest, roosting trees with one flight aisle were highly selected compared to those with no flight aisle (AISLE1 is set to zero), because there were no roosting trees with no flight aisle (see Table 2). Roosting trees were usually closer to a forest edge than control trees (see Fig. 3C). The effects of canopy cover and edge distance differed by site (see Figs. 3B,C and Table 2). Roosting trees in the Black Forest and in the Thuringia Forest were closer to edges and had less canopy cover in the surroundings than control trees. In the Swiss Alps, the opposite was found. In the Swiss Jura, distance to forest edge did not differ between roost and control trees, but canopy cover was 10% higher around roosting trees than around control trees (see
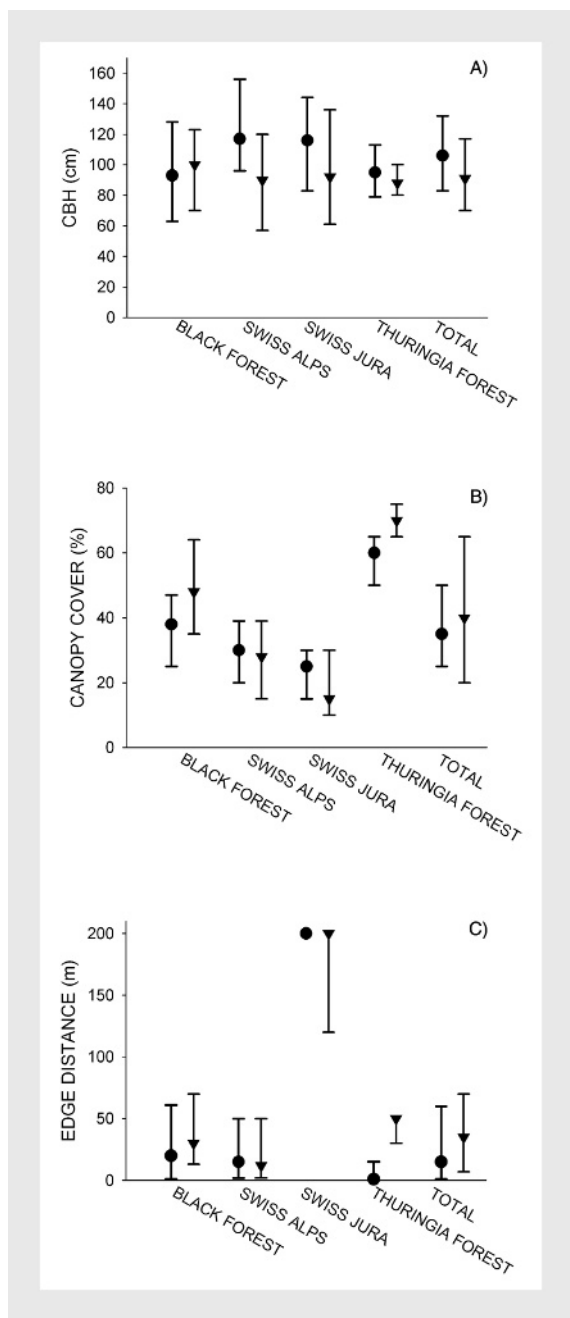
Figure 3. Circumference at breast-height (CBH; in cm; A,), canopy cover (in %; B), and distance to edge (in m; C) of the 508 roost (●) and matched control (▼) trees at the four study sites. The median, 25th and 75th percentiles are shown.

Fig. 3B). The largest odds ratio among the first four interaction terms (AISLE*CANOPY) indicates that the importance of canopy cover in the surroundings differed according to the presence of forest aisles. The median canopy cover around roosting trees without forest aisle was 45 vs 70% for control trees without forest aisle. The canopy
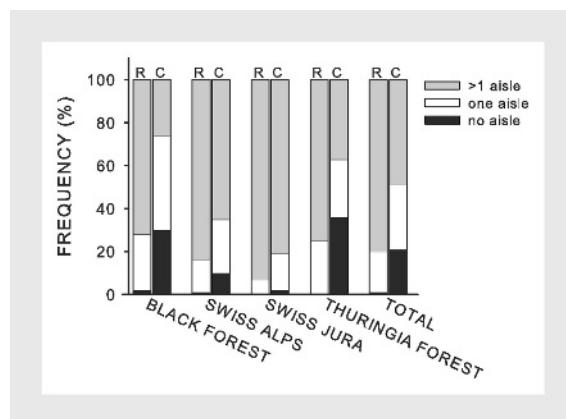

Figure 4. Occurrence of forest aisles in the surroundings of the 508 roost and matched control trees at the four study sites. The percentages sum up to 100% separately for roost (R) and control (C) trees.

cover for roosting trees with one forest aisle was 45 vs 48% for control trees. For roosting trees with > 1 forest aisle, canopy cover was 32 vs 25% for control trees.

In analysis B, we investigated 61 Black Forest tree pairs and measured the DTS value in the circular areas surrounding each tree. AIC$_c$ clearly selected the model including all possible predictor variables, including DTS (Table 3). According to the large odds ratios of the variables TREESPEC and AISLE > 1, roosting trees differed from randomly chosen paired control trees mainly by tree species and the presence of flight aisles (Table 4). Trees offering more than one forest aisle were highly preferred for nocturnal roosting, whereas control trees usually had no or just one forest aisle. Deciduous trees were highly preferred for nocturnal roosting,

Table 3. Model selection results (Analysis B; N = 61) of paired logistic regression models for night roost selection of capercaillie showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AIC$_c$), simple differences (ΔAIC$_c$), and Akaike weights (ωi). Models were numbered according to the number of variables included, the variables being: cbh = circumference at breast-height of the tree, ca = CANOPY, ai = AISLE, e = EDGE, sl = SLOPE, t = TREESPEC, dts = deciduous tree stocking.

Model	Variables	Log L	K	AIC$_c$	ΔAIC$_c$	ωi
7	cbh+ca+ai+e+sl+t+dts	30.42	10	-36.44	0.00	0.88
6	cbh+ca+ai+e+sl+t	26.96	9	-32.40	4.04	0.12
3	cbh+ca+ai	11.53	6	-9.50	26.94	0.00
5	cbh+ca+ai+e+sl	13.33	8	-7.89	28.54	0.00
4	cbh+ca+ai+e	11.90	7	-7.68	28.76	0.00
2	cbh+ca	-3.89	4	16.50	52.93	0.00
1	cbh	-9.83	3	26.08	62.52	0.00

Table 4. Results of the paired logistic regression (analysis B) comparing characteristics of 61 roost trees with 61 paired control trees in the Black Forest (see methods for details). The first category of categorical variables was set at zero and is not shown (AISLE_no and conifer trees in the category TREESPEC). For all variables df = 1 .

Variable	Mean deviance	Parameter estimate	Odds ratio	SE
DBH	0.37	0.07	1.07	0.04
CANOPY	14.90	-0.08	0.92	0.06
AISLE_one	6.05	0.20	1.22	1.08
AISLE>1	21.49	5.70	298.90	2.93
EDGE	0.50	0.02	1.02	0.03
SLOPE	1.86	-0.17	0.84	0.10
TREESPEC	14.20	9.42	12,332.60	4.36
DTS	2.71	-0.03	0.97	0.02

whereas conifer trees were avoided. Of all roosting trees, 64% were deciduous, while only 21% of control trees were deciduous. Forest stands around roosting trees had a significantly higher DTS value (median = 0.74 m^2, range = 0-3.89 m^2) than those around control trees (median = 0.36 m^2, range = 0-2.79 m^2).

Sex differences in nocturnal roosting tree use

In analysis C, coefficients of the three best models selected by AIC$_c$ with combined model weights of 0.93 suggest that tree selection for night roosting differed significantly between the sexes for all predictor variables (Tables 5 and 6). The second and third best models also included one and two interaction terms, respectively. Males usually preferred trees with a greater stem size (CBH) than did fe-

males (Fig. 5A). Compared to females, males preferred forest stands with less canopy cover (see Fig. 5B), situated in less sloped forest stands and closer to forest edges. In the two sites with pines (Swiss Alps and Thuringia Forest), males roosted in pines more often than did females (Fig. 6). In the two sites without pines (Black Forest and Swiss Jura), females roosted more frequently in deciduous trees than in other tree species (see Fig. 6).

Discussion

Capercaillie showed a strong preference for certain tree and forest characteristics for nocturnal roosting in winter. Pines or deciduous trees with more than one forest aisle were strongly preferred for nocturnal roosting, and spruce trees with no forest aisle were avoided. Furthermore, the birds preferred large trees (CBH) in open forest stands close to forest edges, and avoided small trees in relatively dense forest stands. Compared to females, males favoured larger trees in more open stands, closer to forest edges and on gentler slopes.

Night roost selection according to energetic aspects
According to our first hypothesis, capercaillie should roost on the preferred feeding trees to avoid energy-consuming flights. Indeed, if present (Swiss Alps and Thuringia Forest), pines were the most often used trees for night roosting. Several studies have confirmed that capercaillie prefer pine needles

Table 5. Model selection results (Analysis C; N = 508) of logistic regression models for night roost selection differences between capercaillie males and females showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AIC$_c$), simple differences (ΔAIC$_c$), and Akaike weights (ωi). Models were numbered according to the number of variables and interactions terms included, the variables being: cbh = circumference at breast-height of the tree, ca = CANOPY, ai = AISLE, e = EDGE, sl = SLOPE, t = TREESPEC, si = SITE.

Model	Variables	Log L	K	AIC$_c$	ΔAIC$_c$	ωi
7	cbh+ca+ai+e+sl+t+si	-37.58	14.00	104.01	0.00	0.61
8	cbh+ca+ai+e+sl+t+si+e*ai	-37.58	15.00	106.13	2.12	0.21
9	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai	-37.15	16.00	107.40	3.39	0.11
10	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e	-37.15	17.00	109.54	5.53	0.04
15	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e+si*ca+si*sl	-21.10	32.00	110.64	6.64	0.02
11	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh	-35.85	20.00	113.42	9.41	0.01
12	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai	-34.98	23.00	118.24	14.23	0.00
13	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e	-31.91	26.00	118.74	14.73	0.00
14	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e+si*ca	-29.69	29.00	121.03	17.02	0.00
6	cbh+ca+ai+e+sl+t	-51.02	11.00	124.56	20.56	0.00
5	cbh+ca+ai+e+sl	-65.72	7.00	145.66	41.65	0.00
1	cbh	-70.31	3.00	146.66	42.65	0.00
2	cbh+ca	-70.31	4.00	148.69	44.68	0.00
4	cbh+ca+ai+e	-68.40	6.00	148.97	44.97	0.00
3	cbh+ca+ai	-69.93	5.00	149.97	45.97	0.00

Table 6. Results of the non-paired logistic regression (analysis C) comparing characteristics of 312 trees used by males and 196 trees used by females for nocturnal roosting (see methods for details). The first category of categorical variables is not shown (AISLE_no/ one, Norway Spruce in the category TREESPEC, and Black Forest in the category SITE).

Variable	df	Deviance	Mean deviance	Parameter estimates	SE
CBH	1	7.73	7.73	0.99	0.68
CANOPY	1	0.09	0.09	0.01	0.00
AISLE>1	1	0.98	0.98	-0.04	0.01
EDGE	1	3.79	3.79	-0.63	0.30
SLOPE	1	6.80	6.80	0.00	0.00
TREESPEC	4	37.20	9.30	-0.01	0.01
SITE	3	31.80	10.60		

to other needles for feeding (Glutz von Blotzheim et al. 1973, Schroth et al. 2005). In both sexes, habitat selection in winter is mainly determined by the presence of pines for feeding and roosting (Gjerde 1991), and spruce-dominated stands are avoided (Gjerde & Wegge 1989). Lindén (1981) pointed out that pine forest is the most common winter habitat for capercaillie in Finland because the com-

Figure 5. Circumference at breast-height (CBH; in cm; A) and canopy cover (in %; B) of the 508 trees used by males (✚) and females (★) at the four study sites. The median, 25th and 75th percentiles are shown.

bined availability of food and shelter enable the birds to minimise the duration of their activity periods. Therefore, foraging and diurnal and nocturnal roosting can all be done in the same tree or within the same pine forest stand without energy-consuming flights to change trees. Although this has not been investigated with radio-tracking studies, other results point in the same direction, supporting the hypotheses of energy saving and predator avoidance. For example, home ranges are smaller in winter than in summer (Storch 1995), the daily activity period in winter lasts only 2-3 hours (Gjerde & Wegge 1987), and capercaillie confine their movements to small core areas within individual winter home ranges (Gjerde et al. 1985).

Contrary to our first hypothesis, microclimatic conditions did not determine night roost selection in our study sites, although temperatures during most nights were below the thermo-neutral zone of capercaillie, as the lower critical temperature is at -3°C for males and +9°C for females (Rintamäki et al. 1984). Two of our results point in this direction. First, even when snow and temperature conditions were favourable for snow roosts, we did not find any. This is in contrast to northern and boreal capercaillie populations, where capercaillie often roost in snow burrows (Lindén 1981, Klaus et al. 1989), and thus benefit from the higher temperatures within snow roosts (Marjakangas et al. 1984). Snow roosts seem to be used rarely by capercaillie in central Europe (Catusse 1989). Secondly, the windy deciduous trees were highly preferred for nocturnal roosting at sites without pines. Norway spruce was avoided although their dense forest stands and dense canopy cover provided protection against harsh weather conditions. In the few cases where capercaillie used Norway spruce for roosting, they selected trees with few or no branches below the roosting branch. The preference for open roosting trees in capercaillie is in contrast to studies
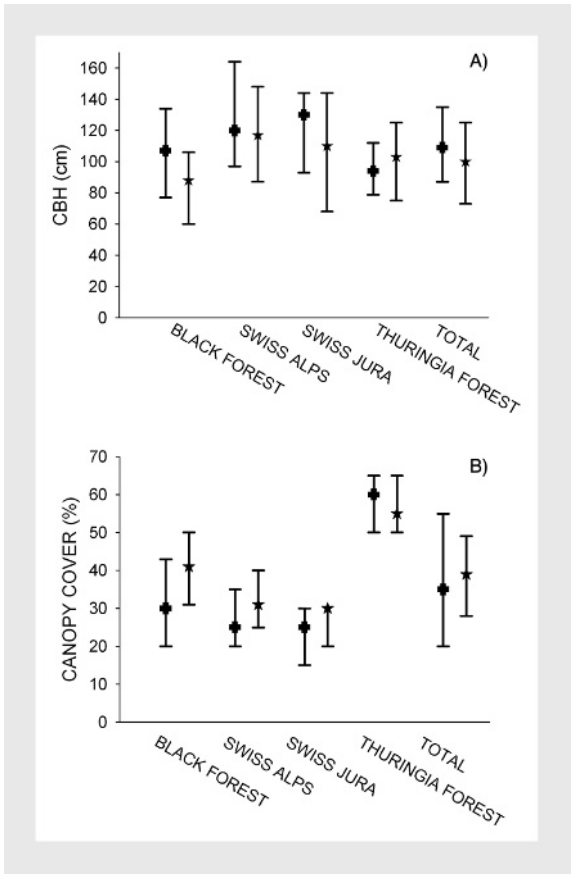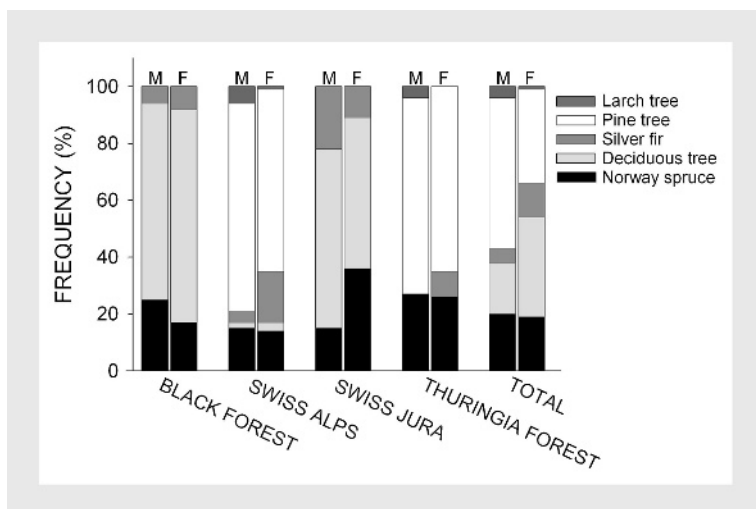
Figure 6. Percentages of tree species of the 508 trees used by males and females in the four study sites. The percentages sum up to 100% separately for trees used by males (M) and females (F).

on winter night roosts of blue grouse *Dendragapus obscurus* (Pekins et al. 1991), hazel grouse (Swenson & Olsson 1991) and ruffed grouse *Bonasa umbellus* (Thompson & Fritzell 1988). Ruffed grouse avoided deciduous trees, hazel grouse preferred to roost in Norway spruce, and all three species preferred dense conifer trees or forest stands with dense canopy cover for nocturnal roosting. The authors interpret these findings with respect to thermal benefits, reduced heat loss and concealment from predators.

Night roosts selection and predator avoidance

Several of our findings indicate that predator avoidance and the availability of escape flight routes strongly influenced night roost selection, which agrees with our second hypothesis. First, capercaillie in our study never used snow roosts, not even when snow conditions would have allowed it. The high densities of red foxes may explain this pattern. Fox densities in central Europe are much higher than in more northern and boreal areas such as Scandinavia (Kauhala et al. 2006), where snow roosting of grouse is mainly explained by microclimatic advantages and predator avoidance (Marjakangas 1990). Secondly, the preferred characteristics of roosting trees were open crowns growing close to forest edges in stands with little canopy cover and with more than one forest aisle available for escape. The highly selected pines grow in open forest stands. Moreover, crowns of pines are less dense than those of spruce trees, which were avoided. Such open forest and open tree structure facilitate both detection of predators and escape flights. Due to the capercaillie's large wing span of

up to 1.2 m (Klaus et al. 1989), flights in many forest stands are restricted to aisles. Interestingly, trees with no forest aisles were used only when these trees were in stands with little canopy cover. The preference for branches pointing down-slope supports the importance of good escape possibilities.

In Scandinavia, major predators of adult capercaillie are goshawks *Accipiter gentilis* and red foxes (Wegge et al. 1987, Gjerde & Wegge 1989). In our study, neither of these predators can be an important threat for capercaillie roosting in trees at night, because foxes hunt on the ground and goshawks and large raptors such as the Golden eagle *Aquila chrysaetos* are diurnal. The nocturnal eagle owl *Bubo bubo* is rare or absent. Other studies confirm that martens are major predators of capercaillie (Schroth 1991, Kurki et al. 1997). Stone martens *Martes foina* and pine martens *M. martes* readily climb trees, are abundant in our study sites and hunt mainly during the night. Martens also travel through forests by jumping between crowns, but preferred roosting sites, such as solitary trees or pines in open stands, are usually isolated enough to prevent this means of access to capercaillie.

Predator avoidance patterns apparently change between day and night. Whereas capercaillie attempt to minimise predation risk at night by selecting open tree and forest structures, the opposite has been found in other studies for diurnal roosts. In Scandinavia, capercaillie selected daytime roosting sites on the ground underneath low branches with good cover at the expense of a good overview (Finne et al. 2000). Similar observations have been made in the Swiss Alps, where capercaillie shifted their daytime roosting sites from tree crowns in ear-

ly winter to the ground in late winter (Bollmann et al. 2005). Therefore, a good strategy for predator avoidance during the day seems to be that of hiding in dense structures with the risk of being killed once detected. At night, the best strategy to reduce predation risk seems to include early detection of predators.

Conflict between predator avoidance and energy saving strategies

In sites without pines, capercaillie cannot simultaneously fulfil the requirements of foraging, predator avoidance and energy saving by roosting in a single tree. In such sites, capercaillie must change trees. This was the case in our study sites in the Black Forest and the Swiss Jura, where capercaillie preferred deciduous trees for roosting despite the thermal disadvantages (Walsberg 1986). In the Black Forest the DTS value around used trees was more than twice as high as that for control trees. In the southern Black Forest, where pines are absent, capercaillie mainly feed on Norway spruce (Lieser 1996). Therefore, the birds must change between foraging and night roosting trees and usually between forest stands varying in tree species composition. The selection of deciduous trees as night roosts in the Black Forest can only be understood in terms of the high priority given to predator detection and escape possibilities. Forests in the Black Forest are mainly dominated by dense Norway spruce stands, and are often cultivated in plantations, thus with much canopy cover and no forest aisles or open forest structures. Deciduous trees within spruce stands are often the only sites with forest openings. Interestingly, most roosting trees were close to edges only in the Black Forest and in the Thuringia Forest, which were characterised by dense spruce stands and dense canopy cover. Furthermore, only in these forests was the canopy cover of stands surrounding roosting trees less than the cover of control trees. In the Swiss Alps and in the Swiss Jura, where the corresponding values were similar between roost and control trees, or even inverse, forests were generally more open.

Sex differences of night roost selection

In accordance with our fourth hypothesis, males preferred slightly larger trees for roosting than females. This pattern can be explained by the pronounced sex dimorphism. The larger males require larger trees with stronger branches. Males also preferred forest stands with less canopy cover. Males

with their larger wing span require more space between trees and a certain width of forest openings to fly through.

Conclusions

Night roost selection by capercaillie is part of a specific temporal and spatial habitat selection. By choosing a specific night roost, capercaillie can reduce predation risk and energy expenditure. The differences in roost sites between day and night, between northern and central Europe, and between sites with and without pines, demonstrate that capercaillie are flexible and optimise their roost sites with regard to foraging, predator avoidance and microclimate. Furthermore, the open forest structure preferred for winter night roosts agrees with the requirement that optimal summer habitats should offer forest openings with a well-developed field layer containing much bilberry *Vaccinium myrtillus* (Storch 1993a). Therefore, forest management practices that favour bilberry also favour ideal winter roosting trees with low predation risk.

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