Resource selection of black grouse in an isolated population in northern Germany – the importance of mixing dry and wet habitats

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Wildlife habitats in general must provide foraging-, hiding and resting places as well as sites for reproduction. In this respect, little is known about habitat selection of black grouse in the lowlands of Central Europe. We investigated habitat selection of seven radio tagged black grouse individuals in an open heath and grassland area surrounded by dense pine forests in the northern German nature reserve Lüneburg Heath. This site carries one of the last remaining black grouse populations in the Central European lowlands. Using resource selection functions based on presence/background data, we determined the probability of black grouse occurrence according to the availability of, or distance to habitat types as well as vegetation diversity indices. Our results show a preference for undisturbed, heterogeneous habitat compositions based on wide sand heaths and natural grasslands intermixed with patches of bog, high diversity of vegetation and food plants, low density of (loose) shrub formations and solitary trees, and sufficient distance from dense forests. We found a particularly high importance of wetland habitats (bogs, mires, fens) in a landscape dominated by dry heaths and grasslands. We projected the model prediction of habitat suitability on the entire nature reserve. As expected, only a minor part (8.8 km² ≙ 3.8%) is suitable for black grouse, as it mainly consists of dense forests. But also, smaller open heath areas are partly unsuitable. Therefore, we argue that it is necessary to increase habitat patch size and connectivity, while providing a mosaic of heterogeneous elements in these habitat islands. Our results may be used to inform and improve black grouse habitat management in the region and elsewhere.

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Abstract

Wildlife habitats in general must provide foraging-, hiding and resting places as well as sites for reproduction. In this respect, little is known about habitat selection of black grouse in the lowlands of Central Europe. We investigated habitat selection of seven radio tagged black grouse individuals in an open heath and grassland area surrounded by dense pine forests in the northern German nature reserve Lüneburg Heath. This site carries one of the last remaining black grouse populations in the Central European lowlands. Using resource selection functions based on presence/background data, we determined the probability of black grouse occurrence according to the availability of, or distance to habitat types as well as vegetation diversity indices. Our results show a preference for undisturbed, heterogeneous habitat compositions based on wide sand heaths and natural grasslands intermixed with patches of bog, high diversity of vegetation and food plants, low density of (loose) shrub formations and solitary trees, and sufficient distance from dense forests. We found a particularly high importance of wetland habitats (bogs, mires, fens) in a landscape dominated by dry heaths and grasslands. We projected the model prediction of habitat suitability on the entire nature reserve. As expected, only a minor part (8.8 $km^2 \triangleq 3.8\%$) is suitable for black grouse, as it mainly consists of dense forests. But also, smaller open heath areas are partly unsuitable. Therefore, we argue that it is necessary to increase habitat patch size and connectivity, while providing a mosaic of heterogeneous elements in these habitat islands. Our results may be used to inform and improve black grouse habitat management in the region and elsewhere.

Introduction

In northern Central Europe, the black grouse has been in severe decline for decades and many populations have gone extinct due to large-scale habitat loss (Ludwig et al. 2009a; Ludwig et al. 2009b; Ludwig et al. 2008; Segelbacher et al. 2014). In northern Germany, the last remaining population is located in the region Lüneburg Heath, Lower Saxony (Strauß et al. 2018). This autochthonous black grouse population is fragmented into five subpopulations distributed among the nature reserve Lüneburg Heath and four neighbouring areas used for military purposes (Strauß et al. 2018). ~~These~~ core areas are surrounded by intensively used agricultural and large contiguous forestry areas (Cordes et al. 1997) and ~~the~~ distances between the core areas are 7 to 15 km (Strauß et al. 2018). ~~The~~ open heath and natural grassland areas that are expected to be potential black grouse habitats in the five core areas cover each between 13 and 86 km² (totalling 197 km²) (Strauß et al. 2018). Despite different protection and biotope improvement measures in the different core areas, such as continuous maintenance of the heath biotopes, removal of regenerating young trees, predator control and visitor guidance (Cordes et al. 1997; Kaiser 2015), the population could not be stabilized at a level of above 200 individuals (Strauß et al. 2018).

After a minimum population size in 1999 with 142 individuals, the population increased to 261 by 2011 and then declined again to a historic minimum of 126 individuals by 2020 (Strauß et al. 2018; Tost et al. 2020).

Previous studies from the nature reserve Lüneburg Heath indicate that the food supply for adult black grouse is sufficient in all seasons and that they have a good physical constitution (Strauß et al. 2018). Furthermore, the population seems to have adapted to anthropogenic influences ~~and can avoid these disturbances, which, however, leads to~~ fragmentation and loss of available habitats in the case of recreational use (Tost et al. 2020). ~~We assume that~~ predation pressure and changing weather conditions can also be considered as further factors (Wegge & Kastdalen 2008). ~~However,~~ habitat quality and quantity are the main prerequisites for stable populations (Klaus et al. 1990) but there are few studies that address resource selection by black grouse (Baines 1994; Immitzer et al. 2014; Patthey et al. 2011; Schweiger et al. 2012; White et al. 2015) and provide management implications that are applicable for the Lüneburg Heath habitats based on landscape characteristics. ~~In most European distribution areas,~~ black grouse habitats are geographically and scenically very different from those in the Lüneburg Heath, with those in the Netherlands and ~~partly in~~ England being the most comparable (Baines 1994). Therefore, we investigated ~~the~~ resource selection (Boyce et al. 2002; Forester et al. 2009; Northrup et al. 2013) and habitat suitability (Hirzel & Le Lay 2008) of black grouse in the Lüneburg Heath.

Generalized linear regression models were calculated using presence and random-background data (Phillips et al. 2009) and environmental data from large-scale vegetation and habitat mapping within the nature reserve Lüneburg Heath.

We hypothesized that 1) densely forested areas, settlements, traffic- as well as hiking trails have a negative effect, 2) large-scale open sandy heaths and natural grasslands, along with small-scale but regularly occurring wetlands and boggy sites, as well as a high structural richness and diversity of flat and medium vegetation have a positive effect on black grouse habitat suitability, and 3) pastures are used according to their availability. Using the model results from the study area, we spatially predicted habitat availability and distribution to the entire nature reserve.

Materials & Methods

Study area

The study area (16.3 km²) is a part of the nature reserve Lüneburg Heath in Lower Saxony, Germany (53.167930° N, 9.939770° E), which covers an area of 235 km² and is composed of 66% forest, 22% heath and grassland, 6% arable land, 5% pasture and 1% paths, buildings and water bodies (Cordes et al. 1997; Kaiser 2015; Strauß et al. 2018). It consists mainly of open heath and natural grassland with small-scattered shrub formations, juniper or pioneer vegetation and is surrounded by dense pine forests. This landscape in the North German lowlands is characterized by sandy ground and terminal moraines with flat undulating relief. The nature reserve's heathlands are the remains of a historic agricultural landscape development (Tost et al. 2020), the preservation of which is realized nowadays by modern mechanized landscape management as well as by sheep farming, and heather burning (Kaiser 2015). This study focuses solely on the nature reserve Lüneburg Heath; the neighbouring black grouse habitats in areas used for military purposes are not considered.

Black grouse data

About one quarter of the northern German black grouse population is located in the nature reserve's open heath and grassland (Strauß et al. 2018). In 2007 78 individuals (45 cocks; 33 hens) were counted during annual censuses conducted by the foundation Stiftung Naturschutzpark Lüneburger Heide and the Lower Saxony Federal Ornithological Station. Since then, numbers have been falling (Tost et al. 2020), with 66 individuals (38; 28) in 2011 and 60 (27; 33) in 2012. In 2021 only 33 individuals (22; 11) were counted in the nature reserve (F Stucke, 2021, pers. comm.).

A total of seven birds were captured and fitted with GPS tags in the eastern part of the nature reserve in 2011 and 2012. All birds were equipped with backpack mounted, battery operated tags with integrated VHF-module and accelerometers (e-obs GmbH, Gruenwald, Germany). Five cocks were fitted with 38 g, and two hens with 28 g tags. One cock was caught and tagged in May 2011, the remaining six birds (four cocks and two hens) were caught and tagged between March and May 2012 (Table 1). One hen (ID 1206) was recaptured and retagged in October 2012. Both hens successfully hatched their clutches, of which one was replaced after loss to predation. Five birds were preyed by goshawks or other predators, one bird (ID 1101) went missing and could not be recovered and one bird's fate (ID 1205) remains unknown after the tag's battery was depleted in December 2012 (Table 1). Depending on survival rates and battery duration, numbers of transmitting days ranged from 61 to 223 days between spring and autumn. GPS-locations were taken at predefined time intervals depending on the tags' programming, usually every three hours between 01:00 and 22:00. In total 2296 locations were taken. The minimum number of locations per individual was 96, the maximum was 546. The observation time ranged between 61 and 222 days. All stages of the animal experiment were conducted under a permit from the Lower Saxony Institute for Consumer Protection and Food Safety (LAVES, Dept. 33 Animal Welfare, permit number: 33.9-42502-04-11/0364). All field experiments were approved by the lower nature conservation authorites of the district Soltau-Fallingbostel (permit number: 09.509 N 24 - Lü 2 - 4) and district Harburg (permit number: 71 21/1.2.1-0.0 - 2011-0081 -Kr).

Environmental data

Habitat data were obtained from vegetation and biotope mapping carried out by Kaiser & Purps (2012) on behalf of the state of Lower Saxony for the baseline survey of the NATURA 2000 area. These data were kindly provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (NLWKN) for our analyses but may not be made publicly available in the original. Mapping was carried out between 2009 and 2011 according to the specifications of the Lower Saxony mapping key (von Drachenfels 2004) in the open heath areas. However, data are missing for parts of the forested areas of the nature reserve. Based on digital aerial photographs and field surveys the large-scale heaths were subdivided into 5698 polygons with a total area of 59.7 km^2 according to their biotope type composition, and then the plots were inventoried during detailed mappings (Kaiser & Purps 2012). Due to the size of the area, some of the surveys were conducted quantitatively along representative transects by recording percentages of the lengths of transect sections with homogeneous biotope characteristics. From this, plant species cover percentages per polygon were derived (Kaiser & Purps 2012).

Data processing

Data processing was performed in R (version 4.1.2) (R Core Team 2021). Modeling of habitat selection was based on the habitat and vegetation mappings, which were available as vector data. The data contained 166 biotope types, which were grouped to reduce the number of independent model variables in the further process (Table S1). The grouping was done according to the Lower Saxony mapping key (von Drachenfels 2004), which can be translated into the habitat types of the EU Habitats Directive (92/43/EEC). In addition, diversity indices were calculated using the mapping inventory of 511 plant species at polygon level (summed cover rate of food plants (Strauß et al. 2018), number of plant species, Shannon index of plant species, coefficient of variation of vegetation). The edited vector data were then rasterized into 10 × 10-meter cells, with grouped biotope types coded as presence (1) / absence (0). To account for heterogeneous edge effects, habitat layer boundaries were fanned out using focal weight with a radius of 25 meters, converting the binary data to continuous values between 0 and 1 (Hijmans 2021). In case of sparsely distributed or apparently unused structures distance rasters were created instead (Table 2).

In the next step, background points (n = 14,000) were spatially randomly distributed (Hijmans et al. 2021) within the home ranges of the seven tagged birds plus a buffer radius of 603 meters, which was calculated as the 95th percentile of step distances of successive GPS positions (Boyce 2006). This served to provide a clear spatial boundary for the model area based on realistic movement distances of black grouse rather than an arbitrarily defined reference area (Senay et al. 2013; VanDerWal et al. 2009). The data table for model building was then generated by extracting the raster values of all biotope and diversity index layers at the background and telemetry point locations.

Data analysis of resource selection

Resource selection was analysed using generalized linear mixed-effects models (R package lme4) with logistic regression (binomial error structure) (Bates et al. 2015; Kuznetsova et al. 2017), where the dependent variable was composed of GPS-locations (presence) and random background points (Phillips et al. 2009) as binary response (Brotons et al. 2004). To account for repeated measurements, individuals were considered as random factors. Data analyses were again performed in R (R Core Team 2021). Diversity indices and both habitat availability and distance values were included as predictor variables, excluding correlating variables (Spearman's Rho > 0.7). We performed manual stepwise forward model selection using the Akaike Information Criteria (AIC) for model evaluation. Models were built using simple and squared terms, with squared terms discarded if they did not improve model prediction (Brotons et al. 2004). Following stepwise model selection, interaction terms were added based on a priori hypotheses.

Results

Habitat selection

Forward model selection resulted in all variables entering the final model as squared terms, except for the variable availability of sand heaths and the two diversity indices summed cover rate of food plants and Shannon index of plant species (Table 3). Based on correlation analyses, number of plant species was previously discarded as a diversity variable in favour of the Shannon index of plant species. Also, ruderal and agricultural areas were discarded because their inclusion did not improve the model. Interactions were modelled for the two dominant habitat types, sand heaths (hc) and natural grasslands (r), each in interaction with the variables raised bogs, mires, and fens (mun), distance to dunes (dd), and summed cover rate of food plants (DG). Sand heaths were additionally interacted with shrub formations (buh) and the Shannon Index (siveg). However, for natural grasslands these two interactions (buh and siveg) were dropped in preference of a more parsimonious model due to high variances.
Because inventories of plant species in the forested peripheries of the study area were often not available, diversity indices (DG and siveg) could not be calculated and were therefore excluded entirely in one of the final models (Table 3b). In the other model, diversity indices were included but data points with missing values in the surrounding forests were omitted (Table 3a).
Both models show basically similar results for all predictor variables, with the difference that in model b) all main effects and interaction effects are generally mitigated, in particular for sand

heaths and natural grasslands. However, the pattern of effects is consistent between both models. The models explain increased black grouse presence in areas of high diversity of (food) plant species (DG and siveg) with a good availability of sand heaths (hc) and natural grasslands (r) in the vicinity of raised bogs, mires and fens (mun) and with low-density shrub formations (buh) and patches of open soil / dunes (dd) (Fig. 1 and 2). As shrub formations (buh) became denser in open sand heaths, probability of black grouse presence decreased. Resource selection by black grouse was highest at distances of 500 to 600 m from infrastructure (dpuo) and dense forests (dw). It also increased significantly starting 400 m away from pastures (dg), though the vicinity to pastures still indicated marginal habitat selection. When availability of raised bogs, mires and fens was high, interaction effects showed strong positive trends in habitat suitability for sand heaths and non-dominant natural grasslands (Fig. 2).

Projection of habitat suitability

Projection of the model predictions returned several large suitable habitat patches throughout the belt of open heath and grassland (southwest to northeast), as well as in the southern peripheral heaths (Fig. 3). The westernmost patches of the reserve were predicted to be more suitable than the large eastern patch from where we gathered our black grouse movement data. Some smaller habitat patches had only low predicted suitability for black grouse (e.g., north and south of our telemetry study area). In total, only 88.3 ha or 0.37% of the entire nature reserve (235 km^2) have a very high suitability (i.e., probability of black grouse presence is $p > 0.75$). In relation to only the open heath and grasslands, the area percentage of very high suitability is 1.9%. 285.7 ha (or 6% of open heath) have moderate to high suitability ($0.5 < p < 0.75$), and 512.9 ha (10.5% of open heath) have low to moderate suitability ($0.25 < p < 0.5$). The greatest part of the nature reserve consists of forest (66%) which accounts for a major part of the low to unsuitable areas (226 km^2; $p < 0.25$). However, 81.6% of the open heathland is also among these least suitable areas.

Discussion

Habitat selection

The final model described highly suitable black grouse habitats as undisturbed areas with sufficient patches of bog in structurally rich, heterogeneous heathland or natural grassland with enough distance from dense forests. The variable distance to infrastructure (dpuo) emerges as the strongest effect. This confirms previous findings on the avoidance of human disturbance (e.g. hiking trails) in the same study area as in this study (Tost et al. 2020) as well as in alpine habitats (Immitzer et al. 2014; Patthey et al. 2011), thus emphasizing the need for undisturbed black grouse habitats as refuge areas.

The availability of wetlands proved to be particularly important for black grouse habitat selection. According to our model, the interaction between bog patches and sand heaths turned out to be a favourable habitat combination, with increasing availability of both bogs and heaths significantly increasing the predicted probability of black grouse occurrence. A clear preference by black grouse for habitat compositions with moorland has been described for Scottish and northern English populations (Baines 1994; White et al. 2015). However, this habitat type makes up a significant portion of areas inhabited by black grouse in these regions. In contrast, the (dry) sand heaths and natural grasslands are the most common habitats in the nature reserve Lüneburg Heath, while bogs occur only rarely and cover a relatively small area. Thus, our results indicate a selective use of the few available bog patches. These findings may have important implications for conservation management not only in the nature reserve but also at the landscape scale, because most black grouse sites that went extinct in the federal state Lower Saxony until the mid-1980s were in regions with raised bogs and mires (Ludwig et al. 2008), exploited for peat mining (Ludwig et al. 2009b). Consequently, the significant renaturation of wet habitats not only inside existing black grouse habitats but also within dispersal distance is probably one of the most important measures to strengthen and increase the black grouse metapopulation.

Black grouse chickens need high availability of arthropods during their first weeks (Klaus et al. 1990; Wegge & Kastdalen 2008). There is possibly a higher arthropod availability in the nature reserve's wet valleys than in the dry sand heaths of the terrain ridges (Baines 1994; Patthey et al. 2011; Schweiger et al. 2012), allowing for a higher reproduction rate in these areas. However, we lack detailed knowledge about arthropod abundances in the different heathland habitats, making qualified assessments of breeding and rearing areas difficult. For the mixture of bog and natural grassland, the positive effect was less pronounced in our model. Here, the probability of black grouse occurrence was increased only when the availability of natural grassland was low to moderate, and the availability of bogs was high, thus supporting the hypothesis that wet habitats are preferred by black grouse and should be promoted by conservation management. It is possible that heather is preferred as hiding cover (Immitzer et al. 2014; Patthey et al. 2011; Wegge & Kastdalen 2008) over natural grassland near bog areas. Nevertheless, natural grasslands might be of importance during other phases of the black grouse life cycle, e.g., as display or nesting sites – both tagged hens placed their nests in grass-dominated areas.

Heterogeneity and patchiness of habitats and vegetation are key factors for black grouse habitat selection, as elaborated in several studies (Immitzer et al. 2014; Patthey et al. 2011; Schweiger et al. 2012; White et al. 2015). In our study area, such a positive effect was explained in our models both, by cover of nutrient plants and the Shannon index as measures of heterogeneity.

Furthermore, when combining sand heaths and wet habitats in an interaction, resource selection by black grouse was especially pronounced. The positive effect of sand heaths was strongly enforced when wet habitats became dominant. This finding should further encourage black grouse managers to create and maintain mosaics of these two important habitats.

According to our results, dominant cover rates of shrub formations did not improve habitat suitability. Plots with high shrub proportions even reduced selection. However, this only applied to areas with high density of predominantly scattered shrubs. For areas with lower abundance of these, this observation did not apply. Field observations showed that hens and cocks use solitary pines and birches as lookouts, especially during the mating season. In addition, mature trees act as an important food source during spring (Strauß et al. 2018). In fact, an adequate supply of low-density woody plants should be provided, as they promote the availability of anthills as essential chick food (Schweiger et al. 2012; Signorell et al. 2010; Wegge & Kastdalen 2008). According to Wegge & Kastdalen (2008), young black grouse broods in Norwegian boreal forest preferred pine bogs with lower tree and shrub density, but higher potential predation risk over denser, bilberry-dominated forest types, which were rather used by capercaillie broods. Our study showed that dense forested areas surrounding the core habitats, but also dense woodlands in open heathland, were entirely avoided by black grouse. This likely serves the purpose of predator avoidance (Brown et al. 1999; Laundre et al. 2010) but may also be due to a ground vegetation unfavourable for mobility and feeding. In Scotland, mosaics of young forests (younger than 14 years) within moorlands are important habitats for winter and spring foraging, but also act as lek sites, breeding grounds, and shelter from predation. However, these benefits are lost in old growth forests due to the change towards a less suitable ground vegetation (White et al. 2015). Alpine black grouse habitats are known to span above the timberline with preference for semi-open heterogeneous patches of alpine meadows and (dwarf) shrubland, intermixed with low-density young and mature trees (Immitzer et al. 2014; Patthey et al. 2011; Schweiger et al. 2012). Given the avoidance of forest edges in the nature reserve Lüneburg Heath and the positive habitat suitability of forest transition zones according to previous studies, it is recommended to lighten the edge structure, away from a vertical forest edge to a gradual transition from open land to forest area, with associated understory of heather and berry bushes (Vaccinium and Empetrum).

Interestingly, black grouse habitat selection increased remarkably when distance to pastures was higher than 400m. While extensive pasture farming was beneficial for black grouse in the 1950s and -60s (Ludwig et al. 2009a; Ludwig et al. 2009b), contemporary intensive pasture management with low plant diversity and high nutrient influx might be detrimental for the species. Despite pasture management in the nature reserve is still carried out conservatively and without fertilization, these areas, as well as the surrounding heaths and natural grasslands, are affected by significant atmospheric nutrient deposition. However, pastures play only a minor role in the black grouse's habitat mix in the nature reserve Lüneburg Heath. Studies in the Alps (alpine meadows) as well as in England assessed pastures rather positively (insect availability) (Baines 1994; Patthey et al. 2011), as long as grazing was neither too intensive (Calladine et al. 2002) nor too light (Immitzer et al. 2014; Schweiger et al. 2012), and concealment was provided nearby (Signorell et al. 2010). Incidentally, these statements on grazing are particularly applicable to extensive sheep grazing in the open heath landscape of the nature reserve. Regarding monotonous, fenced pastures, the positive effects might only apply seasonally with corresponding vegetation height.

Our results apply primarily to spring and summer, and to a limited extent to autumn, due to the coverage period of the telemetry study. Resource selection during autumn and winter might differ from our results. For instance, during past years, groups of black grouse have occasionally been sighted in winter on farmland in the nature reserve (extensive cultivation, e.g., buckwheat). However, farmland could not be incorporated into our model due to lack of presence data.

Projection of habitat suitability

Our model predicted well-suited habitats in the nature reserve's central belt of open heath and grassland, which are known to be selected by black grouse throughout the year, based on annual population censuses and incidental records from long-term observations, scat sample locations and camera trap surveys. While core habitats in the western part of the nature reserve appear to be connected (relatively low fragmentation), projection of our models revealed a possible isolation of the core habitat in the eastern part. However, the vast heathland areas that lie between these two core areas are largely unsuitable habitats, which may be due to the high density of trails, an important local road and some settlements and single buildings in this area. Our model predicted good habitat suitability for the southernmost heathlands, but these have not been populated by black grouse for several years. We suspect that this discrepancy may relate to nearby wind turbines (Coppes et al. 2019; Coppes et al. 2020) to the east and a waste disposal facility and conventional farms to the west, adding to other disturbances within the habitats. Although several further sites of open heathland remain in the nature reserve Lüneburg Heath, they seem to be of poor suitability for black grouse according to model predictions. Again, this is probably due to the high density of trails and the proximity to older forests. Observations during annual black grouse censuses and reports of incidental observations support this prediction. This implies that numerous considerable parts of the open heaths – mainly in the nature reserve's periphery – are effectively inaccessible to the local population, which is instead restricted to the larger, centrally located heathland areas. These peripheral areas, however, are important for habitat connectivity with the southern adjacent military training areas and thus for dispersal between the fragmented subpopulations (Andrén 1994; Hanski 2008). Thinning of forest edges could increase attractiveness of such areas, provided they are undisturbed, unfragmented areas of sufficient size in the first place.

Management and research implications

There are a variety of management implications, accordingly the following actions are recommended: 1) creation of small scale habitat mosaics of heterogeneous dry heaths and grassland with high diversity of food plants throughout the open landscape, 2) restoration and promotion of wet habitats (mires, raised bogs) where topographically possible, 3) avoidance of large, monotonous heath and grassland areas, 4) reduction of regeneration stage of young, emergent trees (pioneer vegetation), but preservation of solitary trees (pines, birches, juniper) as food source and shelter, 5) thinning of forest edges and creation of transition gradients over several hundred meters, 6) providing micro patches of open soil, 7) visitor guidance and enforcement of its compliance, relocation of infrastructure to less exposed areas or landscaping to provide visual cover by vegetation, and reduction of tourism pressure if possible, 8) mixing pastures with habitat elements such as dunes, loose shrub formations for concealment, and wet zones, 9) improvement of habitat connectivity: consideration of fragmentation effects and thus reduction isolation inside as well as outside the nature reserve's borders by creation of heterogenous habitats beyond the core areas. However, these measures are recommended regardless of the individual interests of the various stakeholders and any resulting conflicts.

Next steps in local black grouse research should focus on microhabitats by examining vegetation species composition in detail, monitoring arthropod abundances in different habitat types, and incorporating landscape management practices, e.g., heath mowing, sod cutting, heath burning, and sheep grazing. In addition, the overlap of black grouse habitats with those of the most common predators are currently being investigated, thus identifying conflict zones. Further telemetry studies with higher sample sizes (more individuals, longer duration, shorter timing of fixes) and new study areas would be desirable. However, pragmatic reasons might complicate the realization regarding the low chances of success in catching animals in the nature reserve (only 33 individuals counted in 2021) or on the closed military training areas. An alternative could be a scientifically supervised translocation of Swedish black grouse to the Lüneburg Heath, as it is already done in the Bavarian Rhön and in the Dutch Sallandse Heath. With no doubt, the prevailing metapopulation context is one of the central reasons that black grouse still exist in the Lüneburg Heath area. Therefore, dispersal between military training areas and the nature reserve as well as the individual roles of the five subpopulations for long-term survival of the entire metapopulation should be given special attention in future studies.

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References

Andrén H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos 71:355-366. 10.2307/3545823

Baines D. 1994. Seasonal Differences in Habitat Selection by Black Grouse Tetrao-Tetrix in the Northern Pennines, England. Ibis 136:39-43.

Bates D, Mächler M, Bolker B, and Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1-48. 10.18637/jss.v067.i01

Boyce MS. 2006. Scale for resource selection functions. Diversity and Distributions 12:269-276. 10.1111/j.1366-9516.2006.00243.x

Boyce MS, Vernier PR, Nielsen SE, and Schmiegelow FKA. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300. https://doi.org/10.1016/S0304-3800(02)00200-4
Brotons L, Thuiller W, Araújo MB, and Hirzel AH. 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27:437-448. https://doi.org/10.1111/j.0906-7590.2004.03764.x
Brown JS, Laundré JW, and Gurung M. 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. Journal of Mammalogy 80:385-399. 10.2307/1383287
Calladine J, Baines D, and Warren P. 2002. Effects of reduced grazing on population density and breeding success of Black Grouse in northern England. Journal of Applied Ecology 39:772-780. 10.1046/j.1365-2664.2002.00753.x
Coppes J, Braunisch V, Bollmann K, Storch I, Mollet P, Grünschachner-Berger V, Taubmann J, Suchant R, and Nopp-Mayr U. 2019. The impact of wind energy facilities on grouse: a systematic review. Journal of Ornithology 161. 10.1007/s10336-019-01696-1
Coppes J, Kämmerle J-L, Grünschachner-Berger V, Braunisch V, Bollmann K, Mollet P, Suchant R, and Nopp-Mayr U. 2020. Consistent effects of wind turbines on habitat selection of capercaillie across Europe. Biological Conservation 244:108529. 10.1016/j.biocon.2020.108529
Cordes H, Kaiser T, v. d. Lancken H, Lütkepohl M, and Prüter J. 1997. Naturschutzgebiet Lüneburger Heide. Bremen: H. M. Hausschild GmbH.
Forester JD, Im HK, and Rathouz PJ. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554-3565. 10.1890/08-0874.1
Hanski I. 2008. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17-38. 10.1111/j.1095-8312.1991.tb00549.x
Hijmans RJ. 2021. raster: Geographic Data Analysis and Modeling. R package version 3.5-9. https://CRANR-projectorg/package=raster.
Hijmans RJ, Phillips S, Leathwick J, and Elith J. 2021. dismo: Species Distribution Modeling. R package version 1.3-5. https://CRANR-projectorg/package=dismo.
Hirzel AH, and Le Lay G. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45:1372-1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x
Immitzer M, Nopp-Mayr U, and Zohmann M. 2014. Effects of habitat quality and hiking trails on the occurrence of Black Grouse (Tetrao tetrix L.) at the northern fringe of alpine distribution in Austria. Journal of Ornithology 155:173-181. 10.1007/s10336-013-0999-3
Kaiser T. 2015. Das Naturschutzgebiet Lüneburger Heide - Natur- und Kulturerbe von europäischem Rang. Teil 2 - VNP-Schriften. Niederhaverbeck
Kaiser T, and Purps J. 2012. Basiserfassung im FFH-Gebiet Nr. 70 Lüneburger Heide. Auftraggeber: Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz: Büro Prof. Dr. Thomas Kaiser (Arbeitsgruppe Land & Wasser). p 95.
Klaus S, Bergmann H, Marti C, Müller F, Vitovic O, and Wiesner J. 1990. Die Birkhühner (Tetrao tetrix und T. mlokosiewczi). Wittenberg, Lutherstadt: A. Ziemsen Verlag.

Kuznetsova A, Brockhoff PB, and Christensen RHB. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1-26. 10.18637/jss.v082.i13
Laundre J, Hernández L, and Ripple W. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. The Open Ecology Journal 3:1-7. 10.2174/1874213001003030001
Ludwig T, Storch I, and Gärtner S. 2009a. Large-scale land use change may explain bird species declines in semi-natural areas: the case of Black Grouse population collapse in Lower Saxony, Germany. Journal of Ornithology 150:871-882. 10.1007/s10336-009-0410-6
Ludwig T, Storch I, and Graf R. 2009b. Historic landscape change and habitat loss: the case of black grouse in Lower Saxony, Germany. Landscape Ecology 24:533-546. 10.1007/s10980-009-9330-3
Ludwig T, Storch I, and Wübbenhorst J. 2008. How the Black Grouse was lost: historic reconstruction of its status and distribution in Lower Saxony (Germany). Journal of Ornithology 149:587-596. 10.1007/s10336-008-0306-x
Northrup JM, Hooten MB, Anderson CR, Jr., and Wittemyer G. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456-1463. 10.1890/12-1688.1
Patthey P, Signorell N, Rotelli L, and Arlettaz R. 2011. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. European Journal of Wildlife Research 58:59-70. 10.1007/s10344-011-0540-z
Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, and Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19:181-197. https://doi.org/10.1890/07-2153.1
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria: URL https://www.R-project.org/.
Schweiger AK, Nopp-Mayr U, and Zohmann M. 2012. Small-scale habitat use of black grouse (Tetrao tetrix L.) and rock ptarmigan (Lagopus muta helvetica Thienemann) in the Austrian Alps. European Journal of Wildlife Research 58:35-45. 10.1007/s10344-011-0537-7
Segelbacher G, Strand T, Quintela M, Axelsson T, Jansman HH, Koelewijn H-P, and Höglund J. 2014. Analyses of historical and current populations of black grouse in Central Europe reveal strong effects of genetic drift and loss of genetic diversity. Conservation Genetics 15:1183-1195. 10.1007/s10592-014-0610-3
Senay SD, Worner SP, and Ikeda T. 2013. Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling. PLoS One 8:e71218. 10.1371/journal.pone.0071218
Signorell N, Wirthner S, Patthey P, Schranz R, Rotelli L, and Arlettaz R. 2010. Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse Tetrao tetrix hens: habitat management implications. Wildlife Biology 16:249-257. 10.2981/09-028

Strauß E, Tost D, Ratsch C, Kulow J, Stolter C, Wormanns S, and Siebert U. 2018. Bestandsentwicklung und Nahrungsökologie des Birkhuhns Tetrao tetrix in Niedersachsen. Der Ornithologische Beobachter 115:261-280.

Tost D, Strauss E, Jung K, and Siebert U. 2020. Impact of tourism on habitat use of black grouse (Tetrao tetrix) in an isolated population in northern Germany. PLoS One 15:e0238660. 10.1371/journal.pone.0238660

VanDerWal J, Shoo LP, Graham C, and Williams SE. 2009. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecological Modelling 220:589-594. 10.1016/j.ecolmodel.2008.11.010

von Drachenfels O. 2004. Kartierschlüssel für Biotoptypen in Niedersachsen unter besonderer Berücksichtigung der nach § 28a und § 28b NNatG geschützten Biotope sowie der Lebensraumtypen von Anhang I der FFH-Richtlinie. Naturschutz und Landschaftspflege in Niedersachsen. 6. ed. Hannover: Niedersächsischer Landesamt für Ökologie, . p 121.

Wegge P, and Kastdalen L. 2008. Habitat and diet of young grouse broods: resource partitioning between Capercaillie (Tetrao urogallus) and Black Grouse (Tetrao tetrix) in boreal forests. Journal of Ornithology 149:237-244. DOI 10.1007/s10336-007-0265-7

White PJC, Warren P, and Baines D. 2015. Habitat use by Black Grouse Tetrao tetrix in a mixed moorland-forest landscape in Scotland and implications for a national afforestation strategy. Bird Study 62:1-13. 10.1080/00063657.2014.1000261

Figure 1

Predicted probability of black grouse occurrence (pb) as function of independent distance variables (left), habitat availability variables (middle) and diversity indices (right).

Habitat availability variables are given as continuous values of their respective area coverage. The main effects relate to the model including diversity indices (Table 3a).

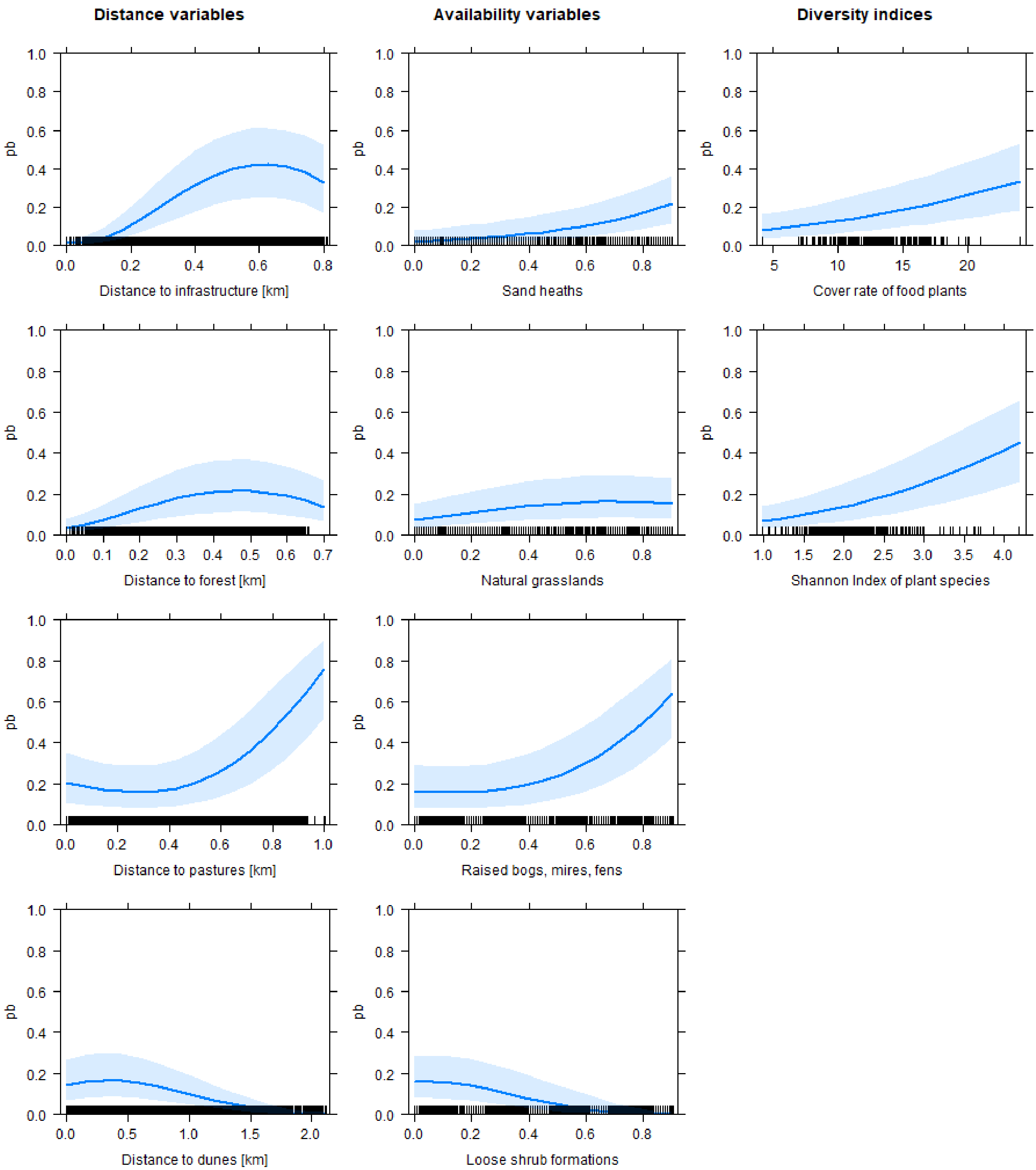
Distance variables
Availability variables
Diversity indices
pb
Distance to infrastructure [km]
Sand heaths
Cover rate of food plants
Distance to forest [km]
Natural grasslands
Shannon Index of plant species
Distance to pastures [km]
Raised bogs, mires, fens
Distance to dunes [km]
Loose shrub formations

Figure 2

Predicted probability of black grouse occurrence (pb) as function of interaction terms.

Availability of sand heaths (left), availability of natural grasslands (right); mun = raised bogy, mires, fens; buh = shrub formations; dd = distance to dunes in km; DG = summed cover rate of food plants; siveg = Shannon Index of plant species.

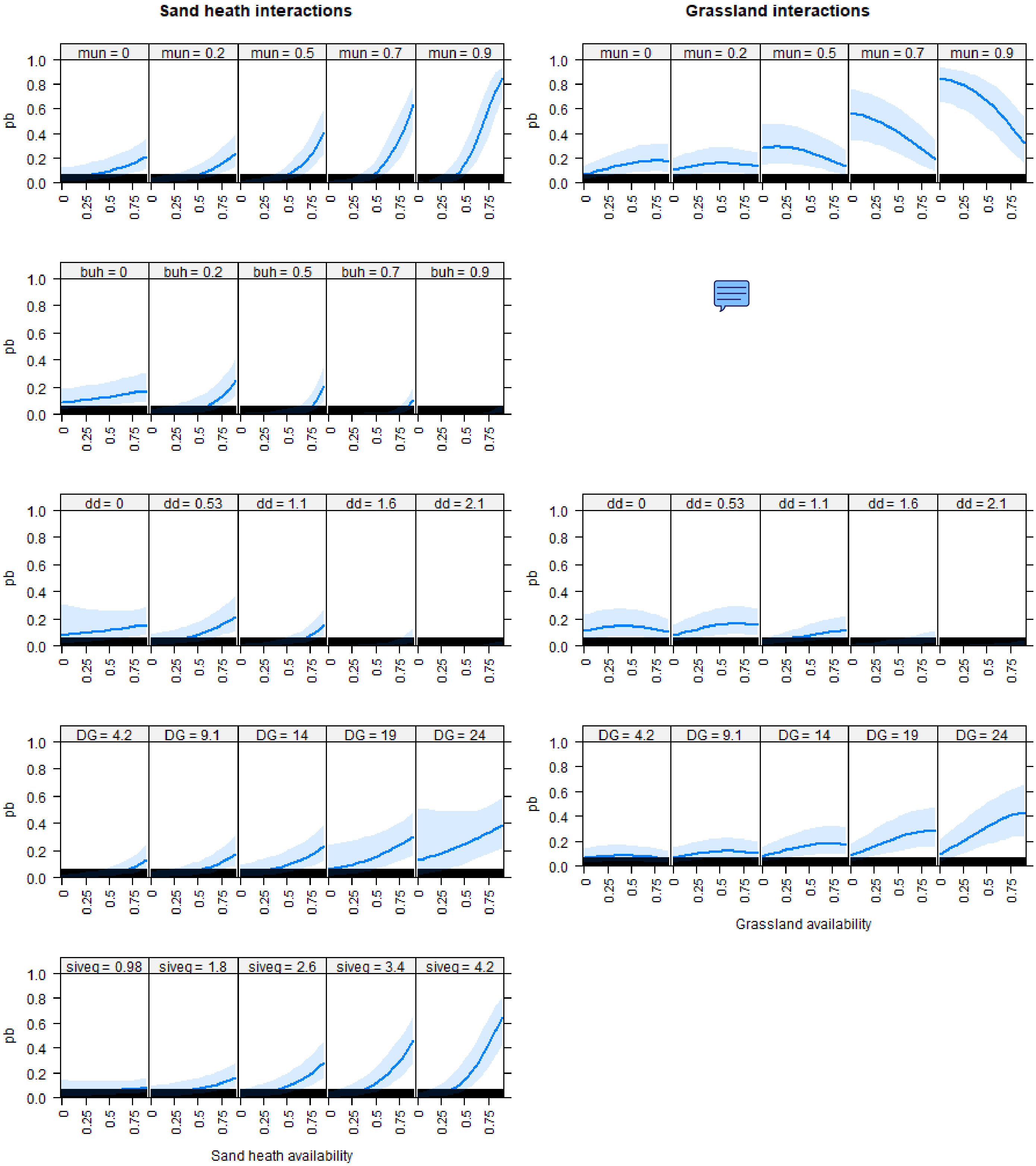
Sand heath interactions
Grassland interactions
mun = 0
mun = 0.2
mun = 0.5
mun = 0.7
mun = 0.9
buh = 0
buh = 0.2
buh = 0.5
buh = 0.7
buh = 0.9
dd = 0
dd = 0.53
dd = 1.1
dd = 1.6
dd = 2.1
DG = 4.2
DG = 9.1
DG = 14
DG = 19
DG = 24
siveg = 0.98
siveg = 1.8
siveg = 2.6
siveg = 3.4
siveg = 4.2
pb
Sand heath availability
Grassland availability

Figure 3

Areal projection of predicted habitat suitability shows the restriction of suitable black grouse habitats to the open heath areas of the nature reserve Lüneburg Heath.

General map (left) and predicted habitat suitability (right). Dashed black line on the left indicates the study area, black lines on the right highlight the extent of open heath landscapes for orientation.

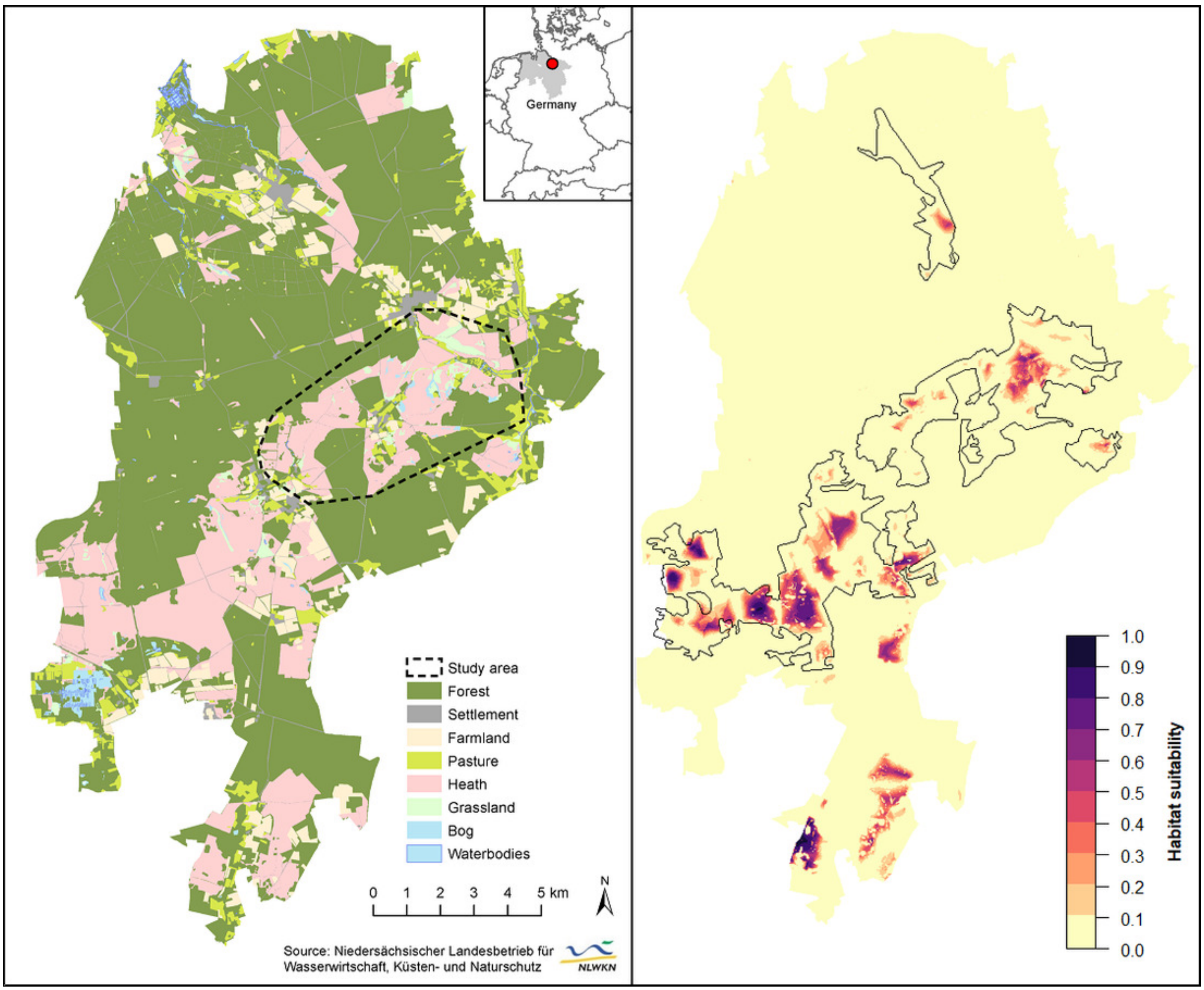

Table 1 (on next page)

Summary of tagged black grouse individuals including number of GPS locations, date of capture and duration of data collection.

Home range size was calculated as 95% kernel.

Animal ID	**Sex**	**Number of locations**	**Date tagged**	**Last position**	**Home range [ha]**	**Age**	**Weight [g]**
1101	m	159	08.05.2011	12.07.2011	39.05	adult	1304
1201	m	452	25.03.2012	08.09.2012	132.99	adult	1361
1202	m	408	01.04.2012	10.09.2012	50.93	adult	1365
1204	m	199	02.05.2012	02.07.2012	197.75	adult	1287
1205	f	436	04.05.2012	03.12.2012	97.51	adult	947
1206	f	546	06.05.2012	15.12.2012	192.31	adult	991
1207	m	96	09.05.2012	30.07.2012	77.78	yearling	1189

Table 2(on next page)

List of habitat and diversity variables

Type	Variable	Variable description
Distance to habitat type	dpuo	Distance [km] to infrastructure (settlement, roads, trails)
	dw	Distance [km] to forest
	dg	Distance [km] to grassland (pastures)
	dd	Distance [km] to open soil (dunes)
Availability of habitat type	hc	Sand heaths
	r	Natural grasslands
	mun	Raised bogs, mires, and fens
	buh	shrub formations (solitary trees and scattered shrub)
Diversity indices	DG	Summed cover rate of food plants
	nveg	Number of plant species
	siveg	Shannon Index of plant species

Table 3(on next page)

Results of black grouse resource selection calculated using generalized linear mixed models.

Diversity indices are included in (a) and excluded in (b). Squared terms are indicated as x^2.

		a) diversity indices included AIC 8265.7 Observations 13004 df 12977			b) diversity indices excluded AIC 8519.3 Observations 16297 df 16275		
Type	Variable	Estimate	SE	p	Estimate	SE	p
	Intercept	-5.37	0.79	1.03E-11	-5.53	0.49	2.16E-29
Distance	dpuo	13.39	0.73	2.93E-74	15.17	0.73	3.46E-97
	dpuo^2	-11.06	0.95	2.53E-31	-14.4	0.9	3.92E-57
	dw	8.68	0.94	2.26E-20	9.38	0.9	1.98E-25
	dw^2	-9.47	1.32	7.00E-13	-9.5	1.25	2.75E-14
	dg	-2.51	0.6	2.57E-05	-4.33	0.55	3.79E-15
	dg^2	5.02	0.8	3.02E-10	7.42	0.72	9.19E-25
	dd	-2.91	0.78	2.04E-04	-3.94	0.64	6.02E-10
	dd^2	-1.36	0.27	3.39E-07	-1.18	0.25	2.28E-06
Availability	hc	-3.57	0.82	1.37E-05	-1.29	0.41	1.46E-03
	r	0.28	0.84	7.35E-01	2.21	0.53	3.16E-05
	r^2	-1.78	0.47	1.33E-04	-1.99	0.43	4.41E-06
	mun	-4.06	0.87	3.40E-06	-2.22	0.71	1.67E-03
	mun^2	3.76	0.71	1.45E-07	3.11	0.69	6.31E-06
	buh	-17.23	7.02	1.42E-02	-16.98	6.04	4.95E-03
	buh^2	-6.23	1.03	1.62E-09	-4.87	1.01	1.46E-06
Diversity	DG	0.11	0.05	2.49E-02			
	siveg	-0.45	0.19	2.07E-02			
Interaction heath	hc:mun	7.19	0.86	6.30E-17	6.76	0.69	1.08E-22
	hc:buh	23	8.03	4.18E-03	21.72	6.89	1.61E-03
	hc:dd	3.76	0.95	7.51E-05	4.66	0.8	6.88E-09
	hc:DG	-0.12	0.07	8.67E-02			
	hc:siveg	1.55	0.28	4.11E-08			
Interaction grassland	r:mun	-4.4	0.6	2.97E-13	-5.07	0.58	3.62E-18
	r:dd	1.81	0.45	6.16E-05	1.97	0.43	5.52E-06
	r:DG	0.12	0.04	5.47E-03			