

Black woodpecker *Dryocopus martius* (L., 1758) distribution, abundance, habitat use and breeding performance in a recently colonized region in SW Europe

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Abstract

At the southwestern edge of its global distribution, the Pyrenean population of the black woodpecker *Dryocopus martius* has increased its range during the last three decades, colonizing new areas where the species was previously unknown. This is the case for Gipuzkoa, where a systematic survey was performed in the breeding season of 2013 aimed at describing the species distribution, abundance, habitat use and reproductive performance. Potential locations were identified using forest inventories and were visited since January until March. Locations were considered occupied when nests or pairs were found, or single individuals were detected during three consecutive visits. Breeding performance in active nests was monitored during May and June. We found 21 breeding home ranges, mainly distributed across the Eastern and Southern fringes of the study area. The environmental variables positively related to the presence of breeding home ranges were higher proportions of canopy cover, mature structure of the stand, cover of beech *Fagus sylvatica*, mixed deciduous and black pine *Pinus nigra* stands, and unfragmented forest patches. Monterey pine *P. radiata* plantations and low tree heights were negatively selected. Preferred foraging areas comprised proportions of American oak *Quercus rubra* and black pine plantations. Thirteen active nests were found. All nests but two were excavated in beech trees. Breeding success was high (92%) but fledging success (1.8) was below the average reported in Europe, suggesting intrinsic limitations associated to a peripheral population.

Key words: Picidae, bird census, range increase, beech forests, pine plantations, Basque Country.

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Resumen

En el límite suroccidental de su distribución mundial, la población pirenaica de picamaderos negro *Dryocopus martius* ha incrementado su área de ocupación durante las últimas tres décadas, colonizando nuevas zonas donde la especie era previamente desconocida. Este es el caso de Gipuzkoa, donde se efectuó un censo durante la temporada de cría de 2013, con el objetivo de describir la distribución, abundancia, uso del hábitat y éxito reproductivo. Se identificaron localidades potenciales utilizando inventarios forestales, y cada localidad fue visitada durante el periodo enero-marzo. Las localidades ocupadas se consideraron "dominios vitales reproductivos" cuando se pudo comprobar el emparejamiento o la nidificación, o cuando se registró presencia de individuos en un mínimo de tres visitas consecutivas. Se vigiló el desarrollo de la reproducción en nidos activos durante mayo y junio. Se detectaron y cartografiaron 21 "dominios vitales reproductivos", distribuidos fundamentalmente a lo largo de las franjas oriental y meridional del área de estudio. Las determinantes ambientales relacionadas positivamente con la presencia de "dominios vitales reproductivos" fueron elevada cobertura arbolada, estructura madura, superficies de haya *Fagus sylvatica*, bosque mixto caducifolio y pino laricio *Pinus nigra*, y parcelas forestales poco fragmentadas. Las plantaciones de pino de Monterrey *P. radiata* y las alturas bajas del arbolado se seleccionaron negativamente. Las parcelas de alimentación preferidas incluyeron proporciones de roble americano *Quercus rubra* y plantaciones de pino laricio. Se detectaron trece nidos activos. Todos los nidos salvo dos fueron excavados en hayas. El éxito de cría fue elevado (92%) pero la tasa de vuelo (1.8) estuvo por debajo de los promedios descritos en Europa, lo que podría indicar limitaciones intrínsecas en esta población periférica.

Palabras clave: Picidae, censo de aves, expansión de la distribución, hayedos, plantaciones de pino, País Vasco.

Laburpena

Espeziearen mundu mailako banaketaren hego-mendebaldeko mugan, Pirinioetako okil beltza (*Dryocopus martius* (L., 1758)) populazioaren banaketa eremua azken hiru hamarkadetan zabaldu egin da eta espezieak leku berriak kolonizatu ditu. Gipuzkoan 2013. urteko ugaltze garaian espeziearen banaketa, ugaritasuna, habitat erabilera eta ugaltze-arrakasta deskribatzeko asmoz egindako zenbaketetan hori bera behatu da. Baso inbentarioak erabilia espeziearentzako eremu potentzialak identifikatu ziren eta eremu horietako bakoitza urtaril eta martxo bitartean bisitatu zen. Espeziea agertzen zen eremuak "ugaltze bizi eremu" izendatu ziren parekatzea zegoela edo habia egiten zutela baieztatzen zenean, edo jarraian egindako hiru bisitetan aleak bazeudela baieztatzen zenean. Maiatza eta ekaina bitartean habietako ugalketaren garapena ikuskatu zen. 21 ugaltze bizi eremu aurkitu eta kartografiatu ziren; horiek batez ere ikerketa eremuaren ekialde eta hegoaldean kokatzen ziren. Ugaltze bizi eremuekin eragin positiboko ingurugiro baldintzak honakoak izan ziren: zuhaitz estaldura zabala, egitura heldua, pago (*Fagus sylvatica* L.) eremuak, hostoerorkor baso-mixtoa, larizio pinua (*Pinus nigra* J.F. Arnold) eta gutxi fragmentatutako baso partzelak. Ordea, intsignis pinu (*Pinus radiata* D. Don) landaketak eta zuhaitzen altuera txikiak eragin negatibokoak zirela antzeman zen. Bazkarako gogokoan zituzten

partzelek haritz amerikar (*Quercus rubra* L.) proportzioak eta larizio pinu landaketak zituzten. Hamahiru habi aktibo aurkitu ziren. Bitan izan ezik, habia guztiak pagoetan zeuden. Ugaltze arrakasta altua izan zen (%92), baina hegaldi tasa (1.8) Europarako deskribatutakoen azpitik zegoen eta horrek bazter populazio periferiko honek berezko mugak dituela adieraz lezake.

Gako hitzak: Picidae, hegazti zentsoa, banaketa eremuaren zabalkuntza, pagadiak, pinu landaketak, Euskal Herria.



Introduction

At the margins of a species range, habitat selection, breeding performance and population dynamics can show varying patterns if compared to core areas (Guo *et al.*, 2005; Tellería, 2014). For instance, the abundant-centre hypothesis states that species are most abundant in the centre of their range and decline towards the edge, but such general assumptions have infrequently been tested empirically (Sagarin & Gaines, 2002). In particular, when colonizing novel, peripheral areas as a consequence of range expansion, individuals can be exposed to different environmental conditions than those prevailing at the source areas, which may lead to maladaptation (Martin *et al.*, 2014). Observational approaches are needed to describe habitat requirements, abundance and reproductive behaviour across entire species ranges (Fuller, 2002; Sagarin *et al.*, 2006), to better understand demographic and genetic responses of populations and environmental limits at the macroecological scale (Mehlman, 1997; Pigot *et al.*, 2010).

The black woodpecker (*Dryocopus martius* L. 1758) is a widely distributed avian species, which occurs throughout the temperate and boreal regions of the Palearctic (Gorman, 2011). Its global range, estimated at around 20,000,000 km², lies at its southwestern limits in the northern Iberian Peninsula (BirdLife International, 2014). Two disjunct populations have been recognized here, each occupying one of the two main mountain ranges in the region: the Pyrenean and the Cantabrian (Simal & Herrero, 2003), separated by c. 175 km. The Pyrenean population has experienced a remarkable range expansion since the 1990's. At the eastern edge of this range, formerly vacant areas in Catalonia have been colonized (Martínez-Vidal, 2004). This expansion has been tentatively explained by the combined increase of forest surface due to natural regeneration and plantations, and of stand maturity as a result of forest ageing (Gil-Tena *et al.*, 2010). Westward of the Pyrenees, a range increase has also been described, filling the intermediate gap between the Pyrenean and the Cantabrian subpopulations across the Basque mountains (Gainzarain & Fernández-García, 2013). The black woodpecker is regarded as a keystone species in managed forest ecosystems, because it provides cavities for secondary users, otherwise constrained

by the lack of these elements in anthropogenic habitats (Wesolowski, 2007; Konsinski *et al.*, 2010).

This study aims to document the range increase of the black woodpecker west of the Pyrenees, an area that has been recently colonized, and where the species was absent before the 1990's. By describing the species distribution, abundance, habitat use and breeding performance, our intention is also to check whether this species' ecological niche in this peripheral area departs from the cores of its range, and to provide insights into the conservation prospects for the population.

Methods

Study area

The study area was the province of Gipuzkoa (Basque Country, N Spain) comprising 1,977 km². Gipuzkoa is situated on the Gulf of Biscay, within the Atlantic biogeographic region. Altitude gradually rises from north to south, from the coastal fringe to the narrow interior valleys and the mountain slopes, reaching 1,500 m above sea level at the highest peak. About 62.9% of the province surface is covered in woodlands, of which 37.8% are plantations of Monterey pine *Pinus radiata*, 5.6% plantations of black pine *P. nigra*, 5.2% plantation of larch *Larix* spp., 14.6% temperate mixed forests, 14.2% beech *Fagus sylvatica* forests, 6.8% penduline oak *Quercus robur* forests, and the rest several other minor types of plantations and semi-natural forests (Área de Inventario y Estadísticas Forestales, 2013).

Sampling and data analyses

Potential forest patches were selected using digital vegetation maps (Gobierno Vasco, 2007) and Geographic Information System (GIS) software (gvSIG 1.12), on the basis of the habitat selection of the black woodpecker previously known in Spain (Camprodon *et al.* 2007). These patches were beech forests and pine (*P. radiata*, *P. nigra* and Scots pine *P. sylvestris*) plantations. Then, 98 sampling itineraries totaling 612.82 km ($X=6.25$, $s=3.46$, range 0.68-15.59), including the selected patches and their surrounding areas, were designed. These itineraries globally sampled through patches of beech (25.91%), Monterey pine (22.93%), larch (8.94%), black pine (5.75%), mixed deciduous (5.72%), penduline oak (5.66%), Douglas fir *Pseudotsuga menziesii* (3.87%), American oak *Quercus rubra* (2.05%), Lawson cypress *Chamaecyparis lawsoniana* (1.01%) and smaller proportions of other types, apart from unforested patches (13.66%).

During the 2013 breeding season, nine observers with previous experience in bird censuses and the black woodpecker, surveyed the itineraries on foot at least four times between January and March, storing in a Global Position System device the precise location of sightings, hearings, nest holes and foraging signs of black woodpeckers. The surveys were mostly carried out in the morning under favourable weather and wind conditions.

The protocol took advantage of the vocal activity of the species and its relatively high probability of detection during pair formation and courtship periods (Bocca *et al.*, 2007). Recordings of the species' calls were not used in order to avoid unnecessary disturbance. Some feeding marks on trees were photographed to confirm the field identification, using descriptions by Gorman (2004).

Breeding and pairing records of the black woodpecker were plotted on the Universal Transverse Mercator (UTM) grid with a 100 km² resolution, a classical and comparable pattern-based technique to model species' distributions (Fuller *et al.*, 2011). Foraging signs and hollows in trees were used as a surrogate to model the spatial range and densities of the black woodpecker at a geographical scale with a kernel estimator (Fortin & Dale, 2005) implemented in the Sextante software (Universidad de Extremadura, 2008).

We defined a black woodpecker breeding home range (BHR) when a pair was detected, an active nest was found or a single individual was recorded in the same area during three consecutive visits spaced at least 10 days in between (Tjernberg *et al.*, 1993). The term "territory" was avoided as territorial behaviour excluding other birds has not always been confirmed (Bocca *et al.*, 2007). On the basis of existing literature (Tjernberg *et al.*, 1993; Fernández & Azkona, 1996; Bocca *et al.* 2007; Van Manen, 2012; review in Gorman, 2011), each BHR was assumed to cover 250 ha. These ranges were mapped as circular plots with the centre at the nest or where pairing behaviour was observed.

We measured variables that were expected to be potentially important in explaining the habitat selection of forest birds and that were readily available using remote databases. The surface coverages of five features (canopy cover, natural or man-made origin of the forest, dominant tree species, stand maturity and tree height) were measured in each separate habitat patch over each BHR's surface (i.e. 250 ha) with gvSIG 1.12, using the data layer provided by the Spanish Forest Inventory (Área de Inventario y Estadísticas Forestales, 2013) and a Laser Imaging Detection and Ranging (LIDAR) image (Diputación Foral de Gipuzkoa, 2008). Canopy cover was assessed with four percentage intervals (<25, 25-50, 50-80 and >80); origin with semi-natural and plantation; dominant tree species with the main ten species; stand maturity with mature (average tree diameter >20 cm), young (diameter 10-20 cm) and replanted stages (diameter <10 cm); and tree height with three intervals (<10 m, 10-20 m, >20 m). Then we used the Fragstat v4 algorithm (McGarigal *et al.*, 2012) to describe the spatial structure of the patches inside the territories, after transforming vectorial data layers to raster images with a pixel size of 100 m². We calculated the Edge Density (ED, the sum of the lengths of all edge segments among patch types divided by the total area) and the Largest Patch Index (LPI, a measure of patch dominance) as fragmentation descriptors, and the Landscape Shape Index (LSI, a standardized measure of edge density that increases as the landscape becomes more irregular) as descriptor of spatial complexity. Extended details on these metrics and their utility can be found in Leitao *et al.* (2006). Finally, we measured the distance from the centre of each of the BHR to the centroid of the nearest UTM 100 km² square where the black woodpecker was found breeding during 1998-2001 (Simal & Herrero, 2003).

The same procedure was applied to a second set of 21 plots of 250 ha each, the centres of which were chosen randomly, but restricted to itineraries where black woodpecker BHR were not detected during field work and separated at least 3 km apart to reduce spatial autocorrelation. Regarding collinearity, variables showing $r > 0.75$ were excluded from further analysis.

Differences between BHR and random plots were explored first with a principal component analysis (Dytham, 2003). After checking for equality of variances with Levene's test, t-test bivariate analyses were performed. Only those independent variables that showed an association ($p < 0.05$) with the dependent variable (presence-absence of BHR) were included in a subsequent multivariate binary logistic regression, using the forward stepwise procedure and the likelihood ratio as criteria for entering or extracting variables from the model (Ferrán, 2001). The goodness-of-fit of the model was assessed using the Hosmer-Lemeshow test. Statistical analyses were produced with PASW 18.0.

The tree species composition of forest patches where black woodpecker foraging signs were found, as provided in data layers from Área de Inventarios y Estadísticas Forestales (2013), was used to describe the foraging habitat. The selection of foraging patches was assessed with the Savage index (W) and its level of significance (Manly *et al.*, 1993), using the proportion of patches across sampling itineraries as an indicator of availability.

Active nests found were monitored during May and June 2013 on a 4-5 day frequency basis, paying visits of 2-3 hours each and recording activities from a hide 30-50 m away from the nest, to minimize disturbance. The number of different full-grown chicks was recorded at the final stage of the nesting period (from day 20), when chicks are fed at the hole entrance by the adults (Gorman, 2011). Several feeding visits per nest (3-5) were videotaped and watched afterwards to count the chicks. These were sexed on the basis of the extension of the red crown (Gorman, 2011). The nest success (defined as the percentage of nests that produced at least one fledgling relative to all nests), the fledging success (number of young per successful nest shortly before leaving the nest) and the day of fledging were recorded for each one of the nests.

Results

Abundance and distribution

Twenty-one BHR were inventoried in the study area. Active nests were located in 13 of them; pairing behaviour was observed in five; and regular presence was recorded in three more. The BHR covered 13 UTM 100 km² and active nests were found in nine of them (fig. 1). The species breeding range occupied the eastern and southern halves of the study area. Two core areas showing higher densities of foraging signs and holes ($N=109$) were identified in the northeastern (Añarbe, Aiako Harria) and south-central (Alto Deba, Elgea, Aizkorri) fringes of the study area (fig. 2), the latter showing both west and eastward extensions (Arlaban and Aralar).

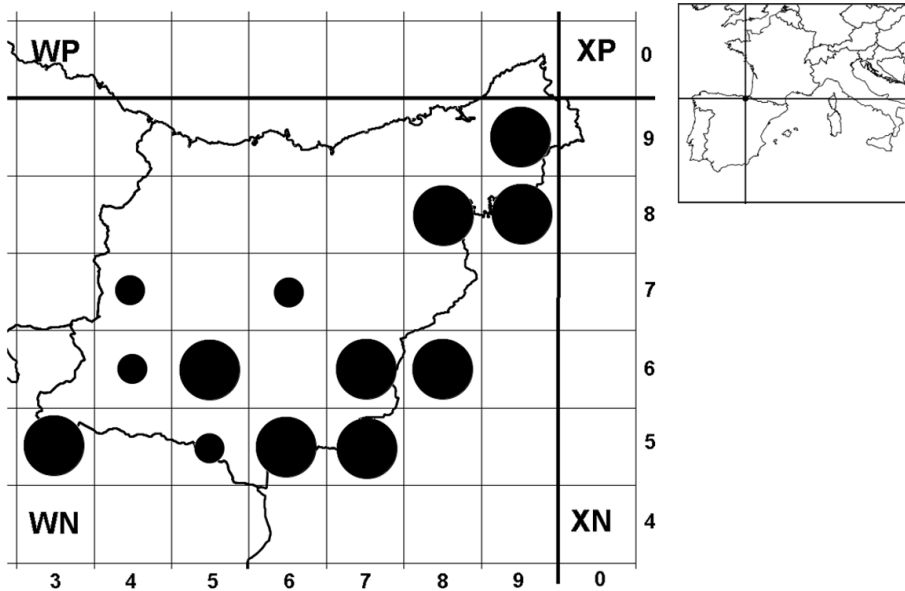


Fig. 1.- Distribution of the black woodpecker *Dryocopus martius* in Gipuzkoa during the breeding season of 2013, referred to UTM 100 km² squares. Big dots highlight squares where active nests were found; smaller dot squares refer to pairing or regular presence confirmed.

Fig. 1.- Distribución del picamaderos negro *Dryocopus martius* en Gipuzkoa durante la temporada de cría de 2013, referida a la malla de cuadrículas UTM de 100 km². Los puntos grandes señalan cuadrículas donde se encontraron nidos activos; los puntos más pequeños, cuadrículas en las que sólo se registró emparejamiento o presencia regular.

Breeding habitat use

Black woodpeckers active nests were always located in beech patches (n=13). From these, 11 nests had been excavated in beech trees and two in American oak trees. Around 88.9% of the combined surface of the 21 BHR (5,149 ha) was woodland, including plantations (51.6%) and semi-natural forests (37.3%; fig. 3). Beech was the dominant tree in the semi-natural stands, whereas in plantations the species composition was more evenly distributed, including relevant proportions of Monterey pine, black pine and other coniferous species. The proportion of stands with thick trunks (>20 cm diameter) was greater in semi-natural patches than in plantations. Semi-natural patches included a broader coverage of higher trees than plantations, and also the proportion of bare ground was smaller, meaning that coniferous stands included younger trees and a less mature forest structure on average (table 1).

The BHR were placed mostly along the negative section of the first axis of the principal component analysis plane (fig. 4), while random plots showed a slightly more dispersed distribution. Variables showing higher weightings (>0.65) on the negative section of the

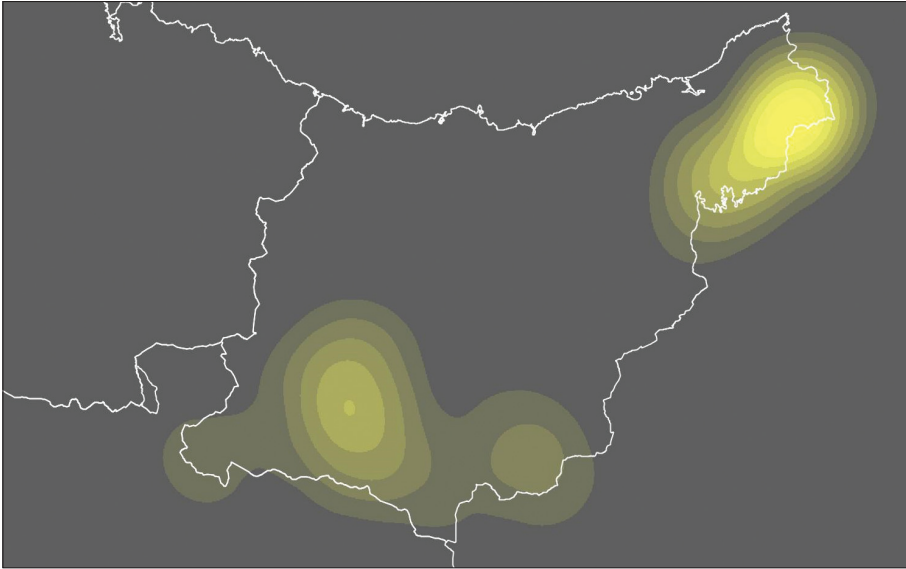


Fig. 2.- Kernel estimator (90 %) for geographical densities of the black woodpecker *Dryocopus martius* in Gipuzkoa, using records of foraging and nesting activity.

Fig. 2.- Estimador kernel (90 %) de las densidades geográficas del picamaderos negro *Dryocopus martius* en Gipuzkoa, a partir de los registros de actividad de alimentación y nidificación.

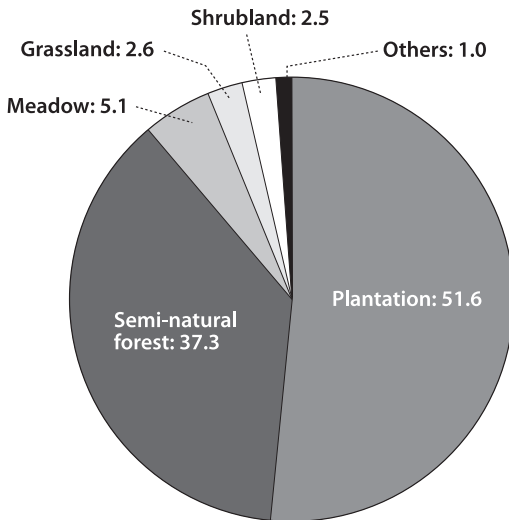


Fig. 3.- Coverage (%) of habitat types within the combined black woodpecker *Dryocopus martius* "breeding home ranges" assessed in Gipuzkoa during the breeding season 2013 (N=21).

Fig. 3.- Cobertura (%) de tipos de hábitat en el conjunto de los "dominios vitales reproductores" de picamaderos negro *Dryocopus martius* identificados en Gipuzkoa durante la temporada de cría de 2013 (N=21).

Semi-natural forests (1,919.4 ha)				Plantations (2,655.8 ha)		
	Category	X	s	Category	X	s
% Species	<i>Fagus sylvatica</i>	66.7	23.6	<i>Pinus radiata</i>	35.4	5.5
	<i>Quercus robur</i>	14.4	17.5	<i>Pinus nigra</i>	25	5.6
	<i>Quercus spp.</i>	3.2	5.9	<i>Larix spp.</i>	14.5	5.7
	Mixed forest	13.3	3.1	<i>Quercus rubra</i>	6.3	7.3
	Others	5.6	3.5	Others	18.6	2.8
% Trunk diameter	≥ 20 cm	82.5	22.2	≥ 20 cm	66.5	5.7
	10-20 cm	13.8	3.1	10-20 cm	15.1	5.2
	≤ 10 cm	3.6	9.1	≤ 10 cm	13.9	4.4
	Felled and planted areas	0	-	Felled and planted areas	4.6	3.8
% Tree height	≥ 30 m	1.5	1.6	≥ 30 m	1.6	3.4
	21-30 m	22.5	15.8	21-30 m	10.9	13
	11-20 m	32.1	21.5	11-20 m	19.9	15.9
	0-10 m	43.9	22.9	0-10 m	67.6	51.5
% Canopy cover	76-100	90.8	14.4	76-100	63.5	4.8
	51-75	5.6	18.7	51-75	8.3	11.3
	26-50	3.5	2.7	26-50	11	5.6
	0-25	0.1	1.6	0-25	17.2	2.6

Table 1.- Parameterization (X, mean; s, standard deviation) of four descriptors of forest composition and structure for the combined black woodpecker *Dryocopus martius* "breeding home ranges" assessed in Gipuzkoa during the breeding season 2013 (N=21), separating patches of semi-natural forests and plantations.

Tabla 1.- Parametrización (X, media; s, desviación estándar) de cuatro descriptores de la composición y estructura forestal en el conjunto de los "dominios vitales reproductivos" de picamaderos negro *Dryocopus martius* identificados en Gipuzkoa durante la temporada de cría de 2013 (N=21), diferenciando parches de bosque seminatural y plantaciones.

first axis were canopy cover >80%, shrub cover <25%, semi-natural, beech and mature stands, LPI and tree height >20 m.

The variables that were significantly associated with the occurrence of the black woodpecker BHR in the bivariate analyses were canopy cover 50-80% and >80%, shrub cover 50-80% and >80%, beech, mixed stand, Monterey pine, black pine, mature stands, ED, LSI, LPI and tree height <10 m. The best model for the binary logistic regression correctly classified 90.5 % of the predicted cases. The variables included in the regression function were coverages of Monterey pine, black pine, stands with trees <10 m high and LPI (table 2).

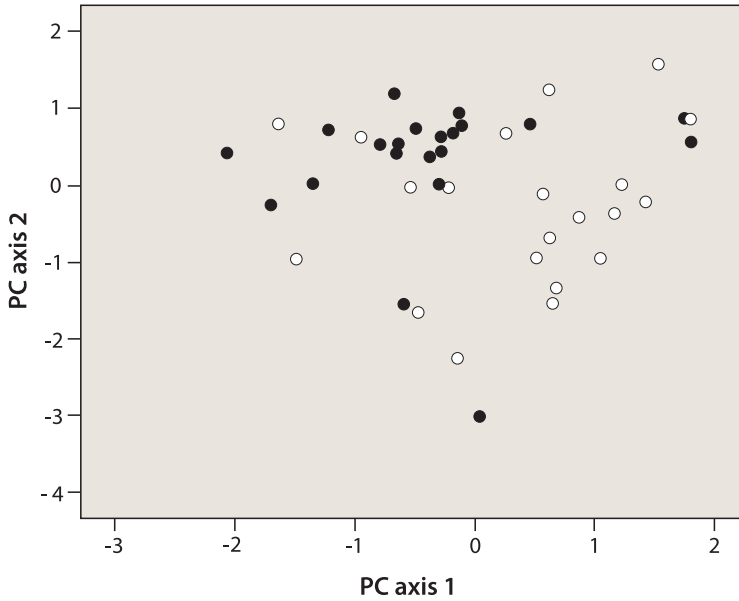


Fig. 4.- Scatterplot of the black woodpecker *Dryocopus martius* “breeding home ranges” in Gipuzkoa (filled circles) and random plots (white circles) positioned on the plane defined by the two axis of the principal component analysis over the habitat variables measured.

Fig. 4.- Gráfico de situación de los “dominios vitales reproductores” de picamaderos negro *Dryocopus martius* en Gipuzkoa (círculos negros) y de parcelas al azar (círculos blancos) sobre el plano definido por los dos ejes del análisis de componentes principales efectuado sobre las variables de hábitat medidas.

Variable	B	SE	Wald	p	Exp (B)
<i>Pinus radiata</i>	0.07	0.03	5.7	0.02	1.1
<i>Pinus nigra</i>	0.13	0.05	7.5	0.01	1.1
LPI	2.5	1.1	5.1	0.02	12.2
Tree height <10 m	-0.08	0.03	6.9	0.01	0.9

Table 2.- Binary logistic regression model for the probability of detection of the black woodpecker *Dryocopus martius* “breeding home ranges” in Gipuzkoa. B, regression coefficient; SE, standard error.

Tabla 2.- Modelo de regresión logística binaria para la probabilidad de detección de “dominios vitales reproductivos” de picamaderos negro *Dryocopus martius* en Gipuzkoa. B, coeficiente de regresión; SE, error estándar.

Foraging habitat use

Eighty-seven foraging signs were recorded. A total of 91.3% were located in mature forest stands, and 52.2% in plantation stands. Beech stands accounted for 28.3%, black pine for 17.4%, American oak for 17.4%, penduline oak for 6.5%, larch for 6.5% and Monterey pine for 4.4%. There was a strong selection in favour of American oak ($W=8.5$, $p<0.01$) and black pine stands ($W=3.03$, $p<0.05$), and against Monterey pine stands ($W=0.2$, $p<0.01$) and un-forested patches ($W=0.4$, $p<0.05$). Selection was not demonstrated for the rest of the tree species. The average proportion of canopy cover in foraging patches was 91.6% ($s=25.1$, range 0-100) and 97.9% ($s=5.9$, range 70-100) excluding the three marks that were located outside forest stands but close to them.

Breeding performance

Thirteen nests were regarded as active because adults were observed visiting the hole on a regular basis. The presence of chicks was confirmed in twelve of them (table 3).

BHR	Habitat use	Regular presence	Pairing behaviour	Active nest	Nestlings	Fledglings
1	X	X				
2	X	X				
3	X	X				
4	X		X			
5	X		X			
6	X		X			
7	X		X			
8	X		X			
9	X			X		
10	X			X	X	
11	X			X	X	X
12	X			X	X	X
13	X			X	X	X
14	X			X	X	X
15	X			X	X	X
16	X			X	X	X
17	X			X	X	X
18	X			X	X	X
19	X			X	X	X
20	X			X	X	X
21	X			X	X	X

Table 3.- Number of "breeding home ranges" (BHR) of the black woodpecker *Dryocopus martius* in Gipuzkoa where habitat use and breeding performance was assessed.

Tabla 3.- Número de "dominios vitales reproductivos" (BHR) del picamaderos negro *Dryocopus martius* en Gipuzkoa en los que se evaluó el uso del hábitat y los parámetros reproductivos.

In one case, one dead chick was found on the ground close to the nest-tree, but evidences of predation were not clearly identified. In another case, two chicks were found dead inside one flooded nest, so hypothermia was the plausible cause of death. The mean number of full-grown chicks recorded was 1.8 ($s=0.7$, range 1-3, $N=11$). Therefore, a total of 20 chicks fledged from 11 broods. Nine of the 16 chicks that could be sexed were males. The earliest day of fledging was May 15, and the latest June 13.

Discussion

The colonizing process

The absence of paleozoological records for the black woodpecker in Europe west and south of the Alps might suggest that the species is a historic colonizer of the Atlantic section of the continent (Arribas, 2004; Holm & Svenning, 2014). During the 20th century, considerable range expansions have been described in The Netherlands, Belgium, France and Italy, with birds invading lowland, reforested regions (Cuisin, 1985; Mikusinski, 1995; Cuisin, 1998; Ceccarelli *et al.*, 2008). In Northern Iberia, at the south-western edge of the global distribution, the black woodpecker has also increased its breeding range, colonizing formerly vacant areas over the last 30 years (Martínez-Vidal, 2004; Camprodon *et al.*, 2007). In Gipuzkoa, the first report of the black woodpecker dates back to the 1960's (Noval, 1967), but until the 2000's the species was extremely rare and irregular (Gainzarain, 1998; Aierbe *et al.*, 2001). In 2011, the first successful reproduction was confirmed (Ruiz de Azua, 2012), though, without doubt, the Black Woodpecker was already breeding a few years before (T. Aierbe, com. pers.).

This particular colonizing event is part of the wider range expansion across the Basque Mountains, which is currently filling the intermediate gap between the Pyrenean and the Cantabrian populations (Gainzarain & Fernández-García, 2013). The geographic origin of this recent population is unknown so far. There is not genetic or ringing information to support a Cantabrian or Pyrenean origin, which are the closest source areas. However, based on the favourable population trend of the neighbouring Pyrenean population (Martínez-Vidal, 2004), opposite to the Cantabrian one (Simal & Herrero, 2003; García, 2008; Sánchez *et al.*, 2009), it is plausible to speculate about a Pyrenean origin.

The black woodpecker fulfills several biological features that Mikusinski (2006) related to decline-prone woodpecker species in transformed landscapes, like large body size and extensive home-ranges, therefore needing a network of vast forest tracts to maintain viable populations. But, on the the other hand, this species maintains a huge distribution indicating adaptability (Crocì *et al.*, 2007), is relatively tolerant to forestry practices (Cárcamo, 2006) which associates to rapid occupation of vacant habitats (Villard & Taylor, 1994), and has good dispersal abilities, in turn related to the velocity of expansion (Lensink, 1997). Although there are hardly any studies in Europe reporting on emigration and immigration rates (Passinelli, 2006), recoveries of ringed birds show a noticeable proportion of long

post-juvenile movements (Gorman, 2011) and high average natal dispersal distance (16.25 km in Denmark; Christensen, 2002). Both this kind of life-history traits and tolerance to disturbance are fair predictors of colonizer birds (Shigesada & Kawasaki, 2002) and may explain the black woodpecker capability to expand its distribution, as shown from our study area.

At the continental scale, the expansion of the black woodpeckers' range has been attributed to extensive coniferous reforestation (Mikusinski, 1995), but at the regional scale more emphasis is placed on forest maturation, due to a decline in timber exploitation (Gil-Tena *et al.*, 2010). The occupancy of patches in Gipuzkoa did not seem to be influenced by distance to population sources, which was not unexpected given the comparatively small scale of our study area. In the Eastern Pyrenees, about three times larger, the pattern of colonization by the black woodpecker was mediated by connectivity among forest patches, depending in turn on distance to source and forest structure (i. e. basal area; Gil-Tena *et al.*, 2013). The availability of a network of stepping stones is crucial to explain the progressive spread of the population (Saura *et al.*, 2014). Such spatially explicit models could be improved if indicators of foraging quality, such as availability of dead wood, are taken into account (see below). Foraging quality enhances breeding performance and the production of a surplus of individuals than can disperse to non-occupied patches (Newton, 1998).

Plantations and the black woodpecker

The black woodpecker inhabits several different types of Palearctic boreal and temperate forests, including coniferous plantations (Mikusinski, 1995; Gorman, 2011). In boreal and hemiboreal forests, the species is tolerant to plantation managing, provided that thick trunks (diameter >40 cm) for excavating nests remain, and decaying trees are also left as foraging substrates (Angelstam & Mikusinski, 1994). In the framework of worldwide afforestation and reforestation activities for commercial purposes, intense debates focus on the effect of plantation forestry on biodiversity (Bremer & Farley, 2010). As for birds, meta-analyses in Europe have shown that landscape history and spatial structure (patch size, matrix pattern) are probably more informative in explaining species richness than management at the stand scale (Paillet *et al.*, 2009).

Extensive Monterey pine plantations in Northern Spain have contributed to the restoration of forest bird communities (Carrascal & Tellería, 1990), but for the black woodpecker in particular our study has found a number of limitations. Plantations of this pine species in the Basque region are a novel habitat for the black woodpecker across its entire range (Mead, 2013). The species' selection for nesting habitats is rather demanding, both for cavity-trees and cavity-tree plots (Martínez-Vidal, 2001; Camprodon *et al.*, 2007; Pirovano & Zecca, 2014). Preference for beech as nesting substrate has been demonstrated over much of Western Europe (Gorman, 2011; Zahner *et al.*, 2012), and our own data supports this view. Beech trees provide less accessible nests: high holes and smooth bark are associated to lower predation pressure (Zahner & Bauer, 2014). But pine trees (i.e. black pine, Scots

pine) are also used in some mountain regions, like the Pyrenees and the Alps, in similar proportion to their availability on the landscape (Martínez-Vidal, 2001; Bocca *et al.*, 2007). In Gipuzkoa, the avoidance of Monterey pine patches deserves further research, but the reason may lie on the combined absence of suitable (i.e. thick, tall and debranched) nesting trees and the scarcity of foraging resources in dense, shaded stands (see below). On the contrary, stands of mixed deciduous trees were favoured because they probably supply hole-trees (beech and American oak, even though these two species do not dominate such stands). Because of the forest history of the study area, mixed deciduous stands appear scattered at lower altitudes, surrounded by the matrix of Monterey pine plantations. Similarly, Bocca *et al.* (2007) found a negative selection for the mountain pine *Pinus uncinata* in the Alps -in spite of accounting for half of the surface of their study area- attributed to the unsuitable tree conformation and the dense structure of this kind of forest.

The role of habitat fragmentation

An interesting outcome was the influence of the spatial structure of the habitat on the presence of black woodpecker BHR. Fragmentation of suitable forest patches embedded in a matrix dominated by intensively managed plantations largely determines the composition of bird assemblages (Estades & Temple, 1999) but in a species-specific-way (Mönkkönen *et al.*, 2014). Woodpeckers are thought to be relatively tolerant to fragmentation because, as primary cavity-nesters, they avoid the increasing effect of predation while decreasing patch size. This seems to be the case for the black woodpecker, whose density and breeding performance was not influenced by fragmentation in Sweden (Tjernberg *et al.* 1993) or landscape structure in Finland (Brotons *et al.*, 2003).

But more detailed analyses have shown differences referred to patch size and density of edges in another generalist species, the great spotted woodpecker *Dendrocopos major* (Mazgajski & Rejt, 2006; Barbaro *et al.*, 2007). Reduced clutch size, low number of fledglings and delayed breeding phenology were observed in smaller woodlots. Therefore even generalist woodpeckers can be sensitive to fragmentation processes, and this could also apply to the black woodpecker (Mikusinski, 1995). The preference for larger, less complex forest patches in our study area, as opposed to the pattern over much of the species range (Rueda *et al.*, 2013), might indicate that the spatial structure plays an increasing role as departing from the range core. This idea is also supported by the fact that such a preference has also been described in other peripheral areas, namely Northern Scandinavia and the Pyrenees (Tjernberg *et al.*, 1993; Garmendia *et al.*, 2006), regardless of their varying degree of forest fragmentation at the European landscape level (Estreguil *et al.*, 2013).

Is breeding performance limited by habitat or demography?

A high percentage of the monitored nests produced fledglings. The review of Passinelli (2006) reported a median breeding success of 80.2% (55-96% in 12 studies from France, Germany, Denmark, Sweden and Finland); the figure in our study area was close to the highest section of that range. This might be an artifact because precision of nest success estimates depends on sample size (Paclík *et al.*, 2009) and breeding failures at the stages of nesting and incubation are more difficult to detect, but the same could be applied to the mentioned studies, and the intensity of our field effort suggests that the breeding success was indeed relatively high. On the contrary, the number of fledglings per successful nest was low, if compared to the average 3.3 given over of the above referred studies (Passinelli, 2006). Our figure is based on a one-year monitoring, but additional data from previous years were in accordance with this (Ruiz de Azua, 2012; T. Aierbe, pers. com.).

Although clutch size has been reported to be influenced by latitude in many bird species, other breeding parameters such as the number of fledglings per successful nest probably depend less on geographical determinants (Sanz, 1998). Reproductive performance in the black woodpecker is influenced by territory quality (Rolstad *et al.*, 2000) and, possibly, by age, experience, duration of bond and kinship between the pair members, although these latter aspects have seldom been investigated in European woodpeckers (Christensen & Kampp, 2003; Passinelli, 2006). Regarding our study area, we do not have data to exclude any of these hypotheses. As for the first, the high proportion of exotic tree stands in black woodpecker territories may limit the availability of invertebrates as foraging resources, and drive higher chick mortality, as has been suggested for forest passerines in Monterey pine plantations (De la Hera *et al.*, 2013). Epigeal ant and beetle abundances are very impoverished in Monterey pine plantations from Australia and South America, where this tree is also alloctonous (Gunther & New, 2003; Sinclair & New, 2004; Corley *et al.*, 2006; Paritsis & Aitzen, 2008).

In our study area, Alberdi *et al.* (2012) measured a lower frequency of occurrence of ground-dwelling ant (*Lasius* spp., *Formica* spp.) mounds on Monterey pine plots (11%, N=392), beech (7 %, N=157), black pine (7 %, N=54) and larch, Douglas fir and Lawson cypress (9 %, N=118), as opposed to oak and mixed deciduous plots (19 %, N=209). This data does not explain the foraging use by the black woodpecker, possibly because the abundance of ground-dwelling ants is not a reliable indicator of foraging habitat quality in our study area. Although these ants are known to be a part of the black woodpecker's diet, arboreal carpenter ants (*Camponotus* spp.) are the staple food in Europe (Rolstad *et al.*, 1998; Gorman, 2011). The abundance of carpenter ants and saproxylophagous prey is primarily related to the shading and canopy cover (Dolek *et al.*, 2009; Lemperiere & Marage, 2010). In Gipuzkoa, black pine stands are more sun-exposed than Monterey pine and beech stands, as deduced by the average herbaceous covers (28.5, 18.6 and 12.1 % respectively). In the Pyrenees, unmanaged patches of black pine are known to be good foraging sites (Camprodon *et al.*, 2007).

Overall, these differences may account for the foraging habitat use of the black woodpecker, even acknowledging the need for in-site field data to counteract the presumed high variability in determinants of foraging habitat quality (González & Villate, 2003; Pirovano & Zecca, 2014). Being a “generalist-forager” species, the black woodpecker is able to exploit several forest development phases (Begehold *et al.*, 2015) in search of the most available prey types, thriving on dead wood (arboreal ants, saproxylophagous beetles) or on alternative substrates (ground-dwelling ants). Its dependence on dead wood volume seems not to be as intense as in other European woodpeckers (Garmendia *et al.*, 2006; Lohmus *et al.*, 2010; Camprodon, 2013).

As for the second hypothesis, poor reproduction may be associated to demographic issues. For instance, if a greater proportion of young, dispersing birds from the core range was present in this area of recent colonization, lower breeding output could be expected (Karvonen *et al.*, 2012). Peripheral populations may experience continual gene flow from central parts of the range, slowing the rate of adaptation to local conditions (Kawecki, 2008; Martin & Liebl, 2014). This kind of population can turn into demographic sinks, the persistence of which is favoured by dispersers from core areas with higher survival and reproduction (Newton, 2003). We do not have data to support or dismiss this hypothesis, but it deserves future study, because understanding demographic and spatial dynamics across central and marginal range sectors is key to determine the conservation status and perspectives of populations (Passinelli, 2006).

Additional comments

One limitation of our habitat analysis was the assumed shape and size for BHR, even though this is well supported by the literature in Spain (Fernández & Azkona, 1996; García & Sánchez, 2002; Camprodon *et al.*, 2007). The number of such ranges was not taken into account as a population size or density indicator, because radiotracking studies have shown that extensive overlap among black woodpecker individual territories can occur (Bocca *et al.*, 2007), although definite spacing and territorial behaviour has also been described (Tjernberg *et al.*, 1993). On the other hand, topographic variables (slope, altitude, exposure) were not measured over BHR because presumably they were not relevant at the scale of our study (Fernández & Azkona, 1996).

Finally, as a methodological conclusion, knowledge about habitat occupancy and selection by forest birds and woodpeckers in particular can be aided by using forest inventory databases, which capture and store environmental, compositional and structural metrics on a standardized basis (Angelstam *et al.*, 2004; Müller *et al.*, 2008; Walczak *et al.*, 2013). Although inner heterogeneity can remain at the stand level, forest inventories provide readily available predictors at the home range scale and above, that can be analyzed on a GIS platform. Besides, these scales have proved to be more meaningful when searching for woodpecker-habitat correlations (Angelstam *et al.*, 2002). Therefore the use of forest inventories is encouraged in species ecological modelling research, but they should pay

more attention to some relevant biotic features generally overlooked, like volumes of decaying wood and basal areas, and supply more precise metrics, like tree diameter intervals.

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Bibliography

- Aierbe, T., Olano, M., Vázquez, J. 2001. Atlas de las aves nidificantes de Gipuzkoa. *Munibe, Cienc. nat.* 52: 5-136.
- Alberdi, I., Hernández, L., Saura, S., Barrera, M., Gil, P., Condés, S., Cantero, A., Sandoval, V.J., Vallejo, R., Cañellas, I. 2012. *Estimación de la biodiversidad forestal en el Tercer Inventario Forestal Nacional. País Vasco-Euskadi*. Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid.
- Álvarez, J., Bea, A., Faus, J.M., Castién, E., Mendiola, Í. *Atlas de los vertebrados continentales de Álava, Vizcaya y Guipúzcoa (excepto Chiroptera)*. Gobierno Vasco. Bilbao.
- Angelstam, P., Breuss, M., Mikusinski, G., Stenström, M., Stighäll, K., Thorell, D. 2002. Effects of forest structure on the presence of woodpeckers with different specialization in a landscape history gradient in NE Poland. In: *Avian Landscape Ecology. Pure and Applied Issues in the Large-scale Ecology of Birds*. D. Chamberlain, A. Wilson (Eds.): 25-38. University of East Anglia. Norwich.
- Angelstam, P., Mikusinski, G. Woodpecker assemblages in natural and managed boreal and hemiboreal forest: a review. *Ann. Zool. Fennici* 31: 157-172.
- Angelstam, P., Roberge, J.M., Löhmus, A., Bergmanis, M., Brazaitis, G., Dönz-Breuss, M., Edenius, L., Kosinski, Z., Kurlavicius, P., Lärmanis, V., Lūkins, M., Mikusinski, G., Račinskis, E., Strazds, M., Tryjanowski, P. 2004. Habitat modelling as a tool for landscape-scale conservation. A review of parameters for focal forest birds. *Ecol. Bull.* 51: 427-453.
- Área de Inventario y Estadísticas Forestales. 2013. *Cuarto inventario forestal nacional. Comunidad Autónoma del País Vasco*. Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid.
- Arribas, Ó. 2004. *Fauna y paisaje de los Pirineos en la era glaciár*. Lynx. Barcelona.

- **Barbaro, L., Rossi, J. P., Vetillard, F., Nezan, J., Jactel, H.** 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. *J. Biogeogr.* 34: 652-664.
- **Begehold, H., Rzanny M., Flade, M.** 2015. Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests. *J. Ornithol.* 156: 19-29.
- **BirdLife International.** 2014. *Species factsheet: Dryocopus martius.* Available from: <http://www.birdlife.org> on 29/09/2014.
- **Bocca, M., Carisio, L., Rolando, A.** 2007. Habitat use, home range and census techniques in the black woodpecker *Dryocopus martius* in the Alps. *Ardea* 95:17-29.
- **Bremer, L.L., Farley, K.A.** 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodivers. Conserv.* 19: 3893-3915.
- **Brotans, L., Mönkkönen, M., Huhta, E., Nikula, A., Rajasärkkä, A.** 2003. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Land. Ecol.* 18: 377-393.
- **Camprodon, J.** 2013. *Ecologia i conservació dels ocells forestals. Un manual de gestió de la biodiversitat en boscos catalans.* Centre Tecnològic Forestal de Catalunya. Solsona.
- **Camprodon, J., Campión, D., Martínez-Vidal, R., Onrubia, A., Robles, H., Romero, J. L., Senosiain, A.** 2007. Estatus, selección del hábitat y conservación de los pícidos ibéricos. In: *Conservación de la biodiversidad y gestión forestal.* J. Camprodon, E. Plana (Eds.): 391-434. Universidad de Barcelona. Barcelona.
- **Cárcamo, S.** 2006. Evolución de las poblaciones de pito negro (*Dryocopus martius*) y pico dorsiblanco (*Dendrocopos leucotos lilfordi*) en los montes de Quinto Real (Navarra) y su relación con la gestión forestal. *Pirineos* 161: 133-150.
- **Carrascal, L.M., Tellería, J.L.** 1990. Impacto de las repoblaciones de *Pinus radiata* sobre la avifauna forestal del norte de España. *Ardeola* 37: 247-266.
- **Ceccarelli, P.P., Agostini, N., Milandri, M., Bonora, M.** 2008. Il picchio nero *Dryocopus martius* (Linnaeus, 1758) nel Parco Nazionale delle Foreste Casentinesi (Aves Piciformes Picidae). *Quad. Studi Not. Storia Naturale della Romagna* 27: 143-154.
- **Christensen, H.** 2002. Spredning af unge Sortspætter *Dryocopus martius* iforbindelse med indvandringen til Sønderjylland. *Dansk Ornithol. Foren. Tidsskr.* 96: 161-167.
- **Christensen, H., Kampp, K.** 2003. Inbreeding in a black woodpecker *Dryocopus martius* population. *Dansk Ornithol. Foren. Tidsskr.* 97: 222-225.
- **Corley, J., Sackmann, P., Rusch, V., Bettinelli, J., Paritsis, J.** 2006. Effects of pine silviculture on the ant assemblages (Hymenoptera: Formicidae) of the Patagonian steppe. *For. Ecol. Manag.* 222: 162-166.
- **Croci, S., Le Quilliec, P., Clergeau, P.** 2007. Geographical range as predictor of spatial expansion of invading birds. *Biodivers. Conserv.* 16: 511-524.
- **Cuisin, M.** 1985. Range expansion of the black woodpecker in Western Europe. *British Birds* 78: 184-187.

- **Cuisin, M.** 1998. L'expansion du pic noir *Dryocopus martius* (L.) en France n'a pas encore pris fin. *Alauda* 66: 131-134.
- **De la Hera, I., Arizaga, J., Galarza, A.** 2013. Exotic tree plantations and avian conservation in northern Iberia: a view from a nest-box monitoring study. *An. Biodivers. Conserv.* 36: 153-163.
- **Diputación Foral de Gipuzkoa.** 2008. *Imagen vuelo LIDAR*. Available from: <http://gipuzkoa.net>.
- **Dolek, M., Freese-Hager, A., Bussler, H., Floren, A., Liegl, A., Schmidl, J.** 2009. Ants on oaks: effects of forest structure on species composition. *J. Insect Conserv.* 13: 367-375.
- **Dytham, C.** 2003. *Choosing and Using Statistics. A Biologist's Guide*. Blackwell. Oxford.
- **Estades, C. F., Temple, S. A.** 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecol. Appl.* 9: 573-585.
- **Estreguil, C., Caudullo, G., de Rigo, D., San Miguel, J.** 2013. *Forest Landscape in Europe: Pattern, Fragmentation and Connectivity*. Publications Office of the European Union. Luxembourg.
- **Fernández, C., Azkona, P.** 1996. Influence of forest structure on the density and distribution of the white-backed woodpecker *Dendrocopos leucotos* and black woodpecker *Dryocopus martius* in Quinto Real (Spanish western Pyrenees). *Bird Study* 43: 305-313.
- **Ferrán, M.** 2001. *SPSS para Windows. Análisis estadístico*. Mc Graw Hill. Madrid.
- **Fortin, M.J., Dale, M.** *Spatial Analysis. A Guide for Ecologists*. Cambridge University Press. Cambridge.
- **Fuller, R.J.** 2002. Spatial differences in habitat selection and occupancy by woodland bird species in Europe: a neglected aspect of bird-habitat relationships. In: *Proceedings of the 11th Annual IALE Conference*. D. Chamberlain, A. Wilson (Eds.): 25-38. University of East Anglia. Norwich.
- **Fuller, R.A., Ladle, R.J., Whittaker, R.J., Possingham, H.P.** 2011. Planning for persistence in a changing world. In: *Conservation Biogeography*. R.J. Ladle, R.J. Whittaker (Eds.): 163-189. Blackwell. Oxford.
- **Gainzarain, J.A.** 1998. Pito negro. In: *Vertebrados continentales. Situación actual en la Comunidad Autónoma del País Vasco*. A. Bea, J.A. Fernández de Mendiola (Eds.): 240-241. Gobierno Vasco. Vitoria.
- **Gainzarain, J.A., Fernandez-García, J.M.** 2013. Black woodpecker *Dryocopus martius* (L., 1758) recent range expansion leads to the coalescence of the two former distribution areas in northern Spain. *Munibe, Cienc. nat.* 61: 103-115.
- **García, J.** 2008. Pito negro. In: *Atlas de las aves reproductoras de León*. J. García, L.A. Ramos, X. Vázquez (Eds.): 155-156. Diputación de León. León.
- **García, A., Sánchez, M.** 2002. El pito negro en Uceda. *Locustella* 1; 96-98.
- **Garmendia, A., Cárcamo, S., Schwendtner, Ó.** 2006. Forest management considerations for conservation of black woodpecker *Dryocopus martius* and white-backed woodpecker *Dendrocopos leucotos* populations in Quinto Real (Spanish Western Pyrenees). *Biodivers. Conserv.* 15: 1399-1415.

- Gil-Tena, A., Brotons, L., Saura, S. 2010. Effects of forest landscape change and management on the range expansion of forest bird species in the Mediterranean region. *For. Ecol. Manag.* 259: 1338-1346.
- Gil-Tena, A., Brotons, L., Fortin, M.J., Burel, F., Saura, S. 2013. Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: forest management implications. *Eur. J. For. Res.* 132: 181-194.
- Gobierno Vasco. 2007. *Mapa de hábitats del País Vasco. Sistema de clasificación EUNIS*. Available from: <http://geoeuskadi.net>.
- González, J., Villate, I. 2003. *Trabajos de gestión en las áreas de elevado interés faunístico del Parque Natural de Aiako Harria*. Unpublished report for the Provincial Council of Gipuzkoa.
- Gorman, G. 2004. *Woodpeckers of Europe. A Study of the European Picidae*. Coleman. Berkshire.
- Gorman, G. 2011. *The Black Woodpecker. A Monograph on Dryocopus martius*. Lynx. Barcelona.
- Gunther, M.J., New, T.R. 2003. Exotic pine plantations in Victoria, Australia: a threat to epigaeic beetle (Coleoptera) assemblages? *J. Insect Conserv.* 7: 73-84.
- Guo, Q., Taper, M., Schoenberger, M., Brandle, J. 2005. Spatial-temporal population dynamics across species range: from centre to margin. *Oikos* 108: 47-57.
- Holm, S.R., Svenning, J.C. 2014. 180,000 years of climate change in Europe: avifaunal responses and vegetation implications. *Plos One* 9 (4): e94021. doi:10.1371/journal.pone.0094021.
- Karvonen, J., Orell, M., Rytönen, S., Broggi, J., Belda, E. 2012. Population dynamics of an expanding passerine at the distribution margin. *J. Avian Biol.* 43: 102-108.
- Kawecki, T.J. 2008. Adaptation to marginal habitats. *Annu. Rev. Ecol. Evol. Syst.* 39: 321-342.
- Konsinski, Z., Bilinska, E., Derezinski, J., Jelen, J., Kempa, M. 2010. The black woodpecker (*Dryocopus martius*) and the European beech (*Fagus sylvatica*) as keystone species for the stock dove (*Columba oenas*) in western Poland. *Ornis Polonica* 51: 1-13.
- Lemperiere, G., Marage, D. 2010. The influence of forest management and habitat on insect communities associated with dead wood: a case study in forests of the southern French Alps. *Insect Conserv. Biodiver.* 3: 236-245.
- Leitão, A.B., Miller, J., Ahern, J., McGarigal, K. 2006. *Measuring Landscapes: A Planners Handbook*. Island Press. Washington DC.
- Lensink, R. 1997. Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual diffusion model. *J. An. Ecol.* 66: 811-826.
- Lohmus, A., Kinks, R., Soon, M. 2010. The importance of dead-wood supply for woodpeckers in Estonia. *Baltic Forestry* 16: 76-86.
- Manly, B.J., McDonald, L.L., Thomas, D.L. 1993. *Resource Selection by Animals. Statistical Design and Analysis for Field Studies*. Chapman & Hall. London.
- Martin, L.B., Liebl, A.L. 2014. Physiological flexibility in an avian range expansion. *Gen. Comp. Endocrinology* 206:227-234.

- **Martin, L.B., Coon, C., Liebl, A.L., Schrey, A.W.** 2014. Surveillance for microbes and range expansion in house sparrows. *Proc. Royal Soc. B* 281(1774). doi:10.1098/rspb.2013.2690.
- **Martínez-Vidal, R.** 2001. Hábitat de cría del pito negro en las sierras del Cadí y Moixeró (Prepirineo oriental): caracterización, tipología y pérdidas de árboles-nido. In: *Conservación de la biodiversidad y gestión forestal*. J. Camprodon, E. Plana (Eds.): 321-330. Universidad de Barcelona. Barcelona.
- **Martínez-Vidal, R.** 2004. Picot negro *Dryocopus martius*. In: *Atlas dels ocells nidificants de Catalunya 1999-2002*. J. Estrada, V. Pedrocchi, L. Brotons, S. Herrando (Eds.): 320-321. Lynx. Barcelona.
- **Mazgajski, T., Rejt, L.** 2006. The effect of forest patch size on the breeding biology of the great spotted woodpecker *Dendrocopos major*. *Ann. Zool. Fennici* 43: 211-220.
- **McGarigal, K., Cushman, S.A., Ene, E.** 2012. *Fragstats v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps*. University of Massachusetts. Amherst. Available from: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- **Mead, D.J.** 2013. *Sustainable Management of Pinus radiata Plantations*. Food and Agriculture Organization of the United Nations. Rome.
- **Mehlman, D.W.** 1997. Change in avian abundance across the geographic range in response to environmental change. *Ecol. Appl.* 7: 614-624.
- **Mikusinski, G.** 1995. Population trends in black woodpecker in relation to changes and characteristics of European forests. *Ecography* 18: 363-369.
- **Mikusinski, G.** 2006. Woodpeckers: distribution, conservation and research in a global perspective. *Ann. Zool. Fennici* 43: 86-95.
- **Mönkkonen, M., Rajasärkkä, A., Lampila, P.** 2014. Isolation, patch size and matrix effects on bird assemblages in forest reserves. *Biodivers. Conserv.* 23: 3287-3300.
- **Müller, J., Pöllath, J., Moshhammer, R., Schröder, B.** 2008 Predicting the occurrence of middle spotted woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data. *For. Ecol. Manag.* 257: 502-509.
- **Newton, I.** 1998. *Population Limitation in Birds*. Academic Press. London.
- **Newton, I.** 2003. *The Speciation and Biogeography of Birds*. Academic Press. London.
- **Noval, A.** 1967. Estudio de la avifauna de Gipuzkoa. *Munibe* 19: 5-78.
- **Paclík, M., Misík, J., Wiedinger, K.** 2009. Nest predation and nest defence in European and North American woodpeckers: a review. *Ann. Zool. Fennici* 46: 361-379.
- **Paillet, Y., Bergés, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastián, M., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R.** 2009. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24: 101-112.
- **Paritsis, J., Aizen, M.A.** 2008. Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. *For. Ecol. Manag.* 255: 1575-1583.

- **Passinelli, G.** 2006. Population biology of European woodpecker species: a review. *Ann. Zool. Fennici* 43: 96-111.
- **Pigot, A.L., Owens, I.P., Orme, C.D.** 2010. The environmental limits to geographic range expansion in birds. *Ecol. Letters* 13: 705-715.
- **Pirovano, A.R., Zecca, G.** 2014. Black woodpecker *Dryocopus martius* habitat selection in the Italian Alps: implications for conservation in Natura 2000 network. *Bird Conserv. Int.* 24: 299-315.
- **Rolstad, J., Majewski, P., Rolstad, E.** 1998. Black woodpecker use of habitats and feeding substrates in a managed Scandinavian forest. *J. Wild. Manag.* 62: 11-23.
- **Rolstad, J., Rolstad, E., Saeteren, O.** 2000. Black woodpecker nest sites: characteristics, selection and reproductive success. *J. Wild. Manag.* 64: 1053-1066.
- **Rueda, M., Hawkins, B.A., Morales-Castilla, I., Vidanes, R.M., Ferrero, M., Rodríguez, M.Á.** 2013. Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. *Glob. Ecol. Biogeography* 22: 1282-1292.
- **Ruiz de Azua, N.** 2012. El picamaderos negro *Dryocopus martius* en Guipúzcoa/Gipuzkoa. *Foresta* 55: 44-45.
- **Sagarin, R.D., Gaines, S.D., Gaylord, B.** 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecol. Evol.* 21: 524-530.
- **Sánchez, T., González-Quirós, P., Vázquez, V. M.** 2009. El pico mediano (*Dendrocopos medius*), el pico menor (*Dendrocopos minor*) y el picamaderos negro (*Dryocopus martius*), (Picidae, Aves) en el Principado de Asturias (España). *Bol. Cienc. Nat. Real Inst. Estud. Astur.* 50: 281-302.
- **Saura, S., Bodin, Ö., Fortin, M.J.** 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J. Appl. Ecol.* 51: 171-182.
- **Sagarin, R., Gaines, S.** 2002. The "abundant centre" distribution: to what extent is it a biogeographic rule? *Ecol. Lett.* 5: 137-147.
- **Sanz, J.J.** 1998. Effects of geographic location and habitat on breeding parameters of great tits. *Auk* 115: 1034-1051.
- **Shigesada, N., Kawasaki, K.** 2002. Invasion and the range expansion of species: effects of long-distance dispersal. In: *Dispersal Ecology*. J.M. Bullock, R.E. Kenward, R.S. Hails (Eds.): 350-373. Blackwell. Oxford.
- **Simal, R., Herrero, Á.** 2003. Picamaderos negro *Dryocopus martius*. In: *Atlas de las aves reproductoras de España*. R. Martí, J.C. del Moral (Eds.): 354-355. Ministerio de Medio Ambiente. Madrid.
- **Sinclair, J.E., New, T.R.** 2004. Pine plantations in south eastern Australia support highly impoverished ant assemblages (Hymenoptera: Formicidae). *J. Insect Conserv.* 8: 277-286.
- **Tellería, J. L.** 2014. The decline of a peripheral population of the European robin *Erithacus rubecula*. *J. Avian Biol.* 46: 159-166.
- **Tjernberg, M., Johnsson, K., Nilsson, S.G.** 1993. Density variation and breeding success of the black woodpecker *Dryocopus martius* in relation to forest fragmentation. *Ornis Fennica* 70: 155-162.

- **Universidad de Extremadura.** 2008. *Manual práctico de Sextante para gvSIG*. Universidad de Extremadura. Badajoz.
- **Van Manen, W.** 2012. Broedbiologie van de Zwarte Specht in Nederland. *Limosa* 85: 161-170.
- **Villard, M.A., Taylor, P.D.** 1994. Tolerance to habitat fragmentation influences the colonization of new habitat by forest birds. *Oecologia* 98: 343-401.
- **Walczak, L., Kosinski, Z., Stachura, K.** 2013. Factors affecting the occurrence of middle spotted woodpeckers as revealed by forest inventory data. *Baltic For.* 19: 81-88.
- **Wesolowski, T.** 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. *J. Ornithol.* 148: 395-405.
- **Zahner, V., Bauer, R.** 2014. Predation in vertebrate communities of black woodpecker (*Dryocopus martius*) cavities and the behavioral response to predation risk. In: *7th International Woodpeckers Conference. Book of Abstracts*. J.M. Fernández-García, G. Passinelli, H. Robles, J. Rubines (Eds.): 32. Diputación Foral de Álava. Vitoria.
- **Zahner, V., Sikora, L., Pasinelli, G.** 2012. Heart rot as a key factor for cavity tree selection in the black woodpecker. *For. Ecol. Manag.* 271: 98-103.



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