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Habitat use by Black Grouse *Tetrao tetrix* in a mixed moorland-forest landscape in Scotland and implications for a national afforestation strategy

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SUMMARY

Capsule

Long-term conservation of Black Grouse in Scotland may rely upon the retention of sufficiently large and well-connected patches of moorland and a diversity of adjacent forest types.

Aims

To study Black Grouse habitat use within a moorland-forest mosaic and make recommendations for their conservation in more heavily forested future landscapes.

Methods

We carried out radio-telemetry on Black Grouse over three years to investigate individual habitat use. We used compositional analyses to investigate habitat selection in different seasons. We examined whether this matched previous population-level patterns and whether it differed between males and females. We used logistic regression to examine whether movements into large-scale commercial forests were restricted to the periphery relative to random locations.

Results

Males used seasonal ranges of >200 ha and females >70 ha. Birds selected strongly for moorland throughout the year, matching other population-level studies. Underlying this, however, males and females differed in their use of forests, with males associated with broadleaf woodland, whilst females preferred new native pinewoods in spring-summer or commercial conifer forests in autumn-winter. Use of commercial plantation forests was generally limited to their periphery, particularly to within < 300 m of the forest edge.

Conclusion

When planning afforestation, moorland patches of at least 200 ha must be retained and their fragmentation should be minimised, particularly as young forests may provide breeding habitat over a limited duration. However, mature forests also form an important habitat component and, at a local scale, both coniferous and broadleaf forests should be made

available to provide resources for both sexes. As such, some management decisions will need to be made at the landscape-scale to balance broad national targets with individual landowner/contractor decisions.

TEXT

INTRODUCTION

Forests can act as major carbon sinks (Pan *et al.* 2011) and so forest expansion is considered a key mitigation measure against anthropogenic climate change (Zomer *et al.* 2008). Though the case for protection of existing native forests to conserve biodiversity is strong (e.g. Brooks *et al.* 2002; Pandit *et al.* 2007), the likely impact of new afforestation strategies on biodiversity is less clear. The effects may depend upon the nature of the new forest, the scale and duration of any original loss of primary forests, connectivity between new and existing forests and the land-uses that are replaced (Rudel *et al.* 2005).

The Scottish government aims to increase forest cover from the current 18% to 25% by 2050 (Forestry Commission Scotland 2006). The target is split as commercially productive conifer forests (60%) and non-commercial native forest (40%) (Woodland Expansion Advisory Group 2012). Such rapid, large-scale and centrally-driven land-use change necessitates questions such as where new forests should be sited, which land-uses should be replaced (Towers *et al.* 2006; Woodland Expansion Advisory Group 2012) and what the likely impacts on threatened species might be (e.g. White *et al.* 2013). Scotland contains a significant proportion of the world's sub-montane Heather *Calluna vulgaris* moorland, a habitat of unique ecological character (e.g. in plant communities and bird assemblages) and international importance, which substantially declined in extent during the 20th century (Thompson *et al.* 1995). Losses have in part been attributed to a previous period of commercial afforestation in the 1940s-1980s, which led to an increase in forest cover from 5% to 14%, almost all of which was on heather moorland (decreased from 19% to 15%), blanket mire (29% to 23%) and rough grassland (30% to 28%) (Mackey *et al.* 1998).

Black Grouse *Tetrao tetrix* are red-listed in 16 nations in Central and Western Europe (Storch 2007). In the UK they have declined in range (Balmer *et al.* 2013; Hancock *et al.* 1999) and counts of displaying males fell from 25 000 in the early 1990s to 5 000 in 2005 (Baines & Hudson 1995; Sim *et al.* 2008). In Scotland, they are associated with mosaics of moorland, moorland-fringe, young coniferous forest and broadleaf forest (Baines *et al.* 2000; Cramp & Simmons 1980). Declines in the 1990s were linked to maturation of commercial forests planted in the 1970s-1980s (Pearce-Higgins *et al.* 2007). Between 1992 and 2010 lek (the communal display site of males) extinctions were associated with increases in adjacent commercial conifer forest, while lek establishments were associated with planting of new native pinewoods (White *et al.* 2013). However, there is a strong and consistent association between leks and moorland (Geary *et al.* 2013; White *et al.* 2013) and, over the long-term, replacement of moorland with forest has led to local declines (Baines *et al.* 2000; Pearce-Higgins *et al.* 2007). Given Scotland's afforestation strategy, the composition and extent of moorland-forest mosaics is likely to change rapidly.

While population-level studies of Black Grouse have described broad, landscape-scale associations, far less is known about how individuals use moorland-forest mosaics. In order to assess habitat use and the potential impacts of national afforestation policy on Black Grouse we used radio-telemetry to record individual-scale habitat use in a landscape of large-scale commercial plantations, young native forests and moorland. We investigated: (1) whether habitat selection patterns at the individual scale match those seen at the lek scale in the same population (White *et al.* 2013), (2) whether these patterns differ between males and females, and (3) to what extent birds use large-scale mature commercial forests, likely to become increasingly prevalent under afforestation targets.

METHODS

Study areas

The study was carried out in a mixed moorland-forest landscape in North Perthshire, Scotland, that included the 3 100 ha Tummel Forest and the 1 100 ha Talladh-a-Bheithe Forest in the Scottish Highlands (Figure 1). These two state-owned commercial plantations differed in their age-structure, with 79% of Tummel Forest planted in the 1950s to 1960s compared to 79% of Talladh-a-Bheithe Forest planted in the 1980s. The study areas covered an altitudinal range 140-580 m above sea-level. The main land-uses were Sheep *Ovis aries* and Cattle *Bos primigenius* grazing, commercial timber forestry and Red Deer C*ervus elaphus* stalking. Red Grouse *Lagopus lagopus scotica* shooting has declined and is now limited to low intensity shoots. Some land has been non-commercially afforested during the last two decades for biodiversity benefits, typically via government grant schemes and are called ‘new native pinewoods’ due to their role of re-creating native Scots Pine *Pinus sylvestris* forest.

Habitats and mapping

We categorised the study areas into three non-forest and four forest habitats (Table 1). Commercial forests were categorised as either closed-canopy stands or clearings. Densities of birds counted in August in commercial plantings have been shown to reach zero when trees are approximately 14 years old (Baines *et al.* 2000) so we defined closed-canopy compartments as those aged 14 years or more since planting. Forestry clearings consisted of either pre-thicket stands less than 14 years since planting (24% area of clearings), clearfells (20%) or unplanted patches left in the forest between stands, including tracks and rides (56%). We mapped habitat patches using satellite images, field visits and forestry stock-maps, which consist of information about the species and planting-year of stands, and digitised them using MapInfo GIS software (MapInfo Corporation 2011) and checked the data via field-visits.

Radio-telemetry

Between August 2009 and March 2012 we caught 89 Black Grouse either using both pointing-breed dogs and a drag-net, or at night-time roosts using a high-power lamp and hand-net (Baines & Richardson 2007) (catch locations in Figure 1). We fitted them with Biotrack TW-3 or Holohil RI-2B or RI-2D necklace tags using fixed-length Dacron polyester cord. Suitable cord lengths for each tag type were determined for each sex by examining dead adult specimens held by the Game & Wildlife Conservation Trust. Tags had battery lives of 15-30 months and masses of 9-17 g, equating to less than 2% adult body-mass. Radio-tagged birds were assigned as juveniles (≤ 1 year old at catching) and adults (> 1 year old or more at catching).

To enable generality of the results, it was important that habitats at catch locations were representative of the habitats available to the wider population. A lek survey, fully encompassing the study area (53 000 ha) was carried out in 2010, which is likely to have recorded most leks present as it involved whole-area searches (White *et al.* 2013). The proportion of habitat types present within 1 km of leks (of ≥ 2 males), a radius which is believed to represent a majority of habitat used by birds (see White *et al.* 2013), is given in Table 2. Catches for the present study were initially carried out in brood-rearing areas (n = 73) and subsequently using follow-up catches at roost sites (n = 16). For efficiency, only ‘open’ habitats suitable for brood-rearing (moorland, new native pinewood and forestry clearings; farmland was not considered suitable breeding habitat due to lack of ericaceous shrub layer for nesting or wet-flush areas for young broods) were targeted for brood catches. All follow-up roost catches happened to be on moorland or in new native pinewood (roost catches were achieved by identifying roost areas of tagged birds and catching new birds in that vicinity). Although catch habitats did not represent the farmland, broadleaf woodland and closed-canopy forestry present around leks, there was a close correspondence between the composition of suitable brood-rearing habitats around leks and the composition of catch habitats, whether this included only brood catches or both brood and roost catches (Table 2). No birds were caught within forestry clearings, but these only comprised 1% of habitat within 1 km of leks. These data suggest that the habitat composition the tagged sample is likely to be representative of the habitats that birds would be caught in if using the same methods over a wider area.

The annual cycle was divided into autumn-winter (1 October - 31 March) and spring-summer (1 April - 30 September), divisions approximating to the start of the peak mating period and end of brood break-up periods respectively, and broadly matching spring and autumn female dispersal (Caizergues & Ellison 2002; Warren & Baines 2002). Radio-telemetry was carried out between August 2009 and September 2012 inclusive, covering three autumn-winter and three spring-summer seasons. We recorded diurnal radio-locations by flushing birds at arbitrary times, typically between 0800 h and 1800 h GMT. The median inter-flush interval for locations that contributed to range calculations (below) was 7 days (inter-quartile range [IQR] 5-11 days) and radio-locations were manually recorded using a handheld GPS device (precision 3 m). Weekly flushes were not expected to affect survival (Baines & Richardson 2007; Thirgood *et al.* 1995). Females were flushed only once from nests to record clutch size and when with broods were not flushed but closely triangulated (to within c. 25 m). Where a nest was located, we recorded the habitat-type that it occupied.

We described a 100% minimum convex polygon (MCP_{100}) to represent a bird's seasonal range which is the smallest polygon containing all radio-locations with external angles greater than 180° (Kenward 2004). MCP_{100}s were produced for autumn-winter and spring-summer seasons separately, only where at least 10 live radio-locations had been recorded per bird per season and where these spanned at least 90 days, equivalent to half a season.

Ten radio-locations was selected as a minimum because it has been used to assess the utilisation distribution in other species (Conner 2001), and logistical constraints of radio-telemetry in rugged terrain meant that for some birds this was the maximum number that could be collected within a season.

We tested whether 10 radio-locations was likely to describe a substantial proportion of seasonal range of an individual by analysing the change in cumulative size of MCP_{100}s with addition of new locations. Each of 90 bird-seasons in our sample was represented by a set of n locations (n_1, n_2… n_i, where i represents the number of locations recorded for that bird-season). For each bird-season we randomly selected five locations (the minimum for which an MCP could be calculated in R) and calculated the MCP_{100} area. We then incrementally added each additional location in a random order, estimating the MCP_{100} area each time until all n_i had been included (Kenward 2004). Then for each bird season we converted areas for each iteration into a percentage of its maximum MCP_{100} area (containing all n_i locations). Across all 90 bird-seasons we took the mean value for each quantity of locations between n_5 and the maximum of n_i for that bird-season (up the maximum of 25). We fitted an asymptote model to the data using a negative exponential $y = 100(1+e^{-ax})$ (Colwell & Coddington 1994) where y was the percentage of maximum area (for a given run), x was the number of locations used, and a is an estimated parameter, estimated using the ‘manipulate’ package in RStudio 0.98.501 (RStudio 2012) to test the fit of the model. The asymptotic model (Figure 2) predicted that ten radio-locations would give a mean of 76% of the maximum expected MCP_{100} area for a bird-season which we considered sufficient as an estimate of habitat use of an individual.

MCP_{100}s have been used to estimate Black Grouse home-ranges in previous studies (Starling-Westerberg 2001; Caizergues & Ellison 2002). They were originally recommended for use in compositional analysis (Aebischer *et al.* 2003), and use of alternative range estimates for describing second-order habitat utilisation has been discouraged (N. J.

Aebischer, Game & Wildlife Conservation Trust, pers. comm.). However, there is a potential for MCP_{100}s to be subject to the influence of outliers. One source of outliers could come from dispersal movements, which in Black Grouse are made by first-year females (Cramp & Simons 1980; Warren & Baines 2002). We defined dispersal as a movement of greater than 1 km from any previous location with no subsequent return to within 1 km. To remove the effect of dispersal-based outliers, if a first-year female dispersed in autumn, the pre-dispersal locations did not contribute to the autumn-winter range. Similarly, if a first-year female dispersed in spring, the post-dispersal locations did not contribute to the prior autumn-winter range, nor did the pre-dispersal locations contribute to the following spring-summer range.

To test the potential impact of any non-dispersal outliers on MCP_{100}s we additionally estimated ranges based on methods likely to reduce the influence of such outliers and compared them to the MCP_{100}s. Firstly, we estimated both a 90% MCP (MCP_{90}) and an 80% MCP (MCP_{80}) for each bird-season. Because the minimum number of locations used to estimate a range was 10 (see below), an MCP_{90} would require the removal of at least one outlier location, and an MCP_{80} would require the removal of at least two outliers. Secondly, we estimated 75% reference kernels (RK_{75}) for each bird-season, using the ‘adehabitat’ R package (Calenge 2006) with the default ‘ad hoc’ smoothing parameter estimate, which assumes the utilisation distribution is bivariate normal. RK_{75}s were selected as they are considered relatively insensitive to outliers (Kernohan *et al.* 2001) and they have been used to calculate individual ranges of Lesser Prairie Chickens *Typmpanuchus pallidicinctus* and Greater Prairie Chickens *Typmpanuchus cupido*, two other lekking species of grouse (Pruett *et al.* 2009).

We then tested a Pearson’s correlation between the square-root transformed MCP_{100} and the square-root transformed RK_{75}, extracting the correlation coefficient (r) and its 95% confidence interval (CI_{95}), and then did the same for the MCP_{90} and the RK_{75} and the MCP_{80} and RK_{75} in turn. The RK_{75} was significantly correlated with each of the MCP_{100} (t_{69} = 15.7, P

< 0.01), MCP_{90} ($t_{69} = 17.2$, $P < 0.01$) and MCP_{80} ($t_{69} = 14.5$, $P < 0.01$). The correlation coefficient was not significantly smaller for the MCP_{100} ($r = 0.88$, $CI_{95} = 0.82$-0.93) than for the 90% MCP ($r = 0.90$, $CI_{95} = 0.84$-0.94) or the 80% MCP ($r = 0.87$, $CI_{95} = 0.80$-0.92). Because the correlation coefficient between the RF_{75} kernel (considered to have low bias due to outliers) and the MCPs was not significantly improved by removal of potential outliers (i.e. from MCP_{100} to MCP_{90} to MCP_{80}), it suggested that outliers had not adversely affected the ability of the MCP_{100} to estimate the range (and thus habitat utilisation) of birds. Hereafter a ‘range’ refers to an MCP_{100}.

Statistical analyses

Statistical analyses were carried out in R 2.11.0 (R Development Core Team 2010). All tests used a significance threshold of $P = 0.05$. Range-level analyses were carried out separately for autumn-winter and spring-summer. Sample sizes of ranges were insufficient to examine all sex, age and year combinations, particularly in habitat selection analyses where a minimum sample of 10 individuals is recommended (Aebischer *et al.* 1993). Therefore ages were grouped within analyses because sex differences in habitat are expected to be more prominent than age differences (Grant & Dawson 2005) due to the pronounced sexual dimorphism in the species (Cramp & Simmons 1980).

We tested whether square-root transformed range sizes for each season differed by sex and year using a two-way analysis of variance (ANOVA) and whether habitat composition within ranges differed by sex and year using non-parametric multivariate analysis of variance (MANOVA) (Anderson 2001). We used likelihood-ratio tests with the *F*-distribution to compare full sex*year interaction models with simplified versions of the models, first removing the interaction term and then the year and sex terms in turn. The ‘other’ habitat category was excluded from all analyses because no birds were recorded within it. Because components within the composition of a range are not independent, we rendered them linearly independent by taking log-ratios of each habitat against moorland and substituting zero values with 0.01% (Aebischer *et al.* 1993).

To assess habitat selection within groups we compared use and availability of habitats using compositional analyses at two scales (Aebischer *et al.* 1993) using the R package ‘Adehabitat’ (Calenge 2006). Firstly, we examined habitat selection at the scale of ranges within the study area, where composition within range describes habitat use and composition within the study area defines habitat availability. Secondly, we examined selection at the scale of locations within ranges, where composition across radio-locations describes habitat use, and composition within ranges describes habitat availability. The study area component was formally defined as a larger 100% MCP containing each bird-season range, computed separately for the Tummel Forest and the Talladh-a-Bheithe Forest study areas. Within each analysis, habitats not used by at least two birds or available to at least half of birds were excluded. We tested the null hypothesis that use did not significantly differ from availability using MANOVA with the test statistic Wilk's Λ (Aebischer *et al.* 1993). To avoid pseudo-replication a maximum of one spring-summer and one autumn-winter range for each individual was included in analyses, selected as the first chronological recorded range of that season.

If the null hypothesis was rejected, indicating habitat selection, we then ranked habitats by order of relative use, by comparing the difference in the log-ratios (the natural logarithm of use/availability) of all pairs of habitats and ranking them by the number of habitats they exceeded. We used randomisation tests to examine if pairwise differences were significant. Multiple pairwise tests are standard within compositional analyses (Aebischer *et al.* 1993) and we did not adjust our α-level (Gotelli & Ellison 2004). These results were displayed in the form of a ranking matrix (Aebischer *et al.* 1993).

Movement into commercial forestry

To examine the extent to which birds moved into commercial forestry we measured the straight-line distance to forest edge for each radio-location recorded within commercial forestry. We did this for two types of patches. Firstly, we defined a patch type ‘commercial forestry’ composed of both closed-canopy forestry and forestry clearings combined to represent all commercial plantations, with patch boundaries occurring where these met external habitats. Secondly, we considered closed-canopy patches alone, with patch boundaries occurring where these met any other external habitat, including forestry clearings. We also generated 200 random points with commercial forestry, 143 of which fell in closed-canopy patches.

We used a generalised linear mixed model with binomial errors and logit-link function, using the ‘lme4’ R package. The response variable was binary, describing whether a point was either a bird location or a random location. Square-root transformed distance-to-edge of commercial forest or closed-canopy patch (m) was included as a fixed effect and bird identity as a random effect to account for repeated-measures within individuals. To allow the random effect, each random point was also randomly assigned to an individual bird represented in the sample of bird locations, separately for commercial forestry and closed-canopy patches. The back-transformed predicted response for a given distance-to-edge can be interpreted as the probability that a point at that distance is either a bird location or a random location. If birds restrict movement into commercial forestry or closed-canopy patches, then we would expect a significantly negative relationship between distance-to-edge and probability that a point at that distance is a bird location. Using a likelihood-ratio test with the X^2 distribution we tested the effect of distance-to-edge and, where the effect was significant, used model parameters to predict the threshold distance at which there was an equal probability (0.5) of a location coming from a bird or from a random location.

RESULTS

Habitat use and selection

Seventy seasonal ranges were recorded from 47 individual birds. Forty-two individuals did not contribute sufficient data to estimate ranges because, prior to meeting the criteria for range estimation, they were a confirmed dead (n = 24), their radio-signal was no longer detectable (potentially due to dispersal outside of the study area, tag malfunction, or a tag being damaged or removed by a predator or scavenger) (n = 15), their tags were found shed but with no evidence of mortality (n = 2) or the project period finished with insufficient data collected (n = 1). Sample sizes of estimated ranges by season, sex and year are shown in Table 3. For range size in both autumn-winter and spring-summer the sex*season interaction was not significant ($F_{2,36}$ = 1.3, P = 0.29; $F_{2,23}$ = 1.2, P = 0.31). Ranges in both autumn-winter and spring-summer did not differ in size between years ($F_{2,38}$ = 2.2, P = 0.01; $F_{2,25}$ = 1.0, P = 0.40) but differed between sexes ($F_{1,38}$ = 8.1, P = 0.01; $F_{1,25}$ = 4.6, P = 0.04). Median MCP size for males was 228 ha (IQR 144-343 ha) in autumn-winter and 259 ha (IQR 141-342 ha) in spring-summer. For females it was 92 ha (IQR 48-203 ha) in autumn-winter and 70 ha (IQR 28-112 ha) in spring summer.

As with range size, for habitat composition within ranges in both autumn-winter and spring-summer the interaction term was not significant ($F_{2,36}$ = 1.5, P = 0.16; $F_{2,22}$ = 0.5, P = 0.83). Habitat composition within ranges did not differ between years ($F_{2,38}$ = 2.2, P = 0.07; $F_{2,24}$ = 0.2, P = 0.99) but differed between sexes ($F_{1,38}$ = 3.3, P = 0.02; $F_{1,24}$ = 9.0, P < 0.01). Habitat compositions within ranges by sex for autumn-winter and spring-summer are given in Table 4, along with the composition across locations and the compositions across the two study sites for comparison. When comparing habitat composition within ranges to habitat composition within study areas, use differed from availability for females in both autumn-winter (Λ = 0.31, P = 0.01) and spring-summer (Λ = 0.05, P < 0.01) and also for males in both autumn-winter ($\Lambda = 0.26$, $P < 0.01$) and spring-summer ($\Lambda = 0.11$, $P < 0.01$). Ranking matrices for these are in Table 5.

Moorland was the top-ranked habitat across males and females in both seasons and was significantly selected relative to all other habitats in each group. Beyond this, however, there were differences between sexes. For males in autumn-winter broadleaf woodland and farmland were ranked most highly following moorland, and both were significantly selected relative to closed-canopy forestry, with broadleaf woodland additionally being selected relative to forestry clearings and new native pinewood. A very similar pattern existed for males in spring summer, except that farmland was ranked above broadleaf woodland both were significantly selected relative to the three conifer forest habitats. In both seasons, conifer forest types (closed-canopy forestry, forestry clearings and new native pinewood) filled the lowest three rankings. Conversely, in females, farmland and broadleaf woodland were either low-ranked or not utilised sufficiently to be considered in analyses. In spring-summer, new native pinewood was ranked second after moorland, although it was not significantly selected relative to any lower ranked habitats. In autumn-winter, however, closed-canopy forestry and forestry clearings were ranked second and third after moorland, and were both significantly selected relative to farmland.

When comparing habitat composition across locations to habitat composition within range, use differed from availability for males in autumn-winter ($\Lambda = 0.18$, $P < 0.01$), but not for males in spring-summer ($\Lambda = 0.95$, $P = 0.87$) or females in autumn-winter ($\Lambda = 0.49$, $P = 0.18$) or spring-summer ($\Lambda = 0.40$, $P = 0.11$). For males in autumn-winter, habitats were ranked moorland, farmland then broadleaf woodland, with both moorland and farmland significantly selected relative to broadleaf woodland. Sixteen nests of radio-tagged females were located during the study, of which 12 were on moorland and four in new native pinewoods.

Movement into commercial forestry

Twenty-six individual birds used commercial forestry (145 locations) and 18 used closed-canopy patches within this (64 locations). The median distance-to-patch-edge in closed-canopy patches for bird locations was 70 m (IQR 23-157 m) and for random points was 89 m (IQR 43-165 m). For commercial forestry, the median distance-to-forest-edge for bird locations was 224 m (IQR 83-692 m) and for random points was 1 134 m (IQR 531-2 442 m). Distance-to-edge had a significant negative effect on whether a point was a bird location within commercial forestry ($X^2_1 = 56.7$, $P < 0.01$) (Figure 3) but no effect was found within closed-canopy patches ($X^2_1 = 2.9$, $P = 0.09$). The model estimated that a point was more likely to be a bird (probability > 0.5) than a random point within 266 m of the forest edge.

DISCUSSION

The individual selection patterns presented here show a strong preference for moorland across sexes, a pattern which matches that observed when considering habitat composition within 1 km of leks of the same population (White *et al.* 2013). Moorland comprised most of the habitat used by both sexes and contained the majority (12/16) of nests. It is a key habitat for both breeding and lekking (Baines 1990; Parr & Watson 1988) and provides vegetation forming major dietary components of Black Grouse (Beeston *et al.* 2005). However, there was a subtler underlying pattern of between-sex differences in the selection for different forest components. The importance of forests for winter (particularly above-snow) feeding (Warren *et al.* 2013), as a protein resource in spring (Baines 1990) and for shelter from predation (Signorell *et al.* 2011) has been observed, but sex-differences in their use may not have been previously noted.

The results suggest that a mosaic consisting of core moorland or young forest habitats for breeding and ground-feeding, interspersed with mature broadleaf and conifer forest components, may provide an optimum habitat mosaic for Black Grouse in Scotland. The productivity of females, and therefore the availability of high quality breeding habitats, is likely to be the key driver of Black Grouse populations (Baines *et al.* 2007; Grant *et al.* 2009) and management for Black Grouse may have to focus on conserving breeding habitats at the landscape scale over the long-term. Moorland and young forest contained most lek sites (White *et al.* 2013) and breeding sites (this study) in the study area. Previous studies have demonstrated a strong positive population or distributional response of Black Grouse to young forest (Klaus 1991; Baines *et al.* 2000, Pearce-Higgins *et al.* 2007; White *et al.* 2013), and the observed selection by breeding females could be a principal driver of this pattern. It is likely to be the increased growth of ground vegetation as a result of reduced grazing and browsing that leads to population increases in young forest, as opposed to the presence of the trees *per se* (Baines *et al.* 2000), although there is some evidence the presence of young trees may be favoured by females with broods as it provides increased shelter from aerial predators (Signorell *et al*. 2010).

Populations only tend to increase in new commercial forest for several years before declining sharply, and it is unlikely to form suitable breeding habitat beyond 14 years as tree growth restricts ground vegetation growth (Baines *et al.* 2000; see also Pearce-Higgins *et al.* 2007). The rotation period of commercial plantations is typically 40-60 years (Mason 2007), so any breeding benefits of young forest relative to moorland that it replaces may be positive for a shorter period than it is negative. This presents a management trade-off, since young forest may potentially provide higher quality breeding habitat than moorland, but moorland provides breeding habitat over a longer period. Managing forest rotations to maintain a relatively constant area of young forest in a landscape over time could present a significant logistical challenge. As an illustration, during the expansion of commercial afforestation in Perthshire in the late 20th century, new forest was planted on moorland over a period of four decades (1950s-1980s) but by the end of the century there was very little pre-thicket (<1%) commercial forestry left in the landscape (White *et al.* 2013). The current afforestation strategy considers new planting over a similar four-decade timeframe (to a target date of 2050) (Forestry Commission Scotland 2006), and could leave some landscapes with relatively little young forest during some periods, as well as a reduced moorland component.

The non-commercial component of the afforestation target (40%) is not intended for harvest and re-stock so, unless these can provide longer-term breeding habitat within their ‘open’ components, they may remove breeding habitat from the landscape in the long-term. Due to their lower stem density and larger open ground component (existing new native pinewoods planted contain c. 20% open ground), new native pinewoods may potentially retain Black Grouse breeding populations for a longer period than has been observed in commercial plantations. However, it has been demonstrated that leaving 15% open space in commercial plantings has only a limited benefit in extending the period of breeding suitability (Baines *et* *al.* 2000). Knowledge of what density of trees might allow continued Black Grouse breeding, albeit at lower densities, after the pre-thicket growth stage is not well established (see review by Grant & Dawson 2005). Under the proposed new Scottish Rural Development Programme 2014-20, low density native woodland would be offered as a subsidised management option, which would contain a higher proportion of open space and a lower planting density than current new native pinewoods (Scottish Government, 2014). The long-term effects of both current new native pinewoods, and proposed low density native woodlands, on Black Grouse populations require further investigation using long-term population data.

Due to the difficulties in long-term provision of young forest habitat at a landscape scale, and the uncertainty around the long-term impacts of non-commercial forests on Black Grouse populations, it will be important that moorland components are conserved as a key long-term breeding habitat for Black Grouse in the Scottish landscape. It is inevitable that moorland extent will decrease under afforestation plans, and prioritisation of moorland patches to conserve will require consideration of their size, connectivity and quality. We did not consider relative habitat quality in this study, but moorland quality for Black Grouse may be improved via sympathetic management, for example via alterations in grazing regimes (Calladine *et al.* 2002). The size of a suitable breeding habitat patch can influence the probability of occurrence of a Black Grouse breeding population. For example, in Sweden, it was found that a patch must be c. 1.5 km^2 to contain a lek and 5 km^2 to contain more than one lek and, at a landscape-scale, about 22% of the area needed to be suitable breeding habitat to have a 90% chance of containing leks (Angelstam 2004). Studies at national (White *et al.* 2013) and regional (Geary *et al.* 2013) scales in Scotland show a relatively consistent pattern of c. 60% of areas within 1 km of leks consisting of moorland, equating to c. 200 ha. Our data also suggest that individual males typically use an area greater than 200 ha in each season. Management for Black Grouse conservation may therefore need to ensure that moorland patches are not reduced below this threshold. However, given apparent differences in habitat use between sexes, and the fact that males and females demonstrate further differences in diet (Beeston *et al.* 2005), this threshold may need to be larger.

Moorland patches will also need to be connected to allow dispersal between populations, and maintain genetic exchange (Höglund *et al.* 2011). In England, more than 50% of first-year females dispersed ≤ 5 km in autumn, and ≤ 3 km in spring, and so moorland patches may need to be relatively close together to facilitate dispersal. The use of large-scale commercial plantations in this study was restricted to the external edges, typically to within 300 m of external habitats, and they could therefore substantially fragment moorland landscapes and restrict birds from utilising multiple fragmented moorland patches within the vicinity of their associated lek. This also indicates that sympathetic management of forests should be concentrated at their periphery, adjacent to external moorland components. Because the majority of a forest-cycle consists of growth stages unsuitable for Black Grouse breeding, forest management for the species should consider the habitat mosaic that will be present during the post-thicket stage. Given partitioning in forest-type use between males and females seen in this study, both broadleaf and conifer components should be provided within close proximity at a scale that would make them available to a single lekking group and associated female population.

Forest expansion targets present both challenges and opportunities for Black Grouse conservation. Set against the challenges are the competing demands for forest expansion to capture carbon, increase timber supply and provide other ecosystem services (Scottish Government 2009). As with large-scale afforestation that occurred during the 20th century, Black Grouse populations may respond positively to initial increases in the extent of young forest in Scotland (White *et al.* 2013), but it will be important for conservation managers to take a long-term view, ensuring that when forests mature and in landscapes where a ‘bottleneck’ in the availability of young forest habitats is possible, that there is a sufficient moorland component in the landscape to maintain viable breeding populations. Both broadleaf and conifer forest components should be available to these populations. The combination of broad national targets and landowner-scale decision making may not be sufficient to provide these resources, so a landscape-scale management approach and decision-making process may be required (see Sayer *et al.* 2004).

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TABLES

Table 1. Descriptions of habitats defined in the study and their dominant tree-layer and field layer components.

Habitat	Description
NON-FOREST	
Moorland	Open land previously/currently managed for red deer and/or red grouse shooting; some low intensity Domestic Sheep or Domestic Cattle grazing; little deer exclusion. Rarely few scattered trees/scrub with field dominated by either Heather, Purple Moor-grass *Molinia caerulea* or peat mosses *Sphagnum spp.*.
Farmland	More intensively grazed pasture typically at lower altitudes; generally improved; few cereal fields. Occasional tree line along boundary. Grass dominated field layer.
Other	Areas unsuitable for Black Grouse, e.g. buildings, roads and water bodies.
NON-COMMERCIAL FOREST	
Broadleaf woodland	Typically along riparian habitats or moorland margins. Birch *Betula spp.* dominant tree layer with some Rowan *Sorbus aucuparia*, Aspen *Populus tremula* and willows *Salix spp.*, and grass-dominated field layer.
New native pinewood	On previous moorland, 14 years old or less; sparsely planted Scots Pine trees in clumps with approximately 20% open ground in between with some birches, Rowan and oaks *Quercus spp.*. Fenced against Red Deer and Domestic Sheep intrusion. Planted under government subsidy.
COMMERCIAL FOREST	
Closed-canopy forestry	Densely planted commercial forestry stands of primarily Sitka Spruce *Picea sitchensis* and Lodgepole Pine *Pinus contorta* where crop canopy has closed over (14 years or older). Generally little field layer.
Forestry clearings	Either pre-thicket re-stocks (<14 years, planted on previous clearfells), clearfells or areas left unplanted, including tracks and rides. Field layer variable, grass or Heather dominated with much brash within clearfells. Natural regeneration of trees often occurring, particularly around clearing edges.

Table 2. Measures of habitat composition within the vicinity of leks and composition of habitats of birds caught in this study. Habitat composition is taken from within 1 km of leks from a 2010 complete survey of the study site and wider area (53 000 ha) (White *et al.* 2013), and is considered for all habitats and for potential brood-rearing habitats alone (*moorland, new native pinewood, forestry clearings). Composition of catching habitats for birds caught is given for brood catches only, and for all catches (both brood and roost).. “-“ represents ‘not applicable’.

Measure	Moorland	Farmland	Broadleaf woodland	New native pinewood	Closed-canopy forestry	Forestry clearings
% habitats around leks (n = 30)	67 ± 4	9 ± 2	5 ± 1	11 ± 4	6 ± 2	1 ± 0
% brood rearing habitats around leks* (n = 30)	84 ± 4	-	-	14 ± 4	-	2 ± 1
% search area for brood catching (47.8 km^2)	58	0	0	38	0	4
% caught (broods only) (n = 73)	84	-	-	16	-	0
% caught (broods + roosts) (n = 90)	87	-	-	13	-	0

Table 3. Sample sizes of Black Grouse ranges recorded by season, sex and year of study (Year 1 = October 2009 to September 2010 inclusive; Year 2 = October 2010 to September 2011 inclusive; Year 3 = October 2011 to September 2012 inclusive).

		Year			
Season	Sex	1	2	3	Total
Autumn-winter	Female	4	10	3	17
	Male	7	11	7	25
Spring-summer	Female	1	6	4	11
	Male	4	8	5	17
	Total	16	35	19	70

Table 4. Percentage habitat composition across radio-locations and within bird ranges (100% MCPs) by season and sex (± SE) and composition of habitats within study areas combined (two combined area 100% MCPs around individual MCPs, one at each study site, totalling 8 948 ha). 'n' refers to sample size of individuals in each group.

Season	Sex	n	Type	Moorland	Farmland	Broadleaf woodland	New native pinewood	Closed-canopy forestry	Forestry clearings
Autumn-winter	Female	17	Locations	56±8	1±1	4±3	22±9	13±6	4±2
			MCP	65±9	1±1	1±0	18±8	13±7	2±1
	Male	25	Locations	54±7	15±5	5±3	13±5	7±3	6±3
			MCP	59±56	9±3	7±2	14±5	7±3	3±2
Spring-summer	Female	11	Locations	70±9	0±0	1±1	21±9	5±3	3±2
			MCP	76±8	0±0	0±0	17±8	5±3	1±1
	Male	17	Locations	63±6	17±5	10±3	7±4	2±1	1±1
			MCP	76±6	11±3	5±2	6±4	2±1	0±0
			Study areas	35	9	7	15	25	10

Table 5. Habitat selection ranking matrices based on comparison of habitat composition within individual 100% minimum convex polygons of radio-locations and composition within study areas, by season and sex. The +/- sign shows that the row habitat was higher/lower ranked than the column habitat with respect to the appropriate analysis and is tripled (+++/---) where the pairwise difference was significant at α = 0.05. Row habitats are ranked according to the number of higher rank (+ or +++) positions. Habitats not ranked were excluded because fewer than two individuals utilised the habitat.

			Column habitat						
Season	Sex	Row habitat	Moorland	Farmland	Broadleaf woodland	New native pinewood	Closed-canopy forestry	Forestry clearings	Rank
Autumn-winter	Female	Moorland		+++	+++	+++	+++	+++	1
	(n = 17)	Farmland	---		-	-	-	---	6
		Broadleaf woodland	---	+		-	-	-	5
		New native pinewood	---	+	+		-	-	4
		Closed-canopy forestry	---	+	+	+		-	3
		Forestry clearings	---	+++	+	+	+		2
	Male	Moorland		+++	+++	+++	+++	+++	1
	(n = 25)	Farmland	---		-	+	+++	+	3
		Broadleaf woodland	---	+		+++	+++	+++	2
		New native pinewood	---	-	---		+	+	4
		Closed-canopy forestry	---	---	---	-		-	6
		Forestry clearings	---	---	---	-	+		5
Spring-summer	Female	Moorland			+++	+++	+++	+++	1
	(n = 11)	Farmland							
		Broadleaf woodland	---			-	+	-	4
		New native pinewood	---		+		+	+	2
		Closed-canopy forestry	---		-	-		----	5
		Forestry clearings	---		+	-	+++		3
	Male	Moorland		+++	+++	+++	+++	+++	1
	(n = 17)	Farmland	---		+	+++	+++	+++	2
		Broadleaf woodland	---	-		+++	+++	+++	3
		New native pinewood	---	---	---		+	-	5
		Closed-canopy forestry	---	---	---	-		-	6
		Forestry clearings	---	---	---	+	+		4

LEGENDS TO FIGURES

Figure 1. Habitat map of study areas in Perthshire with catch locations of 89 Black Grouse fitted with radio-tags (black circles, some overlain): (a) Tummel Forest and (b) Talladh-a-Bheithe Forest, with (c) their approximate location within Scotland. Study area boundaries are depicted as the smallest rectangles containing all subsequent live radio-locations. The Talladh-a-Bheithe Forest study area is 5 km west of Tummel Forest study area.

Figure 2. The percentage of maximum area of (100%) minimum convex polygon (MCP) (y) against number of radio-locations recorded for 90 bird-seasons within the study (x). Only five or more locations are considered because the software (R Development Core Team 2010) did not calculate MCPs with fewer. The fitted line is a negative exponential model $y = 100(1-e^{-0.4074x})$ ($t_1 = 46.1$, $P < 0.01$), which is solid across the fitted x values and dashed for extrapolation to the origin.

Figure 3. Predicted probability of a point within commercial forestry being a bird location or a random location, as a function of distance-to-forest-edge from a generalised linear mixed model (see text). The solid line represent the predicted probability, and the dashed lines the standard error around the prediction. The dotted line indicates where the probability is 0.5. The distribution of distances to forest edge for bird locations (n = 145; top) and random locations (n = 200; bottom) are illustrated as vertical bars to illustrate their relative distributions.