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**Effects of density on lek-site selection by Black Grouse (*Tetrao tetrix*) in the Alps**

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**Capsule** The Black Grouse is a primarily lekking species, but low population density and lack of suitable habitat can lead to establish non-lekking populations.

**Aims** To understand if differences in density could be related to differences in the lekking system, if there were differences in lek-site selection, and if there was a direct effect of habitat on the lek size.

**Methods** We compared two Black Grouse populations with different male density. We carried out counts from randomly chosen sample points and estimated population density by distance sampling. We compared the differences in the lek size distribution between the two study areas by a permutation chi-square test. We considered land-cover categories, landscape metrics and orographic variables and computed the Ivlev's Electivity Index to evaluate habitat selection of males in the two study areas. We performed a general linear model of the number of males attending the lek vs. habitat variables to evaluate if the habitat had an effect on male abundance on lek sites.

**Results** We couldn't demonstrate the direct effect of density on the displaying behavior but we found strongly different patterns of lek-site selection and different effects of habitat on lek size according to the population density.

**Conclusions** We concluded that the high quality habitat for Black Grouse on the Alps should be considered case by case, not considering only what literature reports.

**Keywords:** Black Grouse, displaying behavior, habitat selection, mating system, male density, lek, *Tetrao tetrix*.

## INTRODUCTION

Mating systems are usually reported as being species-specific but intra-specific variation may be observed for many taxa, mostly due to ecological factors (Lott 1984). The Black Grouse (*Tetrao tetrix*) is well known to be a primarily lekking species (Alatalo *et al.* 1992), in which males aggregate in groups during the mating season to display and fight while females attend leks along boundaries to observe males. Yet this behavior is not obligate and different studies in the last decades have described non-lekking populations, in which males tend to attract females with solitary displays (Hoglund & Stohr 1997, Angelstam 2004, Svobodová *et al.* 2011, Chamberlain *et al.* 2012). Hoglund & Stohr (1997) gave four possible explanations, describing a non-lekking population of Black Grouse: 1) low population density: the frequency of interactions between males, and thus lekking behavior, would increase with male density; 2) lack of suitable habitat for establishing leks, as open bogs and clear cuts, 3) high proportions of yearling birds in the population and 4) genetic differences in the propensity of lekking between individuals and populations.

The first two hypothesis are the most likely to be the cause of the absence of leks. These were described for Black Grouse and also for other and non-grouse lekking species. In the study of Hoglund & Stohr (1997) they found that all solitarily displaying males were adults so they discarded the third hypothesis and suggested low density and lack of suitable habitats as the main causes of the lek absence. Warren & Baines (2008) found that in North England a very productive metapopulation of Black Grouse was characterized by a lower proportion of solitary males compared with another declining and isolated British population. Pearce-Higgins *et al.* (2007) indicated in habitat change as the decreasing of open-canopy forest one of the main causes of the decline of a Black

Grouse population in the Scottish Highlands from 1990 to 2002 with a direct effect on both lek occurrence and lek size (i.e. number of males attending the lek). Angelstam (2004), studying a population of Black Grouse in Sweden, found a clear threshold effect of the percentage of suitable habitat, represented by young forest and open bog, in predicting the presence of single or lekking Black Grouse males, in other words in the choice of mating system. He found also that the presence of lekking Capercaillie (*Tetrao urogallus*) was positively related to the amount of suitable habitat, represented by old thinning and final felling forest and forested bog. Hamilton & Manzer (2011) combined lek surveys and spatial modelling for Sharp-tailed Grouse (*Tympanuchus phasianellus*) in a large area of Alberta and they found that lek occurrence was positively related to the abundance of high-quality habitat for the species. Chamberlain *et al.* (2012) analyzed data from 25-year surveys of an increasing Black Grouse population on the Italian Alps and they found that the lekking proportion in their population reached an apparent threshold while the number of solitary displaying males continued to increase. They concluded that suitable lek habitat was not limiting but they also showed that with the increase of population the solitary displaying males expanded their range into higher and, possibly, less suitable altitudes.

The genetic aspect of the Black Grouse mating system was recently investigated by Svobodová *et al.* (2011) who compared the genetic diversity between lekking and non-lekking populations, finding higher genetic diversity in lekking populations than in non-lekking-ones, but in their conclusion no suggestion was given to understand if the genetic diversity can be ascribed to the differences in mating system.

European populations of Black Grouse show clear fluctuations in the last 50 years (Storch 2007, Geary *et al.* 2012). Although the IUCN (International Union for

Conservation of Nature) classifies Black Grouse as Least Concern species, in Europe it is listed as SPEC 3 with the “Vulnerable” status (Papazoglou & van Bommel 2004) and it is in Annex I of the European Bird Directive (Council Directive 2009/147/EC of 30 November 2009 on the conservation of wild birds). The Alpine population decline is clear (Storch 2007), yet the Italian law (Legge n. 157/92) allows the harvest of Black Grouse.

Understanding the mechanisms that drive the mating system and the spatial distribution of a species of conservation concern as the Black Grouse is therefore important to plan correct management measures. Using the information about which habitat variables influence the lek occurrence and male attendance in leks can help wildlife managers in prioritizing management activities.

The main aim of our study was then to verify the first two hypotheses for the non-lekking mating system, comparing two Black Grouse populations on the Italian Alps, one with low male density and one with high male density. In particular we wanted to understand 1) if differences in density can be related to differences in the lekking system, 2) if there were differences in habitat selection between the two populations, and 3) if there was a direct effect of habitat on the number of males attending the leks.

Our predictions were 1) that the population with higher male density had a higher percentage of lekking males, 2) that solitary and lekking males of the two populations selected different habitats and 3) that the lek size was positively affected by high quality habitat.

## **METHODS**

### **Study area**

We selected two study areas in the Piedmont Region on the western Alps (Fig. 1). The choice of the study areas, as being representative of low and high density, derived from data collected by Natural Park wildlife managers. Both study areas were selected on a belt along the timber line, in the ecotonal zone between forest and alpine meadows. The first study area (22.4 km<sup>2</sup>) was located in the northern part of the Orsiera-Rocciavre Natural Park (ORNP), at altitudes ranging from 1352m to 2526 m a.s.l. and slopes from 2.3° to 46.2°. Larch forest (33.8%), subalpine scrubland (19.4%) and alpine grasslands (18.9%) were the dominant land cover types. Average yearly temperature was 6.9 °C, with an average minimum in January of 0.7 °C and an average maximum in July of 14.9 °C. Precipitation averaged 837 mm per year, with the maximum falling as rain from April to June (1,670 m a.s.l. meteorological station, data from 1997 to 2011). ORNP was expected to be the study area with the low density population. Recently Viterbi *et al.* (2015) analyzed the population dynamics of the same Black Grouse population, through the years 1991-2009. They reported average densities ranging from 2.49 to 4.83 males/km<sup>2</sup>, with no linear trends over time with exception of a weak but no significant decline in one of their sampling areas. The second study area (9.5 km<sup>2</sup>) was located in the Alpi Marittime Natural Park (AMNP), close to the French border, with altitudes ranging from 1526 to 2606 m a.s.l. and slopes from 0.6° to 48.7°. The dominant cover types were larch forest (23.7%), subalpine scrubland (21.4%) and alpine grassland (13.0%). Average yearly temperature was 5.9 °C, with an average minimum in January of -2.7 °C and an average maximum in July of 15.4°C. Precipitation averaged 1349 mm per year, with the maximum falling as rain from April to June and from September to November (1390 m a.s.l. meteorological station, data from 1997 to 2011). AMNP was the study area with an expected high density population. Giraudo & PNAM (2015)

reported an average density of 9.57 males/km<sup>2</sup>, without a significant trend through the years 1999-2014.

## **Data collection**

### Black Grouse counts

We carried out black grouse counts in 2010 and 2011 from 25 April to 31 May. Since the traditional lek count methods generally don't take into account the single males displaying (Bibby *et al.* 2000), we decided to use a random sampling design because we wanted to have information about the whole male population, i.e. both lekking and not lekking males. We established a total of 40 sample points with a survey effort proportional to the size of each study area, with approximately 1 point/80 ha i.e. 30 points in ORNP and 10 in AMNP. We conducted the counts during the maximal bird-calling activity, in the first hours of the morning from 05:00 to 06:30 (Cayford & Walker 1991). To avoid the effect of our presence on the displaying behavior, we arrived at the point at least 30 minutes before starting the survey, during which we remained motionless and in silence. Each point was sampled twice each year, with an interval of approximately 2 weeks. Data were collected by 4 different operators, one of which surveyed both sites to ensure homogeneity of data collection protocol. Each single male observation was mapped on aerial photographs and then transferred into the software QGIS 2.6 (QGIS Development Team 2014), in case we observed a lek (two or more males) we mapped the centroid of it. We classified the calling males as solitary males when they were at least 150 m apart from another displaying cock, otherwise we classified them as lekking. This distance was chosen as an average distance of what reported by Angelstam (2004) and Chamberlain *et al.* (2012) who used, respectively,



200 m and 100 m. Using the GIS software we measured the radial distance from observer.

#### Habitat variables

Using the GIS and digital maps, we measured habitat variables in a circular buffer around each observation (solitary male or centroid of lek). Recently Geary *et al.* (2013) investigated the occurrence of black grouse leks by comparing models with predictors measured at different radii (from 0.2 km to 3 km) and they showed how all of them had good and comparable predictive power (in terms of AUC), although the effect of some habitat variables slightly varied. We decided to use a fixed radius of 500m as representative of the lek site habitat (Pearce-Higgins *et al.* 2007). In particular we used 6 cover-type variables obtained from a local digital map “Land Cover Forestry Map of the Piedmont Region”, expressed in percentage: scrubland, beech (*Fagus sylvatica*) forest, larch (*Larix decidua*) forest, grassland, rocky grassland and rocks. Furthermore, using the LecoS tool for QGIS (Jung 2013) we calculated 4 landscape metrics: the mean shape index (MSI), given by the sum of each patch's perimeter divided by the square root of patch area for each habitat class, that represent the shape complexity, the mean patch size (MPS), the edge density (ED), that is the amount of edge relative to the 500 m round buffer, and the Shannon diversity index.

Finally we used a 20 m digital elevation model to evaluate the average altitude, expressed in meters, and slope, expressed in degrees, and the amount of solar radiation in each buffer during the period of our study. The latter variable accounts for how daily and seasonal shift of sun angle, along with variation in elevation, orientation (slope and aspect) and shadows cast by topographic features, affect the amount of solar radiation, expressed in Wh/m<sup>2</sup>.

## Data analysis

We estimated the male densities by point transect distance sampling (Buckland 2001, Buckland *et al.* 2004). This method was chosen because was recently proven to provide better estimates, in terms of accuracy and precision, of breeding male black grouse populations on the Alps than more traditional methods (Franceschi *et al.* 2014). We used in particular the conventional distance sampling engine of the Distance software (Thomas *et al.* 2010), pooling the observed distances to obtain a global estimate of the detection function and expected cluster size and we stratified the encounter rate for the two study areas to obtain two density estimates, pooled by years. We performed estimation starting from half-normal, hazard-rate and uniform key functions with Hermite and simple polynomial series adjustment then we chose the best model according to the Akaike's Information Criterion (AIC) and Kolmogorov-Smirnov goodness-of-fit statistics (GOF K-S). To estimate the expected cluster size we averaged the size of detected clusters. The sampling variance was estimated empirically.

For each display site we grouped the maximum number of attending males into 4 classes: 1 male, 2-3 males, 4-6 males and > 6 males. By a permutation chi-square test we tested the differences in the lek size distribution between study areas (Agresti 2007).

To test for difference in habitat structure between the two study areas we compared the habitat variables measured in the circular plots with Kruskal-Wallis one-way non-parametric analysis of variance for the following subsets: pooled data, solitary males, pooled leks and for different lek size categories.

To evaluate habitat selection of breeding Black Grouse males in the two study areas, we computed the Ivlev's Electivity Index (Ivlev 1961) by the formula

$$E_i = \frac{o_i - \hat{\pi}_i}{o_i + \hat{\pi}_i}$$

Where  $E_i$  is the  $i$ -habitat Electivity Index,  $o_i$  is the average proportion of used  $i$ -habitat, measured in the circular plots around each observation and  $\hat{\pi}_i$  is the sample proportion of available  $i$ -habitat, measured in the study area. The index ranges between +1.0 and -1.0, with positive values indicating preferences and negative values indicating avoidance of a particular habitat. The 0 value indicates that the habitat type is used in proportion to its availability. The index was calculated for pooled data, solitary males and leks in each and in pooled study areas. For each subset we followed a bootstrap approach, resampling the original samples 1000 times (Manly 2006) and re-calculating the Ivlev's Electivity Index for each bootstrap sample. We calculated the average index, standard errors and 95% confidence intervals for each habitat. To assess whether selection of vegetation types deviated from randomness (i.e.  $E_i = 0$ ) we checked if the confidence intervals contained the 0 value.

To evaluate if the lek structure had an effect on males abundance on lek sites, we performed a general linear model (GLM) with Poisson distribution (Zuur *et al.* 2009) of the number of displaying males vs. standardized habitat variables and interactions between habitat variables and study areas. For the variables selection we followed the information theoretic approach (Burnham & Anderson 2002), starting from the subsets of variables that resulted significantly different between study areas and between solitary and lekking plots. To validate the models we evaluated the McFadden pseudo- $R^2$  (McFadden 1974, Cameron & Windmeijer 1997, Faraway 2005) and we tested the residual normality by Shapiro-Wilk test (Shapiro 1985) and the residuals autocorrelation by Moran's I test (Dormann *et al.* 2007). For the analyses we used the software R 3.1.2 (R Development Core Team 2014).

## RESULTS

In the two pooled years, we collected 27 observations with a mean cock number of 3.0 ( $\pm 3.40$  SD) in AMNP and 33 observations with a mean cock number of 2.8 ( $\pm 3.03$  SD) in ORNP. The best detection function, in terms of AIC, was a hazard-rate model without series adjustments ( $\sigma = 323.0$ ,  $\beta = 4.95$ , GOF K-S  $P = 0.417$ ). The effective detection radius was 359.3 m and we estimated a density of 9.2 males/km<sup>2</sup> (95% confidence intervals: 7.6 – 10.9) in AMNP and 5.2 males/km<sup>2</sup> (95% confidence intervals: 4.2 – 6.4) in ORNP.

In the two pooled study areas we found that 49.2% of observations were solitary males, 25.4% were leks with 2-3 males, 15.3% leks with 4-6 males and 10.1% leks with more than 6 males. The lek size distribution did not differ between the two study areas (Table 1, Fig. 2).

Pooling all the observations, the AMNP had significantly higher percentage of pioneer vegetation, scrubland, beech forest and rocky grassland, higher values of Shannon diversity index and a lower percentage of larch forest than the ORNP while all the other habitat variables did not show differences (Table 2). Pioneer vegetation was significantly different in particular for pooled and large lek observations but we did not find differences for solitary males. On the contrary, the percentages of scrubland and larch forest were different in solitary male plots. Percentage of beech forest was significantly higher in AMNP both for solitary males and for leks, in particular small and medium leks. On the contrary, the percentage of larch forest was higher in ORNP both for solitary males and for leks but with no differences within the lek size classes. Shannon diversity index was different in particular for solitary males but not for lek observations. All the other landscape metrics were significantly different between the

two study areas. In particular the AMNP had higher edges density while the ORNP had higher mean shape index and mean patch size.

The confidence intervals of Ivlev's electivity indexes never contained the 0 value and all the t-test for difference from 0 were highly significant ( $P < 0.001$ ), indicating a non random use for all the habitat types. The pioneer vegetation was always avoided in ORNP while in AMNP it was avoided by solitary males but positively selected by leks. Scrublands were always selected, except for solitary males in ORNP that avoided it. Larch forests were selected in all considered cases but not in ORNP leks, where they were avoided. Grasslands were always avoided but in AMNP they were selected by leks. Finally Beech forests, rocky grasslands and rocks were always avoided (Table 3).

Ranking the GLM models by  $\Delta AIC_c$ , we only obtained a best model since all the other had a  $\Delta AIC_c > 2$ . The model had a pseudo- $R^2$  of 0.767, a normal distribution of residuals ( $P = 0.375$ ), and absence of spatial autocorrelation ( $P = 0.714$ ). Scrubland and the mean patch size had a significant and positive effect on the number of males attending the leks whereas the mean shape index had a negative effect (Table 4, Fig. 3). The interaction between Shannon index and the ORNP study area had a significant and positive effect. Finally the interaction between scrubland and the ORNP study area had a negative and significant effect on lek size (Table 4).

## DISCUSSION

We compared a high male density population with a low one. The choice to investigate only two populations can represent a limit of our study, however from our results we can draw some suggestions to explain the mating system of Black Grouse populations on the Alps.

According to our first hypothesis, we should have found a higher proportion of lekking males in high male density population. Our two populations had a significantly different male density but we did not find any difference in lek size distribution. In both cases half part of observations were solitary males and half were leks. The two populations indeed had a significantly different male density but anyway both were higher if compared to the study of Hoglund & Stohr (1997). In their study they investigated a non lekking population in central Sweden with very low density, between 0.43 males/km<sup>2</sup> in 1995 and 0.80 males/km<sup>2</sup> in 1996, and they found only one lek with two males in 1995 while all the other observations were solitary males. They concluded that the absence of leks was due mostly to the low population density. In our case we cannot draw neither similar nor opposite conclusion but it did not seem to exist a direct effect of density on displaying behavior, at least not at these densities. We can hypothesize that there must be a threshold to which the male density have an effect on the choice of displaying strategy but to demonstrate it for the Alpine population we probably need to compare a higher number of populations, taking into consideration a wider range of density level, starting from those comparable to the low density of the study of Hoglund & Stohr (1997).

Since there were no substantial differences in mating system, we could not verify the second hypothesis for our populations, i.e. lack of suitable habitat to establish leks. Notwithstanding, we found that the two populations showed some differences in habitat selection though the two study areas had few differences in habitat composition, suggesting that male density could have an effect on the choice of habitat to establish leks.

The more evident difference in habitat structure was the percentage of beech and larch forests: beech was significantly higher in low density area and larch was significantly higher in high density area. Nevertheless, in both populations the Ivlev's electivity index indicated that males avoided beech forest and positively selected larch forest. This indeed can be the reason for the different males density, since beech forest on the Alps is characterized by closed canopy and thus low quality habitat for Black Grouse (Pearce-Higgins *et al.* 2007)..

Pioneer vegetation, according to the pooled observations, was selected by males of high density population and avoided by those of low density population. At a first sight we may conclude that pioneer vegetation represent a low suitable habitat because when competition is low, all males tend to prefer better quality habitat but when the competition is high we expect that even poor habitats are selected (Fretwell & Lucas 1970, Van Horne 2002). The presence of pioneer vegetation on the Alps is often a consequence of pasture abandonment that lead to a decrease in open ground habitat and reduces heterogeneity in the landscape (Laiolo *et al.* 2004). The British populations of Black Grouse are negatively affected by the maturation of plantation forestry (Pearce-Higgins *et al.* 2007, Geary *et al.* 2013, White *et al.* 2013). If this is true also for the Alpine populations we would expect that solitary males in high density area were the most likely to select pioneer vegetation, yet we found an avoidance of it by solitary males in both populations and a selection by leks in high density area. Evaluating the selection for grasslands, we found exactly the same result: avoidance by solitary males in low density area and selection by solitary males in high density area, yet a preference by leks in high density area. These two results may indicate that the density-dependence on the selection of these two habitats acts mostly on leks, and not on solitary males.

Scrublands were positively selected by pooled and lekking males in both and in pooled study areas but solitary males of low density population avoided it. It is known that open bogs with sparse scrubland is a high quality habitat for Black Grouse because it allows to gather in leks both in Britain (Watson & Moss 2008) and on the Alps (Immitzer *et al.* 2014) but solitary males during the breeding season tend to display on the top of larch trees (Hoglund & Stohr 1997), more than on the ground and actually larch forest was the only habitat positively selected by solitary males of low density population.

For the British population of the species it was demonstrated that the quantity of each habitat that is considered suitable changes at different radii around leks and in particular that Black Grouse prefers a complex mosaic with different mixes of habitat immediately around the lek (Geary *et al.* 2013). For our Alpine population we can draw similar conclusion, as our results showed that in almost all considered cases the species positively selected both scrublands and larch forests.

From the regression analyses we found that the interaction between scrublands and the low density area had a negative effect on the number of males attending the lek. In contrast in the high density area scrublands have a positive effect on the number of males attending the lek.

It also emerged a clear avoidance of low altitude habitats as beech forests and high altitude habitats as rocks and rocky grassland in all considered cases.

Besides the differences in habitat composition, the two study areas had difference in habitat structure, as emerged from the comparison between the landscape metrics. High density area had greater habitat diversity with smaller and more complex patches. This may indicate that a more complex habitat is linked to a higher population density.



Patthey *et al.* (2012), analyzing habitat preference of both male and female Black Grouse in different study sites of Swiss and Italian Alps, showed that patchy and heterogeneous microhabitats played an essential role for the occurrence of the species. Schweiger *et al.* (2012) also found that a mosaic structure of dwarf shrubs and grassy patches (i.e. high patchiness) generally increased the probability of Black Grouse presence. Nevertheless from our regression analysis we found that the mean shape index had a negative effect on the number of males attending the lek. MSI is equal to 1 when all patches are circular and it increases with increasing patch shape irregularity so a negative effect of it indicates that plot with more complex shapes have a negative effect on males number in leks. So we may conclude that more complex habitats have indeed a positive effect on population density but that it acts mostly on solitary males rather than on lekking males. The positive effect of mean patch size and the negative effect of the diversity index, although not significant, seem to lead the same conclusion. Finally in the best model we found a positive effect of the interaction between the Shannon index and the low density study area, so we may conclude that a more complex habitat, besides favoring solitary males, has a greater effect on the lek size in low density population, rather than in high density population.

Geary *et al.* (2012) identified a clear effect of lek size on lek longevity and resilience, indicating that maintenance of large leks is crucial in buffering the population against declines. This can potentially complicate our findings, because it may be possible that large leks are now present where habitat has changed. We didn't have data about habitat change and not even precise location of single males and leks through the years but it would be interesting to extend our research to a longer term research, following a

similar approach done by White *et al.* (2013), who investigated the role of habitat change in lek establishments and extinctions.

When dealing with habitat and resource selection, the choice of the detail level at which carrying out the analyses, can affect the quality of the results (Brambilla *et al.* 2009). Pearce-Higgins *et al.* (2007) obtained good results on modelling Black Grouse occurrence and lek size when considering the effect of variables such as forest maturation, undergrowth characteristics and moorland habitat composition. In a previous work on habitat selection by breeding Rock Ptarmigan males, we compared the habitat variables obtained from the same land cover digital map that we used in the present work (Land Cover Forestry Map of the Piedmont Region) with a more detailed phytosociological map (Nelli *et al.* 2013). Unfortunately, the same detail level was not available for our two Black Grouse study areas. For the Rock Ptarmigan, with the fine-scale map we obtained more interesting results on habitat selection of the species, but with the forestry map we obtained good predictive models and we were able to obtain useful information as well (Nelli *in press*).

Concluding, with the present study we were not able to properly answer our main question, as we couldn't demonstrate that Black Grouse populations with different density have a different lekking system. Nevertheless from our results we stressed the fact that the patterns of habitat selection in Black Grouse may strongly vary according to the population density. Some normally considered high quality habitat and habitat complexity may in fact play a different role on selection by solitary or lekking males when different population density are considered. Thus we suggest that this remarks should be acknowledged when management decision are taken, in particular it should be

necessary to evaluate the potential high quality habitat case by case, considering more than just what has been reported in the literature.

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## LITERATURE CITED

- Agresti, A.** 2007. *An Introduction to Categorical Data Analysis*. Wiley, New York.
- Alatalo, R.V., Höglund, J., Lundberg, A. & Sutherland, W.J.** 1992. Evolution of black grouse leks: female preferences benefit males in larger leks. *Behav. Ecol.* **3**: 53-59.
- Angelstam, P.** 2004. Habitat Thresholds and Effects of Forest Landscape Change on the Distribution and Abundance of Black Grouse and Capercaillie. *Ecol. Bull.* **51**: 173-187.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H.** 2000. Counting individual species. *Bird census techniques*. 130-152. Academic Press, London.
- Brambilla, M., Casale, F., Bergero, V., Crovetto, G.M., Falco, R., Negri, I., Siccardi, P. & Bogliani, G.** 2009. GIS-models work well, but are not enough: Habitat preferences of *Lanius collurio* at multiple levels and conservation implications. *Biol. Conserv.* **142**: 2033-2042.
- Buckland, S.T.** 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L.** 2004. *Advanced Distance Sampling: Estimating abundance of biological populations*. Oxford University Press, Oxford.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

- Cameron, A.C. & Windmeijer, F.a.G.** 1997. An R-squared measure of goodness of fit for some common nonlinear regression models. *Journal of Econometrics* **77**: 329-342.
- Cayford, J.T. & Walker, F.** 1991. Counts of male black grouse *Tetrao tetrix* in North Wales. *Bird Study* **38**: 80-86.
- Chamberlain, D.E., Bocca, M., Migliore, L., Caprio, E. & Rolando, A.** 2012. The dynamics of alternative male mating tactics in a population of Black Grouse *Tetrao tetrix* in the Italian Alps. *J. Ornithol.* **153**: 999-1009.
- Dormann, C.F., Mcpherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuehn, I., Ohlemueller, R., Peres-Neto, P.R., Reineking, B., Schroeder, B., Schurr, F.M. & Wilson, R.** 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**: 609-628.
- Faraway, J.J.** 2005. *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Chapman & Hall, London.
- Franceschi, S., Nelli, L., Pisani, C., Franzoi, A., Fattorini, L. & Meriggi, A.** 2014. A Monte Carlo Appraisal of Plot and Distance Sampling for Surveys of Black Grouse and Rock Ptarmigan Populations in Alpine Protected Areas. *J. Wildl. Manage.* **78**: 359-368.
- Fretwell, D.S. & Lucas, H.L.** 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**: 16.
- Geary, M., Fielding, A. & Marsden, S.** 2012. The anatomy of population change in a black grouse population 1992–2008. *Oecologia* **168**: 73-81.
- Geary, M., Fielding, A.H. & Marsden, S.J.** 2013. Designing mosaic landscapes for Black Grouse *Tetrao tetrix* using multi-scaled models. *Ibis* **155**: 792-803.
- Giraud, L. & Pnam, P.N.a.M.** 2015. Black Grouse spring counts 2000-2015 in Alpi Marittime Natural Park. *Unpublihed raw data*.
- Hamilton, S. & Manzer, D.** 2011. Estimating Lek Occurrence and Density for Sharp-tailed Grouse. *Ecology, Conservation, and Management of Grouse*: 33-49.
- Hoglund, J. & Stohr, S.** 1997. A non-lekking population of black grouse *Tetrao tetrix*. *J. Avian Biol.* **28**: 184-187.
- Immitzer, M., Nopp-Mayr, U. & 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. *J. Ornithol.* **155**: 173-181.
- Ivlev, V.S.** 1961. *Experimental Ecology of the Feeding of Fishes*. Yale University Press, Yale.
- Jung, M.** 2013. LecoS - A QGIS plugin for automated landscape ecology analysis. *PeerJ PrePrints*: 1:e116v2.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A.** 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* **41**: 294-304.
- Lott, D.F.** 1984. Intraspecific Variation in the Social Systems of Wild Vertebrates. *Behaviour* **88**: 266-325.
- Manly, B.F.J.** 2006. *Randomization, Bootstrap and Monte Carlo Methods in Biology, Third Edition*. Chapman & Hall, London.
- Mcfadden, D.** 1974. Conditional Logit Analysis of Qualitative Choice Behavior. In Zarembka, P. (ed), *Frontiers in Econometrics*. 105-142. Academic Press, New York.
- Nelli, L., Meriggi, A. & Franzoi, A.** 2013. Habitat selection by breeding rock ptarmigan *Lagopus muta helvetica* males in the western Italian Alps. *Wildl. Biol.* **19**: 382-389.
- Nelli, L.** *in press*. Habitat suitability models and carrying capacity estimations for rock ptarmigans in a protected area of the Italian Alps. *Riv. Ital. Ornitol.*
- Papazoglou, C. & Van Bommel, F.** 2004. *Birds in the European Union: A Status Assessment*. BirdLife International.

- Patthey, P., Signorell, N., Rotelli, L. & Arlettaz, R. 2012. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. *Eur. J. Wildl. Res.* **58**: 59-70.
- Pearce-Higgins, J.W., Grant, M.C., Robinson, M.C. & Haysom, S.L. 2007. The role of forest maturation in causing the decline of Black Grouse *Tetrao tetrix*. *Ibis* **149**: 143-155.
- Qgis Development Team. 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- R Development Core Team, 2014. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Schweiger, A.K., Nopp-Mayr, U. & Zohmann, M. 2012. Small-scale habitat use of black grouse (*Tetrao tetrix* L.) and rock ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. *Eur. J. Wildl. Res.* **58**: 35-45.
- Shapiro, S.S. 1985. An analysis of variance test for normality (complete samples). *Current Contents/Social & Behavioral Sciences*: 14-14.
- Storch, I. 2007. *Grouse: Status Survey and Conservation Action Plan 2006-2010*. IUCN and World Pheasant Association, Glann and Fordinbridge.
- Svobodová, J., Segelbacher, G. & Höglund, J. 2011. Genetic variation in Black Grouse populations with different lekking systems in the Czech Republic. *J. Ornithol.* **152**: 37-44.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* **47**: 5-14.
- Van Horne, B. 2002. Approaches to habitat modeling: the tensions between pattern and process and between specificity and generality. In Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., W.A., W. & F.B., S. (eds), *Predicting species occurrences: issues of accuracy and scale*. 63-72. Island Press, Washington D.C.
- Viterbi, R., Imperio, S., Alpe, D., Bosser-Peverelli, V. & Provenzale, A. 2015. Climatic Control and Population Dynamics of Black Grouse (*Tetrao tetrix*) in the Western Italian Alps. *J. Wildl. Manage.* **79**: 156-166.
- Warren, P. & Baines, D. 2008. Current status and recent trends in numbers and distribution of Black Grouse *Tetrao tetrix* in northern England. *Bird Study* **55**: 94-99.
- Watson, A. & Moss, R. 2008. *Grouse: The Natural History of British and Irish Species*. Collins, Glasgow.
- White, P.J.C., Warren, P. & Baines, D. 2013. Forest expansion in Scotland and its potential effects on black grouse *Tetrao tetrix* conservation. *For. Ecol. Manage* **308**: 145-152.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

**Table 1** - Percentage of lek size distribution in the two separated and pooled study areas and permutation chi-square test. ORNP: Orsiera-Rocciavrè Natural Park; AMNP: Alpi Marittime Natural Park.

<b>Lek size</b>	<b>ORNP</b>	<b>AMNP</b>	<b>Pooled</b>
solitary males	50.9	48.2	49.2
small lek (2-3 males)	31.3	18.5	25.4
medium lek (4-6 males)	6.3	25.9	15.3
big lek ( $\geq 7$ males)	12.5	7.4	10.1
$\chi^2 = 5.034$			
df= 3			
P = 0.169			

**Table 2** - Average values (SE) of habitat variables in the circular plot around the observations of Black Grouse and significance of Kruskal-Wallis ANOVA between the two study areas, divided by pooled observations, solitary males and leks.

Variables	Pooled Observations		Solitary males		Leks	
	ORNP	AMNP	ORNP	AMNP	ORNP	AMNP
Pioneer vegetation	0.6 (0.37)	6.6 (2.10)**	1.0 (0.73)	4.1 (1.72)	0.1 (0.09)	8.8 (3.7)*
Scrubland	26.3 (4.14)	26.9 (4.37)	14.8 (4.78)	31.8 (6.53)	37.7 (5.49)	22.3 (5.81)
Beech forest	2.1 (1.56)	17.9 (4.08)**	4.2 (3.08)	17.3 (5.05)*	0.0 (0.02)	18.4 (6.51)**
Larch forest	42.1 (5.07)	15.7 (4.54)**	49.8 (7.04)	17.0 (7.69)*	34.3 (6.97)	14.5 (5.34)*
Grassland	18.9 (2.7)	17.2 (2.77)	22.2 (4.32)	15.7 (3.69)	15.6 (3.17)	18.6 (4.19)
Rocky grassland	4.6 (1.47)	6.1 (1.41)	5.1 (2.19)	6.5 (1.73)	4.1 (2.02)	5.8 (2.26)
Rocks	5.1 (1.57)	9.6 (3.21)	2.0 (0.87)	7.5 (3.36)	8.2 (2.85)	11.6 (5.43)
Altitude	1927 (26.9)	1845 (32.7)	1900 (46.0)	1857 (45.4)	1954 (28.0)	1835 (48.3)
Slope	24.6 (0.49)	25.3 (0.64)	24.9 (0.74)	25.8 (0.91)	24.2 (0.65)	24.8 (0.92)
Solar radiation $\times 10^3$	88.4 (0.90)	87.1 (0.90)	89.4 (1.64)	87.5 (1.66)	87.5 (0.76)	86.8 (0.88)
MSI	1.7 (0.02)	1.6 (0.01)**	1.8 (0.03)	1.6 (0.01)**	1.7 (0.04)	1.6 (0.02)*
MPS $\times 10^3$	61.6 (4.71)	31.9 (3.84)**	73.2 (7.95)	25.8 (4.55)**	50.0 (3.22)	37.6 (5.84)*
ED	6.9 (0.26)	10.4 (0.47)**	6.4 (0.44)	11.2 (0.65)**	7.3 (0.23)	9.6 (0.61)*
Shannon	1.6 (0.1)	2.0 (0.08)*	1.5 (0.15)	2.0 (0.14)*	1.7 (0.12)	1.9 (0.08)

ORNP: Orsiera-Rocciavre Natural Park

AMNP: Alpi Marittime Natural Park. MSI – mean shape index

MPS – mean patch size

ED – edge density

\* - significant difference at 0.05

\*\* - significant difference at 0.001

**Table 3** – Average values (SE) of Ivlev’s electivity indices for habitat selection of Black Grouse on the Italian Alps. Positive values indicate preferences and negative values indicate avoidance of a particular habitat.

Habitat	Pooled observations			Solitary			Lekking		
	ORNP	AMNP	PSA	ORNP	AMNP	PSA	ORNP	AMNP	PSA
Pioneer vegetation	-0.34 (0.010)	0.19 (0.005)	-0.21 (0.005)	-0.12 (0.014)	-0.04 (0.007)	0.05 (0.006)	-0.80 (0.004)	0.30 (0.007)	0.28 (0.008)
Scrubland	0.07 (0.002)	0.14 (0.002)	0.17 (0.002)	-0.23 (0.005)	0.22 (0.003)	0.08 (0.003)	0.25 (0.002)	0.03 (0.004)	0.24 (0.002)
Beech forest	-0.34 (0.011)	-0.14 (0.004)	-0.05 (0.004)	-0.03 (0.014)	-0.17 (0.005)	-0.01 (0.005)	-0.99 (0.000)	-0.15 (0.006)	-0.11 (0.007)
Larch forest	0.10 (0.002)	0.14 (0.004)	0.01 (0.002)	0.18 (0.002)	0.12 (0.008)	0.08 (0.003)	-0.01 (0.003)	0.09 (0.006)	0.09 (0.003)
Grassland	-0.12 (0.002)	0.02 (0.002)	-0.08 (0.002)	-0.04 (0.003)	-0.03 (0.004)	-0.06 (0.002)	-0.22 (0.003)	0.05 (0.003)	-0.11 (0.002)
Rocky grassland	-0.15 (0.005)	-0.26 (0.003)	-0.17 (0.003)	-0.13 (0.007)	-0.24 (0.004)	-0.14 (0.004)	-0.22 (0.008)	-0.31 (0.006)	-0.22 (0.005)
Rocks	-0.31 (0.004)	-0.22 (0.005)	-0.22 (0.004)	-0.65 (0.004)	-0.35 (0.006)	-0.43 (0.005)	-0.10 (0.006)	-0.15 (0.007)	-0.08 (0.005)

PSA: pooled study areas

ORNP: Orsiera-Rocciavré Natural Park

AMNP: Alpi Marittime Natural Park.



**Table 4** – Coefficients ( $\beta$ ) of general linear model for Poisson distribution of lek size vs. habitat variables in the two considered study areas.

<b>Variable</b>	<b><math>\beta</math></b>	<b>LCI</b>	<b>UCI</b>	<b><i>P</i></b>
(Intercept)	1.390	1.039	1.715	< 0.001
Scrubland	0.329	0.075	0.577	0.010
MPS	0.257	0.057	0.455	0.011
MSI	-0.455	-0.718	-0.191	0.001
Shannon	-0.123	-0.618	0.357	0.620
Study area (ORNP)	0.435	-0.042	0.907	0.359
Scrubland*Study_area(ORNP)	-0.878	-1.286	-0.477	< 0.001
Shannon*Study_area(ORNP)	0.625	0.110	1.159	0.019
LCI= 95% lower confidence interval				
UCI = 95% upper confidence interval mean patch size				
MPS = mean patch size				
MSI = mean shape index				

**Figure 1** – Location of the two study areas in Piedmont Region on the Western Italian Alps. ORNP: Orsiera-Rocciavré Natural Park; AMNP: Alpi Marittime Natural Park.

**Figure 2** – Lek size distribution in the two separated and pooled study areas. ORNP: Orsiera-Rocciavré Natural Park; AMNP: Alpi Marittime Natural Park.

**Figure 3** – Number of males attending the leks in the two pooled study areas as a linear function of percentage of scrubland, mean patch size (MPS) and mean shape index (MSI) in a 500m circular plot around the lek.

Figure 1

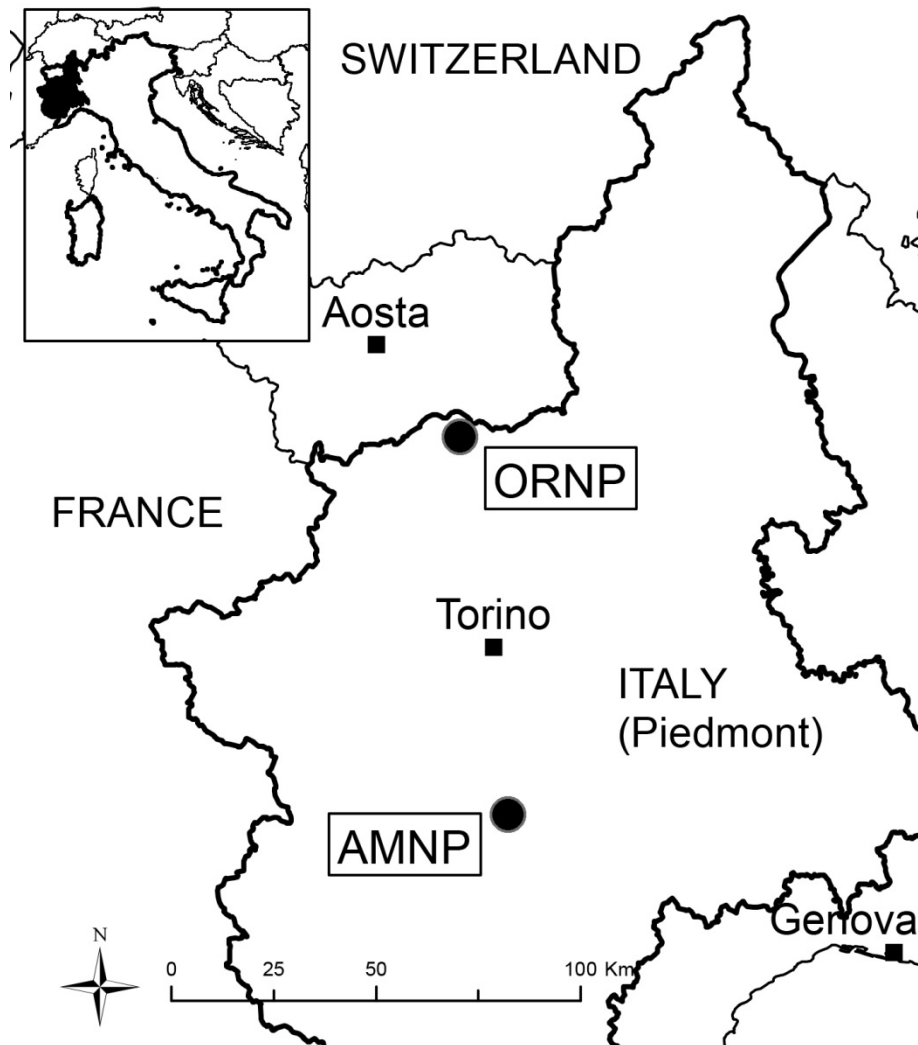


Figure 2

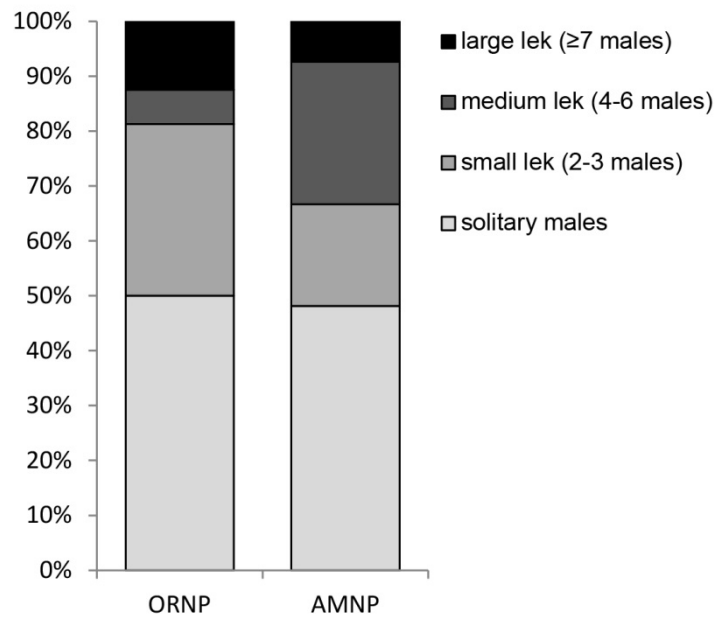


Figure 3

