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Fine-scale habitat use by black woodpecker *Dryocopus martius*: a year-round study in the Hyrcanian forest, Iran

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Abstract. We investigated the fine-scale habitat use by black woodpeckers all year round. We aimed to describe what environmental factors mostly affect species occurrence at a fine-grained scale in the Caspian Hyrcanian forest, Northern Iran, in a poorly studied portion of the species range. Presence and absence of birds and habitat variables (forest cover types, structural and complexity characteristics of vegetation and topography) were measured within a 25-m radius at 103 sampling points, and seasonal models for habitat selection were built. Plots occupied by woodpeckers consistently showed typical characteristics of old forests, with a high number of snags and many large trees (diameter at breast height > 20 cm and tree height > 20 m). Despite such a consistent association, the comparison of occurrence probability according to the most supported models across different seasons showed significant differences in habitat suitability between summer and autumn and between autumn and spring ($P < 0.05$), and marginally significant differences between winter and spring and winter and summer ($P < 0.1$). Such a difference revealed the occurrence of slight seasonal variation in habitat use at a fine scale. Due to the marked preference shown by black woodpecker for forest habitats with beech cover type and mature forest structure, it is essential to control severe exploitation of such habitats. Habitat suitability is strongly affected by the abundance of snag and old trees, the conservation of which is crucial for the species and likely for several other ones dwelling in the same forest habitats. black woodpeckers are associated with mature forest and the species conservation depends to a large extent on how forests are managed.

Key words: conservation, forest management, habitat requirements, Hyrcanian Forest, primary hole nester.

Introduction

Forest birds have attracted attention in environmental impact studies in the last decades because they have often been suggested as reliable indicators or monitors of healthy forest ecosystems (Furness & Greenwood 1993). Within this framework, woodpeckers (Aves: Picidae) have been proposed as indicators for forest biodiversity in several different contexts (Mikusiński & Angelstam 1998, Drever et al. 2008, Nappi et al. 2015, De Gasperis et al. 2016). Woodpeckers include several woodland species that are sensitive to anthropogenic changes in forest environments (Mikusiński 2006). Clearing of forests and conversion of naturally dynamic forests to production landscapes have led to the drastic decline and sometimes extinction of the more specialized species. Many woodpecker species are known to be sensitive to the removal of dead wood (Czeszczewik et al. 2013, Nappi et al. 2015). Due to this incompatibility, several woodpecker species have been recognized as surrogates for the assessment of forest avian diversity and forest biodiversity in general (Roberge et al. 2008, Drever & Martin 2010). Woodpeckers might function as umbrella species for other specialized forest organisms. In general, the autoecology of most woodpecker species has been investigated exclusively during the breeding season, whereas information for the non-reproductive phases is very sparse and mostly anecdotal, to the point that the most important drivers of species occurrence or habitat use outside the breeding season are generally unknown.

The black woodpecker *Dryocopus martius*, the largest woodpecker of the Palearctic region, uses different forest habitats both for breeding and feeding (Cramp 1988, Brambilla & Saporetti 2014) and plays an important ecological role in forest ecosystems as a keystone species for large-sized cavity nesting birds. It is the only woodpecker which creates breeding holes which other large hole nesters may use as well (Johnsson et al. 1993, Kosiński et al. 2011). Some studies carried out in Europe considered the black woodpecker as an indicator of old-growth forest conditions (Fernandez & Azkona 1996). However, also evidence against this hypothesis has been provided (Rolstad et al. 1998). Black woodpecker is mainly sedentary and is widely distributed throughout northern and temperate forests of Europe and Asia. Habitat use is presumably most related to its nesting/roosting and peculiar food requirements, especially carpenter ants (Rolstad & Rolstad 2000, Brambilla & Saporetti 2014). This species generally prefers woodland with large trees, favouring tall trunks of many coniferous and broad-leaved trees forming extensive forests (Cramp 1985). In Iran the black woodpecker is a scarce resident species in the Hyrcanian forest, which covers a narrow strip along the south margin of the Caspian Sea. In this portion of its range, the ecology of the black woodpecker is poorly known. Khanaposhtani et al. (2012) studied the habitat requirements of the black woodpecker in spring season at Kheyrood forest and suggested that tall and large diameter trees, high volumes of coarse woody debris and dense canopy cover, are significantly higher in areas where the black woodpecker occurs. The lack of information about the species ecology in other areas and in other periods of the year prevents the definition of well targeted conservation measures for this keystone species.

The aim of this study was thus to identify the habitat characteristics affecting habitat use by black woodpeckers throughout the year, in order to provide the knowledge requested for woodpecker conservation by means of adequate conservation and management of its habitat. Considering its value as an umbrella and a keystone species, other woodpecker species as well as the community of secondary cavity nesters would also benefit from woodpecker-oriented conservation measures (Balen et al. 1982).

Materials and methods

Study area

The research was carried out from June 2010 to June 2011, in Shast Kalate Forest (36°41' to 36°45' N, 54°20' to 54°24' E), an educational and research forest area, in the Caspian Hyrcanian mixed forests, in the Alborz Mountains in Northern Iran (Fig. 1). This forest is located around 6 km South-West of Gorgan, Golestan Province. The annual average temperature varies between 11.5 to 17.5 °C; the absolute minimum temperature is -25 °C and the reported maximum is 45 °C. Mean annual precipitation is 650 mm. The climate of the study area is relatively cold and wet, having a temperate summer with a short dry season.

The area covers about 37 km² and is largely covered by broad-leaved forests, ranging from 210 to 1960 m a.s.l. For forestry purposes, the Shast Kalate Forest is divided into two districts: a first district (c. 1700 ha), mostly exploited by means of strip cutting and mostly single and group tree selective cutting, and a second district (c. 2000 ha), which is unmanaged and being never harvested is representative of the original forest vegetation of the region. Survey points occur predominantly in the first (managed district), both in points interested by forestry and in other untreated plots, and secondarily in the second, unmanaged district. The study area can be roughly divided into three main sectors: a low-elevation belt (below 400 m a.s.l.), mostly containing *Parrotia-Carpinus-Quercus* forest type, an intermediate belt (400-700 m a.s.l.), dominated by *Carpinus-Parrotia* and *Parrotia-Carpinus* forest type, and a higher-elevation type (700-1000 m a.s.l.), where beech is the dominant tree species. The dominant tree species below 500-700 a.s.l. are hornbeam *Carpinus betulus* and ironwood tree *Parrotia persica*, whereas above this altitude, oriental beech *Fagus orientalis* becomes the dominant species. These species are mostly found together with other non-dominant species in mixed stands.

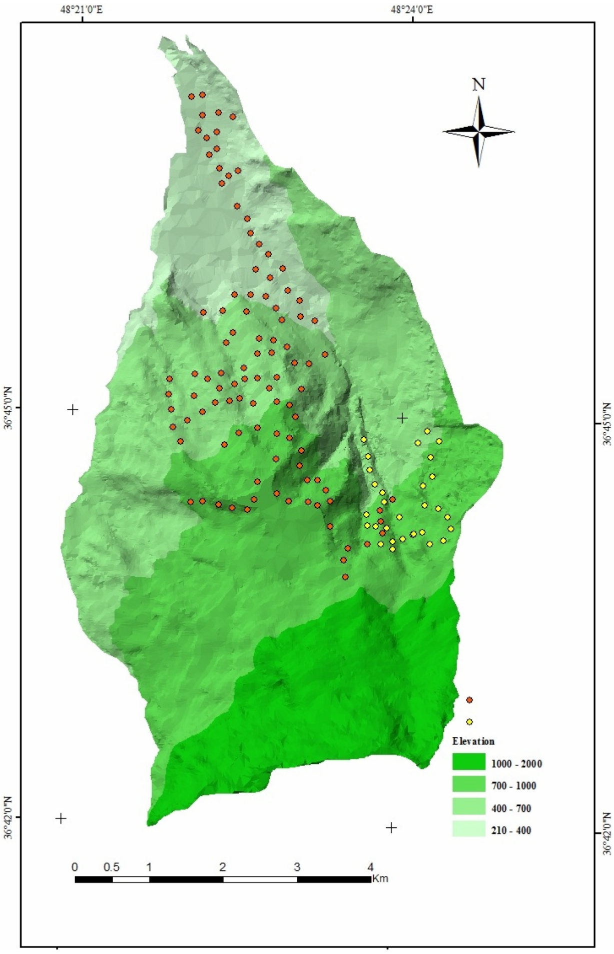

Figure 1. Geographic position of the study site, distribution of sampling points for modelling and for post-modelling field surveys in Northern Iran.

Environmental data

Twenty-three environmental factors potentially affecting the habitat suitability for black woodpecker were considered. Environmental variables, including forest cover types, structural and complexity characteristics of the vegetation and topography were measured within a 25-m radius of each of 103 sampling points distributed

Table 1. Habitat variables used to model black woodpecker presence/absence at the fine scale.

N.s	The number of snags
N.f	The number of fallen dead trees
H>20 m	The number of trees with height more than 20 m
H<20 m	The number of trees with height less than 20 m
H10-20 m	The number of trees with height between 10-20 m
DBH >20 cm	The number of trees with diameter at breast height (DBH) more than 20 cm
DBH <20 cm	The number of trees with DBH less than 20 cm
BSA	Basal area, m²
Vow	Volume of wood, m³
N.st	The number of stratum
H.s	Mean height of each story
P.s	Percent of each story
P.tb	Percent of timber and branch
S>20	Upper story
S10-20	Middle story
S<10	Lower story
Cc	Canopy cover
As	Aspect (n, s, e, w, or none)
Al	Elevation (m)
Sl	Slope (%)
Ca_1	Axis 1 of the correspondence analysis for tree species ordination
Ca_2	Axis 2 of the correspondence analysis for tree species ordination
Ca_3	Axis 3 of the correspondence analysis for tree species ordination

throughout the study area (Table 1). We included in the inventory only the variables that were expected to be potentially important in explaining habitat use of black woodpeckers. We did not include climatic data because the climate is suitable for woodpeckers within the whole study area (Cramp 1985), and the limited variations are mostly due to elevation.

In each plot, we recorded some variables describing the dominant vegetation structure: the tree species, tree height and the diameter at breast height (DBH-M) of all living trees, with DBH over 4 cm e.g. (Díaz 2006). Other factors representing vegetation structure and complexity included tree number, number of strata, percentage of each story and percentage of timber and branches. Dead tree number was recorded, including snags and fallen dead trees (Appendix 1). An index of south–north and east–west orientation was calculated using the sine and cosine of aspect, respectively (Díaz 2006). The basal area of each tree was calculated with the basal area function (Elledge & Barlow 2010), equation number 1:

$$Bsa = \frac{d^2 \pi}{4} \qquad (1)$$

Where Bsa = Basal Area (m^2), π= Constant (3.142) and d = Diameter at breast height (M).

Volume of wood was obtained following Küchler (1967), equation number 2:

$$V = \frac{d^2 \pi}{4} \times h \times 0.9 \qquad (2)$$

Where V is the volume, d is tree DBH (M) and h is the tree height (M).

Canopy cover was quantified using a spherical densitometer at 103 points within each plot (with four readings taken per point; see Lemmon 1957).

Fieldwork

We sampled bird species occurrence using sampling points (Bibby et al. 2000), enumerating woodpeckers in each of 103 point distributed at least 200 m apart across study sites. Stratified random sampling was used considering each elevation class as a stratum (210-400 m a.s.l.: 32 points; 400-700 m: 36 points; >700 m: 35 points), in order to sample adequately all the elevational belts corresponding with the main forest types (see above). Totally, we had 26 points in not used stands and 87 points in harvested stands. The occurrence of the black woodpeckers in the Shast Kalateh forest plots was established by direct observation (i.e. visual sightings; 33 sightings in summer, 45 in autumn, 36 in winter, 45 in spring), nest location (8 nests, added to spring samples) and signs of wood-boring (considered only for winter; 5 records, added to winter samples); all contacts were collected within a 25-radius from each point. Individuals flying over the plots or calling in not well-defined locations were not included. Bird sampling was carried out separately for each season to investigate the habitat use and relative variations over the year (summer: 1-11 August 2010; autumn: 1-11 November 2010; winter: 30 January-9 February 2011; spring: 30 April-10 May 2011). Bird surveys were carried out between 7:00 a.m. and 10:00 a.m., when the weather was favourable (i.e. avoiding rainy and windy days). This census period was considered as appropriate, because during the surveys birds' activity tended to be high during the whole morning. All bird observations were performed by one person (SK) to avoid observer bias. Sit-and-wait method was used at each sampling point to record black woodpecker. Following a 2-minute rest period, species observations were recorded in each plot as present or absent for a period of 10 minutes (Marsden et al. 2001).

Modelling habitat use

Habitat suitability modelling has been used to evaluate wildlife habitat and the effects of management activities. These models are based on functional relationships between wildlife and habitat variables (Rushton et al. 2004).

We used the widely adopted binomial logistic regression analysis to investigate black woodpecker habitat use. To evaluate the parameters potentially relevant for the species' occurrence, each parameter was entered individually into a binary logistic regression and the relative *P*-value was assessed. The parameters that did not result in a statistically significant effect ($P > 0.05$) were eventually removed. Significant variables were used as potential predictors in a logistic regression analysis to compare present and absent site (Appendix 2). We first verified the main tree species gradient of the study area with Correspondence Analyses (CA) for the tree species matrix (103×15). We extracted the first three axes of this analysis, which explained 72% of tree species variances in the study area, and used them as habitat explanatory variables for regression analysis (Fig. 2). The third axis was allocated to *Alnus subcordata, Quercus castaneifolia, Acer insigne* and *Diospyros lotus* in the CA analysis. The first axis was allocated to *Fagus orientalis* and *Carpinus betulus* in the CA analysis. The correlation structure of measured variables was investigated before running the analysis.

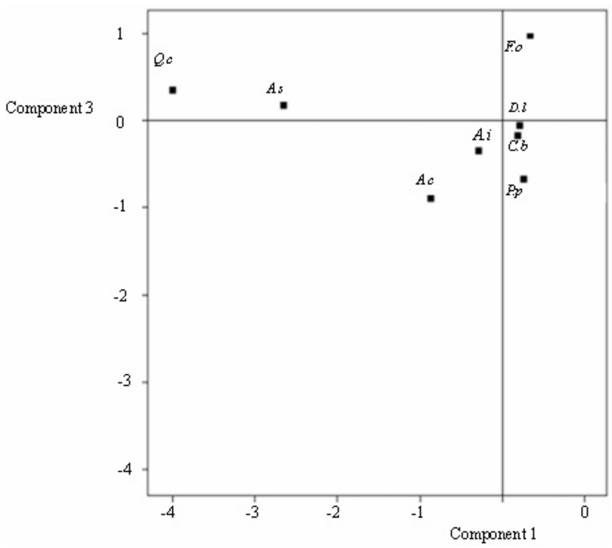

Figure 2. Classification of 8 tree species in Correspondence analysis, first and third axes. The first and the third axes showed significant relationship so were used them to model building. First axis separates *Fagus orientalis (F.o)*, *Carpinus betulus (C.b)*, *Parrotia persica (P.p)*, *Diospyros lotus (D.l)* from *Acer insigne (A.i)*, *Acer cappodocicum (A.c)*, *Quercus castaneifolia (Q.c)* and *Alnus subcordata (A.s)*, third axis separate *Fagus orientalis*, *Alnus subcordata*, *Quercus castaneifolia* from other species.

A coefficient matrix was made with the STATISTICA software (StatSoft 2004) to investigate the potential correlation among significant parameters. For each pair of highly correlated variables (Spearman correlation coefficient $r > |0.7|$; Dormann et al. 2013), the choice of the variable to be removed was based on the results of a logistic regression analysis (Hosmer Jr & Lemeshow 2004). We verified high correlation between S10-20 and H10-20 as well as basal area and volume of wood, and selected one of them as a potential predictor in different seasons.

We carried out a model selection procedure according to the information-theoretic approach (Burnham & Anderson 2002), which takes both descriptive accuracy and parsimony into account (Wagenmakers & Farrell 2004). For each season, all possible models were built considering the pre-defined set of variables and then ranked according to the relative Akaike Information Criterion corrected for small sample sizes (AICc). After model ranking, for each season we built an average model, considering the most supported models (those with ΔAICc < 2), after excluding 'uninformative parameters' (cf. Arnold 2010). The latter are those variables which are included only in 'complex' models, which comprise more parsimonious models as nested ones (Ficetola et al. 2011; Jedlikowski et al. 2016). When models with ΔAICc < 2 included only the most parsimonious model and others with uninformative parameters, we took the former as 'final' model for that season. Model ranking for all season and model averaging were carried out by means of the package "MuMIn" (Bartoń 2016) in software R (R Development Core Team 2016).

Given that our data have a strong spatial structure and that the occurrence records may be somewhat affected by the home-range of the single individuals belonging to the surveyed population, we checked for the potential occurrence of spatial autocorrelation in final models' residuals by calculating Moran's I and associated P-value, using the software SAM (Rangel et al. 2010).

Model validation over independent data sets

The best approach to evaluate a predictive map probably is to get out in the field and look for the target element in areas predicted as either suitable or unsuitable. This has a lot of appeal, especially since the sampling can be planned in ways that best test the model (Vaughan & Ormerod 2003). For this purpose, to obtain an unbiased estimate of the models' predictive performance, evaluation is best undertaken with independent data collected from sites other than those used to develop the model, so 30 new sampling points (Fig. 1) were observed in summer 2011 in Shast Kalateh forest and environmental variables and present/absent of black woodpecker were recorded at these points. As percentage of middle story (a variable included in the summer model; see Results) was not recorded at these additional points, we assigned to all the new samples the average value of the original points. A chi-square test was performed to check whether a significant association exists between predictions and observations and the Area under the Curve of the Receiver operating characteristic (AUC of the ROC plot) was calculated to evaluate the model's discriminatory ability over the new data.

Results

Habitat use: common patterns

The number of snags was a highly significant predictor and had a positive influence on woodpecker occurrence in all the most supported models for each period. Similarly, elevation was always included with a positive effect on species occurrence. The average characteristics of used and unused plots according to the factors selected by the models are reported in Table 2.

In all season-specific models, data were not overdispersed and residuals were not spatially autocorrelated, based on Moran's *I* and associated *P*-value (all $P > 0.1$). Therefore, habitat models are unlikely to be affected by spatial biases.

Summer

Regression models were developed to evaluate woodpecker presence/absence in relation to 13 significant ($P \lesssim 0.05$) variables (N.s, N.f, H>20 m, H10-20 m, DBH <20 cm, BSA, Vow, upper story, middle story, Al, Sl, CA1, CA_3). The other variables did not have a significant relationship with black woodpecker occurrence (all $P > 0.05$). The most parsimonious model (Table 3) included three variables: the number of snags, elevation (with positive effect) and the percent of middle story (with negative effect). Other models with ΔAICc < 2 included the most parsimonious model plus uninformative parameters.

Autumn

In autumn 14 variables significantly differed ($P < 0.05$) between black woodpecker presence and absence sites (N.s, N.f, H>20 m, H10-20, DBH <20 cm, DBH >20 cm, BSA, Vow, upper story, middle story, Al, Sl, CA1, CA3). Two different models had comparable support (Table 4). The averaged model revealed a positive and significant effect of DBH >20 cm, elevation and number of snags, whereas H10-20 had a negative (and non-significant) effect.

Winter

In winter 11 variables significantly differed ($P < 0.05$) between black woodpecker presence and absence sites (N.s, H>20 m, H10-20, DBH <20 cm, DBH >20 cm, upper story, middle story, Al, Sl, CA3, CA1). Two models showed a comparable support (Table 5). The averaged model revealed a positive and significant effect of DBH >20 cm, elevation and number of snags, a positive (but not significant) effect of slope, and a negative (significant) effect of H10-20.

Spring

In spring 11 variables significantly differed ($P < 0.05$) be-

Table 2. Average characteristics of used and unused plots according to the factors selected by the models.

	Summer		Autumn		Winter		Spring	
Variable	Used	Unused	Used	Unused	Used	Unused	Used	Unused
Snag	0.97±1.11	0.52±0.83	0.96±1.00	0.45±0.86	0.90±1.05483	0.51±0.85	0.94±1.13	0.54±0.83
Elevation	694.97±124.41	494.01±173.19	668.78±144.14	476.22±168.41	678.69±136.29	478.87±169.09	677.85±120.27	502.45±183.60
Middle story	1.53±0.51	2.41±0.96					1.50±0.51	2.42±0.95
Dbh>20			17.02±4.72	13.57±5.69	16.40±4.19	14.16±6.16		
H 10-20			4.53±3.42	7.90±4.82	3.71±2.36	8.30±4.78		
Slope					25.26±10.68	16.90±11.30		

Table 3. Most supported models (ΔAIC < 2) for habitat use by black woodpecker in summer.

Model	Intercept	Number of snags	Elevation	Middle story	R^2
Most parsimonious	-3.16+1.55	0.76+0.30**	$(7.27+2.03)*10^{-3}$***	-1.38+0.46**	0.37

Table 4. Most supported models (ΔAIC < 2) for habitat use by black woodpecker in autumn.

Model	Intercept	Number of snags	DBH >20 cm	Elevation	H10-20 m	AICc	Weight	R^2
1		+	+	+	+	91.06	0.244	0.44
2		+	+	+		92.06	0.144	
Averaged	-11.16+2.61	1.00+0.32**	0.28+0.08***	$(1.04+0.26)*10^{-2}$***	-0.09+0.10			
Importance		1.00	1.00	1.00	0.63			

Table 5. Most supported models (ΔAIC < 2) for habitat use by black woodpecker in winter.

Model	Intercept	Number of snags	DBH >20 cm	Elevation	H10-20 m	Slope	AICc	weight	R^2
1		+	+	+	+	+	91.05	0.218	0.44
2		+	+	+	+		92.00	0.173	
Averaged	-7.12+2.27	0.72+0.31*	0.22+0.08**	(6.90+2.20)*10^{-3}**	-0.36+0.11**	(2.52+3.10)*10^{-2}			
Importance		1.00	1.00	1.00	1.00	0.56			

Table 6. Most supported models (ΔAIC < 2) for habitat use by black woodpecker in spring.

Model	Intercept	Number of snags	Elevation	Middle story	R^2
Most parsimonious	-1.37+1.43	0.63+0.28*	(5.05+1.80)*10^{-3}**	-1.53+0.45***	0.33

tween black woodpecker presence and absence sites (N.s, N.f, H>20 m, H10-20, DBH <20 cm, upper story, middle story, Al, Sl, CA3, CA1). The most parsimonious model included three variables (Table 6): the number of snags and elevation (with positive effect), and the percent of middle story (with negative effect). Other models with ΔAICc < 2 included the most parsimonious model plus uninformative parameters.

The difference between predicted occurrence probability across final models for different seasons was calculated. Based on the results there were significant differences between predicted presence probability of summer-autumn models and spring-autumn models, marginally significant (0.05<P<0.1) differences between winter-spring and winter-summer models, and no differences for winter-autumn models (Table 7).

Table 7. Results of T-test comparisons for predicted occurrence probability according to the most supported models across different seasons.

Comparison	t	Df	P
Autumn vs. Winter	-0.55	203.99	0.579
Autumn vs. Spring	-2.46	196.35	0.015
Autumn vs. Summer	-2.40	200.08	0.017
Winter vs. Spring	-1.87	196.78	0.064
Winter vs. Summer	-1.82	200.41	0.070
Summer vs. Spring	3.65*10^{-12}	03.29	~1

Table 8. Cross-table showing model performance over the 30 new sampling sites.

	Observed	Presence	Absence
Predicted	19	3	22
Suitable	0	8	8
Unsuitable	19	11	30

<u>Model validation</u>

The Chi-square results of the comparison between predicted and observed woodpecker occurrence in the new dataset (Table 8) revealed a significant value (Pearson's X^2 = 5.17, df = 1, P = 0.023), and the AUC of the ROC plot was equal to 0.88, suggesting model efficacy on the independent points (even if one the variables included in the model was kept constant at its average value, given that measures were not available for the new data).

Discussion

Our work is virtually the first attempt to model year-round habitat use in the black woodpecker, and one of the few contributions about its ecology in Iran, after the work carried out by Khanaposhtani et al (2012). We found evidence for a highly significant relationship between the occurrence of black woodpecker at a fine spatial scale and environmental variables describing forest structure. The number of snags and a specific vegetation structure (characterized by larger trees) were the most important determinants of habitat use by black woodpeckers in the Hyrcanian forest in all the seasons, although specific patterns emerged and occurrence probability at a given point was quite different according to season-specific models. Woodpeckers occurred and nested (S.K. unpublished data) in some of the largest (in diameter and height) trees in the Shast Kalateh Forest, and in particular made a more frequent use of parcels with high number of snags and lower number of smaller trees (all seasons), preferring plots with larger trees (and generally higher basal area of boles: no presence data was detected in plots with a TBA below 10 m^{2}ha^{-1}).

Those results agree with previous findings of studies carried out in other geographical portions of the species range, which also reported the species to select mature stands and/or larger and older trees (e.g. Fernandez & Azkona 1996, Imbeau et al. 2003, Pirovano et al. 2005, Garmendia et al. 2006, Bocca et al. 2007). Taller tree height, higher amounts of dead wood and larger tree DBH are all characteristics typical of mature stands and have an important effect on habitat use by black woodpecker in the study area, coherently with findings of studies carried out elsewhere (Díaz 2006, Gil-Tena et al. 2007, Khanaposhtani et al. 2012). Notably, even if we found some differences in habitat use across seasons (see also below), habitat traits associated with woodpecker occurrence indicated a constant preference for mature forests, with dead wood and larger trees. black woodpeckers choose the best conserved beech forests, which, in the Shast Kalateh forest, are found at high altitude and on steep slopes with humid directional exposures, in agreement with the generally positive effect of broadleaved woodland, elevation and slope reported in the Prealps (Brambilla & Saporetti 2014). The substantial use of mature stands of oriental beech *Fagus orientalis* on high slopes is consistent with previous studies on microhabitat selection, which revealed the outstanding importance of beeches as foraging and nesting trees (Arisawa 1991, Zahner et al. 2012, Pirovano & Zecca 2014). The availability of snags (and of dead trees in general), suitable for foraging woodpeckers, is also a critical factor according to both our results and previous information (e.g. Garmendia et al. 2006). The access to rich food resources in vertical elements (snags, infected trees) containing beetle larvae or large carpenter ant colonies, is crucial for winter survival. These resources are easily available in natural forest, and even with deep snow cover, they can thus be intensively used in winter. However, in managed forest the amount of both snags and old trees is much lower. According to our results, there is no significant relationship between fallen dead trees and species occurrence in winter, likely because of the high snow cover at higher elevation (where the most suitable habitats for the species occur), which may dramatically reduce access to fallen dead trees. Other studies show that, where the snow depth is below 1 m, birds were feeding on carpenter ants in stumps and dead downed wood, but at snow depths above 1 m birds increasingly feed on carpenter ants at the base of trunks of infested living trees, and on bark beetles and beetle larvae in dead standing trees (Rolstad & Rolstad 2000). Habitat use by black woodpeckers was positively affected by slope in winter and spring, but not in summer and autumn, likely because of the avoidance of areas with higher or more persistent snow cover. Coherently, the number of records increased in winter in parcels at lower elevation (450-700 m), probably because of limited resources (or limited accessibility to resources because of snow cover) at higher elevation and/or of seasonal changes in resource distribution.

Canopy cover did not affect habitat use by black woodpecker in the Hyrcanian forest. This is potentially due to the rather homogeneous, extensive canopy cover of Persian ironwood, which is the dominant tree species at low elevation forest parcels (below 700 m). This is also the likely reason (most of the Persian ironwood trees are thick, with DBH> 20 cm) why there is no significant relationship between numbers of trees with diameter at breast height more than 20 cm and species occurrence in most seasons. On the other side, the negative effect of the number of trees with DBH<20 cm clearly highlighted the avoidance of stands dominated by young trees.

Study assumptions and potential caveats

Our approach allowed an investigation of fine-scaled habitat use in black woodpecker along the four seasons. The use of multiple records from the same individuals/pairs, which is unavoidable at such a fine spatial scale with this species, did not result in problems due to spatial dependence (as confirmed by the lack of spatial autocorrelation in models' residuals), but could potentially lead to habitat preferences somewhat affected by individual traits. However, the general agreement with previous information available on the species suggested the overall validity of our findings.

The use of indirect signs of occurrence (signs of wood-boring), for which a correct assignment to a given season could be difficult, may potentially result in lower differences in habitat use across seasons than expected. Nevertheless, we use only five records of wood-boring, all likely being 'true' winter records, and differences among seasons emerged, leading to a seasonal variation in fine-scale habitat suitability, as suggested by the statistical comparison of predicted occurrence probabilities.

Conservation and management implications

Woodpeckers are keystone species whose occurrence provides critical resources in the community of vertebrates that require, but cannot create, cavities, and therefore deserve specific monitoring and management efforts (Drever & Martin 2010). Although their importance may vary with forest type (Wesołowski 2007, Cockle et al. 2011), woodpecker holes may be crucial for several species (e.g. Brambilla et al. 2013), and thus woodpecker conservation is particularly important, especially in managed forests. In general, black woodpecker relies on mature, tall stands, and tends to disappear when the forest is degraded (Cramp & Brooks 1992, Fernandez & Azkona 1996). In our study area, forestry (timber production) and the black woodpecker seem to prefer the same large beech trees with strong boles. Our results highlighted the importance of snags and of mature large trees, likely determinant as source of food and of potential breeding trees, respectively. The strong effect of dead wood availability on habitat use suggests that conserving enough dead wood and in particular preserving snags (the main foraging habitats for black woodpecker, especially in autumn and winter) are the most important recommendations for forest management in areas of black woodpecker occurrence. A well-regulated use of forest resources can be beneficial for this species if small clearings are created and a considerable amount of standing dead wood is left over in the harvesting process, as such forestry practices can increase the availability of woodpecker preys (Cramp & Brooks 1992, Brambilla & Saporetti 2014). On the other side, frequent harvesting leading to thinning would be highly detrimental, favouring the occurrence of young and thin trees (DBH<20 cm), which are avoided by the species in all seasons.

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Appendix 1. Mean number ±SD of living trees, snags and fallen dead trees measured per plot.

Point	Mean±SD	Point	Mean±SD	Point	Mean±SD	Point	Mean±SD
1	2.36±3.20	35	2.18±3.92	64	2.82±6.52	92	1.45±2.58
2	2.36±3.38	36	1.82±3.40	65	0.91±2.39	93	1.45±2.54
3	1.55±2.38	37	1.55±3.24	66	1.91±5.68	94	2.27±3.07
4	1.91±4.18	38	2.36±4.15	67	1.45±2.81	95	1.73±2.20
5	2.09±3.08	39	2.00±3.13	68	2.18±3.89	96	1.45±2.38
6	2.45±4.16	40	1.45±3.33	69	2.36±3.98	97	1.73±3.52
7	1.91±3.36	44	2.27±4.63	70	2.36±3.53	98	1.55±2.25
8	1.45±2.88	45	1.82±4.21	71	2.64±5.01	99	1.73±2.05
9	1.45±2.58	46	1.91±4.28	72	2.00±3.07	100	2.55±4.03
10	1.82±3.84	47	3.09±5.58	73	1.82±3.60	101	1.82±3.12
11	1.55±3.33	48	3.09±7.52	74	3.91±5.38	102	1.73±2.49
13	2.45±8.14	49	2.27±4.03	75	3.09±6.19	103	1.27±2.41
14	0.64±1.21	50	1.91±3.05	78	1.55±2.38	104	2.09±2.34
15	1.64±2.69	51	3.36±6.85	79	1.82±3.46	105	2.09±2.34
16	1.82±3.97	52	2.36±4.72	80	1.27±3.35	107	1.91±2.30
17	2.09±6.30	53	1.82±2.86	81	1.55±3.86	108	1.64±2.06
22	1.91±3.94	54	1.64±2.69	82	1.55±2.98	109	2.00±2.53
23	2.36±6.22	55	2.27±5.62	83	2.45±3.59	110	1.91±2.59
24	2.00±3.55	56	3.00±5.44	84	2.55±4.23	111	2.00±2.79
28	2.36±4.48	57	2.45±6.23	85	2.09±3.51	113	1.64±2.62
29	1.82±3.03	58	1.452.46	86	1.55±2.54	115	2.27±3.72
30	2.36±3.61	59	2.55±6.52	87	1.91±3.62	116	1.55±3.24
31	2.18±3.63	60	0.82±1.54	88	2.73±3.66	117	1.45±3.30
32	2.91±3.65	61	1.91±3.81	89	1.73±2.49	118	1.73±4.45
33	2.82±5.27	62	1.73±4.03	90	1.82±3.22		
34	1.73±3.20	63	1.36±3.04	91	1.36±2.80		

Appendix 2. Measurements for variables that were selected by the models.

Point	Snag	Fallen dead trees	H>20	H10-20	Basal area	Ca3	DBH>20	DBH<20	Middle story	Upper story	Slope	Elevation
1	3	2	15	6	18.512	0.355	18	5	2	3	20.9	448
2	3	6	10	7	9.789	0.648	12	6	2	3	45.41	521
3	0	0	6	11	10.630	0.338	7	6	3	3	28.74	580
4	1	4	13	1	22.125	-1.368	19	0	1	4	30.19	664
5	2	0	17	4	31.641	-0.18	16	2	2	3	49.32	611
6	0	3	22	2	38.201	-0.045	24	0	2	4	15.12	587
7	1	0	17	3	29.909	0.513	19	1	1	4	37.75	552
8	3	0	12	1	9.796	-0.324	13	10	1	4	11.34	273
9	0	0	1	12	1.915	0.277	3	10	4	1	4.24	273
10	1	0	6	12	3.183	0.04	2	16	4	1	2.98	293
11	0	0	1	10	4.448	0.193	7	13	4	1	8.71	309
12	0	0	0	22	3.504	-0.279	0	22	4	1	9.39	309
13	0	1	2	5	5.020	-0.428	4	3	4	1	0	305
14	0	0	8	10	3.387	0.103	8	10	3	2	6.54	288
15	1	0	7	12	8.218	0.543	13	6	3	2	0	257
16	0	0	19	4	17.859	0.176	23	0	1	4	8.38	268
17	4	3	13	1	4.101	-1.459	14	1	1	4	11.83	951
18	1	1	20	4	25.213	-1.382	20	4	1	4	27.45	896
19	1	0	14	3	21.625	-0.289	15	2	1	4	20.84	827
20	1	4	13	8	32.983	-0.977	13	8	2	3	23.2	830
21	2	4	5	6	18.232	-0.595	9	2	3	3	1.23	858
22	0	3	19	4	25.589	-0.428	19	4	2	3	27.75	847
23	2	1	11	10	26.695	-0.618	14	7	2	3	27.03	803
24	1	5	18	7	35.239	-0.237	19	6	2	3	49.62	808
25	1	5	22	2	6.385	-1.024	23	2	1	4	12.42	780
26	0	2	14	3	29.362	-0.874	15	2	1	4	20.75	717
27	0	1	21	2	29.375	-0.537	20	3	1	4	19.04	803
28	0	0	17	3	19.466	-0.613	16	4	1	4	23.1	794
29	0	0	10	3	11.230	-0.669	8	5	2	3	31.02	816
30	0	1	19	5	26.560	-0.62	20	6	1	4	16.73	800
31	1	0	20	1	12.706	-0.455	19	2	1	4	11.86	786
32	0	0	11	5	15.082	-1.04	12	6	2	3	31.6	824
33	0	0	17	8	28.168	0.638	24	1	1	4	13.76	392
34	0	0	14	6	35.375	0.863	20	0	2	3	24.89	414
35	1	0	14	6	19.418	0.824	20	0	2	3	17.52	440
36	0	1	23	10	14.911	0.455	23	10	2	3	19.82	451

Point	Snag	Fallen dead trees	H>20	H10-20	Basal area	Ca3	DBH>20	DBH<20	Middle story	Upper story	Slope	Elevation
37	0	6	13	15	13.405	0.333	25	3	3	2	19.63	475
38	0	3	16	6	15.434	-0.692	16	6	2	3	24.69	469
39	0	1	12	8	14.423	0.727	18	2	3	2	20.31	478
40	1	1	23	6	8.640	0.077	23	6	1	4	36.77	427
41	0	1	19	6	15.553	0.599	23	3	2	3	22.53	417
42	0	0	8	8	14.370	0.265	14	2	3	3	23.45	386
43	0	0	11	7	16.552	0.62	17	1	2	3	17.67	402
44	1	0	16	8	21.017	0.939	24	0	2	3	8.97	382
45	1	5	15	12	23.651	0.693	25	2	3	3	0	382
46	1	0	18	8	11.613	0.33	22	4	2	3	11.49	478
47	0	0	9	8	13.891	0.267	14	2	4	1	23.72	339
48	1	0	6	20	14.194	0.907	22	4	4	1	0	332
49	0	0	2	9	5.392	0.623	8	3	4	1	6.79	326
50	1	0	12	8	14.754	0.759	19	1	2	3	6.77	319
51	0	0	10	9	11.235	0.812	10	9	4	1	6.75	313
52	0	0	5	12	5.775	0.41	7	10	2	1	7.43	283
53	3	0	12	18	11.724	-0.066	19	11	3	2	0	269
54	0	0	5	8	2.126	-0.382	7	6	4	1	12.34	263
55	1	0	2	17	3.797	1.009	7	12	4	1	3.78	246
56	0	0	7	9	6.182	0.616	8	8	3	2	4.82	285
57	1	2	17	11	22.695	0.823	15	2	2	3	16.04	531
58	0	2	11	6	25.468	0.484	15	3	3	3	29.43	560
59	2	2	15	6	17.427	0.641	17	2	1	4	31.11	570
60	0	5	9	13	24.709	0.883	15	3	3	2	33.22	530
61	0	1	7	12	13.945	0.658	16	3	3	2	24.11	530
62	0	1	14	3	28.585	0.885	17	0	2	4	9.13	370
63	0	3	20	18	19.832	0.645	29	9	2	3	10.24	360
64	1	1	20	10	22.196	0.498	17	10	2	3	3.84	369
65	0	1	12	4	8.813	-0.272	12	4	2	3	54.1	742
66	1	0	17	2	27.233	-0.768	17	2	1	4	29.86	754
67	0	0	13	1	77.237	0.875	13	1	2	3	28.31	757
68	0	1	12	3	19.130	-1.311	12	3	2	3	18.18	787
69	0	1	14	2	22.578	-1.008	15	1	2	3	23.92	789
70	2	3	14	8	24.960	-0.489	20	2	2	3	44.3	694
71	0	0	21	7	22.974	-0.462	26	2	2	3	25.14	673
72	3	2	16	2	18.385	-0.851	17	1	4	1	41.25	648
73	0	1	10	6	22.007	0.643	13	3	2	3	20.3	615
74	0	4	2	15	7.087	0.808	13	4	2	4	24.67	553
75	1	4	18	7	30.122	-0.251	21	4	2	4	30.46	664
76	0	5	12	2	17.338	0.145	13	1	1	4	25.04	614
77	0	3	16	1	37.794	-0.462	17	0	1	4	24.55	577
78	0	1	7	7	14.663	0.784	12	2	2	3	29.83	539
79	0	2	5	9	8.517	0.46	10	4	3	3	33.1	591
80	0	0	11	5	27.176	0.495	13	3	2	3	28.25	605
81	0	4	11	9	15.866	0.651	13	7	2	3	20.45	656
82	1	2	11	2	25.629	-0.051	12	1	2	4	21.1	646
83	0	1	12	2	18.716	-0.351	12	2	2	4	22.38	608
84	2	2	13	2	25.938	-1.095	12	1	2	3	10.52	620
85	2	2	11	3	12.141	-0.195	9	4	2	3	12.2	582
86	1	4	13	1	14.694	-0.36	10	4	1	4	24.09	564
87	2	3	12	12	12.545	0.419	16	8	3	3	32.76	530
88	0	0	15	5	11.891	0.62	15	3	2	4	29.54	513
89	0	0	15	4	9.470	-0.214	14	5	2	4	13.88	594
90	0	0	11	3	19.623	0.328	14	0	2	4	33.64	640
91	2	2	11	5	11.038	-0.258	14	2	2	3	12.07	639
92	2	2	9	5	13.387	-0.258	14	2	2	3	12.07	639
93	0	2	15	2	13.387	-0.275	17	0	1	4	18.37	684
94	0	1	16	1	4.412	-0.127	18	1	1	4	10.41	649
95	3	3	11	3	15.805	-0.349	9	4	2	3	24.15	580
96	0	4	18	1	22.452	-0.531	18	1	1	4	17.83	533
97	2	2	15	3	17.785	-0.04	13	3	2	4	27.35	500
98	0	0	14	4	19.260	-0.464	10	5	2	3	30.29	770
99	0	1	22	2	22.977	-0.413	17	3	1	4	24.28	751
100	0	0	13	4	24.124	-0.462	10	7	2	4	16.3	703
101	0	0	16	1	18.707	-0.946	10	6	1	4	28.19	768
102	1	1	13	2	24.412	-1.279	13	2	1	4	31.51	750
103	0	1	21	5	19.063	-0.178	19	7	1	4	11.76	729