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Habitat selection of sympatric Siberian Grouse and Hazel Grouse in natural and exploited forests of the lower Amur region

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The Siberian Grouse (*Falcipennis falcipennis*), which is endemic to the “dark-needle” taiga of the Russian Far East, is one of the least studied grouse species in the world. We examined post-breeding habitat selection of Siberian Grouse and contrasted it with that of the better examined Hazel Grouse (*Tetrastes bonasia*) in two areas near Komsomolsk na Amure, Russia. To infer species-specific preferences, we used field sampling, logistic regression, and AIC model selection, and compared late summer habitats of Siberian Grouse and Hazel Grouse in a mountain- and hilly area in the dark needle taiga. Our study is the first to explain Siberian Grouse habitat relationships with an empirical modelling approach. Results indicate proportions of coniferous/ pioneer trees forest and rejuvenation to be the most important covariates separating Siberian and Hazel Grouse observation sites in forests from both areas. Siberian Grouse tended to select sites with low proportions of pioneer trees and rejuvenation but availability of dwarf shrubs. Bunchberry (*Cornus canadensis*) appeared to be of high importance for the presence of Siberian Grouse in both regions. Hazel Grouse were common in places dominated by pioneer trees with high canopy cover, and high proportions of grass/herb cover. Hazel Grouse also occurred more often in forest sites with dense vertical layering and rejuvenation. Modern forestry, which results in increasing amounts of forests at younger successional stages, is likely to favour the Hazel Grouse at the expense of the Siberian Grouse.

1. Introduction

Boreal forest ecosystems are characterised by disturbance processes and natural dynamics that create and sustain habitat heterogeneity (Angelstam 1998, Cook *et al.* 2006, Drapeau *et al.* 2000, Niemelä 1999, Smith 2012). Owing to their specific habitat requirements and life histories, boreal forest grouse are representatives of different forest successional stages (Angelstam 2004, Swenson & Angelstam 1993). Yet, they are susceptible to human land use and forest grouse are often referred to as indicators of ecosystem health (Barnagaud *et al.* 2011, Storch 2007) and species diversity (Fischer & Storch 2001, Pakkala *et al.* 2003, Suter *et al.* 2002). Primeval boreal forests are mosaics of different successional stages that permit the coexistence of different grouse species in the same area. Sympatric occurrence of sensitive forest grouse can thus be regarded a signal for biodiversity and forests with high resilience. Therefore, knowledge about forest structure and composition in areas of sympatric occurrence of forest grouse is of great importance for forest biodiversity conservation and sustainable forestry.

Habitat selection of Black Grouse (*Tetrao tetrix*), Hazel Grouse (*Tetrastes bonasia*) and Capercaillie (*Tetrao urogallus*) have been reviewed throughout their large distribution ranges (Bergmann *et al.* 1996, Klaus *et al.* 1989, 1990, Storch 2007) and diverse Eurasian study cases address the sympatric occurrences of these grouse species (Lande *et al.* 2014, Melin *et al.* 2016, Sachot *et al.* 2003, Storaas & Wegge 1987, Swenson & Angelstam 1993, Wegge & Rolstad 2011). In North American forests, ruffed grouse (*Bonasa umbellus*) and spruce grouse (*Falcipennis canadensis*) have been studied in sympatry (Bendell & Bendell-Young 1993, Pietz & Tester 1982). However, little is known about sympatric occurrence of grouse in boreal Russia. Siberian Grouse (*Falcipennis falcipennis*) is endemic to the Russian Far East, from about 120°E to the shores of the Sea of Okhotsk and Sakhalin Island, south from the Sikhote-Alin mountains/ lower Amur region to a northern distribution limit at about 57°N (Klaus & Andreev 2003, Potapov 1985, Storch 2007). The species has apparently been extirpated from Xiao Hinggan Ling mountains in Heilongjiang, China (Storch 2007). Siberian Grouse is distributed within the vegetation type "Okhotsk taiga" or the so-called dark needle taiga with stands of Ajan spruce (*Picea ajanensis*), white bark fir (*Abies nephrolepis*), Dahurian larch (*Larix gmelina*), and occasionally Korean pine (*Pinus koraiensis*) (Hafner & Andreev 1998, Klaus *et al.* 1995, 2018, Klaus & Andreev 2003). Habitat loss, fragmentation, and deterioration due to forestry are considered main threats to Siberian Grouse (Andreev *et al.* 2001, Hafner & Andreev 1998, Potapov & Flint 1989). The species´ status in the IUCN red list is "near threatened", its population trend assumed to be decreasing (BirdLife International 2017). Alongside, habitat requirements of Siberian Grouse are not yet fully understood, also because the species uses a variety of forest types over the year. Mature spruce/fir but also old larch stands with spruce and fir in the understory and middle layer have been reported to be most important for Siberian Grouse (Andreev & Hafner 2011, Hafner & Andreev 1998, Klaus *et al.* 2018). However, functional habitat associations of Siberian Grouse have not yet been empirically tested. Mosaic cycle dynamics of dark needle versus larch taiga have been described by Klaus *et al.* (1995, 2018).

In contrast to Siberian Grouse, the Hazel Grouse has a huge Palaearctic distribution range (Bergmann *et al.* 1996, Klaus *et al.* 2003) and the species is listed as "least concern" (BirdLife International, 2016). Hazel Grouse habitats are well described and comprise of vertical and horizontal well structured forests with young successional stages, providing a sufficient amount of pioneer trees and shrubs as food resource, a diverse field layer and an adequately dense structure for cover (Åberg *et al.* 2003, Hofstetter *et al.* 2015, Ludwig & Klaus 2017, Mathys *et al.* 2006, Matysek *et al.* 2020, Swenson 1995, Swenson & Angelstam 1993).

In this study, we empirically examined the functional association between habitat resources and occurrence patterns for sympatric Siberian Grouse and Hazel Grouse at the local scale of forest plots. We used an information theoretic approach (Burnham & Anderson 2002) together with descriptive habitat associations for Siberian Grouse and published results for Hazel Grouse as a priori hypotheses to be tested in a model selection framework (multi-model inference).

We aimed 1) to empirically explain key structural parameters of post-breeding (late summer) habitat of Siberian Grouse, 2) to detect how sympatric occurrences of Siberian and Hazel Grouse are separated along environmental gradients, and 3) to describe both species´ habitats in natural mountain forests and exploited forests at lower elevations that are characterised by intensive forestry with large-scale clear-cutting.

2. Methods

2.1. Study area

We collected our data from two areas located 70 km west and 100 km northeast from the city Komsomolsk na Amure (Fig. 1). Myaochan mountain ridge (50°49’ N, 136°23’ E, 800–1.300 m a.s.l.) is a north-east extention of the “Dzhaki-Unakhta-Yakbyana” mountains, bordering left side of Amur valley near Komsomolsk, being approximately 200 km in length and 50 km in width with mountains around 1,500 m height. We performed field work right north of lake Amut, which is a shallow accumulation of a creek with the same name. To date of our field work, forests were nearly untouched. There was some minor influence only in the vicinity of the sport camp “Amut “. The nearly untouched mountain forests in this area were dominated by Ajan Spruce and Manchurian fir with admixtures of Erman´s birch (*Betula ermanii*), Siberian dwarf pine (*Pinus pumila*), and Siberian rowan (*Sorbus sibirica*)

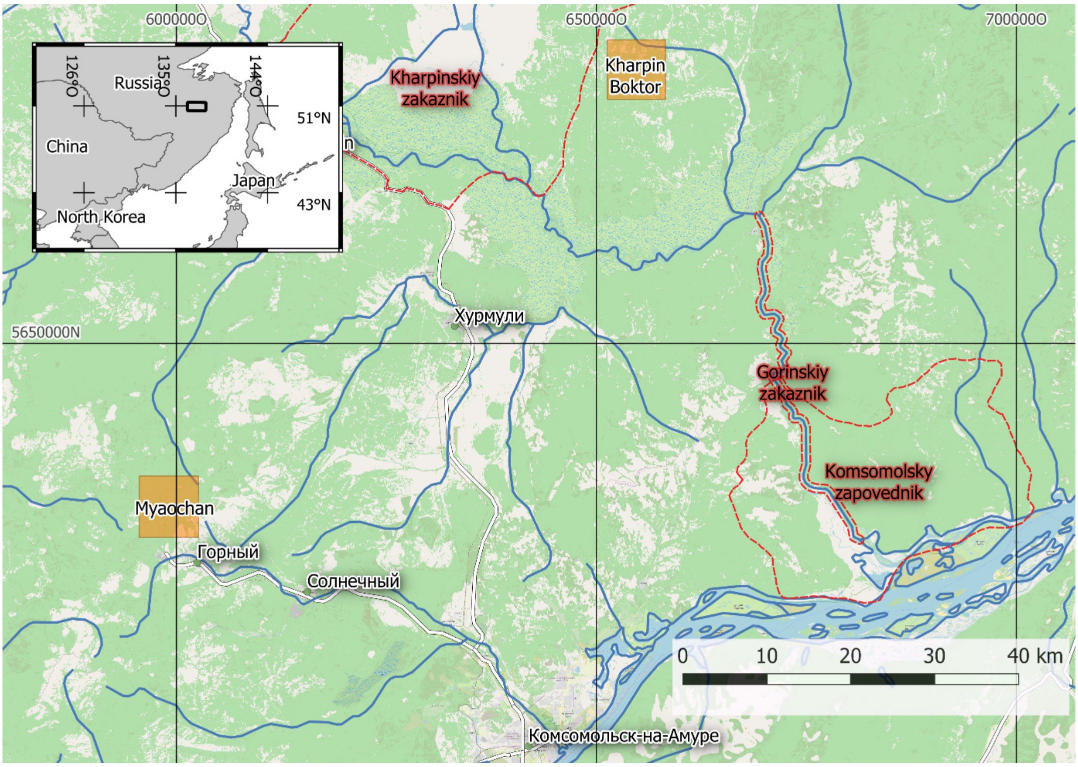

Fig. 1. Location of the two study areas “Myaochan” and “Kharpin-Boktor” in the Amur region (orange rectangles). The black box in the inset map (upper left corner) shows the position of the main map in the Russian Far East. Settlements are given in Cyrillic letters. The city Komsomolsk na Amure is located at the southern map edge. Reserves (zapovednik and zakaznik) are delineated with red broken lines. Coordinate systems are WGS84/ UTM zone 53N (EPSG:32653) for the main map and WGS84 (EPSG:43426) for the inset map. Base map: © OpenStreetMap contributors (www.openstreetmap.org/copyright). Data: WWF Amur Branch (http://amur-heilong.net/Gis_site/gis_index.html) and Global Forest Watch (Hansen *et al.*, 2013).

and high proportions of strongly dimensioned standing and downed dead wood. We found pure stands of dwarf pine at the edge of boulder fields and some hilltops. Between June and September 2019, logging activity reached the area and took timber from about 1km² coniferous forests (www.globalforestwatch.org). At a larger scale extent, intensive clear-felling occurred further westward at lower elevations.

Kharpin-Boktor (river names) interfluve (51°16’ N, 137°13’ E, 100–400 m a.s.l.) as the second study area is a hilly region characterized by old and young stands of larch, Ajan spruce and Manchurian fir or mixed stands of these species with additional presence of Manchurian birch (*Betula platyphylla*), Manchurian oak (*Quercus mongolica*), and admixtures of Korean pine, aspen (*Populus tremula*), alder (*Alnus hirsute*), maple (*Acer spec.*), willow (*Salix spec.*), and hazel (*Corylus manchurica*). Ongoing clear-cut forestry has been conducted in the interfluve since the 1970s with areas between 20 ha and several square kilometers. Therefore, the area is characterized also by larger forest patches and stands at younger successional stages.

Maple (*Acer mono*) was characteristic for both study sites (though only on northward slopes at Myaochan), as well as patchy growth of raspberry. The main differences between both areas were 1) the presence of *Vaccinium myrtilloides* at Myaochan, an important year-round food for Siberian Grouse although berries are not available every year, 2) occurrence of larch and Korean pine at Kharpin-Boktor, and 3) a wide distribution of *Rhododendron dauricum* in Kharpin-Boktor uplands. A comprehensive summary of the forest vegetation is given by Krestov (2003).

2.2. Field methods and habitat sampling

We chose late summer for our field period to maximise the indirect detection of grouse from moulting feathers and dust bathing sites. Between August 25th and September 26th in 2014 as well as from 5th to 23rd September 2015, we collected species and habitat data along Myaochan mountain ridge. From September 2014 7th to 21st, we visited the hilly area Kharpin-Boktor interfluve. In both areas, we sampled direct and indirect signs of Siberian Grouse and Hazel Grouse (feathers, faeces, dust bathes) along forest roads, ski runs (Myaochan) and off-track routes. With the field camp at their start and end, all routes were circular and layout such that we covered all cardinal directions during the available field period (Fig. 2).

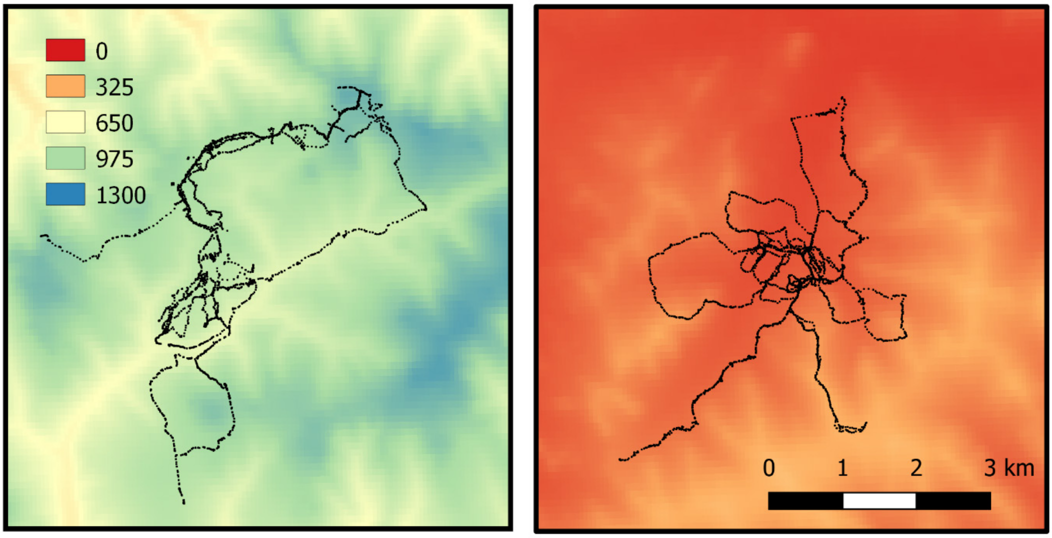

Fig. 2. Enlargements of the inset maps from Fig. 1 with GPS tracks of the mapping routes. (left: Myaochan, right: Kharpin-Boktor). The legend of the height above sea level (in meter) and the scale bar apply to both maps.

We walked 48 routes (33 in Myaochan and 15 in Kharpin-Boktor) with a total route length of 292 km (mean 6.1 km/ route). We found dust bathes and moulting feathers especially along forest road edges as well as in the roots of large, fallen trees inside the forest. Furthermore, we collected direct presence observations of Hazel Grouse by mimicking songs of territorial males with a whistle, following the method described by Swenson (1991). We also trapped Siberian Grouse with the "Dersu-Uzala method" (Arsenyev 1965), using a soft noose attached at the end of a telescopic pole (Schroeder 1986, Zwickel & Bendell 1967) and equipped these birds with necklace transmitters (different brands, 8–18 g) for daily location. The confiding behaviour of Siberian Grouse (Potapov & Flint 1989) allowed catching with comparatively little stress for the birds and less effort than in other methods. Altogether, we mapped 82 plots with Siberian Grouse presence (eight of which in Kharpin-Boktor), 54 plots with Hazel Grouse presence (Kharpin-Boktor: 6) and 11 plots with signs from both species (Kharpin-Boktor: 0). The number of random plots without a species sign was 78 (Kharpin-Boktor: 7). The proportion of direct observations was 50% for Siberian Grouse and 59% for Hazel Grouse.

For all indirect signs and direct observations as well as for additional random points at minimum distances of 200 m to other points, we measured habitat as forest and vegetation structure variables on a 20 m radius forest plot as follows. We described the tree layer with the shares of spruce/fir and pioneer trees (birch, willow, rowan) and six forest stage categories (young, thicket, pole, mature, old, mixed age). We estimated the number of vertical tree layers (1–3) as well as canopy cover as the proportion of the sky that was covered, and estimated the density of standing dead wood and downed dead wood as the proportion of stems with diameter of more than 20 cm. Further, we measured ground vegetation height, and recorded presence of forest gaps and anthills. Percent cover within the plot was estimated also for rejuvenation and to describe the ground layer vegetation: mosses (*Hylocomium, Pleurozium*), ferns (*Dryopteris, Phegopteris*), grasses and sedges (*Calamagrostis, Carex*), dwarf shrubs (*Vaccinium, Ledum, Rhododendron*), and herbs (*Maianthemum, Chamaepericlymenum, Streptopus, Huperzia*, *Smilacina, Solidago*). For a subset of Siberian Grouse sites and random plots, we separately estimated bunchberry (*Cornus canadensis,* also known as *Chamaepericlymenum canadense*) as the proportion of total herb cover. As a variable for forest density, we estimated a mean sighting distance from the position of the observer to the nearest tree vegetation cover over all cardinal directions. Details of discrete and ordinal variables are presented in Table 1. Both field mappers compared and calibrated their estimates at the beginning of the field session.

2.3. Statistical analyses

To explain and compare post-breeding habitat selection of Siberian Grouse and Hazel Grouse, we applied generalized linear models (GLM) with logit-link function and binomial error distribution (logistic regression) to our species observations (1) and random plots (0). Rather than testing many statistical models that arise from dredging potential variables in a dataset, we considered and compared a predefined set of models (Burnham *et al.* 2010) under a model-selection framework that compares different candidate hypotheses (Burnham & Anderson 2002). Following Dochtermann & Jenkins (2011), we therefore made use of previous research results combined with exploratory analyses and model simplification to generate and evaluate these hypotheses.

For each species, we first built univariate models to test linear and non-linear relationships with the response variable using second-order polynomials. Although variation in elevation along routes was low (740–1,144 m Myaochan, 119–218 m Kharpin-Boktor), we also tested this variable as well as slope and aspect as predictors in our analyses. However, we skipped these variables from further analyses because they did not contribute to either of the species´ models.

We then calibrated sets of candidate habitat models based on AIC (Akaike´s Information Criterion) to find the most parsimonious model with data from both study areas (N = 169). We added year as a covariate to account for different detection probabilities in 2014 and 2015. Anthill presence and share of bunchberry within the herbal layer were available only for a subset of

Table 1. Details of discrete candidate variables used to explain probability of Siberian- and Hazel Grouse occurrence in the two study areas. For species specific values see Table 2 and 3.

	Myaochan				Kharpin-Boktor			
Variable	N	Mean	SD	Range	N	Mean	SD	Range
Downed dead wood (% of stems)	149	14.67	10.57	0–60	21	8.95	6.71	0-30
Standing deadwood (% of stems)	149	11.92	12.1	0–90	21	2.24	4.48	0–20
Canopy cover (%)	149	68.96	11.5	30–100	21	79.29	21.17	0–95
Spruce–fir (%)	149	80.36	23.55	0–100	21	44.76	29.64	0–95
Pioneer trees (%)	149	20.76	18.14	1–93	21	23.19	23.46	1–90
Birch (%)	149	16.77	14.8	0–60	21	14	18.47	0–75
Rejuvenation (%)[a]	149	26.91	14.29	0–80	21	12.95	15.94	0–50
Vegetation height (cm)[b]	149	34.43	14.8	10–100	21	30.24	17.14	10–70
Mosses and ferns (%)	149	47.65	32.24	0–100	21	23.57	30.91	0–90
Grass cover (%)	149	39.77	18.77	0–90	21	38.57	25.16	0–90
Herbs (%)	149	23.37	15.43	0–70	21	25.71	18.39	0–70
Dwarf shrubs (%)	149	6.84	9.61	0–40	21	2.19	5.12	0–20
Bunchberry (% of herbs)	148	34.16	18.56	10–100	21	29.05	31.21	5–100
Sighting distance (m)[c]	86	34.78	28.55	0–100	20	34.25	28.25	0–70

a Minimum height 130 cm; b Maximum height 130 cm; c Mean circular distance from observer to the nearest tree vegetation cover

our data (*N* = 74). To include these variables, we therefore calibrated another set of habitat models. We checked coefficients and their signs for ecological plausibility and further improved candidate models by inclusion of non-linear relationships that have ecological meaning for the species. We ranked models based on Akaike´s Information Criterion with an adjustment for small sample size (AICc), and calculated Akaike weights (*w*). We also included an intercept only model in all logistic regression analyses, which served as a benchmark for the influence of the covariates in our statistical models. Collinearity between predictor variables was not a problem in any of our candidate models. Spearman’s ρ for all pairs of continuous variables was between –0.4 and 0.6. Additionally, we checked variance inflation factors (VIF) of each model, all of which were well below 3.

We evaluated all Siberian and Hazel Grouse habitat candidate models by means of five-fold cross-validation. The dataset was divided into five bins and the best models were run with four fifth of the data. For evaluation, we used the remaining fifth of the data to report the threshold-independent area under the receiver operating curve (ROC) and its standard deviation (SD). We also validated the models specific for Myaochan with the dataset from Kharpin-Boktor, thus testing generality of our models. The area under the ROC curve (AUC) provides a measure of whether a model’s discrimination ability is better than a random presence-absence classification (Guisan & Zimmermann 2000). Its critical value is at 0.5, when probability of occurrence from a randomly chosen presence point has only a 50% chance of being larger than that of a randomly chosen absence point. Values larger than 0.7 and > 0.8 are considered to represent good and excellent discrimination ability of the model, respectively (Hosmer & Lemeshow 2000).

Cohen’s kappa (κ) is a threshold-dependent measure of model performance that consists of actual model agreement minus the agreement expected by chance. We report κ at the optimized threshold, i.e., at the probability cut-off level that maximises the coefficient of prediction agreement. Agreement is moderate at κ-values from 0.4 to 0.55, good at κ-values from 0.55 to 0.7, very good from 0.7 to 0.85, and excellent from 0.85 to 0.99 (Monserud & Leemans 1992).

To visualize how well model predictions fit the observed data, we plotted calibration curves for the best model of each species. Therefore, we ordered the predictions and aggregated them into five equal bins with a range of 0.2. For each bin, we calculated the proportion of presence points. The location of binned proportions along the diagonal expresses the reliability of the model. The refinement or sharpness is the range of predictions along the x-axis (Pearce & Ferrier 2000).

For explanations of habitat relationships, we plotted the fitted habitat relationship for both species with the most important covariates while keeping the other predictor variables constant at their median values. We accounted for uncertainty in model explanations by bootstrapping of these species-environment effect plots. Bootstrapping selects random subsamples with replacement from the data thus yielding a dataset with the same size, but some cases selected more than once. We performed 100 bootstraps. For all statistical analyses, we used the open source statistical software RStudio version 1.2.5019 (RStudio Team 2020), with the packages Hmisc (Harrell Jr *et al.* 2020), MASS (Venables & Ripley 2002), MuMin (Barton 2013), and PresenceAbsence (Freeman & Moisen 2008).

3. Results

3.1. Study area characteristics

The means of most of our estimated field variables differed significantly between study areas and demonstrated both areas contrasting characteristics. Mean proportions of downed dead wood (14.7%) and standing deadwood (11.9%) in Myaochan were significantly higher than in Kharpin-Boktor with 8.9% downed dead wood and 2.2% standing deadwood (Table 1, Wilcoxon rank sum test $p < 0.01$ and $p < 0.001$). Mean rejuvenation cover in Myaochan with 26.9% was more than twice as high as in Kharpin-Boktor ($p < 0.001$). Similarly, proportion of coniferous trees was much higher in Myaochan (80.4%) than in Kharpin-Boktor (44.8%, $p < 0.001$) as was the proportion of mosses and ferns (47.6% vs. 23.6%, $p < 0.001$) and dwarf shrubs (6.8% vs. 2.2%, $p < 0.001$). Only canopy cover in Kharpin-Boktor with 79.3% was significantly higher than in the Myaochan (69%, Wilcoxon rank sum test $p < 0.001$), corresponding with a significant shorter sighting distance of 29 m (35 m in Myaochan, Table 1, Wilcoxon rank sum test $p < 0.05$). Another difference was a larch proportion of 26.4% in Kharpin-Baktor while this tree species was absent from Myaochan.

3.2. Habitat associations

3.2.1. Siberian Grouse

The most parsimonious models highlighted the importance of pioneer trees and rejuvenation as negative predictors of Siberian Grouse occurrence. The average proportion of pioneer trees at Siberian Grouse sites in both areas was about 12% (Table 2). Presence probability for the species dropped sharply already at low proportions and decreased by 23% for each 5% increase in pioneer trees. It was reduced by half at about 30% pioneer trees in the forest and reached zero beyond 40% pioneer trees proportion (Fig. 3). Proportion of pioneer trees was contained in models both, without bunchberry proportion and anthill presence ($N = 169$) and with their inclusion ($N = 74$). With the smaller dataset however, a model without pioneer trees proportion performed nearly as good as the best model (Table 4). Substitution of pioneer trees with proportion of coniferous trees marginally lowered the explained deviance from 30% to 28% but still resulted in good discrimination ability of the model (kappa = 0.59, Table 4). Siberian Grouse exhibited a positive response to the proportion coniferous trees (4% higher presence probability for a five percent increase, Fig. 3). Average proportions of coniferous trees around Siberian Grouse sites were 86% in Myaochan and 62% in Kharpin-Boktor. The species exhibited a similar response to increasing canopy cover, which was 74% on average. The mean proportion of rejuvenation at Siberian Grouse sites was 24% in Myaochan and 6% in Kharpin-Boktor (Table 2). Siberian Grouse clearly responded negatively to increasing rejuvenation cover (19% decrease for a 5% increase, Fig. 3).

Table 2. Siberian Grouse site characteristics in the Myaochan mountains and Kharpin-Boktor interfluve, 2014–2015.

	Myaochan				Kharpin-Boktor			
Variable	N	Mean	SD	Range	N	Mean	SD	Range
Downed dead wood (% of stems)	42	14	9.9	0–40	8	9.4	4.2	5–15
Standing deadwood (% of stems)	42	11.2	9.7	0–40	8	1.5	2.2	0–5
Canopy cover (%)	42	69.4	11.4	50–100	8	86.3	8.8	70–95
Spruce-fir (%)	42	86.2	19.4	5–100	8	61.9	20.9	40–95
Pioneer trees (%)	42	13.1	10.4	2–44	8	11.1	6.5	4–21
Birch (%)	42	11.2	9.6	1–40	8	6.9	6.9	0–20
Rejuvenation (%) [a]	42	23.9	11.6	0–60	8	6.3	6.4	0–20
Vegetation height (cm) [b]	42	33.5	14.3	15–70	8	23.8	12.8	10–45
Mosses and ferns (%)	42	41.2	30.1	0–100	8	25	28.9	0–90
Grass cover (%)	42	34.6	19.5	0–80	8	36.3	25.6	10–90
Herbs (%)	42	19.1	13	0–50	8	31.9	20	5–70
Dwarf shrubs (%)	42	9.1	9.8	0–30	8	2.5	4.6	0–10
Bunchberry (% of herbs)	19	39.1	31.7	1–100	8	55.6	14.5	25–70
Sighting distance (m) [c]	41	36	16.1	10–80	8	16.9	9.2	5–35

a Minimum height 130 cm; b Maximum height 130 cm; c Mean circular distance from observer to the nearest tree vegetation cover

The ground layer covariate dwarf shrub cover appeared in all candidate models that we calibrated with the large dataset (Table 4). The species displayed a positive response to dwarf shrub cover with optimum values between 20% and 30% cover (Fig. 3). However, the mean proportion of dwarf shrubs was low with 6.8% in Myaochan (range 0–40%) and 2.1% in Kharpin-Boktor (range 0–20%, Table 1). The mean proportion of moss and ferns was 48% in Myaochan and 24% in Kharpin Boktor. As with dwarf shrubs, Siberian grouse exhibited a unimodal relationship with that variable, showing intermediate probability of occurrence below 50% cover and decreasing occupancy above this threshold (Fig. 3). Percentage of grasses, which was on average nearly 40% in both areas, was a negative predictor of Siberian grouse occupancy only in forest openings but not in the forest interior.

Proportion of bunchberry was the most important predictor in the habitat models that we calibrated with the reduced dataset. At Siberian Grouse sites in Kharpin-Boktor, mean bunchberry proportion was considerably higher than at sites in Myaochan (55% vs. 39%). The probability of Siberian Grouse occurrence increased by almost 6% with each 5% increase in bunchberry cover (Fig. 3). In the highest-ranking model, the variable was accompanied by covariates rejuvenation cover, proportion of pioneer trees, and anthill presence. Siberian grouse occurrence probability was more than three times higher when anthills were present in a forest plot (odds ratio = 3.2). The least important variable in the Siberian Grouse models was sighting distance. The species showed moderate occurrence probabilities below 40 m sighting distance, approaching a low value (0.1) at 100 m (Fig. 3).

All Siberian Grouse models achieved mean cross-validated AUC-values above or close to 0.75 and Cohen´s kappa values between 0.42 and 0.59 (Table 4). The reliability of the best model was very good as indicated by the wide range of predictions and their close relationship with the observed proportion of occurrence points within each bin (Fig. 4).

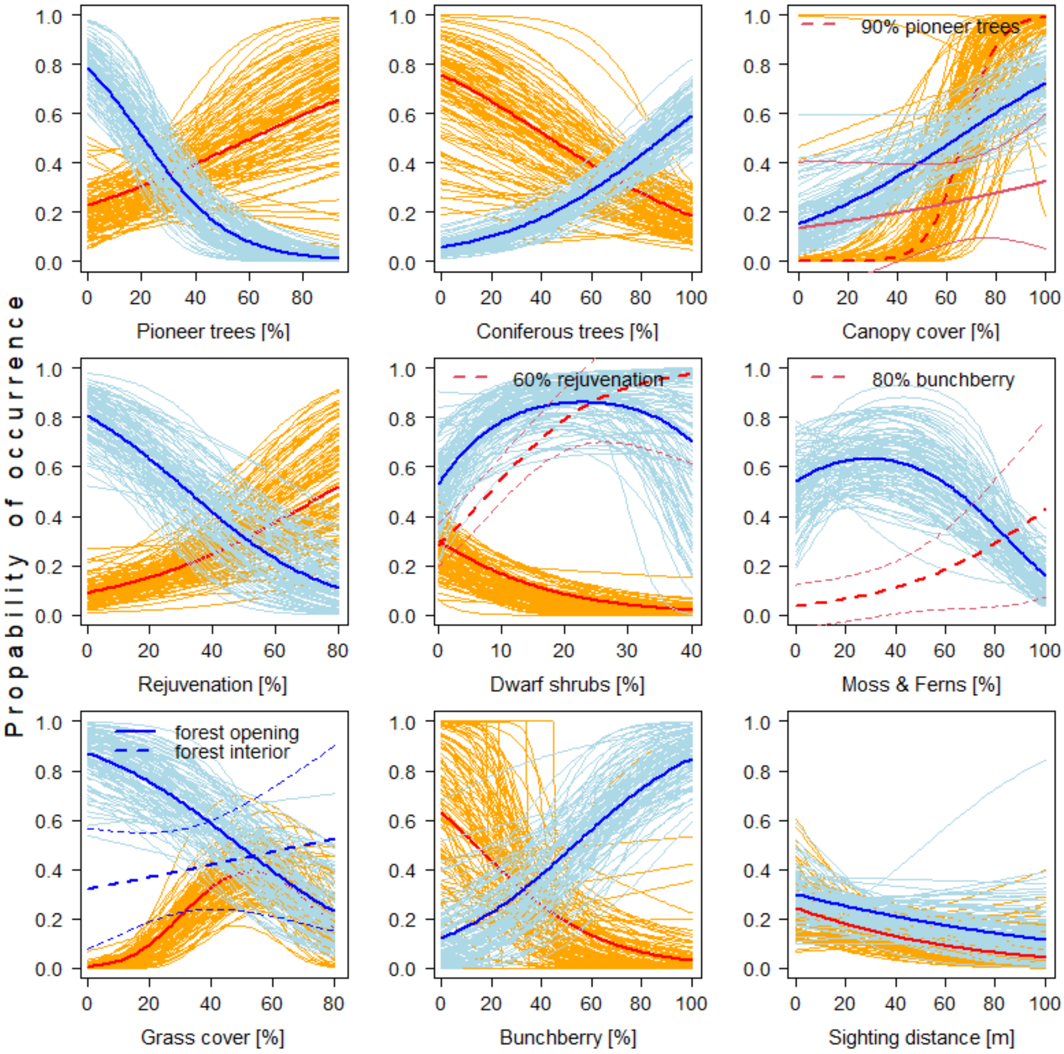

Fig. 3. Partial dependence of Siberian Grouse (light blue) and Hazel Grouse (orange) probability of occurrence on common predictor variables. Graphs were plotted with 100 bootstraps by varying the variable under consideration over the range of values observed in the field and keeping all other predictors in the model at their mean values. The average bootstrapped effects are graphed with bold blue (Siberian Grouse) and red lines (Hazel Grouse). Dashed lines (± 95% confidence limits) show how the effect changes if the interacting variable has values that deviate from the mean (legend in respective plots).

3.2.2. Hazel Grouse

Hazel Grouse occurrence in both study areas was explained by positive effects of pioneer tree proportion, canopy cover, and presence of rowan. Presence of rowan in a forest plot more than doubled Hazel Grouse occurrence probability (odds ratio = 2.2). The highest-ranking models also included grass cover as a quadratic term together with an interaction between proportion of pioneer trees and canopy cover (Table 5). Average proportions of pioneer trees at Hazel Grouse sites were 30% in Kharpin-Boktor and 75% in Myaochan (Table 3). Hazel Grouse showed a strong positive response to proportions of pioneer trees trees in a plot (17% increase for each 5%

Table 3. Hazel Grouse site characteristics in the Myaochan mountains and Kharpin-Boktor interfluve (Central Khabarovsky kray), 2014–2015.

	Myaochan				Kharpin-Boktor			
Variable	N	Mean	SD	Range	N	Mean	SD	Range
Downed dead wood	37	12.3	8.6	0–35	6	6.7	2.6	5–10
Standing deadwood	37	10.4	10.6	0–50	6	1.3	1.9	0–5
Canopy cover	37	74.3	9.2	50–90	6	80.8	15.3	60–95
Spruce–fir (%)	37	70.3	22.9	10–100	6	30.8	19.1	0–50
Pioneer trees (%)	37	30.1	19.4	2–93	6	37.2	19.1	12–60
Birch (%)	37	25.2	16.9	1–60	6	21.7	17.5	0–50
Rejuvenation (%) [a]	37	30.3	14.1	0–60	6	21.7	22.5	0–50
Vegetation height (cm) [b]	37	34.1	8.3	20–50	6	36.7	19.7	20–70
Mosses and ferns (%)	37	35.8	28.3	0–100	6	10	11	0–30
Grass cover (%)	37	44.3	12.3	30–80	6	46.7	20.7	20–70
Herbs (%)	37	27	13.4	5–50	6	29.2	13.6	15–50
Dwarf shrubs (%)	37	5.1	6.8	0–30	6	3.3	8.2	0–20
Bunchberry (% of herbs)	13	36.6	27.2	1–100	2	60	14.1	50–70
Sighting distance (m) [c]	36	27.4	11.1	10–60	6	22.5	12.6	10–45

a Minimum height 130 cm; b Maximum height 130 cm; c Mean circular distance from observer to the nearest tree vegetation cover

Table 4. Ranking of candidate models that assess the influence of vegetation characteristics on occurrence probability of Siberian Grouse during late-summer 2014 and 2015 surveys in Myaochan mountains and Kharpin-Boktor interfluve. See Table 1 for explanation of variables.

Model Description	k	AICc	ΔAIC	ω	AUC5fold(sd)	κ
(a) both study areas						
pioneer + poly(moss.fern,2) + poly(dwarf,2) + open × grass + rjv.cover	10	181.27	0.00	0.76	0.747 (0.049)	0.45
pioneer + moss.fern + dwarf + open + rjv.cover + crown + grass	8	184.65	3.38	0.14	0.756 (0.064)	0.42
pioneer + rjv.cover + year + sightdist + poly(dwarf,2)	7	185.29	4.02	0.10	0.710 (0.073)	0.43
Intercept	1	215.27	30.39	0.00		
(b) both study areas, bunchberry in dataset						
pioneer + dow_herb + rjv.cover + anthills + year	6	77.27	0.00	0.45	0.779 (0.231)	0.57
rjv.cover + dow_herb + year + anthills	5	77.92	0.65	0.33	0.790 (0.150)	0.59
sprfir + dow_herb + rjv.cover + anthills + year	6	78.67	1.40	0.22	0.779 (0.169)	0.59
Intercept	1	93.78	16.51	0.00		

k = Number of parameters; AICc = Akaikes Information Criterion corrected for small sample size; ΔAIC = Change in AICc; ω = Model weight; AUCxfold (sd) = Area under curve from five and threefold cross-validation; κ = Cohen´s kappa; AUC = Area under curve

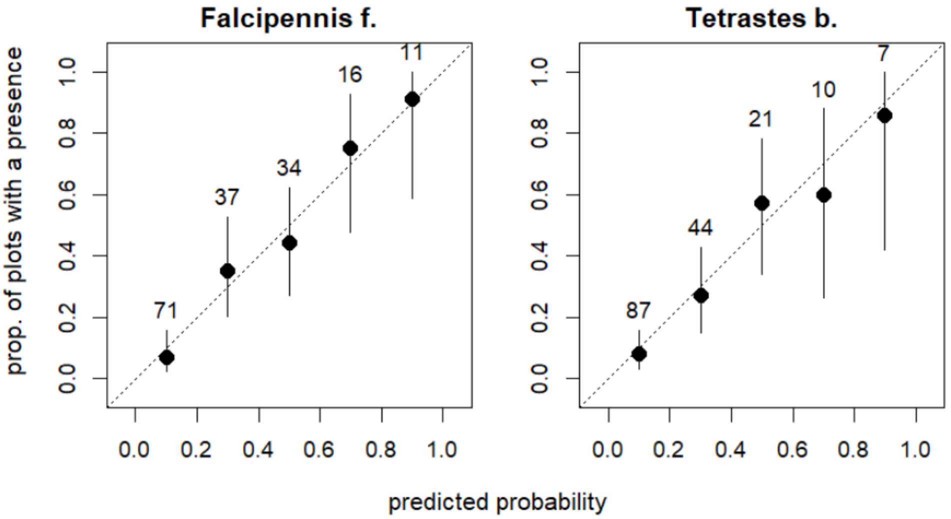

Fig. 4. Calibration plots of generalized linear models for Siberian Grouse (left) and Hazel Grouse (right). Observed occurrences as proportion of plots surveyed are close to the ideal slope represented by the dotted diagonal. Vertical lines represent confidence intervals for a binomial distribution. Figures above the points give the number of cases in each bin.

increase in pioneer trees, Fig. 3) that was related to canopy cover. Likewise, the probability of Hazel Grouse occurrence increased linearly with canopy cover (Fig. 3), which was on average, 74% at Hazel Grouse sites in Myaochan and 84% in Kharpin-Boktor (Table 3). However, a clear threshold starting from 60–70% canopy cover was only visible at a high proportion of pioneer trees (Fig. 3). Occurrence probability of Hazel Grouse also increased by 12% for each 5% increase in rejuvenation cover. The average of this variable was 30% at Hazel Grouse sites in, Myaochan and 15% in Kharpin-Boktor.

Compared to other predictors, dwarf shrub cover was less important in the Hazel Grouse models, but probability of occurrence increased sharply with this variable at high proportions of rejuvenation (Fig. 3). The mean proportion of dwarf shrub cover at Hazel Grouse sites was low in both areas (Table 1) but reached maximum values of 40% in some forest plots. Mosses and ferns were positive predictors of Hazel Grouse occurrence only when bunchberry proportion was high. The uni-modal relationship with proportion of grass cover in the best models had a maximum probability of Hazel Grouse occurrence between 50% and 60% grass cover.

Positive effects of forest and vegetation structure were accompanied by a negative association with forest transparency such that Hazel Grouse probability of occurrence decreased with increasing sighting distance.

All candidate models of Hazel Grouse habitat explained around 25% of the deviance in the data and achieved Cohen´s kappa values between 0.39 and 0.47 (Table 5). Five-fold cross-validation of the candidate models revealed good discrimination abilities of AUC close to 0.80. The wide range of predictions and their close relationship with the observed proportion of occurrence points within each bin indicated a good model reliability (Fig. 4).

4. Discussion

Our results provide empirical explanations for the response of Siberian Grouse to key structural parameters in its post-breeding (late summer) habitat. They furthermore offer details on how Siberian and Hazel Grouse succeed to coexist in natural mountain forests and exploited forests at lower elevations in a central part of the Amurland dark-needle taiga. The evaluation of the models resulted in good discrimination as revealed by

Table 5. Ranking of candidate models that assess the influence of vegetation characteristics on occurrence probability of Hazel Grouse during late-summer 2014 and 2015 surveys in Myaochan mountains and Kharpin-Boktor interfluve. See Table 1 for explanation of variables and footnote to Table 4 for abbreviations.

Model Description	k	AICc	ΔAIC	ω	AUC 5fold (sd)	κ
rowan + canopy × pioneer + sprfir + poly(grass,2)	8	158.06	0.00	0.85	0.828 (0.076)	0.47
pioneer + poly(canopy,2) + poly(grass,2) + rjv.cover + sightdist	8	162.28	4.22	0.10	0.786 (0.092)	0.46
year + rowan + canopy + sprfir + rjv.cover + grass + herbs	8	164.78	6.72	0.03	0.809 (0.049)	0.42
pioneer + canopy + rjv.cover + poly(grass,2)	6	166.33	8.27	0.01	0.805 (0.083)	0.45
pioneer + rowan + canopy + moss.fern	5	167.46	9.40	0.01	0.777 (0.021)	0.39
Intercept	1	193.72	35.66	0.00		

AUC values and calibration plots. Our models indicate as well that the post-breeding habitat relationships found for Siberian Grouse and Hazel Grouse in the mountain area Myaochan also correctly depict the occurrence of both species in the hilly area Kharpin-Boktor. Although we had only a limited amount of testing data, validation results demonstrate the generality and spatial transferability of our models.

4.1. Siberian Grouse habitat

Mature spruce/fir stands, and old larch stands with spruce/fir in the middle layer have been reported as the main habitat types for Siberian Grouse (Andreev & Hafner 2011, Biserov 2011, Hafner & Andreev 1998, Klaus *et al.* 1995, 2018, Klaus & Andreev 2003, Nechaev 1998). Here, we confirmed this notion but also quantified how increasing amounts of pioneer trees in the forest negatively affect Siberian Grouse. Our findings therefore support the opinion that Siberian Grouse is a good indicator species for virgin and mature coniferous forests in the Amurland dark-needle taiga (Klaus *et al.* 2018). These forests seem to be particularly suitable when canopy cover is high as reflected by the positive response of the species to this variable and the moderate negative response to increasing stand transparency or sighting distance. This is in line with results from Canada where the density of the Spruce grouse populations was reported to be proportional to cover density (Huggard 2003). However, our results also suggest that dense understory negatively affects Siberian Grouse habitat because occurrence probability of the species was low at rejuvenation proportions beyond 30%. Gap structures in old forests seem to improve habitat quality for Siberian grouse, a pattern that was also observed in spruce grouse habitats in North America (Aldrich 1963, Lumsden 1961). Small openings in the forest allow for accumulation of snow for snow burrows (Andreev 1990, Andreev & Hafner 2011) but play also an important role during Siberian grouse display and chick rearing (Andreev *et al.* 2001, Hafner & Andreev 1998, Möllers *et al.* 1995).

Replacement of pioneer trees with spruce/fir cover as a variable resulted in Siberian Grouse models with less explanative power. Nevertheless, a positive response of Siberian Grouse to increasing proportions of spruce/fir stands was clearly visible. In the Republic of Sakha, Siberian grouse was associated with dense spruce forests in spring and summer (Isaev 2011). Mature spruce forests with diverse horizontal structuring are preferred also during winter (Andreev 1990). Likewise, North American Spruce grouse tended to select stands where proportions of spruce in both, the canopy layer and understory were higher than average (Robinson 1969). The observation that in our study the proportion of pioneer trees was a better predictor than the amount of spruce and fir suggested that the former restricts Siberian

Grouse habitat at the local scale while conifers are abundant both, locally and at the landscape level, and are thus not limiting. Correspondingly, sampling at relative small-scale extents reduces the probability to find expected habitat associations (Åberg *et al.* 2000). In other words, the expected positive response of Siberian Grouse to increasing proportions of coniferous trees in a forest plot was less evident, probably because we sampled most of our data in suitable mountain habitat, dominated by conifers.For the foothills of Kharpin-Boktor, Hafner and Andreev (1998) reported a minimum spruce proportion of 2–5% on a larch-spruce forest plot to be necessary for Siberian Grouse presence in winter. They observed similar proportions on birch-spruce forest plots with Siberian Grouse presence in Bureinsky reserve, about 150 km northwest from Myaochan.Overall, we found higher proportions of spruce and fir at Siberian Grouse sites in both study areas (Table 2). Our results suggest that for a Siberian Grouse population to sustain, such minimum conifer proportions in a forest plot require the presence of spruce dominated stands at a larger scale extent. Siberian Grouse probability of occurrence was very low beyond 60% pioneer trees and up to 40% coniferous tree proportion (Fig. 3). Mean proportions of coniferous trees in Myaochan and Kharpin-Boktor were 80% and 70% (44% spruce/fir, 26% larch), while pioneer trees proportions were 21% and 23%, respectively (Table 1). Disregarding clear-felling areas at the landscape scale, both areas thus locally met the requirements of Siberian Grouse. We hypothesise that mountain habitats in the Amurland dark-needle taiga likely provide core habitats while mixed forests or forest regeneration after clear-cutting at lower elevations sustain much lower densities of Siberian Grouse (0.13 Siberian Grouse/km in 2014) and may be regarded sink habitats. This must be further investigated in the future. Natural source-sink habitat patch conditions arise in other parts of the Siberian Grouse range such as in Yakutia (Isaev 2011) were hills, covered with spruce and fir are immersed in vast lowland extents of Siberian larch (*Larix sibirca*). For the Bikin river basin (Primorye region), high densities of 4–6 birds per kilometre route have been reported (Pukinskij 2014).

Regarding the ground layer, our models revealed the species preference of sites with high bunchberry proportion in both study areas, the plant being reported as important food source in summer (Hafner & Andreev 1998). Likewise, dwarf shrubs were important habitat components, also representing a food source in late summer and throughout the year (Hafner & Andreev 1998, Potapov & Flint 1989). The unimodal relationship of Siberian Grouse with that variable may be since detection decreased with increasing dwarf shrub cover. However, we found a unimodal response of Siberian Grouse also with moss/fern cover. This suggests that low to intermediate proportions of these habitat components suffice and that a mosaic of various plant species is more important than the dominance of a single component in the ground layer, which was also found for Spruce grouse in North America (Robinson 1969). We suggest that moss and fern cover should be separately estimated in future studies of Siberian grouse small-scale habitat requirements.

Interestingly, Siberian Grouse responded differently to increasing grass cover depending on whether a mapping point was in the interior or at the edge of the forest. Forest edge was mainly shaped through little-used tracks. We found Siberian Grouse on these tracks especially after rain to dry out but also for grit uptake. We also found dust-baths, drinking pools, roosting and display sites. These have been reported to be important structures along undisturbed forest-tracks for other grouse species elsewhere (Klaus & Bergmann 2020, Moss *et al.* 2014). Therefore, a high grass cover on gravel roads seems detrimental to certain behaviours but is probably important in the interior of the forest because of its protective cover effect.

4.2. Sympatric occurrence

Our second goal was to uncover how Siberian and Hazel Grouse are separated along environmental gradients. The effect plots clearly indicated that both species responded differently to patterns in the tree layer. As we found positive responses of Hazel Grouse to pioneer trees and rejuvenation, our results suggest that the niches of sympatric Siberian and Hazel Grouse are separated chiefly along these gradients. Remarkably, both species positively responded to increasing canopy cover in the dark-needle taiga. However, the response of Hazel Grouse was mediated by the proportion of pioneer trees such that very high proportions of deciduous trees resulted in a clear threshold at 70% canopy cover. This is in line with Hazel Grouse habitat characteristics in Finland, where canopy cover was a positive predictor of brood occurrence while canopy height was a negative predictor (Melin *et al.* 2016). Although we did not measure canopy height, the negative response of Hazel Grouse to increasing proportions of coniferous trees suggests similar patterns because forest height in the dark-needle taiga is determined primarily by mature coniferous trees. The high cover requirement of the Hazel Grouse is also met by good shrub cover or number of forest layers (Melin *et al.* 2016, Rhim *et al.* 2015). Forests with a vertically diverse and rich understorey represent dense stand structures and are often described as preferred by Hazel Grouse (Bergmann *et al.* 1996, Koch 1978, Mathys *et al.* 2006, Matysek *et al.* 2020, Müller *et al.* 2009b), providing the particularly needed coverage (Swenson 1995). Sighting distance as an alternative variable for stand density has hardly been recorded in grouse studies so far. In the Bohemian Forest, Ludwig & Klaus (2017) found that forest plots with short sighting distances up to 20 m had the highest probabilities of Hazel Grouse presence. This result coincided with what we found in this study. However, among all variables, sighting distance was less important in explaining Hazel Grouse and Siberian Grouse occurrence. This might be because structured stands and thus good cover are common in forests of the Russian Far East.

For Siberian Grouse, stand density appeared to be less of a priority as shown by the responses of the species to rejuvenation, which was different from those of the Hazel Grouse. Striking however, was the strong negative response of Siberian Grouse to increasing proportions of pioneer trees. In European studies, pioneer trees was shown to be an important winter food and crucial habitat element for the Hazel Grouse (Bergmann *et al.* 1996, Klaus 1996, Matysek *et al.* 2019, Müller *et al.* 2009a, Salo 1971, Schäublin & Bollmann 2011, Swenson 1993). Also, in South Korea, Hazel Grouse prefers forests rich in pioneer trees (Rhim 2013). Winter diet of the species in the Russian Far East depends on birch, willow, and alder in most of the areas (Potapov & Flint 1989). The preferred species of pioneer trees can vary between regions, but European Hazel Grouse often show a bond to rowan *Sorbus spec.*, especially in mountain habitats (Müller *et al.* 2009b, Schäublin & Bollmann 2011, Zellweger *et al.* 2014). As rowan berries are a well-known food source in late summer and autumn (Zbinden 1979), it may explain that rowan appeared in most of our habitat models for Hazel Grouse. We did not find such a response for Siberian Grouse. However, we documented one Siberian Grouse cock feeding on rowan berries during one occasion in 2014. Siberian rowan thus appears to be one of several alternative diets for Siberian Grouse.

Habitat segregation between both species was apparent also by responses to different ground vegetation characteristics. Bunchberry and dwarf shrub cover were important for the Siberian grouse but not for Hazel grouse, in our models. Similarly, presence of anthills was an important predictor in Siberian grouse models only. In some European studies, presence of anthills influenced occurrence of Hazel Grouse positively, which may reflect edge effects and small openings within dense forests, which in turn were preferred by the species (Ludwig & Klaus 2017, Müller *et al.* 2009b, Swenson 1995, Wiesner *et al.* 1977). Perhaps a generally higher number of anthills in the Amurland taiga forests was the reason why we did not find a connection with the hazel grouse. Alternatively, anthills were often found in structures that were too open, which the hazel grouse tended to avoid.

Habitat preferences of the two species were similar when it comes to the presence of large forests landscapes with low human density and disturbance. In geographical space, Siberian Grouse and Hazel Grouse habitat separation was less noticeable than it is for forest grouse communities in European managed forests where habitats are characterized by stands of contrasting age classes (Swenson & Angelstam 1993). Habitat separation in our study areas occurred along forest roads and a natural within forest patchiness. In environmental space, the age of the forest was not as important for the species as were variables of forest composition and structure like proportion of pioneer trees, rejuvenation, and canopy cover. Structural elements like coarse woody debris, canopy gaps, downed and standing deadwood were abundant throughout our two study areas, which is why they did not appear in our habitat models.

4.3. Comparison of habitats from both areas

According to Hafner & Andreev (1998) and Andreev & Hafner (2011), Siberian Grouse can cope with different forest compositions like mature spruce/fir stands with single larch trees, old larch and larch-birch stands with spruce/fir in the middle layer, old larch stands with spruce, birch, and alder, as well as larch-*Ledum* forest. Spruce trees thus seem to be an important habitat requisite both, as a food resource in winter and as a structural component. Especially in larch dominated forests like in Kharpin-Boktor (mean larch proportion = 26%), the importance of Ajan spruce becomes evident.

Siberian Grouse feed upon dwarf shrub berries in late-summer and autumn (Hafner & Andreev 1998). A main difference between Myaochan and Kharpin-Boktor was the presence of *Vaccinium myrtilloides* at Myaochan. This plant with its stems, fruits, leaves, and buds is an important food for Siberian Grouse (Potapov & Sale 2013) even though berries are not annually available. Another major preference is that of raspberry bushes in forest gaps with downed spruce logs, where the species' broods tended to spend much of the days in September during our fieldwork sessions. Important in this respect is a result of Hafner and Andreev (1998) that highest densities of Siberian Grouse in summer occurred in dying spruce-fir forest with dense undergrowth of raspberry and wild rose. Even pure larch stands may suffice if woody shrubs are available. A forest management that simulates natural conditions of small forest openings may thus support Siberian Grouse. Adaptability of the species should be investigated further under that viewpoint.

Another evident feature of Siberian Grouse habitat models for Myaochan was lower presence of anthills in Kharpin-Boktor (mean occupancy = 0.14) compared to Myochan (mean occupancy = 0.56). Our models revealed the importance of anthill presence and thus highlight the greater habitat potential of Myaochan for Siberian Grouse. According to our observations, Siberian Grouse selected mature to old spruce forests in Myaochan that were interspersed with forest gaps. In Kharpin-Boktor, we found the species in mature larch-spruce forests as well as in pure 30-year-old larch stands. Average proportions of coniferous forest around Siberian Grouse sites were larger in Myaochan than in Kharpin-Boktor. In contrast, availability of pioneer trees for Hazel Grouse was much lower in Myaochan than in Kharpin-Boktor. In the latter study area, also multi-layered stands had a lower proportion. These patterns make areas at lower elevations more suitable for the Hazel Grouse and probably create a fragmentation pattern for Siberian Grouse, which is less adapted to forest of young age and high proportions of deciduous trees. Apart from the presence of anthills and dwarf shrub cover, ground layer vegetation in Kharpin-Boktor was suitable because it comprised high proportions of bunchberry. The plant was about equally available in both study areas, but its proportion was considerably higher at Siberian Grouse sites in Kharpin-Boktor. These figures highlight the importance of bunchberry for Siberian Grouse especially at lower elevations where dwarf shrubs are less abundant.

Observations from Kharpin-Boktor (Hafner & Andreev 1998) proposed that the Siberian Grouse performs seasonal movements between larch- (summer) and spruce dominated forests (autumn/winter). An interesting feature therefore was the absence of larch within the direct environments around the Myaochan study area where Siberian Grouse were abundant in September. Larch was more common only about 2.5 km away. This observation suggests that Siberian Grouse can cope without larch at least during the late breeding season. Further investigations in mountain forests in summer will clarify the role of larch for that species.

4.4. Conservation implications

In the Far East of Russia, large-scale clear-cutting threatens the Amurland dark-needle taiga (Vandergert & Newell 2003) and thus also fragments and deteriorates Siberian Grouse habitat, characterised by dense dark-coniferous stands of Ajan spruce and high proportions of deadwood and downed dead wood (Andreev &

Hafner 2011). Timber harvest by clear-felling not only leads to direct habitat loss and fragmentation but also interrupts and changes the natural succession cycle (Klaus *et al.* 1995, 2018, Krestov 2003) over large areas. Our models emphasised the strong relationship between Siberian Grouse and coniferous forests, which are dominated by Ajan spruce and Manchurian fir. They suggested that clear-cutting of coniferous old-growth forests with subsequent young successional stages and an increase in pioneer tree species like birch, willow and larch will result in habitat loss for endemic Siberian Grouse, while Hazel Grouse is likely to benefit. Increasing densities of Hazel Grouse may attract predators, which will then switch to other prey species (Andreev 1990). This functional response in the Russian Far East is likely to pose another potential threat to Siberian Grouse populations. While clear-cutting is most likely to result in regional declines of Siberian Grouse populations, adaptive forest management may be a chance for long-term survival of the species and for a mitigation of fragmentation effects. Possible management scenarios are small-scale felling to simulate forest openings, as well as selective felling within parts of the forest while neighboured forest patches staying untouched. Large-scale clear-cutting of several ten to hundred hectares must be avoided.

Nevertheless, adaptability of grouse species must be considered as well. For example, Capercaillie in Norway were found to breed in middle-aged plantations (Wegge & Rolstad 2011) though they were initially assumed to be negatively affected by commercial forestry that fragmented old forests. Likewise, Siberian Grouse most probably is not an old forest obligate but capable to use younger forest stages as long as the landscape context comprises both, old and middle-aged forest stands, and local vegetation patterns that provide food and meet the species cover requirements. Long-term studies on Siberian Grouse population dynamics are therefore necessary, and to further disentangle both, the species' small-scale habitat requirements and responses to large-scale timber harvest. Due to the vastness and remoteness of the Russian Far East, remote sensing provides an important means to address this issue (Gottschalk *et al.* 2005, Wang *et al.* 2010). It may also help to clarify the range-wide status of the species indirectly (Ludwig & Konovalenko 2012) through an assessment of potentially available habitat, since a reassessment of the species threat category according to IUCN guidelines seems to be warranted (Storch 2007).

Amurinpyyn ja pyyn elinympäristövaatimukset luonnon- ja hoitometsissä Venäjällä

Amurinpyy on kotoperäinen laji Venäjän itäosien taigalla, ja yksi maailman vähiten tunnetuista kanalinnuista. Tutkimme amurinpyyn elinympäristön valintaa itäisellä Venäjällä kahdella alueella, ja vertasimme tuloksia sympatrisesti esiintyvän pyyn elinympäristövaatimuksiin. Keräsimme maastoaineistoa taigalta pesinnän jälkeen ja analysoimme aineistoa mm. AIC-menetelmin. Havupuiden ja nuoren metsän suhteet selittivät eroja kahden pyylajin esiintymisessä. Amurinpyy vältteli nuorta metsää ja suosi alueita, joissa oli matalaa aluskasvillisuutta. Amurinpyitä havaittiin erityisesti alueilla, joissa kasvoi kanadanruohokannukkaa. Pyitä esiintyi paljon nuorissa metsissä ja alueilla, joilla oli heinää tai runsaasti muuta aluskasvillisuutta. Nykyaikainen metsätalous, joka tuottaa paljon nuoria metsiä, todennäköisesti suosii pyytä amurinpyyn kustannuksella.

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