Habitat 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 birds 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 populations in the Central European lowlands. Using resource selection functions based on presence/background data, we estimated the probability of black grouse occurrence ~~according to the~~ availability of, or distance to habitat types as well as vegetation diversity indices. Grouse prefer undisturbed and heterogeneous habitats far from dense forests with wide sand heaths, natural grasslands and intermixed bogs, diverse vegetation and food sources, low density of (loose) shrub formations and solitary trees. Wetlands are extremely important in a landscape that is dominated by dry heaths and grasslands. Only around 4% (8.8 km²) of the nature reserve is suitable for black grouse, mostly because there is too much 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 birds 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 populations in the Central European lowlands. Using resource selection functions based on presence/background data, we estimated the probability of black grouse occurrence according to the availability of, or distance to habitat types as well as vegetation diversity indices. Grouse prefer undisturbed and heterogeneous habitats far from dense forests with wide sand heaths, natural grasslands and intermixed bogs, diverse vegetation and food sources, low density of (loose) shrub formations and solitary trees. Wetlands are extremely important in a landscape that is dominated by dry heaths and grasslands. Only around 4% (8.8 km²) of the nature reserve is suitable for black grouse, mostly because there is too much 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 (*Tetrao tetrix*) 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). Although the ~~species~~ is listed as least concern by the IUCN Red List (IUCN 2016), it is listed as endangered in Germany and critically endangered in the northern German state of Lower Saxony (Krüger & Sandkühler 2022). There, in Lower Saxony, the last remaining population is ~~located~~ in the region Lüneburg Heath (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). Core areas are surrounded by intensively used agricultural and large contiguous forestry areas (Cordes et al. 1997) and distances between the core areas are 7 to 15 km (Strauß et al. 2018). 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 permanently stabilized at a level of above 200 individuals in the past 20 years (Strauß et al. 2018). After a minimum population size in 1999 with 142 individuals, the population temporarily 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).

In its main distribution area of the Eurasian Palaearctic, black grouse inhabit transition zones between forests and habitats of heaths, raised moors and in Asia also of steppes, while old, dense forests are usually excluded from their habitat (Glutz von Blotzheim et al. 1994). Whether in the boreal zone, alpine, upland, or lowland regions, (semi-)open habitats with light-loving dwarf and berry shrubs are preferred (Klaus et al. 1990; Patthey et al. 2011). Being adapted to dynamic environments with changing mosaics of succession stages, grouse are sensitive to anthropogenically homogenized, high-disturbance habitats (Angelstam 2004; Ludwig et al. 2008; Immitzer et al. 2014). Where found elsewhere in Europe, black grouse habitats are geographically and scenically very different from those in the Lüneburg Heath, with those in the Netherlands and England being the most comparable (Baines 1994).

In the nature reserve Lüneburg Heath, black grouse find heterogeneous, open landscapes, seem to have sufficient food in all seasons and individuals are healthy (Strauß et al. 2018), so it is unclear why the population does not grow. Furthermore, the population seems to have adapted to anthropogenic influences that cause fragmentation and loss of available habitats ~~in the case of recreational use~~ (Tost et al. 2020). 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 habitat 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.

~~Therefore,~~ we investigated habitat 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. Model results from the study area were used to spatially predict habitat availability and distribution for the entire nature reserve. These predictions ~~on~~ habitat suitability can then be used to develop or improve conservation strategies for black grouse in the nature reserve and possibly in the neighboring military training areas.

We wished to determine 1) how important different habitats are for black grouse, 2) which of the available habitats are used and which of these are preferred. ~~In this context,~~ we also wanted to answer the question of the role of small-scale wetland sites as well as of areas with high structural richness for black grouse habitat use in this unique landscape.

Materials & Methods

Study area

The study area (16.3 km²), defined by the home ranges of the tagged black grouse, is within the 235 km² nature reserve Lüneburg Heath in Lower Saxony, Germany (53.167930° N, 9.939770° E). The reserve 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). Its core areas consist 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 today by modern mechanized landscape management, sheep farming, and heath burning (Kaiser 2015). The reserve is located in the transition zone between Atlantic and continental climate, with an average annual precipitation of 806 mm and average annual temperature of 9.4°C (CDC 2021). 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 open heath and grassland of the nature reserve (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.).

Data were collected as previously described in Tost et al. (2020). A total of seven birds were captured and fitted with backpack mounted, battery operated GPS tags (e-obs GmbH, Gruenwald, Germany) in the eastern part of the nature reserve in 2011 and 2012. 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). Both hens reproduced successfully, with the first clutch of one hen preyed and a secondary clutch hatched. Five birds were lost to 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). GPS-locations were taken every three hours between 01:00 and 22:00 daily during the entire sampling period. 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. As most important variables mapping included species inventories of flora and fauna, vertical layers (stratification) and horizontal cover rates of vegetation and (bio-)geological parameters as well as types of land use. Based on this, biotope types (Table S1) including their subunits, additional features and their state of conservation were recorded. 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 km² ~~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 different ~~biotope types~~ and their subunits. These were partly grouped within their hierarchical order to reduce the number of independent model variables in the further process (Table S1). Subunits of biotope types were partially grouped at the level of their main units, or biotope types (main units) were grouped at the level of their super units (e.g., 'degraded raised bogs still capable of natural regeneration' (MP) and 'transition mires and quaking bogs' (MW), etc. were grouped to 'raised bogs, mires, and fens' (mun)). Hirarchical 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), and resulted in ten groups of biotope types, eight of which were used for modelling (Table 2). 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 for each grouped biotope type separately and coded as present (1) / absent (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 habitat selection

Habitat 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. 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.

The best model was then used to spatially predict habitat suitability in the entire nature reserve by applying logistic transformation (logit link) to the model equation with the raster values of all biotope and diversity index layers previously used for point extraction.

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 the final model b) (Table 3b). In the other model a), 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. Habitat 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 km²) 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 km²; $p < 0.25$). 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). Although not investigated in this study, arthropod ~~availability~~ may be higher 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), ~~which could allow for higher reproduction rates in these areas~~. ~~However, we lack knowledge about arthropod~~

~~abundances in different heathland habitats, so evaluation of breeding and rearing areas remains uncertain.~~ 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, habitat 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* spp. and *Empetrum* sp.).

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. Habitat 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 (Tost et al. 2020) 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 (White et al. 2015), 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 (Sim et al. 2008; Patthey et al. 2011), 5) thinning of forest edges and creation of transition gradients over several hundred meters (Sim et al. 2008), 6) providing micro patches of open soil (Klaus et al. 1990), 7) visitor guidance and enforcement of its compliance (Immitzer et al. 2014), promotion of environmental education with local schools (Freund et al. 2020), relocation of infrastructure to less exposed areas or landscaping to provide visual cover by vegetation, and reduction of tourism pressure if possible (Tost et al. 2020), 8) mixing pastures with habitat elements such as dunes, loose shrub formations for concealment (Signorell et al. 2010), and wet zones, 9) improvement of habitat connectivity (Andrén 1994): 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 (Patthey et al. 2011) by examining vegetation species composition in detail, monitoring arthropod abundances in different habitat types (Wegge & Kastdalen 2008), 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 (Signorell et al. 2010). 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, F Stucke, 2021, pers. comm.) 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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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).

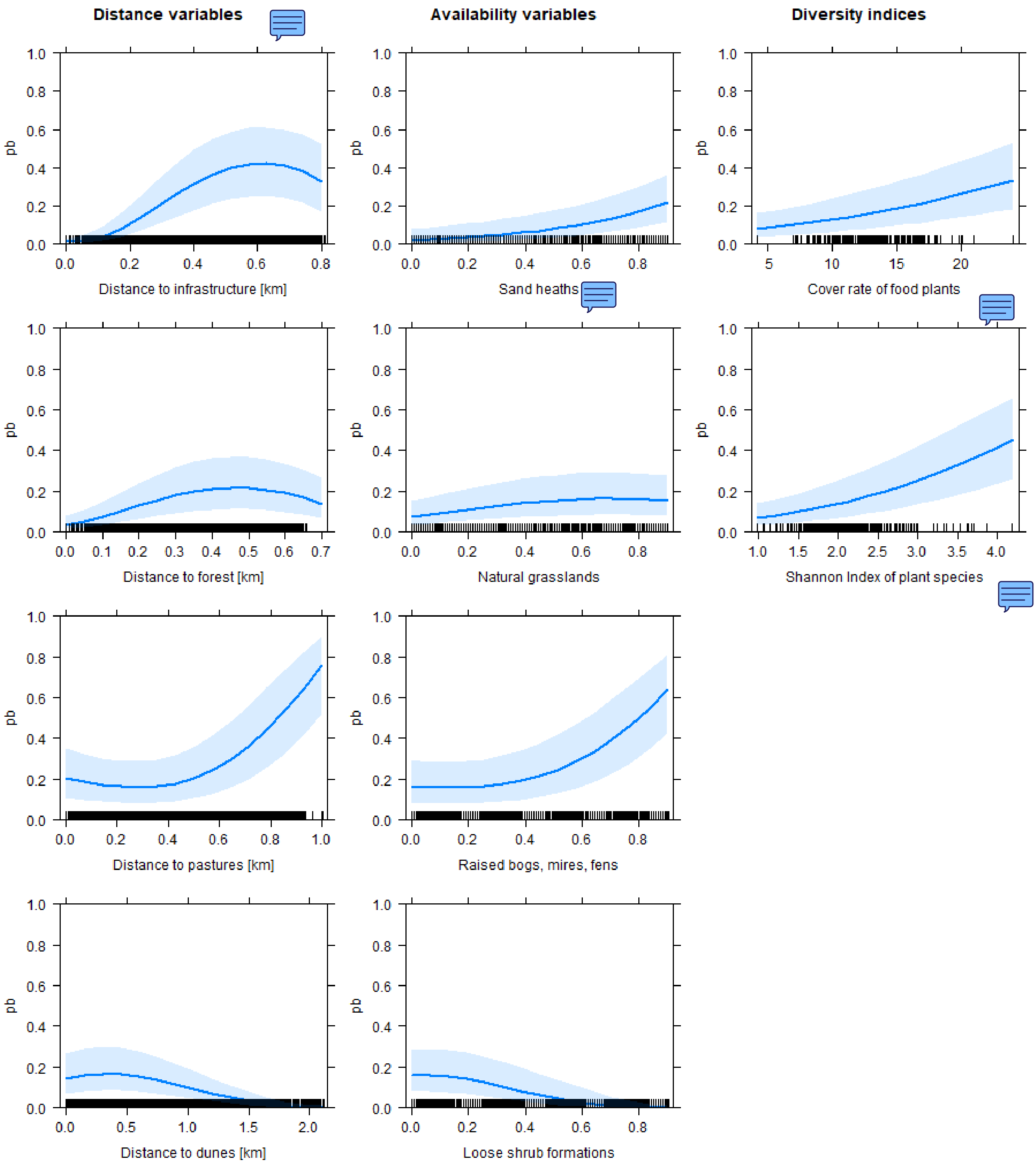
Distance variables
Availability variables
Diversity indices
pb
Distance to infrastructure [km]
Sand heaths
Cover rate of food plants
Distance to forest [km]
Natural grasslands
Shannon Index of plant species
Distance to pastures [km]
Raised bogs, mires, fens
Distance to dunes [km]
Loose shrub formations

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 bogs, mires, fens; buh = shrub formations; dd = distance to dunes in km; DG = summed cover rate of food plants; siveg = Shannon Index of plant species.

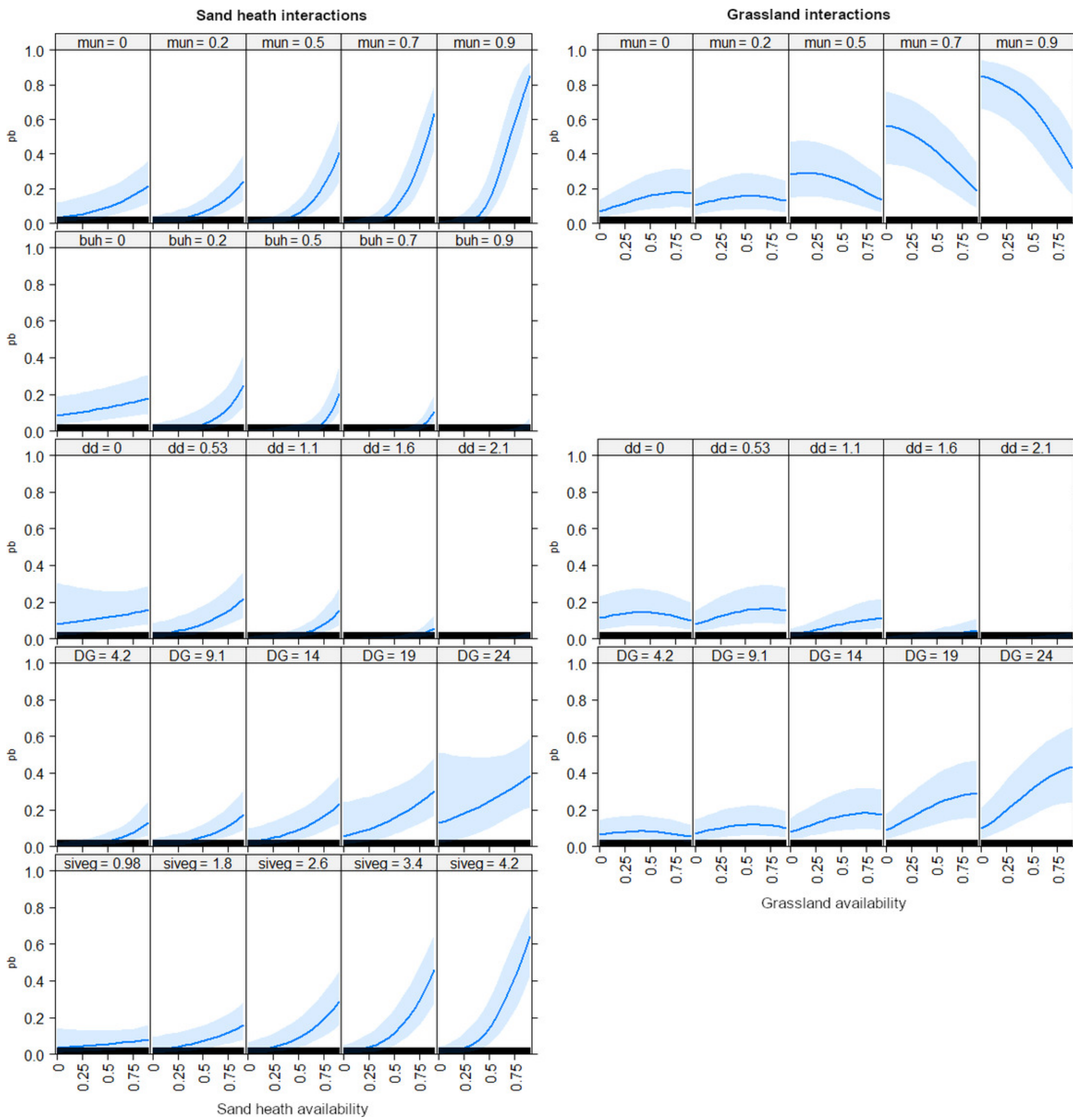
Sand heath interactions
Grassland interactions
mun = 0
mun = 0.2
mun = 0.5
mun = 0.7
mun = 0.9
buh = 0
buh = 0.2
buh = 0.5
buh = 0.7
buh = 0.9
dd = 0
dd = 0.53
dd = 1.1
dd = 1.6
dd = 2.1
DG = 4.2
DG = 9.1
DG = 14
DG = 19
DG = 24
siveg = 0.98
siveg = 1.8
siveg = 2.6
siveg = 3.4
siveg = 4.2
pb
Sand heath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

Left: General map of the nature reserve Lüneburg Heath showing the land use types within its boundaries. Right: predicted habitat suitability, with black lines ~~highlighting the extent of open heath landscapes for orientation~~. Overview map (top) shows the location of the nature reserve in Lower Saxony (grey) and Germany.

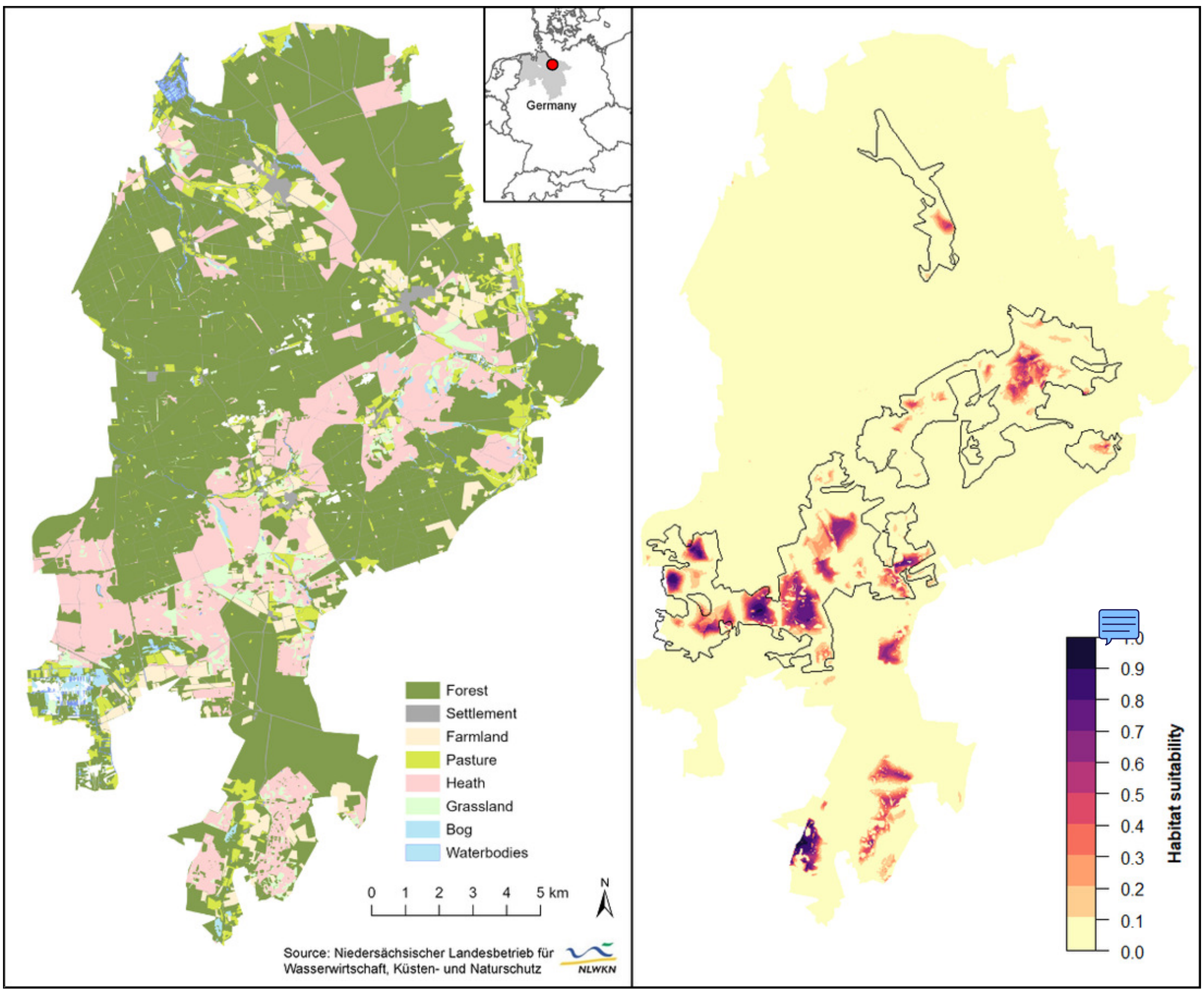

Table 1(on next page)

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	adult	1304
1201	m	452	25.03.2012	08.09.2012	133	adult	1361
1202	m	408	01.04.2012	10.09.2012	51	adult	1365
1204	m	199	02.05.2012	02.07.2012	198	adult	1287
1205	f	436	04.05.2012	03.12.2012	98	adult	947
1206	f	546	06.05.2012	15.12.2012	192	adult	991
1207	m	96	09.05.2012	30.07.2012	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 habitat 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 R^2 0.687 Observations 13004 df 12977			b) diversity indices excluded AIC 8519.3 R^2 0.807 Observations 16297 df 16275		
Type	Variable	Estimate	SE	p	Estimate	SE	p
	Intercept	-5.37	0.79	< 0.001	-5.53	0.49	< 0.001
Distance	dpuo	13.39	0.73	< 0.001	15.17	0.73	< 0.001
	dpuo²	-11.06	0.95	< 0.001	-14.4	0.9	< 0.001
	dw	8.68	0.94	< 0.001	9.38	0.9	< 0.001
	dw²	-9.47	1.32	< 0.001	-9.5	1.25	< 0.001
	dg	-2.51	0.6	< 0.001	-4.33	0.55	< 0.001
	dg²	5.02	0.8	< 0.001	7.42	0.72	< 0.001
	dd	-2.91	0.78	< 0.001	-3.94	0.64	< 0.001
	dd²	-1.36	0.27	< 0.001	-1.18	0.25	< 0.001
Availability	hc	-3.57	0.82	< 0.001	-1.29	0.41	0.001
	r	0.28	0.84	0.735	2.21	0.53	< 0.001
	r²	-1.78	0.47	< 0.001	-1.99	0.43	< 0.001
	mun	-4.06	0.87	< 0.001	-2.22	0.71	0.002
	mun²	3.76	0.71	< 0.001	3.11	0.69	< 0.001
	buh	-17.23	7.02	0.014	-16.98	6.04	0.005
	buh²	-6.23	1.03	< 0.001	-4.87	1.01	< 0.001
Diversity	DG	0.11	0.05	0.025			
	siveg	-0.45	0.19	0.021			
Interaction heath	hc:mun	7.19	0.86	< 0.001	6.76	0.69	< 0.001
	hc:buh	23	8.03	0.004	21.72	6.89	0.002
	hc:dd	3.76	0.95	< 0.001	4.66	0.8	< 0.001
	hc:DG	-0.12	0.07	0.087			
	hc:siveg	1.55	0.28	< 0.001			
Interaction grassland	r:mun	-4.4	0.6	< 0.001	-5.07	0.58	< 0.001
	r:dd	1.81	0.45	< 0.001	1.97	0.43	< 0.001
	r:DG	0.12	0.04	0.005			

1