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Habitat selection and foraging site fidelity in Caspian Terns (*Hydroprogne caspia*) breeding in the Baltic Sea

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Habitat preferences and foraging strategies affect population-level space use and are therefore crucial to understanding population change and implementing spatial conservation and management actions. We investigated the breeding season habitat preference and foraging site fidelity of the under-studied and threatened, Baltic Sea population of Caspian Terns (*Hydroprogne caspia*). Using GPS devices, we tracked 20 adult individuals at two breeding colonies, in Sweden and Finland, from late incubation through chick-rearing. Analyzing foraging movements during this period, we describe trip characteristics for each colony, daily metrics of effort, habitat use, and foraging site fidelity. We found that daily time spent away from the colony increased throughout the season, with colony-level differences in terms of distance travelled per day. In general, terns selected shallow waters between 0–5 meters in depth with certain individuals using inland lakes for foraging. We show, for the first time, that individual Caspian Terns are faithful to foraging sites throughout the breeding season, and that individuals are highly repeatable in their strategies regarding foraging site fidelity. These results fill important knowledge gaps for this at-risk population, and extend our general knowledge of the breeding season foraging ecology of this widespread species.

1. Introduction

Foraging ecology is central to animal biology, influencing individual fitness and shaping the spatial distributions of animal populations (Norberg, 1977; Olsson & Bolin, 2014). During the breeding season, the foraging ecology of colonial birds is constrained by the responsibility of raising young at a fixed location and potential competition for prey (Ricklefs, 1990). Studying the movement patterns of breeding adults can reveal what subset of the surrounding landscape is available to them for foraging and the strategies used to meet the demands of rearing chicks in a competitive context (Wakefield *et al.*, 2009). Habitat preferences and foraging strategies affect population-level space use and are therefore crucial to understanding broader population change and implementing effective area-based conservation and management action (Donazar *et al.*, 1993).

The foraging ecology of seabirds often varies across populations, reflecting potential differences in biotic and abiotic processes (Torres *et al.*, 2015). Caspian Terns (*Hydroprogne caspia*) occur in freshwater and marine coastal ecosystems around the world and despite this wide range, their populations are often disjunct (Craig & Larson, 2017). While there are a number of studies concerning the foraging ecology of Caspian Terns (e.g., Dunlop & McNeill, 2017; Lyons *et al.*, 2005; Sirdevan & Quinn, 1997), there remains a dearth of information on many populations, including the Baltic Sea where the species underwent a serious decline in the 1970s and is conservation-listed in the region (HELCOM Red List Bird Expert Group, 2013). Caspian Terns are considered generalist piscivores, however they are not habitat generalists and are often described as preferring ‘shallow water’ (Koli & Soikkeli, 1974; Lyons *et al.*, 2005). Previous work in the Columbia River estuary in the US showed that certain habitats there, such as ocean jetties and the main river channel, are selected and avoided, respectively (Lyons *et al.*, 2007). This suggests that Caspian Terns indeed prefer shallower water for foraging (Dunlop & McNeill, 2017), however what range of water depths are utilized relative to their availability and how individuals may vary in their habitat use remains unclear.

The energetic demands associated with nesting change across the breeding season, from incubation to chick-rearing, and as chicks grow (Humphreys *et al.*, 2006). Previous work on Caspian Terns identified limited differences between breeding stages in terms of foraging trip characteristics like maximum distance travelled and trip duration (Anderson *et al.*, 2007), suggesting minimal changes in foraging effort throughout breeding. However, foraging effort may not be fully captured by these per trip metrics, as Caspian Terns take multiple trips per day. To better understand how movements related to foraging effort vary across the breeding season, per day metrics of time spent and distance travelled on foraging trips should also be investigated.

When resources are patchy yet predictable in space, individuals may use prior knowledge of sites containing prey to increase foraging success and reduce competition (Weimerskirch, 2007). Termed ‘individual foraging site fidelity’, this phenomenon can arise through different mechanisms, including habitat or prey specialization, and through avoidance or active exclusion of conspecifics (i.e. territoriality) (Piper, 2011; Wakefield *et al.*, 2015). Whether populations show foraging site fidelity is relevant to conservation and management, as the persistence of site use may indicate the efficacy of site-based management strategies (e.g. protected area establishment; Augé *et al.*, 2018). Although foraging site fidelity depends on spatio-temporal prey dynamics, gathering direct information on prey fields remains a challenge, especially in aquatic systems (Birt *et al.*, 1987). In recent years, individual-based tracking data has been used to infer foraging site fidelity in an increasing number of seabird species (Ceia *et al.*, 2014; Irons, 1998; Wakefield *et al.*, 2015). While foraging site fidelity has been described in a number of other larid species (Irons, 1998; Nisbet, 1983), only anecdotal evidence exists to suggest that Caspian Terns re-visit foraging sites during breeding (McNicholl, 1990).

We use GPS-tracking data collected during the breeding period from two colonies of Caspian Terns in the Baltic Sea to investigate the foraging ecology of this under-studied population. First, we describe the foraging trip characteristics of each colony to provide general reference points for comparison with other colonies of this widespread species. Then, we test whether breeding Caspian Terns change their foraging effort as nesting progresses, by modelling the daily time spent on foraging trips and total distance travelled per day. Next, we quantify the habitat use of terns from each colony, to describe the range of seawater depths they use on foraging trips as well as the degree to which they utilize freshwater lakes for foraging. We then test whether terns may show foraging site fidelity during breeding by comparing the spatial overlap of weekly home ranges to that of a null distribution produced under the assumption that individuals do not re-visit sites more than expected at random. Finally, we examine whether the rate of foraging site re-visitation changes predictably across the weeks of nesting and whether individual terns are repeatable (i.e., consistently differ) in the degree of site fidelity shown between weeks.

2. Material and methods

2.1. Study sites and device deployment

We studied two breeding colonies located in the Gulf of Bothnia in the Baltic Sea, on the islands of Norra Stenarna (hereafter 'Stenarna'), in Sweden (60.63°N, 17.92°E), and Gubbstenen, in Finland (62.50°N, 21.10°E) (Fig. 1). The colony on Stenarna is one of the largest in the Baltic, with 110 pairs breeding there during the study periods in 2013 and 2014 and the colony on Gubbstenen hosted 78 breeding pairs during work there in 2016.

At Stenarna, 7 birds were fitted with 7.5 g University of Amsterdam Bird Tracking System GPS-Loggers (model: 2CDSe; Bouten *et al.*, 2013) in 2013 and 2014, respectively. At Gubbstenen, one bird was fitted with a 7 g Ecotone Telemetry Sterna UHF GPS-logger in 2015, and 5 birds with 13 g Ecotone Telemetry UHF GPS-loggers (model: Harrier-L) in 2016. The tracking devices relay information to a remote base station, one of which was placed at the center of each colony to receive data when the birds approached the island. The individual from 2015 continued transmitting data through the 2016 breeding season, with only data from the latter year being analyzed in the present study. All 20 birds captured were breeding adults captured at the nest using either walk-in cage traps with a trip wire-release door, or spring net traps with a trip wire that releases the spring and folds the net over the nest; all loggers constituted < 3% of the body weight of tagged individuals (see Supplementary

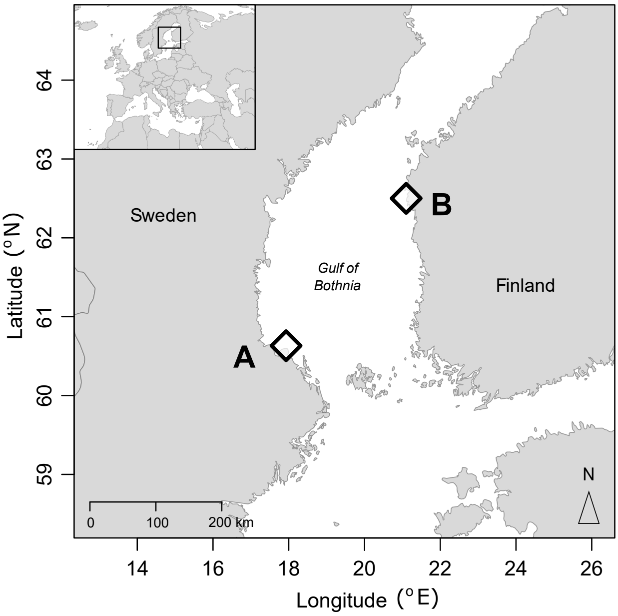

Fig. 1. Location of Caspian Tern breeding colonies in the Gulf of Bothnia of the Baltic Sea. (A) Colony in Sweden on the island of Norra Stenarna, (B) and colony on Gubbstenen in Finland.

Methods for further discussion of device effects). In 2013 and 2014, loggers were attached using the wing-harness method and in 2016 loggers were fitted using the leg-loop method (Thaxter *et al.*, 2014). Teflon ribbon (2013, 2014, 2016) was used to fasten the loggers, and was sewn together using nylon string and glued at the ends using Loctite 406(c) cyanoacrylate glue. The ringing of Caspian Terns in Sweden was performed under Ringmärkningscentralen permit number 710 (to Lennart Söderlund) and tagging under ethical permit from Malmö-Lunds Djurförsöksetiska Nämnd (M470-12, M72/15). Tagging and handling was in accordance with relevant permits as issued by Finnish authorities (ringing permit: 2604; GPS-harnessing permit: VARELY/115/2015).

2.2. Data processing

2.2.1. Nest-phase demarcation

The duration of tracking data for each individual was variable (max: 3 years, min: 2 weeks). To improve comparability among the year-samples from each colony, data were filtered to the years with at least six simultaneously-transmitting devices. Since direct observations of nest-phase progression were unavailable for the tagged birds, tracking data was filtered to the period deemed as best representing active nesting (i.e. incubation, brooding, chick-rearing) based on population breeding phenology information and individual mapping of each track. For all but one bird (ID: SER06), the tracking period began with logger attachment during late incubation. For individual SER06, pre-nesting data was clipped by removing data prior to and including the last absence from the colony of greater than 24 h; an additional 7 days after this final absence were also removed, with the assumption that egg-laying does not occur directly upon arrival (Ludwigs & Becker, 2002).

To identify the end of the nesting period for each individual two different methods were used: for several individuals breeding at Stenarna (ID: 2026, 2027, 2031, 2032, 2033, 2061, 2073, 2086) nest observations from a remote camera were used to identify the date at which the nest failed, or the young fledged. Birds 2027, 2032, and 2033 had their nests predated by a White-tailed Eagle (*Halieatus albicilla*) several days after logger attachment and since all three individuals re-nested, the tracking data from the second nest attempt were analyzed herein. For the remaining individuals, a colony absence of > 24 h was considered a failed or fledged nest. In addition, tracking data beyond the median reported nesting duration (i.e. egg-laying to fledging) for Caspian Terns of 60 days (Barlow & Dowding, 2002) were also excluded. Direct observation of nesting for tracked birds was not practically possible which restricted our ability to attribute tracking data to specific nest phases (e.g., incubation to chick-rearing).

2.2.2. Time interval standardization & trip calculation

Due to differences in the experimental set-up between colony datasets, the time interval at which locations were sampled was heterogeneous. To approximate a standard interval, the data were down-sampled to the lowest common interval of 30 min using custom R code. To calculate general movement characteristics, data were segmented into discrete foraging trips for each individual, and colony-level averages calculated for each characteristic. A trip was considered a period of greater than 40 min spent beyond a 1 km colony buffer.

2.2.3. Geodata and habitat classification

To investigate the habitat selectivity of nesting Caspian Terns, the aquatic environment surrounding each colony was classified into different types. Seawater was separated into depth intervals (0–5, 5–10, 10–20, 20–30, 30–40, > 40 m), and since all freshwater bodies in these regions fall within 0-5 m in depth, a separate category (Inland) was used to distinguish their use.

For the Stenarna colony, bathymetric data at 500 m horizontal resolution was downloaded from the Baltic Sea Bathymetry Database (http://data.bshc.pro), and for Gubbstenen, 20 m resolution data was acquired from the Finnish Environmental Institute (http://paikkatieto.

ymparisto.fi/velmu); these data were respectively aggregated and resampled using nearest bilinear interpolation to 100 m resolution. Shapefiles of inland waters were downloaded from the Swedish Meteorological Institute and the Finnish National Land Survey, and rasterized to 100 m resolution. The aforementioned steps were performed using ArcMap10 v.10.5 (ESRI, 2016).

2.3. Statistical Analyses

2.3.1. Daily foraging effort

The daily foraging effort for each individual was estimated by calculating the total time spent away from the colony (sum of trip durations) and the total distance travelled (sum of total distance per trip). In a linear mixed model framework, each metric of foraging effort was modelled as a function of Julian day of the year (mean-centered) and colony, with individual bird as a random effect to account for the non-independence of observations (R package 'lme4, Bates *et al.*, 2015). Year was not included in the models as they were unique at each site and only one was available for Gubbstenen. A step-wise model selection procedure was used to determine whether colony, its interaction with day of the year, and random slopes or intercepts produced the most parsimonious and informative model. Information criterion (AIC) were calculated using maximum likelihood for fixed effects and restricted maximum likelihood for random effects. Time spent per day and daily distance travelled were visually inspected to ensure they met model assumptions (Fig. S1–2); daily distance travelled was square root-transformed to meet the assumption of normality (Fig. S2).

2.3.2. Habitat use

To quantify patterns of habitat use, Manly's selection ratio with a Type II design was used. In this design, individual habitat use is measured relative to categorical habitat types, and the availability is assumed equal across individuals in the group (Manly *et al.*, 2007), which is an appropriate assumption for colony-breeding birds (Donazar *et al.*, 1993; Tyson *et al.*, 2015). Habitat was considered available within a 'use area' for each colony, and was delineated as the spatial union of 95% minimum convex polygons calculated around the fixes of each individual (Fig. 4A–C; Jones, 2001). Land was not considered as potential foraging habitat and was therefore omitted from calculation of proportional use and availability.

Terns are aquatic foragers, therefore points with an instantaneous speed of less than 1.5 m/s were considered as representing a grounded bird and were filtered out of the dataset (Fig. S3). Then, for each individual, the proportion of off-colony (> 1 km from colony center), in-flight fixes over each habitat type were compared to the proportional availability of each type within the colony use area, using the selection ratio formula (Manly *et al.*, 2007). Chi-squared goodness-of-fit tests were used to test for general selectivity patterns within colonies, testing two null hypotheses: (1) proportional habitat use is identical among individuals (X_{L1}^2), (2) and overall use patterns are proportional to availability (X_{L2}^2) (Manly *et al.*, 2007). For each colony, mean selection ratios were calculated across individuals for each habitat type, with the resulting confidence intervals reflecting the group-level probability of visitation for each habitat type. Use of a habitat type is proportionate to availability when the 95% confidence interval encompasses a ratio of 1, and disproportionate when the variation is above (*selected*) or below (*not selected*) this ratio (Manly *et al.*, 2007). Selection ratio calculations were made using the 'adehabitatHS' package (Calenge, 2006) in R (R Core Team, 2020).

2.3.3. Weekly home range fidelity

To estimate space use patterns, in-flight tracking data was split into weekly bins for each individual and the 95% and 50% utilization distributions (UD), which reflect the probability of occurrence across space (Worton, 1989), were estimated using Kernel Density Estimation, a standard technique (Fig. S4 A–C). A fixed kernel with a smoothing parameter of 1.85 km was used across all birds, which was calculated as half of the median forward displacement distance between in-flight fixes.

Next, to assess whether terns show site fidelity to foraging trip home ranges between weeks of the nesting period, a randomization procedure was conducted. The pairwise spatial overlap among all possible combinations of weekly UDs was calculated within each individual, and a mean overlap was calculated for each individual, and then for the year-samples at each colony (i.e. Stenarna 2013, 2014 and Gubbstenen 2016). This grand mean indicates the group-level degree of site fidelity. Overlap was calculated for both the 95% and 50% UDs using Bhattacharyaa's affinity (BA), an appropriate index when comparing UD similarity, which ranges from 0 (indicating no overlap) to the maximum UD level compared (i.e., 0.95 for the overlap of 95% UDs; indicating full overlap and identical shape) (Fieberg & Kochanny, 2005). To facilitate comparison between the degrees of overlap for the different UD levels, BA values were scaled to 1.

To test whether individual terns are site faithful, the observed mean overlap was compared to a null distribution for each group, which was produced assuming within-individual overlap is equal to between-individual overlap (Carneiro *et al.*, 2017). Within each year-sample, weeks of tracking data were randomly re-assigned to different individuals. So as to maintain the ordinal nature of the weeks, randomization was only done within weekly bins across individuals (Fig. 2). Pairwise overlap was then calculated within each randomized 'individual.' Since the extents of individual tracking periods were heterogeneous, only week-bins with a minimum of 3 simultaneously-tracked individuals were included, and weeks with fewer than 3 days of tracking data were also excluded (Fig. 2). Individual 2032 was excluded from this analysis as there were only 2 weeks of data available. Randomization was permutated 199 times and the group-level mean calculated for each permutation. The proportion of permutations with a mean overlap less than that of the observed mean overlap was taken as a test of the significance, with the p-value being set by the number of permutations (i.e., 199 randomized permutations plus the observed permutation gives a minimum p-value of 0.005) (Baylis *et al.*, 2017).

2.3.4. Weekly foraging site fidelity

To investigate whether foraging site fidelity changes over the season, we identified foraging sites which were revisited for each week. For each

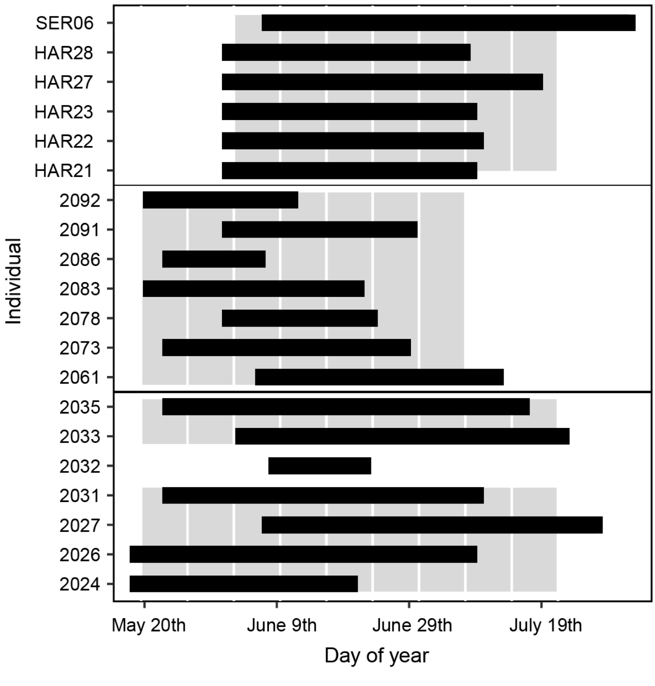

Fig. 2. Tracking periods for individual Caspian Terns tracked with GPS during the breeding season at Stenarna colony in 2013 (bottom) and 2014 (middle), and from Gubbstenen colony in 2016 (top). Black bars represent the extent of tracking data for each individual. The full extent of black bars represents the data used to calculate trip characteristics for each colony, daily foraging effort, and habitat use. Where the black bars overlap grey boxes represent the subset of data used to estimate site fidelity; white vertical lines within the grey boxes signify the weeks of the year, by which the data were partitioned in the randomization procedure testing for foraging site fidelity.

trip, we defined 'foraging sites' as the most-distant point from the colony, and classified revisits as subsequent trips (in a given week) to locations within 500 m of a previously-visited site. Next, in a linear mixed-effects framework, we modelled the proportion of revisit trips per week as a function of the relative week of tracking, with individual tern set as a random effect to account for repeated measures (Bates *et al.*, 2015). To quantify whether individuals consistently differed in the degree of site revisitation, we estimated the repeatability of trip revisits per individual using the R package 'rptR' (Nakagawa & Schielzeth, 2010). The model was identified using a step-wise model selection procedure (Table S5). Only weeks with 7 or more trips recorded and individuals with at least 4 weeks of tracking were retained (7 weeks removed and 16 individuals retained for a total of 94 weeks, IDs: 2032, 2078, 2086, 2092 removed).

3. Results

3.1. Foraging trips and effort

We recorded a total of 1409 foraging trips at Stenarna (897 in 2013, and 512 in 2014) and 1078 trips at Gubbstenen from across the breeding season. Terns at Stenarna took trips which were 18.6 km (IQR 6.7) in maximum distance from the colony and of an average total distance travelled of 39.2 km (IQR 15.5) (Table 1). Foraging trips at Gubbstenen were shorter, with a median maximum distance of 8.5 km (IQR 5.2) and a total distance travelled of 18.1 km (IQR 9.6) (Table 1). The duration of foraging trips was variable among individuals at both colonies, but on average terns at Stenarna took trips of 2 h 18 min compared to trips at Gubbstenen which averaged 1 h 45 min in duration. Birds at Stenarna subsequently took fewer trips per day (2.9, SD 1.2) than those breeding at Gubbstenen (4.4, SD 1.4) (Table 1).

The most parsimonious model identified for daily time spent on foraging trips included day of the year but not colony, as a fixed effect, and random intercepts and slope estimated for each individual tern (Table S3A–B). Based on model predictions, we found that the terns at both colonies spent an average of 10 h 10 min (*SE* 21 min) away from the colony each day, which increased significantly as the nesting season progressed by 3.4 min (*SE* 1.1) per day (Fig. 3A, Table S4; $df = 16.8$, $t = 2.99$, $p = 0.01$, $R^2_{\text{marginal}} = 0.05$). Individual-level differences accounted for 20% of the variation in the model ($R^2_{\text{conditional}} = 0.25$). For daily foraging distance, the most parsimonious model included day of the year and colony as fixed effects, with random intercepts being estimated for each individual tern (Table S3C–D). We did not identify a significant population-level effect of day of the year on the square root of the total distance travelled per day (Table S4, $df = 701$, $t = 1.39$ $p = 0.17$). However, there was a significant difference between the colonies ($df = 17.5$, $t = 4.1$, $p < 0.001$), and a significant interaction between colony and day of the year ($df = 699.5$, $t = 4.1$, $p < 0.001$), with birds at Stenarna travelling further per day and having a steeper, positive relationship with day of the year compared to Gubbstenen birds (Fig. 3B, Table S4). Colony-level fixed effects in the model explained 23% of the residual variation, with individual-level differences explaining an additional 15% ($R^2_{\text{marginal}} = 0.23$, $R^2_{\text{conditional}} = 0.38$).

Table 1. Foraging trip characteristics of Caspian Terns tracked from breeding colonies in Sweden (Stenarna) and Finland (Gubbstenen). The number of individuals tracked and the total number of trips recorded from each colony are indicated by 'n(ID)' and 'n(trips)' respectively. Values represent medians of medians per individual and inter-quartile ranges, and means with standard deviation for trips per day. Values in parentheses represent the first and third quartile values.

Group	n (ID)	n (trips)	Max. distance (km)	Total distance (km)	Duration (min)	Trips per day
Gubbstenen	6	1078	8.5 ± 5.2	18.1 ± 8.6	105 (95–114)	4.4 + 1.4
Stenarna	14	1409	18.6 ± 6.7	39.2 ± 15.5	138 (120–238)	2.9 ± 1.2

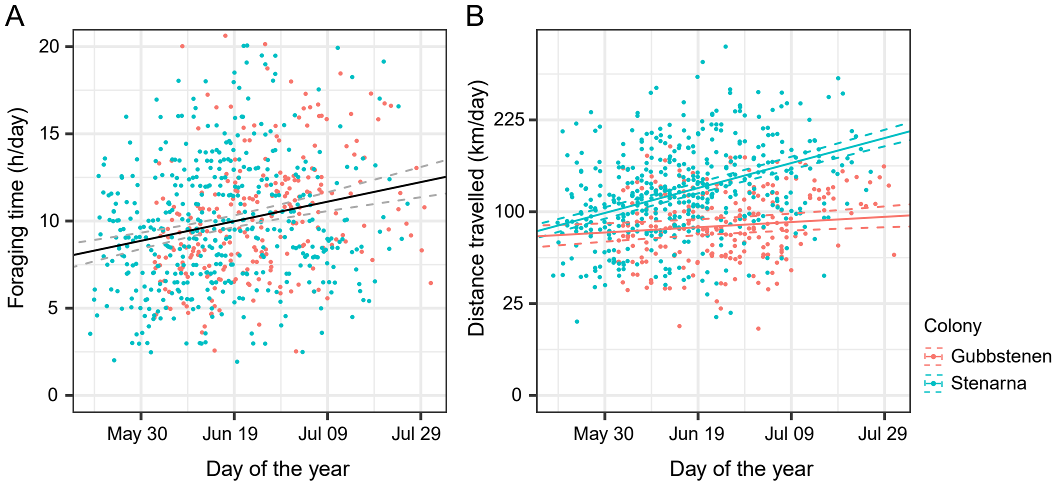

Fig. 3. Association between metrics of daily foraging effort of breeding Caspian Terns and seasonal advancement. (A) The predicted marginal effect of day of the year on daily time spent on foraging trips ($R^2_{\text{marginal}} = 0.05$, $R^2_{\text{conditional}} = 0.25$, $p = 0.01$) is shown as a black line, with dotted lines representing the 95% confidence intervals. (B) Colored lines represent the predicted relationship between day of the year and total distance (on square root scale) travelled per day on foraging trips at each breeding colony ($R^2_{\text{marginal}} = 0.23$, $R^2_{\text{conditional}} = 0.38$, $p = 0.17$). Lines are split by colony to illustrate that the mean distance travelled per day ($p < 0.001$) and the marginal effect of day of the year ($p < 0.001$) differed significantly between terns breeding at Stenarna and Gubbstenen colonies. (A, B) Colored dots represent observed daily estimates of foraging time and distance travelled for individuals from Stenarna and Gubbstenen breeding colonies. Predicted relationships were derived from linear mixed effects models (Table S3–4).

3.2. Habitat use

Tracked Caspian Terns visited waters between 0–40 m in depth, yet when the relative availability and relative use of depth intervals were taken into account the only depth range selected for foraging in seawater habitat was 0–5 m deep water (Fig. 4). Habitat use was significantly non-random (Table S2; Stenarna: $df = 84$, $X_{L2}^2 = 13{,}493$, $p < 0.001$; Gubbstenen: $df = 18$, $X_{L2}^2 = 4454$, $p < 0.001$) and differed among individuals at both colonies (Table S2; Stenarna: $df = 78$, $X_{L1}^2 = 3412$, $p < 0.001$; Gubbstenen: $df = 15$, $X_{L1}^2 = 173$, $p < 0.001$). Freshwater areas represented only 4% and 1% of the water area available at Stenarna and Gubbstenen respectively, and were used in proportion to availability at both colonies. However, selectivity at the individual level was highly variable, with certain individuals selecting inland freshwaters and others not (Fig. 4D–F, Table S2).

3.3. Weekly foraging site fidelity

For birds from Stenarna, the mean overlap of within-individual weekly home ranges was 0.44 (SD 0.008, 95% UD) and 0.30 (SD 0.01, 50% UD) in 2013, and 0.44 (SD 0.03, 95% UD) and 0.23 (SD 0.03, 50% UD) in 2014. At Gubbstenen, the mean overlap was 0.70 (SD 0.1, 95% UD), and 0.36 (SD 0.02, 50% UD). The observed mean overlap was significantly higher than the null distribution in all three year-samples, for both the 95% UD (S-2013: $p = 0.005$, S-2014: $p = 0.005$; G-2016: $p = 0.005$) and the 50% UD (S-2013: $p = 0.005$, S-2014: $p = 0.005$; G-2016: $p = 0.005$) (Fig. 5A), respectively, indicating that individuals overlap spatially with areas used in prior weeks of foraging more than expected by chance.

We estimated that terns revisited foraging sites every 2 d 11.5 h (mean, SD 6 h) per week, and found that the maximum period over which a tern re-visited the same site was 51 d and 6 h. The most parsimonious model identified to explain foraging site re-visitation rate included day of the year as a fixed effect with random

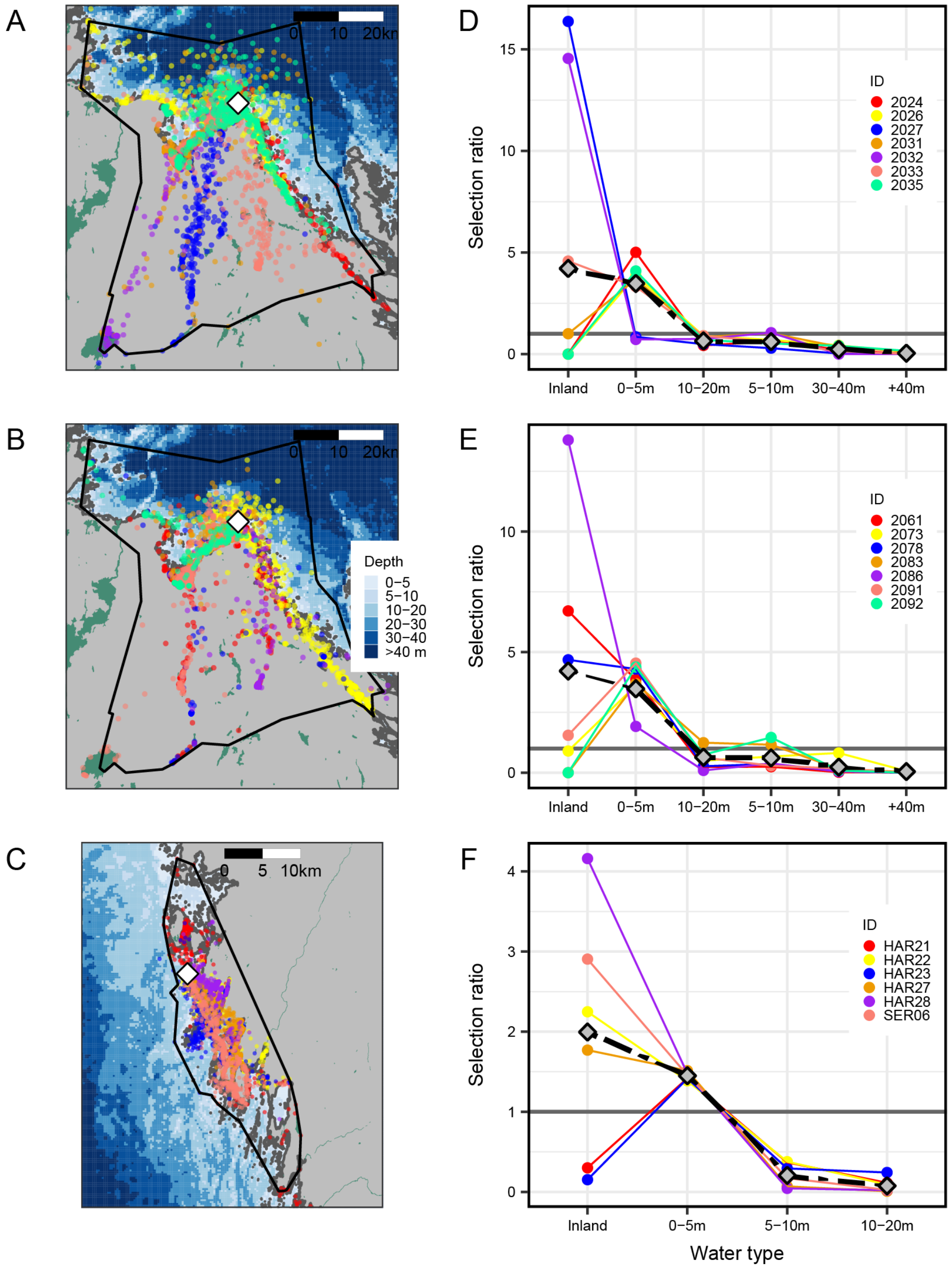

Fig. 4. Tracked movements and habitat selection of Caspian Terns during breeding in the Baltic Sea. Movements of individual terns from the breeding colonies of Stenarna in (A) 2013, (B) 2014, and Gubbstenen in (C) 2016. Dots represent GPS-fixes of birds during flight; each color represents a different individual. Polygon outlines (black) represent the 95% minimum convex polygons within which the availability of water types were calculated at each colony. Seawater bathymetry is scaled from white to dark blue and inland waters are green-blue. Patterns of habitat selectivity of terns tracked from Stenarna in 2013 (D) and 2014 (E) and Gubbstenen in 2016 (F). Habitat use was quantified as a selection ratio, which is the proportional use of a water type over its relative availability around the colony. Grey diamonds represent the group-level mean selection ratio for each water type, of which ratios above and below 1 respectively indicate positive and negative selectivity. Water types are ranked from left to right in order of highest to lowest mean selectivity at the group level. Colored dots and lines signify the habitat use pattern of individual terns. Year-samples from Stenarna were analyzed together and are shown separately for clarity.

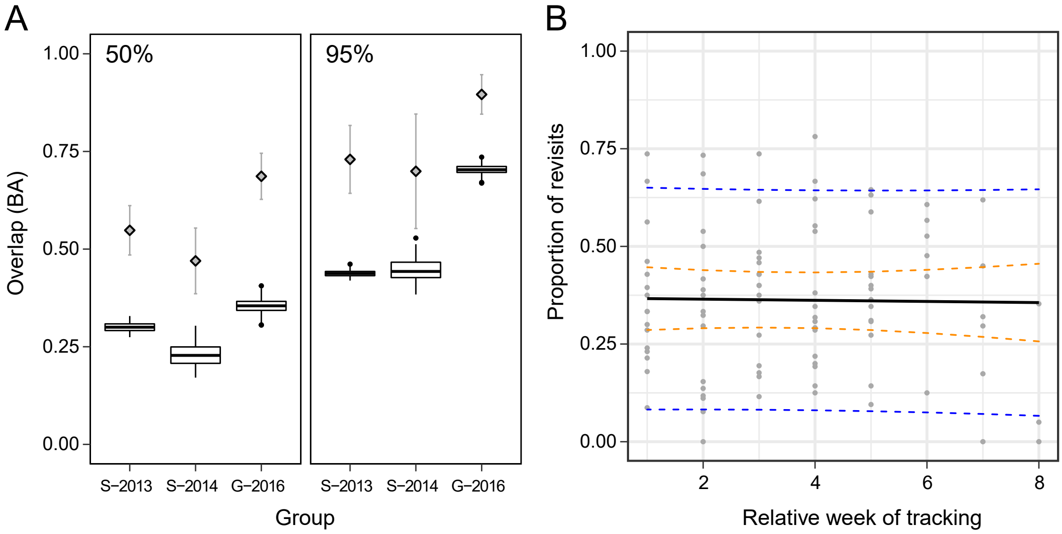

Fig. 5. Foraging site fidelity of Caspian Terns during the breeding season. (A) Resulting distributions from randomization procedure testing whether Caspian Terns tracked from Stenarna (S-2013, S-2014), and Gubbstenen (G-2016) were more faithful to foraging sites than expected at random. Fidelity was estimated as between-week overlap of 50% (left panel) and 95% (right panel) utilization distribution areas, where overlap was quantified using an index of distribution similarity (Bhattacharyaa's affinity). Grey diamonds (mean) and error bars (1 SD) represent the observed within-individual overlap for each tracking sample. Boxes signify the distribution of randomized grand mean overlaps across 199 permutations assuming between-individual overlap is equal to within-individual overlap. The lack of overlap between distributions indicates the observed pattern differs significantly from random. (B) Weekly foraging site re-visitation rate and advancing season. The predicted marginal effect of week of the season (relative to when each individual was tracked) on the rate at which terns revisit foraging sites is shown as a black line. The orange dotted line represents the 95% confidence interval around the mean effect, and the blue line represents the prediction interval, illustrating the large effect of among-individual variation in the linear-mixed effects model.

intercepts estimated for each individual tern (Table S5). The model-estimated weekly change in the proportion of trips which are revisits was –0.001 min (*SE* 0.007), which was not significant (Fig. 5B, Table S6; $df = 80.2$, $t = -0.185$, $p = 0.85$, $R^2_{\text{marginal}} = 0.0002$). However the variation in the estimated mean effect does not discount a possible effect. Individual differences accounted for 47% of the variation explained by the model (Fig. 5B, $R^2_{\text{conditional}} = 0.47$), and individual terns were significantly repeatable in the rate at which they revisited sites among weeks ($R = 0.475$, $SE = 0.118$, $p < 0.001$).

4. Discussion

Habitat use and foraging strategies are central to the foraging ecology of aquatic birds. Here, we revealed aspects of the breeding season foraging ecology of Caspian Terns in the little-studied population of the Baltic Sea. We found that Caspian Terns at two breeding colonies increased their daily foraging effort from late incubation through chick-rearing by spending more time on foraging trips, and that changes in total distance travelled differed at the colony level. Tracked Caspian Terns selected shallow coastal waters, and when available, inland lakes for foraging. We showed that individuals differ in their habitat use patterns and are highly site faithful, maintaining the same foraging areas throughout the breeding season, despite changes in effort. These results further understanding of the roles of habitat availability and individual site fidelity in the foraging ecology of this widespread species (Dunlop & McNeill, 2017; Koli & Soikkeli, 1974; Lyons *et al.*, 2005; McNicholl, 1990).

As we were not able not distinguish between different in-flight behavioral states (e.g., active foraging, transiting), the habitat use patterns described here also reflect the habitats the terns passed over in transit (Bennison *et al.*, 2018). Nevertheless, given that foraging behavior in this species is characterized by sinuous movement within a restricted area, much of the habitat use signal we report likely represent true foraging habitat selection. Our results support the general understanding of this species as a coastal and inland forager (Cramp, 1985; Dunlop & McNeill, 2017). It is apparent from our selection ratio calculations (Fig. 4D–F) that certain individuals visit lakes while others use only coastal waters (Fig. 4D–F). Whether this represents true habitat specialization remains unclear, however as all individuals which visited lakes also used coastal areas, it may more likely represent spatial fidelity.

Our finding that terns re-use foraging areas more than expected by chance, and even revisit the same sites throughout the season is, to the best of our knowledge, the first quantitative evidence of foraging site fidelity in this species. Individual foraging site specialization has been reported for an increasing number of taxa (e.g., Baylis *et al.*, 2017; Drury & Smith, 1968; Hillen *et al.*, 2009; Patrick & Weimerskirch, 2014) and that Caspian Terns also display this behavior suggests that site familiarity is an important part of their foraging strategy (Piper, 2011). Breeding Common Terns (*Sterna hirundo*) are often site-faithful to the point of territoriality (Nisbet, 1983). Although this agonistic behavior has also been reported for Caspian Terns (McNicholl, 1990), it remains unverified as a common strategy. Our observation of site fidelity, combined with a certain degree of spatial and habitat segregation (Fig. 4), indicates that intra-specific competition may indeed influence colony-level space use patterns in this species (Davoren *et al.*, 2003; Sánchez *et al.*, 2018).

We found a difference in foraging range between our study colonies, with the values from the Stenarna colony being similar to published averages from other Caspian Tern populations (Anderson *et al.*, 2007; Oppel *et al.*, 2018) and the maximum distances reached at Gubbstenen being lower. The smaller sample from Gubbstenen may not fully represent colony-level variation, however given that individuals are site faithful throughout the season and variation in trip characteristics was not large (Table 1), this suggests a real difference between the colonies in this respect. The distribution of preferred foraging habitats (shallow coastal water and freshwater) differed between the colonies, which may have affected the distances birds had to travel to reach foraging sites. At both colonies, we found that the daily time spent on trips increased from late incubation through chick-rearing, which could reflect increasing energetic demands of chicks or deteriorating prey availability (Elliott *et al.*, 2009; Humphreys *et al.*, 2006). The total distance travelled per day at Stenarna also increased sharply with time, suggesting that competition there may have been more acute as the season progresses than at Gubbstenen. Stenarna hosts around 40% more breeding pairs than Gubbstenen, which could also contribute to differences in the resource competition (Jovani *et al.*, 2016). Terns are known to use foraging trips as opportunities for self-maintenance (e.g., preening, resting), therefore changes in daily off-colony movements could in part reflect release from responsibility when chicks gain thermoregulatory independence (Palestis & Burger, 1998).

Despite changes in daily foraging trip movements throughout nesting, we found no support for general changes in the degree of site fidelity. Instead, we found substantial among-individual variation in foraging site re-visitation rates and that these differences were consistent across the season. This indicates that as foraging effort changes individuals maintain their strategies, whether that means frequent re-use of the same few sites or more exploratory search behavior. This represents a novel finding regarding Caspian Terns, however recent work has implicated the roles of individual condition, quality, and personality on foraging behavior in a number of seabird species (Geary *et al.*, 2019; Patrick & Weimerskirch, 2014). By combining further tracking with direct observation of nest progression and outcomes, and prey types brought to the nest (e.g., Anderson *et al.*, 2007) future work could reveal the drivers of the foraging strategies described here and clarify whether foraging site fidelity persists across seasons and is associated with habitat specialization in this and similar species.

Konsekvent födosöksbeteende hos en hotad Östersjöhäckande havsfågel

Födosöksstragier och habitatspreferenser är viktiga begrepp för att förstå förändringar av djurpopulationer och hur dessa populationer kan bevaras. I denna studie undersökte vi rörelsemönster hos skräntärnor (*Hydroprogne caspia*) i Östersjön under häckningstiden som tills nu studerats endast till begränsad del. Vi analyserade data från GPS-sändare för 20 individer från två häckningskolonier, en i Sverige och en i Finland. Här beskriver vi de egenskaper som karaktäriserar de dagliga födosöksturerna till och från kolonierna, i vilken typ av vatten de söker föda (vattendjup och insjöar), och i vilken utsträckning individerna använder sig av samma födosöksplatser under hela häckningsperioden. Den dagliga tiden som tärnorna är borta från kolonin för att söka föda ökar signifikant under häckningsperioden. Dessutom verkar kolonierna skilja sig åt angående de dagliga distanserna som tärnorna rör sig för att söka föda. Häckande tärnor väljer att söka föda främst i grunda vatten (0–5 m djup), medan vissa individer sökte föda i insjöar. I studien visar vi för första gången att skräntärnor är trogna specifika födosöksplatser under hela häckningen, men också att individer har olika strategier och att individerna är konsekventa i de strategier som de använder sig av. Resultaten fyller viktiga kunskapsluckor för denna hotade skräntärnepopulation som häckar i Östersjön, och studien bidrar med ny information om födosöksekologin hos individer av den globalt vittspridda art

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Conflict of Interest. Authors report no conflicts of interest.

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Online supplementary material

The supplementary material includes extended methods, as well as figures (Fig. S1–S5) and tables (Table S1–S6) to provide more context to the main analysis.

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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*)

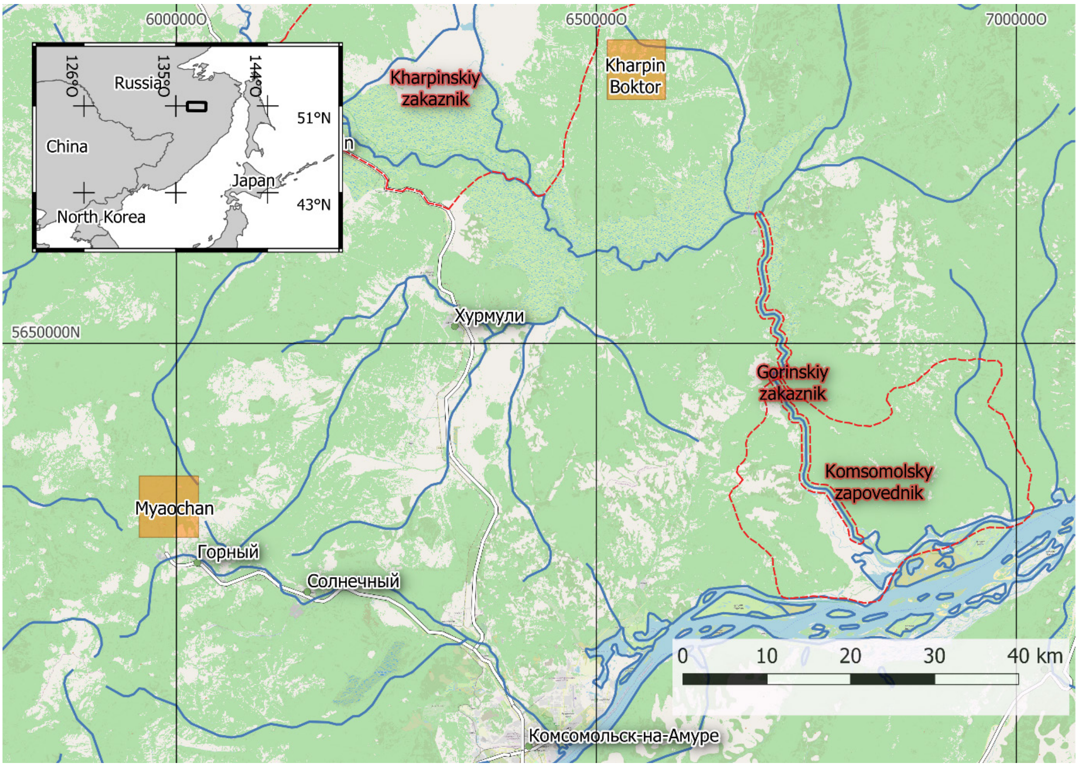

Fig. 1. Location of the two study areas “Myaochan” and “Kharpin-Boktor” in the Amur region (orange rectangles). The black box in the inset map (upper left corner) shows the position of the main map in the Russian Far East. Settlements are given in Cyrillic letters. The city Komsomolsk na Amure is located 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).

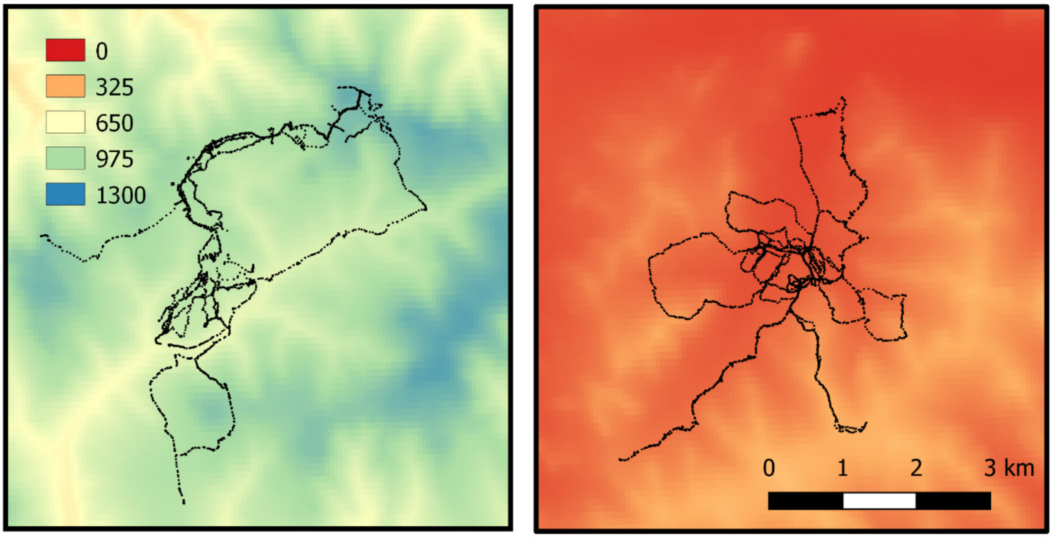

Fig. 2. Enlargements of the inset maps from Fig. 1 with GPS tracks of the mapping routes. (left: Myaochan, right: Kharpin-Boktor). The legend of the height above sea level (in meter) and the scale bar apply to both maps.

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).

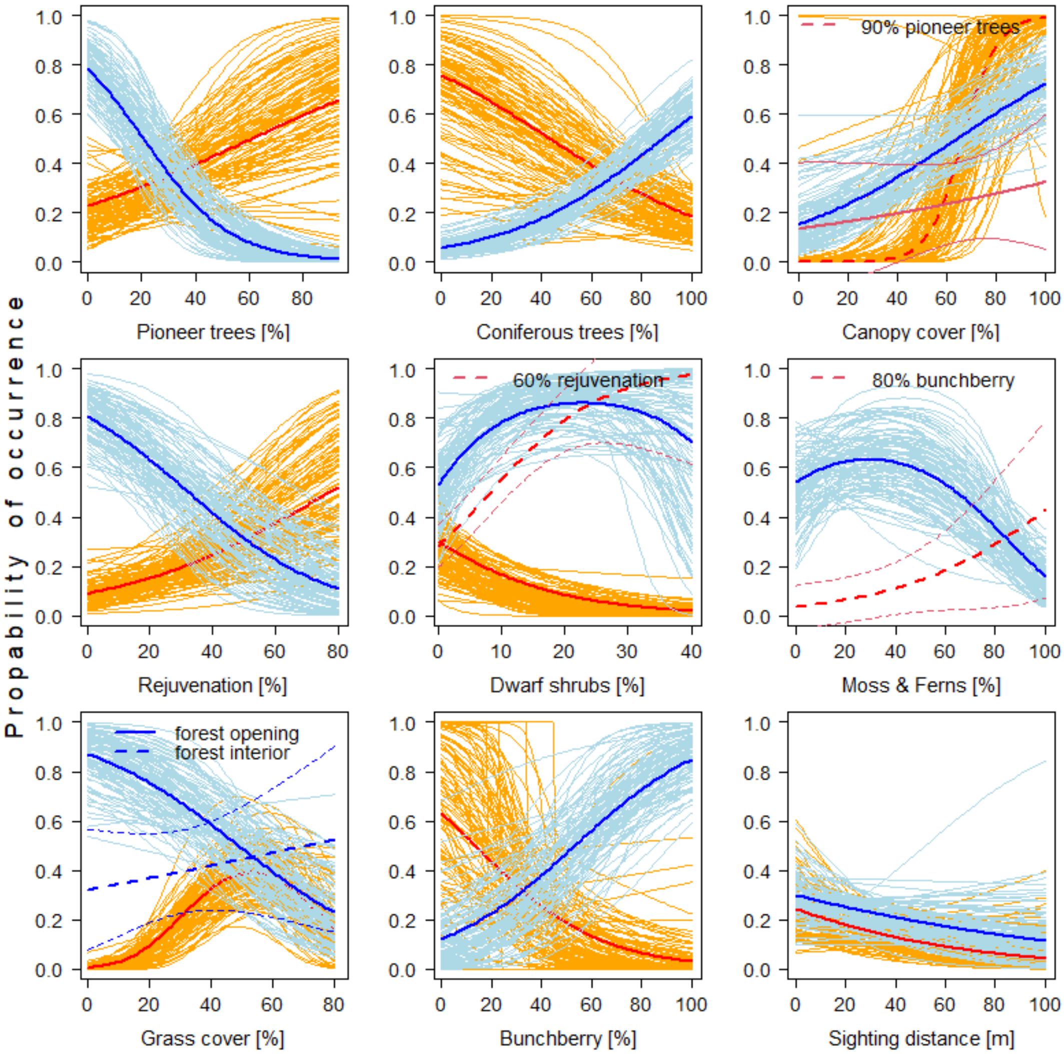

Fig. 3. Partial dependence of Siberian Grouse (light blue) and Hazel Grouse (orange) probability of occurrence on common predictor variables. Graphs were plotted with 100 bootstraps by varying the variable under consideration over the range of values observed in the field and keeping all other predictors 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

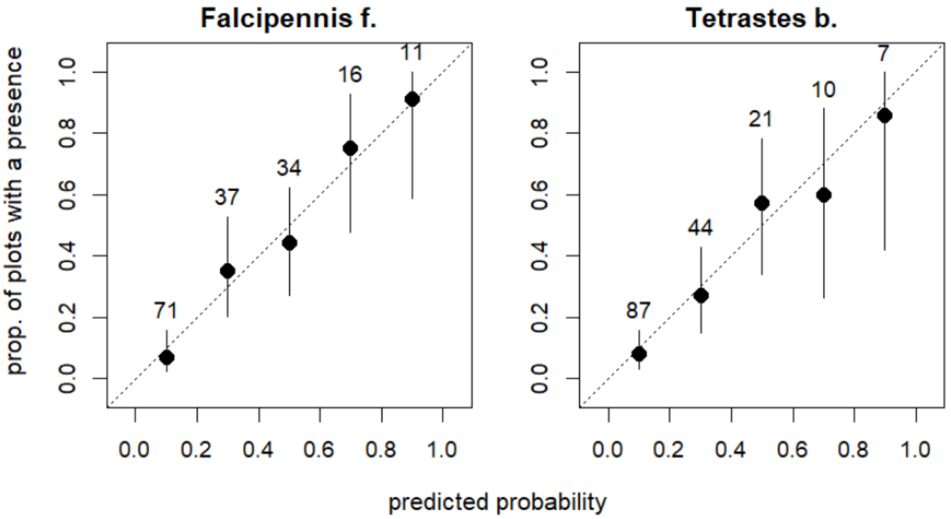

Fig. 4. Calibration plots of generalized linear models for Siberian Grouse (left) and Hazel Grouse (right). Observed occurrences as proportion of plots surveyed are close to the ideal slope represented by the dotted diagonal. Vertical lines represent confidence intervals for a binomial distribution. 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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Association of weather variables with the migration phenology and body conditions of Siberian warblers

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Different elements of weather, such as wind speed, wind direction, precipitation and temperature are very important regulators of bird migration. Weather conditions also play role on the body condition such as body mass and the deposited fat. In this study we selected four warbler species to examine the impact of different weather variables on their spring and autumn migration timing and their body condition in one of the most extreme weather areas of the Earth, at Lake Baikal in Siberia. We also studied the changes in body mass and fat reserves during the spring and autumn migration periods of these species. For the analyses, we used ringing data of 2471 birds from five spring and five autumn seasons during 2015–2019. According to our results, it can be stated that the weather did not have a significant association with the migration timing of the studied warblers, perhaps due to the geographical location of the study site. However, the body mass and the fat reserves of the birds increased during unsuitable weather conditions because of the increased energy requirements. Birds generally migrate with low fat reserves, which is due to the fact that this area is not an important stopover site for these species.

1. Introduction

Birds usually migrate in windless, anticyclonic weather conditions without precipitation or with the support of tailwinds (Alerstam 1990, Gyurácz *et al.* 1997, 2003, Bruderer & Boldt 2001, Erni *et al.* 2002), while cloudy skies, poor visibility, strong head- or crosswinds, and warm or occluded fronts have negative effects on the migration (Åkesson 1993, Pyle *et al.* 1993). The most intense migration occurs in synoptic weather conditions, in the transitional phase on the western side of low-pressure systems and the eastern side of high-pressure areas, when the temperature decreases, the sky clears, the air pressure increases and the wind direction changes (Alerstam 1990). Wind speed and direction are also key regulators of migration (Cochran & Kjos 1985, Weber & Hedenström 2000, Pennycuick &

Battley 2003, Cochran & Wikeski 2005, Bowlin & Wikelski 2008, Shamoun-Baranes & van Gasteren 2011, Bulte *et al.* 2014, Gill *et al.* 2014), even if the observation methods overestimate the effect of wind on the migration (Erni *et al.* 2002). Not only the wind but also the rain determines the end of a stopover period, and these two factors synchronize the flights of most migrants (Schaub *et al.* 2004). Temperature also clearly has an effect on the timing of bird migration. In spring, the local temperature on the breeding grounds affected at least the early subsets of the bird populations (Tøttrup *et al.* 2010). In the case of Pied Flycatcher (*Ficedula hypoleuca*), the progression of spring migration is strongly influenced by temperature en route (Hüppop & Winkel 2006). As a result of global climate change, more and more migratory bird species return to their breeding grounds earlier in spring, which also indicates that temperatures – at least in spring – affect bird migration (Kullberg *et al.* 2015, Bozó & Csörgő 2020).

In the present study, we examined the impact of different weather variables on bird migration in one of the most extreme weather areas of the Earth, near South Siberia. Species migrating there use the East Asian-Australasian migratory flyway, which, despite being extremely species-rich, is the least studied of the migratory systems (Yong *et al.* 2015, 2021). In recent years, intensive research has been conducted in the region (Bozó & Csörgő under review), but the impact of weather on songbird migration has only been studied in the Russian Far East (Bozó *et al.* 2018), not yet in Siberia. We hypothesize that the migration of small songbirds is influenced by the weather, however, based on the results of a similar study in the Russian Far East (Bozó *et al.* 2018), these effects are less significant in spring than in autumn. We also examined how much fat the birds had during the different migration periods, and how much the weather associates with the weight and the stored fat reserves of the birds. Since unsuitable weather conditions increase the energy requirements of the birds (Richardson 1978), we hypothesized that in case of low temperature, rain or strong winds the stored fat of birds is higher than in case of calm weather conditions.In this study, we selected four species of warblers that migrate in large numbers in the study area, but differ in some of their characteristics (body size, size of distribution area, habitat, migration period): the Thick-billed Warbler (*Arundinax aedon*), the Yellow-browed Warbler (*Phylloscopus inornatus*), the Dusky Warbler (*Ph. fuscatus*) *and* the Pallas's Leaf Warbler (*Ph. proregulus*). We chose these four species because we wanted to find out whether closely related species are affected by the same weather factors in the same way or differently under the same conditions.

2. Material and methods

2.1. Study species

The Thick-billed Warbler (18–19 cm body length and 22–31 g weight), breeds mainly in continental lowlands, dense thickets, bushes, tall grasses, edges and clearings of forests, in gardens, along roads, near lakes and in river valleys. It breeds in South-Central Siberia east of the Sea of Japan, and in North China north to the Lake Baikal (Dyrcz 2020). Despite its extremely large distribution range with a total area of 7,180,000 km^2, its population is declining (BirdLife International 2020). The Yellow-browed Warbler is a small leaf warbler (10–11 cm, 4.3–6.5 g), and breeds between 1000 and 2440 meters in a variety of broadleaf forests (Clement 2020a). The Yellow-browed Warbler has the largest distribution area of species in this study with a total area of 15,900,000 km^2, and its population is stable (BirdLife International 2020). It breeds in Northern Russia from middle and upper Pechora and Ural mountains east of East Siberia, south to Northeast Altai, Northwest Mongolia, Baikal Mountains and Northeast China (Clement 2020a). The Dusky Warbler is a small (11–12 cm, 8.5–13.5 g), polytypic leaf warbler with three subspecies. It breeds in scrub and low dense vegetation areas in taiga forests along streams, sedge-swamps and reed-swamps and in floodplain meadows in marshy river valleys (Clement 2020b). The nominate *Ph. f. fuscatus* breeds in Central and East Siberia, Mongolia, Northeast China and in the Russian Far East (Clement 2020b). It has an extremely large distribution area with a total area of 15,600,000 km^2, and its population is stable (BirdLife International 2020). The Pallas's Leaf Warbler is the smallest

Table 1. Number of captured individuals for each species for both spring (Spr) and autumn (Aut) season. Final sample size refers to the data used for the analyses of changes in body mass and stored fat.

	2015		2016		2017		2018		2019		Total		Final sample size	
Species	Spr	Aut	Spr	Aut	Spr	Aut	Spr	Aut	Spr	Aut	Spr	Aut	Spr	Aut
Thick-billed Warbler	38	29	92	108	80	58	88	113	144	116	442	424	442	423
Dusky Warbler	37	41	64	68	56	68	70	41	80	76	307	294	294	285
Yellow-browed Warbler	5	15	12	56	19	79	4	73	17	71	57	294	54	284
Pallas's Leaf Warbler	6	52	12	139	9	156	15	104	12	148	54	599	53	585

of all study species (9–10 cm, 4.5–7.5 g), and has the smallest distribution range with a total area of 6,680,000 km^2 (BirdLife International 2020). It breeds in the taiga coniferous forest or in mixed forest with a high percentage of conifers. Its breeding range is in South-Central and Southeast Siberia from the Altai Mountains east of north Sea of Okhotsk, south to North Mongolia, Northeast China and Sakhalin (Alström *et al.* 2020). Its population is stable (BirdLife International 2020).

2.2. Data collection

Fieldwork was carried out in the buffer zone of Baikalsky State Nature Biosphere Reserve, which is on the southeast coast of Lake Baikal, southwest from the Mishikha River mouth on Pribaikalskaya flatland (51°38'37.5" N 105°31'23.9" E). The surrounding vegetation is dominated by cedar (*Cedrus* sp.) forests mixed with birch (*Betula* spp.), aspen (*Populus* spp.), fir (*Abies* spp.), interspersed with small willow (*Salix* spp.) bushes and grass meadows. The birds were captured with mist-nets with a total length of 210 metres. Mist-nets were checked every 60 minutes from sunrise to sunset, and every 30 minutes during inclement weather. We used data from five spring (from 15 May to 20 June) and five autumn (from 1 August to 25 October) seasons during 2015–2019. Rings were supplied by the Moscow Ringing Centre. Species identification followed Svensson (1992) and Demongin (2016). In this study, we only used the data from transient individuals, excluding possible local breeders (birds with brood patch or long-term recaptures). In addition, we only included data of first captures and excluded all recaptures. From the recorded biometric data, only the body mass and fat score were used for this study. Body mass was measured to the nearest 0.1 g, while fat scores followed Kaiser (1993)

Table 2. Daily percentage distribution of different wind speed and wind direction categories.

	Wind speed		Wind direction	
Day	Spring	Autumn	Spring	Autumn
1	25	30.5	0.6	4.4
2	36.6	33.2	0.6	3.7
3	31.3	22.3	5.7	5.9
4	7.1	12.7	1.3	5.9
5	0	1.3	1.9	6.5
6	0	0	9.4	9
7	0	0	21.4	4.4
8	0	0	13.8	8.1
9	0	0	1.9	13.7
10	0	0	8.8	18.7
11	0	0	5	9.3
12	0	0	5	4.4
13	–	–	10.1	0
14	–	–	6.3	4.4
15	–	–	3.8	1.6
16	–	–	4.4	0

on a scale of 0 to 8. Because of the small sample size, fat scores 4–8 were merged into category 3+, similarly to other studies (e. g. Brown *et al.* 2002, Turcotte & Desrochers 2008). Data analysis was based on 2471 individuals of four species (Thick-billed Warbler, Dusky Warbler, Yellow-browed Warbler and Pallas's Leaf Warbler) (Table 1).

The following weather variables were selected to analyse the association of weather with bird migration timing and the body conditions of the individuals: minimum daily temperature, maximum daily temperature, daily average temperature (°C), precipitation (mm), daily average wind speed (Beaufort scale 0–12) and wind direction. Since the temperature variables are highly correlated with each other in both seasons ($R > 0.7, p < 0.001$ in all cases), only the daily average temperature values were used in the analyses. For the statistical analyses, the wind direction was categorized on a scale of 1–16, at which the tailwind received the highest score in both spring and autumn seasons (in spring the southern, in autumn the northern winds, circular coordinates). In order to illustrate the variability of the wind direction and wind speed data, the percentage of daily different wind speed and wind direction categories is given in Table 2. We used weather data from the nearest meteorological station located in Babushkin. All data were gathered from the website of National Centers for Environmental Information.

Multiple regressions were used to evaluate the impact of weather on the number of birds trapped per day and on the body conditions (deposited fat and body weight) of each trapped individuals. Given that many statistical tests have been carried out, we have taken type 1 errors into account and therefore focus on the biologically strongest effects when evaluating the results. Regressions were used for each species for both spring and autumn season.

According to Berthold (1973), we examined changes in body mass and stored fat over 10-day

Table 3. Results of the multiple regressions regarding to the association of different weather variables with the number of captured individuals. Significant *p*-values are in bold.

		Spring				Autumn			
Species	Variable	Coefficient	*t*	*p*	R^2	Coefficient	*t*	*p*	R^2
Thick-billed Warbler	Temperature	0.089	0.74	0.463	0.0057	0.003	0.03	0.977	0.0026
	Wind speed	–0.075	–0.61	0.541	0.0044	–0.045	–0.67	0.506	0.0082
	Wind direction	–0.086	–0.63	0.531	0.0002	–0.061	–0.58	0.563	0.0041
	Precipitation	–0.041	–0.11	0.910	0.0007	–0.125	–0.96	0.338	0.0070
Dusky Warbler	Temperature	0.045	1.00	0.316	0.0059	0.017	0.84	0.401	0.0138
	Wind speed	–0.013	–0.28	0.778	0.0011	–0.042	–2.30	**0.022**	0.0264
	Wind direction	–0.039	–0.78	0.439	0.0009	0.021	0.70	0.486	0.0018
	Precipitation	0.066	0.50	0.619	0.0006	0.008	0.20	0.843	0.0006
Yellow-browed Warbler	Temperature	–0.055	–2.93	**0.004**	0.0292	–0.011	–0.48	0.629	0.0001
	Wind speed	–0.026	–1.36	0.177	0.0003	–0.023	–1.01	0.311	0.0016
	Wind direction	–0.005	–0.22	0.827	0.0006	0.019	0.48	0.630	0.0001
	Precipitation	–0.072	–1.29	0.198	0.0105	0.007	0.12	0.901	0.0001
Pallas's Leaf Warbler	Temperature	–0.011	–0.75	0.456	0.0000	0.022	0.43	0.671	0.0018
	Wind speed	–0.028	–1.92	0.057	0.0096	–0.059	–1.09	0.276	0.0055
	Wind direction	–0.020	–1.19	0.236	0.0015	0.070	0.80	0.423	0.0000
	Precipitation	0.012	0.27	0.784	0.0003	–0.126	–0.94	0.350	0.0043

periods. Differences among body mass change in subsequent 10-day periods were tested using the Kruskal–Wallis-test. Periods with fewer than 10 individuals per species were excluded from our analysis (Yosef & Chernetsov 2004, Bozó *et al.* 2020a). All statistical analyses were carried out in Past 3.14 (Hammer *et al.* 2001), while figures were created by Microsoft Excel 2013.

3. Results

3.1. Associations between different weather variables and numbers of captured birds

In spring, the lower the temperature, the higher the number of Yellow-browed Warblers caught in the nets (Table 3). In autumn, the stronger the wind, the less Dusky Warblers caught in the nets. (Table 3).

3.2 Fat accumulation and body weight

In spring, in the case of Dusky Warblers, and Pallas's Leaf Warblers, body weight decreased significantly over time (Table 4, Fig. 1). In autumn, for Yellow-browed Warbler and Pallas's Leaf Warbler, both the amount of stored fat and body weight increased over time (Table 4, Fig. 2).

It is the characteristic of all species that they migrate with very low fat reserves both in spring and autumn. The only exception is the Thick-billed Warbler, for which body fat values of 4 or more were measured in nearly 20% of the birds caught in autumn (Fig. 3, Fig. 4).

3.3. Associations between weather variables and the body mass and fat reserves

There were both similarities and differences between spring and autumn in relation to the association of different weather variables with the weight and fat reserves of the birds. We detected significant negative relationships between body condition and temperature, and positive relationship between body condition, wind speed and tailwinds, but these were not uniformly detected in all species and seasons (Table 5).

Table 4. Results of Kruskal–Wallis-test regarding to the changes in body mass and fat over time. Significant *p*-values are in bold.

Species	Season	Variable	*H*	*p*
Thick-billed Warbler	Spring	Body mass	1.99	0.369
		Fat	3.12	0.183
	Autumn	Body mass	2.26	0.520
		Fat	3.72	0.231
Dusky Warbler	Spring	Body mass	29.70	**<0.001**
		Fat	0.12	0.934
	Autumn	Body mass	12.95	**0.024**
		Fat	96.32	**<0.001**
Yellow-browed Warbler	Spring	Body mass	0.03	0.852
		Fat	0.31	0.562
	Autumn	Body mass	36.75	**<0.001**
		Fat	28.57	**<0.001**
Pallas's Leaf Warbler	Spring	Body mass	11.79	**0.003**
		Fat	8.49	**0.010**
	Autumn	Body mass	35.81	**<0.001**
		Fat	39.46	**<0.001**

4. Discussion

According to our results, the various elements of the weather were generally not associated with numbers of birds captured. Only the strength of the wind was associated with migration of the Dusky Warblers: the stronger the wind, the fewer the birds were caught in the nets. However, temperature, wind speed and direction influenced the weight and fat reserves of the birds.

Birds during their migration achieve the fastest, the cheapest or the safest possible migration (optimal migration strategies, reviewed in Alerstam & Hedenström 1998), in which the strength of the wind and its direction play an important role (Richardson 1978). Wind in the right direction and strength contributes to optimal migration, as it allows birds to travel longer distances with a given amount of stored nutrients (Alerstam 1978, Richardson 1978). In strong winds, small birds are not able to compensate for winds in the opposite direction to migration (Elkins 1988). Therefore, in this case, they are

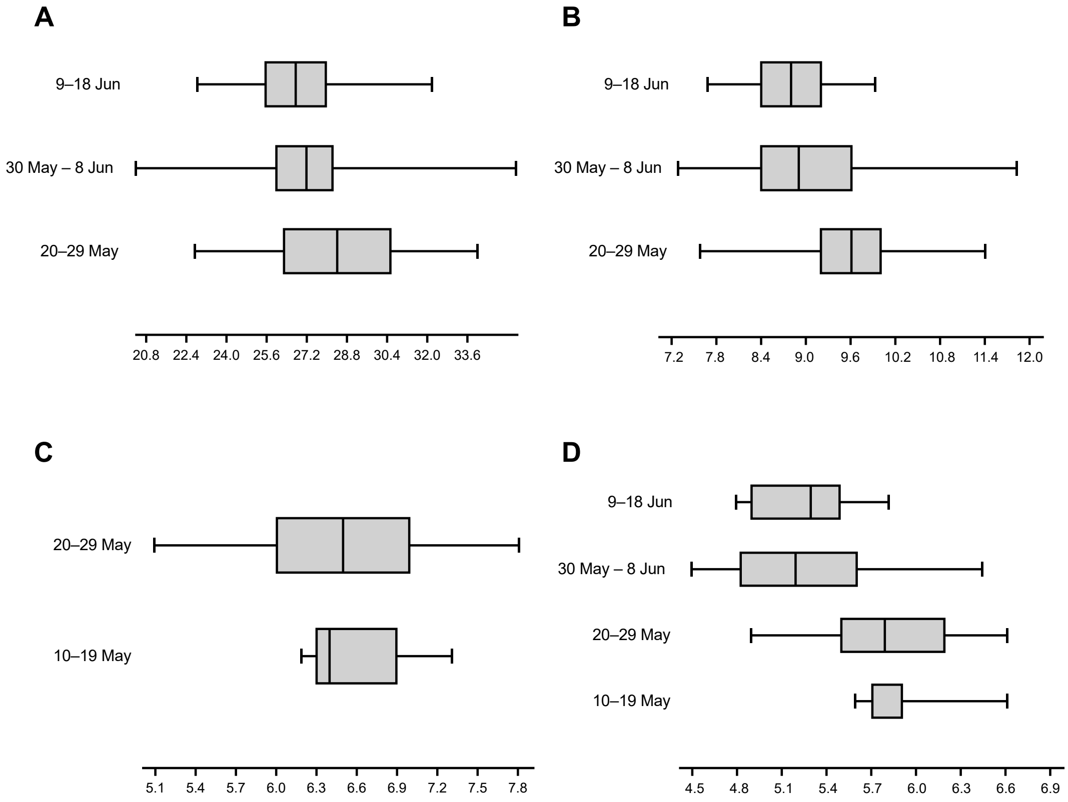

Fig. 1. Changes in body mass (x-axis) during subsequent decades in spring for Thick-billed Warbler (A), Dusky Warbler (B), Yellow-browed Warbler (C) and Pallas's Leaf Warbler (D).

more likely to die or move to suboptimal areas, up to thousands of kilometers away, as in the case of appearances in Europe of several species studied in this study (Baker 1977, Howey & Bell 1985, Baker & Catley 1987). Taking the energy and mortality minimization strategies into account, it is understandable that the studied species migrate in significantly smaller numbers in strong winds than in windless weather. Bozó *et al.* (2018) obtained similar results for the same species in the Muraviovka Park, an important stopover site located in the Russian Far East, 1,500 kilometers east of Lake Baikal. In the case of the Thick-billed Warbler, however, there was no correlation between wind strength and the number of birds, perhaps due to the fact that of the four species studied, it uses the closest, densest habitats nearest to the ground (del Hoyo *et al.* 2006), where the effect of the wind is less pronounced than in the canopy. This is true even if the nets are the same height and do not cover the canopy. Regarding the wind strength, it should be mentioned that in strong winds nets are often incapable of catching because the pockets are tightened and the birds do not get caught in the net. Capture probability varies by species and movement height (Lövei *et al.* 2001). Smaller species have a superior manoeuvring capability and thus avoid capture with a higher probability. For this reason, it is conceivable that the probability of catching decreases due to strong winds, so that the wind strength distorts the results in this form.

Most studies have found a correlation between tailwinds and the number of migratory birds (Emlen 1975, Bloch & Bruderer 1982, Gauthreaux 1982, 1991, Alerstam 1990, Richardson 1990, Åkesson & Hedenström 2000, Bozó *et al.* 2018). Some studies consider the tailwind as a criterion for successful migration in certain cases (Piersma & Jukema 1990, Butler

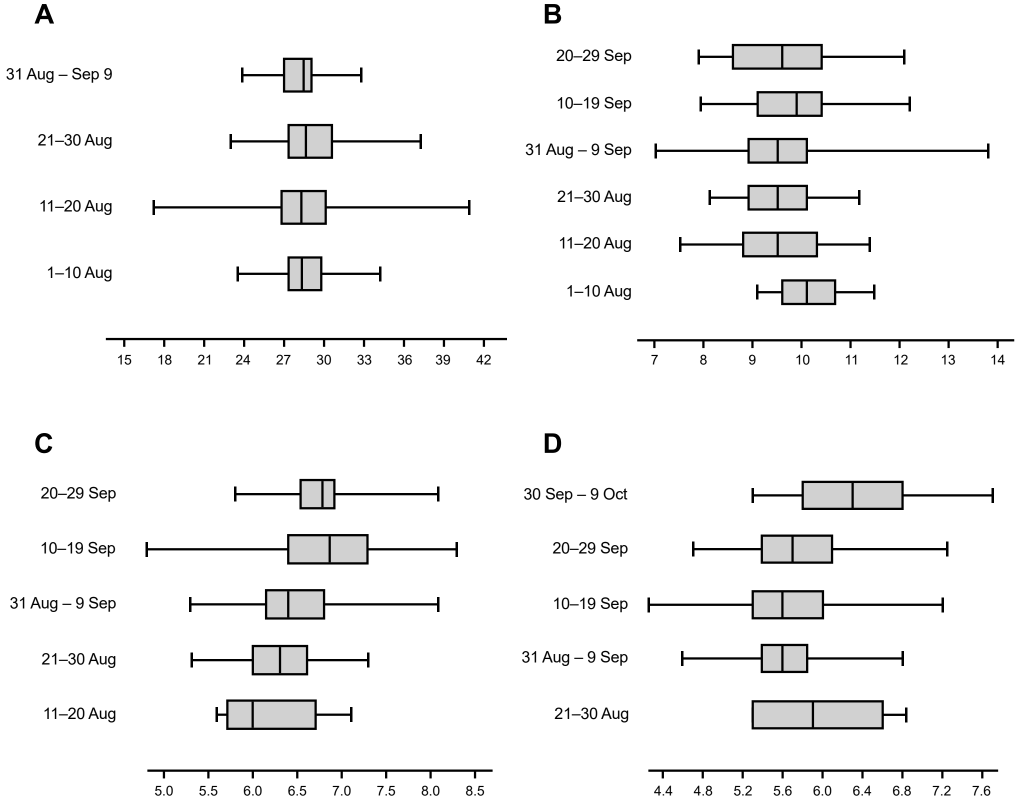

Fig. 2. Changes in body mass (x-axis) during subsequent decades in autumn for Thick-billed Warbler (A), Dusky Warbler (B), Yellow-browed Warbler (C) and Pallas's Leaf Warbler (D).

et al. 1997). Others, such as Fransson (1998) found no correlation between the tailwind and the departure of birds from the stopover site in the case of the Common Whitethroat (*Sylvia communis*). Bozó *et al.* (2018) found a difference in the association of wind direction with migration in spring and autumn, since tailwinds in autumn and crosswinds in spring proved to be decisive for several Siberian *Phylloscopus* species. The study of Erni *et al*. (2002) shows that birds distinguish between favourable and unfavourable weather conditions, however, they observed that birds migrated not only in the case of opposing winds but also in the case of weak crosswinds. This may be due to the fact that western winds predominate in central Europe, so birds generally do not encounter supporting winds. The same may be the case at Lake Baikal, where mainly eastern winds predominate (Lutgens & Tarbuck 2001), so birds cannot use support winds in spring and autumn, so it is understandable that wind direction has no effect on their migration.

Bird migration is also significantly associated with precipitation: birds migrate mainly in rainless weather, while prolonged rainfall slows down the migration (Richardson 1978, Alerstam 1990). In central Europe, relative migration intensity decreased as rain duration increased (Erni *et al.* 2002), and in the Russian Far East, Bozó *et al.* (2018) also found that migration was significantly lower on rainy days. Nevertheless, no correlation was found between the amount of precipitation and the migration (number of captured birds) of the studied species in this study. According to our own observations, certain species (e.g. buntings, finches, thrushes) migrated in huge (ten thousand) masses, concentrated in some areas on some days, while at other times they may have been completely absent. In contrast, this was not the case for the leaf warblers as they were caught in roughly the same amount during the whole migration period, including rainy days. As *Phylloscopus* species migrate from tree to tree during the day over very short distances, their movement is unlikely to be affected to the same extent by rain as species that fly longer distances.

Previous studies have shown that bird migration generally intensifies in the spring as temperatures rise, while in autumn it tends to intensify as temperatures decline (reviewed by Richardson 1978). According to the results of similar studies on *Phylloscopus* species in the Muraviovka Park, temperature proved to be the most important weather variable on the migration (Bozó *et al.* 2018): in the case of Yellow-browed Warblers and Dusky Warblers, most individuals were caught in the nets at higher temperatures in both spring and autumn, while Pallas's Leaf Warblers had the same situation in the spring, but most birds were caught in rising temperature. In the present study, a negative correlation between temperature and the number of birds in spring was only found in the case of Yellow-browed Warblers, which is contrary to the results of most studies. However, e.g. Richardson (1978) found that eastward migration in the northern Yukon tends to occur with low temperature, because in that area following westerly winds tend to be cold. For this reason, it is conceivable that we obtained a negative correlation in spring because the dominant eastern winds are typically cold and birds migrate regardless of its temperature. It should be noted, that given the low sample size and multiple testing, this association needs to be carefully considered.

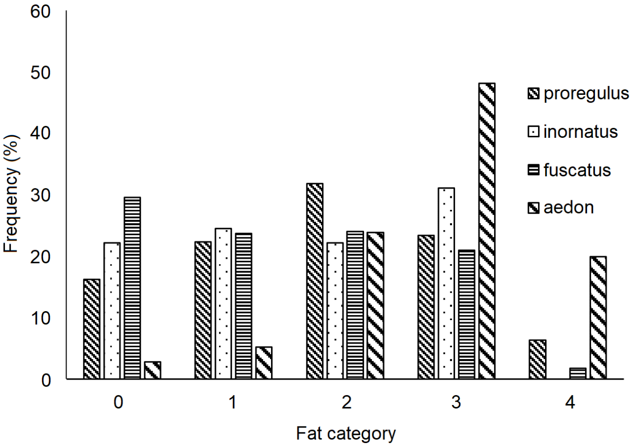

Fig. 4. Frequencies of different fat categories of the study species in autumn.

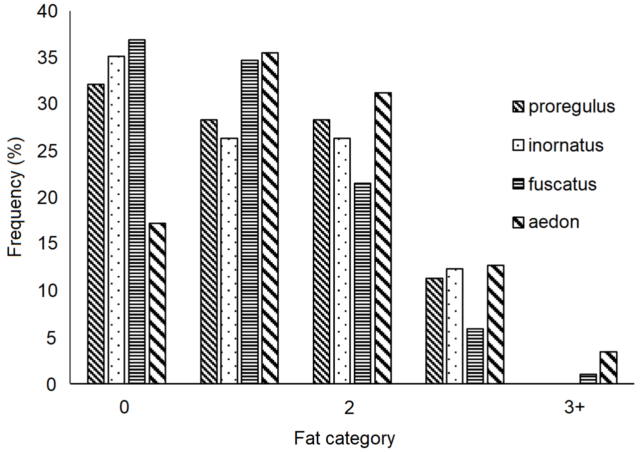

Fig. 3. Frequencies of different fat categories of the study species in spring.

The species studied migrated with very low fat reserves in both spring and autumn. This may be due to the fact that this area is not an important stopover site, birds just migrate through and only replenish their energy stores later. This is also confirmed by the fact that there are no within-season recaptures, the birds quickly moved out of the area. There are no habitat patches for the Thick-billed Warblers where they could stop over for feeding for a longer period, but the taiga forest and its edge would be an optimal habitat for leaf warblers. Yellow-browed Warblers migrating in the Muraviovka Park also had low fat reserves and spent a short time in the area (Bozó *et al.*

Table 5. Results of the multiple regressions regarding to the association of different weather variables (temperature, wind speed, wind direction and precipitation) with the weight and stored fat of the trapped birds. Significant *p*-values are in bold.

			Spring				Autumn			
Species	Constant	Variable	Coef.	*t*	*p*	R^2	Coef.	*t*	*p*	R^2
Thick-billed Warbler	Weight	Temp.	–0.083	–1.91	0.057	0.0110	0.002	0.024	0.981	0.0023
		Wind s.	0.086	2.90	**0.004**	0.0099	–0.015	–0.404	0.686	0.0006
		Wind d.	–0.010	–0.46	0.646	0.0040	0.121	2.647	**0.008**	0.0184
		Prec.	–0.289	–3.54	**0.000**	0.0089	0.020	0.294	0.769	0.0001
	Fat	Temp.	0.027	1.12	0.264	0.0062	–0.052	–2.300	**0.022**	0.0415
		Wind s.	0.028	1.67	0.096	0.0015	0.028	2.250	**0.025**	0.0516
		Wind d.	0.029	2.33	**0.020**	0.0155	0.022	1.422	0.156	0.0237
		Prec.	–0.059	–1.29	0.199	0.0013	0.056	2.352	**0.019**	0.0211
Dusky Warbler	Weight	Temp.	–0.038	–2.17	**0.031**	0.0226	0.002	0.117	0.907	0.0058
		Wind s.	0.013	0.96	0.340	0.0100	0.038	2.308	**0.022**	0.0249
		Wind d.	0.013	0.91	0.364	0.0001	–0.012	–0.701	0.484	0.0058
		Prec.	–0.031	–0.84	0.402	0.0001	–0.014	–0.320	0.749	0.0013
	Fat	Temp.	0.000	0.09	0.927	0.0001	0.000	–1.171	0.243	0.0053
		Wind s.	0.013	0.93	0.355	0.0027	0.074	4.620	**0.000**	0.0787
		Wind d.	–0.002	–0.09	0.927	0.0000	–0.003	–0.142	0.887	0.0088
		Prec.	–0.043	–1.26	0.209	0.0055	0.048	1.230	0.220	0.0076
Yellow-browed Warbler	Weight	Temp.	0.034	1.32	0.194	0.0170	–0.046	–4.510	**0.000**	0.1200
		Wind s.	0.025	1.03	0.306	0.0008	0.020	2.645	**0.009**	0.0826
		Wind d.	0.002	0.09	0.930	0.0003	–0.007	–0.536	0.592	0.0108
		Prec.	–0.251	–1.40	0.166	0.0140	–0.018	–1.081	0.281	0.0002
	Fat	Temp.	0.045	1.04	0.305	0.0137	–0.100	–5.048	**0.000**	0.1258
		Wind s.	0.067	1.63	0.109	0.0393	0.039	2.744	**0.006**	0.0644
		Wind d.	0.058	1.28	0.207	0.0107	–0.062	–2.443	**0.015**	0.0001
		Prec.	0.042	0.14	0.891	0.0277	–0.024	–0.755	0.451	0.0008
Pallas's Leaf Warbler	Weight	Temp.	–0.070	–3.07	**0.004**	0.1800	–0.045	–6.945	**0.000**	0.0644
		Wind s.	–0.027	–1.69	0.098	0.0181	–0.010	–1.790	0.074	0.0001
		Wind d.	–0.007	–0.29	0.776	0.0265	–0.011	–1.520	0.129	0.0016
		Prec.	0.008	0.11	0.911	0.0413	–0.017	–1.068	0.286	0.0012
	Fat	Temp.	0.052	1.16	0.252	0.0095	–0.103	–7.903	**0.000**	0.0970
		Wind s.	0.118	3.64	**0.001**	0.1553	–0.017	–1.445	0.149	0.0050
		Wind d.	0.103	2.25	**0.029**	0.0582	–0.019	–1.302	0.194	0.0000
		Prec.	–0.182	–1.36	0.179	0.0017	0.090	2.812	**0.005**	0.0160

2020a). Among the European species, Common Chiffchaff (*Ph. collybita*) uses the same strategies, which involves migrating shorter distances with low fat reserves (Ścisłowska & Busse 2005, Gyurácz & Csörgő 2009). Within the autumn season Yellow-browed Warblers and Pallas's Leaf Warblers increased body weight and fat reserves, while in spring, increasing fat reserves were detected only for Pallas's Leaf Warblers. Both Pallas's Leaf Warblers and Dusky Warblers decreased body weight in the spring. Autumn body weight and fat gain may be due to the fact that individuals migrating at different times come from different latitudes, so the location of stopover sites may differ. At the same time, it is also inconceivable that later migrants will be forced to migrate with larger energy stores due to more unfavourable weather conditions in order to survive colder, sometimes wetter periods. In spring, there were already species-level differences, probably due to different feeding strategies (Price 1991, Forstmeier *et al.* 2001, Katti & Price 2003, Batova 2011), nesting seasons and habitats (Glutz von Blotzheim & Bauer 1991, del Hoyo *et al.* 2006).

Temperature correlated negatively with body mass and fat score in Yellow-browed Warblers and Pallas's Leaf Warblers, and most strongly in the autumn. This is due to the fact that in general, low temperature increase the energy requirements of the birds (Richardson 1978). In females of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) long days and low temperatures increased body mass and fat reserves. In contrast, not temperature but photostimulation affected the body mass and fat reserves of males (Wingfield *et al.* 2003). In case of Great Tits, residual evening weights were higher during the period of unpredictable temperatures. At the end of the period with unpredictable temperatures, more weight was gained on cold than on warm days (Bednekoff *et al.* 1994).

During stronger winds (especially in Yellow-browed Warblers and Dusky Warblers in autumn, and Thick-billed Warblers and Pallas's Leaf Warblers in spring) and tailwinds (especially in Thick-billed Warblers in autumn) birds also increased their body mass and fat reserves. Birds need less energy under supporting winds the same distance to cover (Tucker 1974, Alerstam 1976). For species crossing large barriers along their migratory journey, sufficient fat reserves and tailwinds are essential (Berger & Hart 1974, Tucker 1974). In addition, especially in spring and in case of species breeding in northern latitudes, there is a great importance of the high fat reserves, since these species often arrive to the breeding grounds very early when the food availibility is poor (Ryder 1971, Irving 2012). In addition, strong winds increase heat loss, therefore the high fat reserves are essential (Richardson 1978). Important to note, however, that all the study species are insectivorous (del Hoyo *et al.* 2006), therefore they would not be able to prey as much insects as they need in rainy days when insect availability is lower. This is likely the reason we observed more fat in Thick-billed Warblers and Pallas's Leaf Warblers on rainy days.

There were also intraspecific differences between seasons, which are likely explained by with different environmental and meteorological conditions and feeding opportunities for different species, and use different migratory strategies. Sample sizes varied between autumn and spring which may also contribute to such differences. A possible response to avoid these difficulties is the loop migration, when birds use different migration routes in spring and in autumn (Thorup *et al.* 2017, Tøttrup *et al.* 2017). Loop migration was studied in some Siberian Passerines, included leaf warblers, but the results showed that these species most likely use the same routes in different seasons (Bozó *et al.* 2020b). The reason for this is that the East Asian-Australasian migratory flyway provides continuous refueling opportunities without extreme barriers (Yong *et al.* 2015). However, as we noted before, these stopover sites may provide different feeding opportunities by seasons, and the birds need to change more or less their migration timing, or the responses to the different weather conditions may also be different between spring and autumn. Given that for some species we worked with a lower sample size than for others, further studies are needed to confirm the species-specific results, yet many of our results are in good agreement with those of similar studies in other migration systems.

Sääolosuhteiden vaikutus kerttujen muuttoon ja kuntoon Siperiassa

Sääolosuhteet, kuten tuulen nopeus ja -suunta, sademäärä ja lämpötila säätelevät lintujen muuttoa. Sääolosuhteet vaikuttavat myös lintujen kuntoon, kuten painoon ja rasvavaraston määrään. Tutkimuksessa selvitimme sääolosuhteiden vaikutusta neljän kerttulajin muuton ajoittumiseen ja kuntoon sekä kevät- että syysmuutolla. Tutkimme myös painon ja rasvan muutoksia kevät- ja syysmuuton aikana. Tutkimusalueena oli Baikaljärven ympäristö Venäjällä, jossa sääolosuhteet ovat hyvin ankarat. Analysoimme aineistoa 2471 linnusta vuosina 2015–2019. Sääoloilla ei näyttänyt olevan vaikutusta muuton ajoittumiseen (lintumääriin). Lintujen paino ja rasvavarastot lisääntyivät huonon sään aikana johtuen suurentuneesta energiantarpeesta. Alueella muuttavien lintujen rasvavarastot olivat suhteellisen vähäiset, mikä voi johtua siitä, että alue ei ole tärkeä pysähtymispaikka.

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