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Available at https://doi.org/10.1080/00063657.2017.1395807

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Author(s): Salvador Rebollo

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BIRD STUDY, 2017
https://doi.org/10.1080/00063657.2017.1395807

Prey preferences and recent changes in diet of a breeding population of the Northern Goshawk *Accipiter gentilis* in Southwestern Europe

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ABSTRACT

Capsule: Northern Goshawk *Accipiter gentilis* diet has changed significantly since the 1980s, probably due to changes in populations of preferred prey species.

Aims and methods: To assess changes to the breeding season diet of the Northern Goshawk in southwest Europe over three decades. We examined prey remains at and around nests and assessed avian prey availability using point count surveys.

Results: During 2008–11, Goshawks mainly ate birds, with Feral Pigeons *Columba livia f. domestica* being the most important prey species. Goshawks preferred prey of 100–400 g and forest prey species to non-forest species. Goshawk diet has changed significantly over recent decades: 22% of current prey items belong to species that were not part of the diet in the 1980s. We suggest that these dietary changes reflect changes in the abundance of prey species of the preferred size caused by changes in land use leading to an increase in forest cover, new prey species colonization and changes in the abundance and management of domestic prey.

Conclusion: This study emphasizes that major transformations occurring in agroforestry systems are affecting the main preferred prey of important forest predators, which may have consequences for conservation of both the predators and their prey.

ARTICLE HISTORY
Received 2 December 2016
Accepted 31 August 2017

European agroforestry systems are undergoing major transformations driven by changes in land use, conservation policies of natural resources and climate change (Klijn 2004). These changes are altering the abundance and distribution of prey of top predators and consequently the populations of these predators (Millon *et al.* 2009). A thorough understanding of predator diets, prey preferences and diet changes is important for developing management and conservation plans for top predators and their prey in changing agroforestry systems.

The Northern Goshawk *Accipiter gentilis* (hereafter Goshawk) is a common top predator in European agroforestry systems. They hunt a variety of prey ranging in size from a few grams, including insects, to several kilograms such as adult Arctic Hares *Lepus arcticus* and Capercaillies *Tetrao urogallus* (Tornberg 1997, Petronilho & Vingada 2002). Goshawks exert significant predation pressure on smaller predators, both diurnal and nocturnal, influencing their abundance and spatial distribution (Petty *et al.* 2003, Lourenço *et al.* 2011). It is the most important predator of some forest species, such as certain grouse species, with annual predation rates reaching more than 50% of the adult population for some species and localities (Tornberg *et al.* 2013). Goshawks also affect species of human interest such as game and domestic species, generating conflicts with hunters, pigeon breeders and farmers (Valkama *et al.* 2005, Rutz *et al.* 2006). Because of these feeding habits, the study of prey preferences and recent changes in the Goshawk diet are interesting as indicators of changes in the food webs of European agroforestry systems.

Numerous studies of Goshawk diet during the breeding season in central and north Europe have been published (see reviews in Cramp & Simmons 1980, Kenward 2006, Rutz *et al.* 2006), but the southwestern region remains understudied (but see Mañosa 1994). Furthermore, most previous studies infer the presence and abundance of prey species from prey remains and pellets, which may lead to some biases (Marti *et al.* 2007, García-Salgado *et al.* 2015). The few studies that made use of more direct methods such as observations from hides or video-monitoring of nests examined few nests, so their results may be influenced by a small sample size (Penteriani *et al.* 2005).

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Supplemental data for this article can be accessed http://dx.doi.org/10.1080/00063657.2017.1395807.

These previous studies of Goshawk diet during the breeding season have also left several questions open. First, few studies have simultaneously analysed Goshawk diet and prey abundance to estimate Goshawk prey preferences (Møller *et al.* 2012). Analysing prey preferences gives insight into the hunting strategy of predators and mechanisms of prey selection (Tornberg 1997), which are crucial for explaining diet and its changes. It also allows researchers to test predictions of optimal foraging theory specifically in the case of highly mobile prey and breeding predators, that is central-place foragers (Sih & Christensen 2001). Second, those few studies that examined changes in Goshawk diet in recent decades have been mostly limited to northern and central Europe (Tornberg & Sulkava 1991, Rutz & Bijlsma 2006, Rutz *et al.* 2006, Lehikoinen *et al.* 2013). The abundance of potential prey species has changed substantially in agroforestry systems in southwestern Europe, which offers a valuable opportunity for researching how predators change their feeding habits and for identifying the most influential prey species, i.e. those prey whose changes in abundance exert more influence in predator diet composition.

The present study analysed the breeding season diet, recent dietary changes and prey preferences in a Goshawk population in southwestern Europe. To do so, we analysed: (1) the current Goshawk diet for the period 2008–2011 based on camera recording in 77 nests and analysis of prey remains; (2) changes in Goshawk diet between the periods 1980–1984 and 2008–2011 based on prey remains; and (3) the current prey preferences of the Goshawk, based on comparison of diet and prey abundance, and factors that might affect prey vulnerability, including prey size, age and habitat.

Methods

Study area

The study area was located in the northwestern Iberian Peninsula (Galicia region, 42° 20′ N, 8° 47′ E). It is a 400 km^2 coastal area divided into two subzones of similar size: Península do Morrazo to the west and Terra de Cotobade to the east (online supplementary material Figure S1). The climate is humid-oceanic, with annual average precipitation of 1586 mm and annual average temperature of 14.4°C (Carballeira *et al.* 1983). The landscape is mountainous and dominated by non-native eucalyptus plantations *Eucalyptus globulus* occupying the upper and middle parts of the slopes. Lower parts of the slopes and valley bottoms are occupied by fields, urban areas and coastal areas. Forest area has increased in recent decades as a result of declining livestock and farming activities and increasing afforestation (MMA 1998). The study area features both high human population density (507 inhabitants/km^2) as well as high Goshawk breeding density at 15.8 nesting territories/100 km^2 (Perez-Camacho *et al.* 2015, Rebollo *et al.* in press).

Diet estimates

Goshawk diet during the breeding season was estimated in both east and west subzones (online Figure S1). During the periods 1980–1984 and 2008–2011, we visited all active Goshawk nests and plucking sites in the study area to collect all uneaten prey remains and pellets available. We performed these surveys at least three times in each territory and year during the second half of the breeding season (May–August). In the period 2008–11, we collected prey remains from the nest cups twice: the first time when we installed the cameras in the nests and ringed the nestlings (see below), and the second time when we removed the cameras from the nests after fledging. In the period 1980–84, we collected prey remains from the nest cups just once, when we ringed the nestlings. We identified feathers, hair and bones to species level and estimated the minimum number of individuals of each prey species, adjusting for repetition of principal feathers and bones. During 2008–11, we also installed digital photo trail-cameras at 77 nests (18–21 nests each year in 29 different nesting territories) to record the prey provided throughout the nestling phase. Cameras were installed when nestlings were an average of 23.7 days old (sd = 3.4). Further details on these methods can be found in García-Salgado *et al.* (2015).

The number of prey items detected from camera images was about three times greater than those identified from prey remains (García-Salgado *et al.* 2015). Thus, estimates of current Goshawk diet (period 2008–11) per year and territory were based primarily on data from camera images. Analysis of prey remains from 2008 to 2011 was used to complement camera-based diet assessment when certain prey species were detected in higher number in remains than in images (e.g. passerines). For each year and territory, we used only the source of data in which we detected the highest number of individuals for any given prey species in order to avoid multiple counting of individuals and get a consensus mixed data set. The rate of prey identification to species level was lower based on camera analysis (70%) than on prey remains (>99%). Some prey items were identified to family or genera but not to species level based on camera images, like prey identified as pigeons but not reliably classifiable as Feral Pigeon or Wood Pigeon (see Table 1 for scientific names of prey species). These prey images were assigned to particular species in the proportions they were reliably identified in camera images and prey remains for a given territory and year. This mixed data set was subsequently used for all analyses. Prey items that could not be identified even to class level (mammal, bird or reptile) based on camera images were excluded from diet assessment. The age of avian prey in prey remains was recorded whenever possible as nestling, fledgling or full-grown according to the growth stage of primary and secondary feathers (Newton & Marquiss 1982). Full-grown avian prey included yearlings in which the inferior umbilicus of the feather is already keratinized.

We estimated the Goshawk diet composition as percentage of different prey by number and by biomass. Prey items were converted into biomass using the mass of the species in the study area when available; otherwise we used the mass reported in the literature (online appendix Table S1). Biomass estimates of prey took into account age classes. For avian prey species, we took into account the proportion of nestlings, fledglings or full-grown individuals in the Goshawk diet. European Rabbits were classified as young, subadult or adult according to their relative size in camera images. We were unable to estimate the age of Red Squirrels from camera images, so we applied the percentage of young Red Squirrels (11%) in the diet of another Iberian Goshawk population at the same latitude (Mañosa 1994). All other mammals and reptiles were considered adults. Main avian prey species were classified as forest or non-forest prey, according to habitat-related prey density estimates (see next section and online Table S2).

To compare the diets for the periods 1980–1984 and 2008–2011, we analysed the prey remains of seven nesting territories studied in both periods (523 prey items in 1980–84, 433 prey items in 2008–11). The same investigators collected and identified the prey in both periods. Diet estimates were compared using the non-parametric Wilcoxon matched pairs test.

Table 1. Relative contributions of prey species to Goshawk diet by number of prey items and by biomass during 2008–2011.

Species or taxonomic group		Percentage by number (se)	Percentage by biomass
BIRDS			
Feral Pigeon	*Columba livia f. domestica*	17.1 (2.5)	25.1
Eurasian Jay	*Garrulus glandarius*	16.8 (1.2)	10.5
Eurasian Collared Dove	*Streptopelia decaocto*	10.8 (0.8)	8.7
European Green Woodpecker	*Picus viridis*	10.4 (0.9)	7.4
Common Wood Pigeon	*Columba palumbus*	9.0 (1.5)	14.4
Eurasian Magpie	*Pica pica*	7.2 (0.2)	4.8
Common Blackbird	*Turdus merula*	5.3 (0.6)	1.9
Great Spotted Woodpecker	*Dendrocopus major*	3.7 (0.6)	1.0
Song Thrush or Mistle Thrush	*Turdus philomelos, T. viscivorus*	2.2 (0.4)	0.6
Small passerines		1.3 (0.3)	0.1
Yellow-legged Gull	*Larus michahellis*	1.0 (0.4)	3.8
Domestic chicken	*Gallus gallus domesticus*	0.6 (0.2)	1.6
European Turtle Dove	*Streptopelia turtur*	0.6 (0.3)	0.3
Spotless Starling	*Sturnus unicolor*	0.6 (0.3)	0.2
Carrion Crow	*Corvus corone*	0.5 (0.1)	1.2
Eurasian Sparrowhawk	*Accipiter nisus*	0.3 (0.1)	0.2
Psittacine sp.		0.3 (0.1)	0.2
European Nightjar	*Caprimulgus europaeus*	0.2 (0.1)	0.1
Tawny Owl	*Strix aluco*	0.1 (0.1)	0.2
Unidentified bird		0.1 (0.1)	0.0
Common Cuckoo	*Cuculus canorus*	<0.1 (0.0)	0.0
Common Quail	*Coturnix coturnix*	<0.1 (0.0)	0.0
Golden Oriole	*Oriolus oriolus*	<0.1 (0.0)	0.0
MAMMALS			
Red Squirrel	*Sciurus vulgaris*	8.5 (1.6)	10.0
European Rabbit	*Oryctolagus cuniculus*	2.3 (0.3)	6.9
Rat sp.	*Rattus* sp.	0.3 (0.1)	0.2
Micromammal sp.		0.2 (0.1)	0.0
European Mole	*Talpa europaea*	0.1 (0.1)	0.0
Least Weasel	*Mustela nivalis*	0.1 (0.1)	0.1
West European Hedgehog	*Erinaceus europaeus*	<0.1 (0)	0.1
American Mink	*Neovison vison*	<0.1 (0)	0.2
REPTILES			
Ocellated Lizard	*Timon lepidus*	0.3 (0.2)	0.1

Note: The percentage of each species by number is the mean for the four years (± 1 se). The percentage by biomass was obtained by converting into biomass the mean percentage of each species by number, while taking age classes into account (see online Table S1). The total number of prey items identified was 2618.

Avian prey abundance estimates

During the breeding seasons of 2011 and 2012, we estimated the abundance of avian Goshawk prey by sampling diurnal birds larger than a House Sparrow (*Passer domesticus*) in the west subzone of the study area. Habitat areas were delineated in a geographic information system (ArcGIS 9.3, ESRI) based on photo-interpretation of satellite images (PNOA 2009 ; AQ8 habitat categories considered can be seen in online Table S2). In June 2011, we sampled 279 point counts, recording all bird contacts within and beyond a threshold distance of 50 m for 5 minutes per station. Between May and September 2012, we surveyed 242 line transects 300 m long recording all bird contacts within and beyond a threshold distance of 30 m in forest habitats, and 50 m in open habitats. The point count stations and the transect lines were independent and randomly distributed in the sampling area, with sampling effort proportional to habitat areas. All species and habitats were sampled with both methods. Censuses were conducted during the first 4 hours after sunrise or the last 3 hours before sunset on days that were not windy or rainy, in order to ensure high bird detectability. The proportional abundance of avian prey species estimated in the nesting territories was similar in both years (Pearson correlation, $r = 0.93$, $P = 0.000002$, 14; see the following *Avian prey preferences* section and online Table S3).

Absolute densities of avian species in each habitat were estimated with the threshold method (Carrascal *et al.* 2010). The threshold method is a distance sampling-related method suitable for estimating avian densities when measuring exact distances to each contact is unreliable, for example, in censuses of assemblages of multiple species, multiple habitats and collaborative field work including several people with different degrees of expertise. The threshold method provides functions to compute estimates of effective strip width (*ESW*, the distance within which detection probability is expected to be 1.0) based on the ratio $d/p(d)$, were d is the pre-established threshold distance and $p(d)$ the proportion of bird contacts within this threshold. Functions provided by the threshold method incorporate a term t, describing the loss of detectability with distance. This is obtained by integral calculation from species simulations with different detection curves and maximum detection distances. It can be empirically demonstrated that the threshold method provides nearly identical estimates of *ESW* to those obtained with the *DISTANCE* regression approach (Carrascal *et al.* 2010). We used the following functions to estimate *ESW* (Carrascal *et al.* 2007, Carrascal & Palomino 2008):

$$ESW(\text{point counts}) = [d/\sqrt{p(d)}] + t,$$
$$t = 1/(0.197 - 0.014) \times \left[d/\sqrt{p(d)}\right]^{0.747},$$

$$ESW\ (\text{line transects}) = \left[\frac{d}{p(d)}\right] + t$$
$$t = 1/(-29.6 + 29.5) \times [p(d)]^{0.0176}.$$

Absolute densities of each avian species per habitat can be calculated by dividing the total number of individuals detected in that habitat by the area effectively sampled according to the following equations:

$$D\ (\text{point counts}) = N/[S \times (\pi \times \text{ESW}^2)],$$

$$D\ (\text{line transects}) = N/[L \times (2 \times \text{ESW})],$$

where D is absolute avian density (birds/km^2), N is the number of individuals detected, S is the total number of point count stations and L is the total length of transects sampled.

Average densities ± 90% confidence intervals per habitat and year were calculated using the following bootstrap procedure. We replaced the original dataset with a randomly selected subset of 80% of bird surveys in each habitat type and year, and estimated the abundance of each species from these subsets. This procedure was repeated 1000 times to give 1000 density estimates for each species. These density estimates were then averaged, and the resulting 5th and 95th percentiles were defined as the lower and upper limits of the 90% confidence interval (Santos *et al.* 2014). We **AQ9** averaged the densities by habitat type in 2011 and 2012 in order to obtain the mean prey density by habitat type. To estimate absolute abundance of prey in the Goshawk nesting territories, we multiplied the averaged density of each prey species in each habitat by the mean area covered by each habitat type in the territories. Territories were defined as circles with a radius of 1500 m surrounding nests (Martinez-Hesterkamp *et al.* 2015), and we assumed that this area included the main hunting grounds of Goshawk pairs during the breeding season. Prey density estimates can be found in online Table S2. Resampling was carried out using *Pop Tools* 3.2.5 in Microsoft Excel (Hood 2010).

To assess recent historical trends in the number and type of pigeon lofts, we conducted a census of pigeon lofts in 1983 and 2011–12 in a representative area of 31 km^2 within the west subzone of the study area (online Figure S1). We also conducted eight interviews with professional pigeon breeders in 2011 and 2012.

Avian prey preferences

In order to assess Goshawk prey preferences, we used Ivlev"s selectivity index (Marti *et al.* 2007). We averaged the percentage of each prey species in the current (2008–11) Goshawk diet of the west subzone of the study area (21 nesting territories), and related it with the current (2011–12) averaged percentage of abundance of each species within these nesting territories. We assume that although prey species densities may change from one year to the next, the percentage of abundance of each species per territory remains more constant (online Table S3). The selectivity index takes the form:

$$S = (r - p)/(r + p),$$

where r is the proportion of prey taken by the predator and p is the proportion of the same prey available to the raptor (Marti *et al.* 2007). The index S

ranges from −1 to + 1. Values near +1, 0 and −1 indicate a prey species preyed on by Goshawk above, at or below the prey's abundance, respectively. Ivlev's index was calculated only for prey species with abundance >1% in the field. The Ivlev's selectivity indexes estimated for the 2011 showed a high correlation with the Ivlev's indices estimated for the overall data set (Pearson correlation $r = 0.96$, $P = 0.000000$, 3).

We used a generalized additive model (GAM) with Gaussian error distribution and identity link function to explore bivariate relationships between Goshawk preference for each avian prey species and prey characteristics. The response variable in the model was preference for prey species (Ivlev's index), and the predictor variables were prey body mass, prey abundance in Goshawk nesting territories, frequency of nestlings and fledglings in the Goshawk diet and the main habitat of prey species. All predictor variables having a statistically significant contribution in these bivariate comparisons ($P < 0.1$) were combined into a final GAM. We limited GAM smoothing (effective degrees of freedom) in order to avoid over-fitting, and we assessed model fit by visualizing standard diagnostic residual plots and with the 'k-index', both provided by the function 'gam.check'. All modelling was carried out using the 'mgcv' package in R (Wood 2011, R core team 2015).

Results

Current (2008–11) goshawk diet

We identified 2618 prey belonging to 34 species or taxonomic groups (Table 1). Most prey were birds, which accounted for 72% of prey species, 88% of prey by number and 82% of prey by biomass; followed by mammals, which accounted for 25% of species, 11.5% of prey by number and 18% of prey by biomass. Reptiles were rare in the diet, accounting for only 0.3% of prey by number; all observed reptiles were Ocellated Lizards *Timon lepidus*.

Among avian prey (Table 1), pigeons and doves were the most important group, accounting for 40% of prey by number (*N*) and 49% by biomass (*B*). At least 25% of Feral Pigeons detected in camera images were banded racing pigeons. Of the 44 rings recovered from prey remains, 48% came from local pigeon lofts, 27% from international (Portuguese) lofts and 25% from other national lofts. Other frequent avian prey groups were corvids (*N* 25%, *B* 16%), woodpeckers (*N* 14%, *B* 8.3%), and thrushes/starlings (*N* 8.1%, *B* 2.8%).

Prey species size ranged from <20 g (small passerines and micromammals) to >1 kg (adult European Rabbits and American Mink). The most frequent prey species

Table 2. Age of avian prey in Goshawk diet during 2008–2011, based on the growth stage of primary and secondary feathers in prey remains.

	N	% full-grown	% fledglings	% nestlings
Eurasian Jay	302	29.5	40.7	29.8
Eurasian Magpie	155	29.7	41.9	28.4
European Green Woodpecker	177	38.4	54.8	6.8
Great Spotted Woodpecker	90	44.4	47.8	7.8
European Turtle Dove	32	46.9	37.5	15.6
Common Wood Pigeon	99	49.5	29.3	21.2
Common Blackbird	133	60.2	28.6	11.3
Domestic chicken	13	61.5	23.1	15.4
Song Thrush, Mistle Thrush	16	62.5	25.0	12.5
European Nightjar	8	62.5	25.0	12.5
Eurasian Collared Dove	204	67.6	26.5	5.9
Carrion Crow	13	69.2	30.8	0.0
Eurasian Sparrowhawk	7	71.4	14.3	14.3
Small passerines	62	74.2	19.4	6.5
Spotless Starling	10	80.0	20.0	0.0
Psittacine sp.	13	84.6	7.7	7.7
Feral Pigeon	273	85.7	13.6	0.7
Yellow-legged Gull	36	100.0	0.0	0.0

in the diet were medium-sized (100−199 g; 47% of prey by number, 33% by biomass) or large-sized (200−400 g; 26% of prey by number, 35% by biomass). Just over half (55%) the avian prey in the Goshawk diet was full-grown individuals; 32% were fledglings and 13% were nestlings (Table 2). According to camera images, 26% of European Rabbits were young, 37% sub-adults and 37% adults.

Goshawk dietary changes between the periods 1980–84 and 2008–11

The diet of Goshawks in 1980–84 and 2008–11 showed similar proportions of birds (93.4% vs. 91.8%), mammals (5.9% vs. 8.2%) and reptiles (0.6% vs. 0%). Eurasian Collared Doves and Red Squirrels were common in the current diet but did not appear as prey in the 1980s (Figure 1). The current diet showed a lower proportion of Feral Pigeon and European Turtle Dove, and a higher proportion of Eurasian Jay and small passerines. Both periods showed a similar low overall proportion of birds of prey in the Goshawk diet (<1% of prey by number).

Our pigeon census indicated that the number of pigeon lofts decreased by 71% from 90 in 1983 to 26 in 2011–12, and that the number of Feral Pigeons decreased by 76% from 4206 in 1983 to 1027 in 2011–12. About 26% of pigeon lofts in 2011–12 hold racing Feral Pigeons, while the rest hold non-racing Feral Pigeons. The eight professional pigeon breeders interviewed reported a general decline in pigeon lofts and in Feral Pigeon numbers but also an increase in the proportion of racing pigeon lofts since the 1980s.

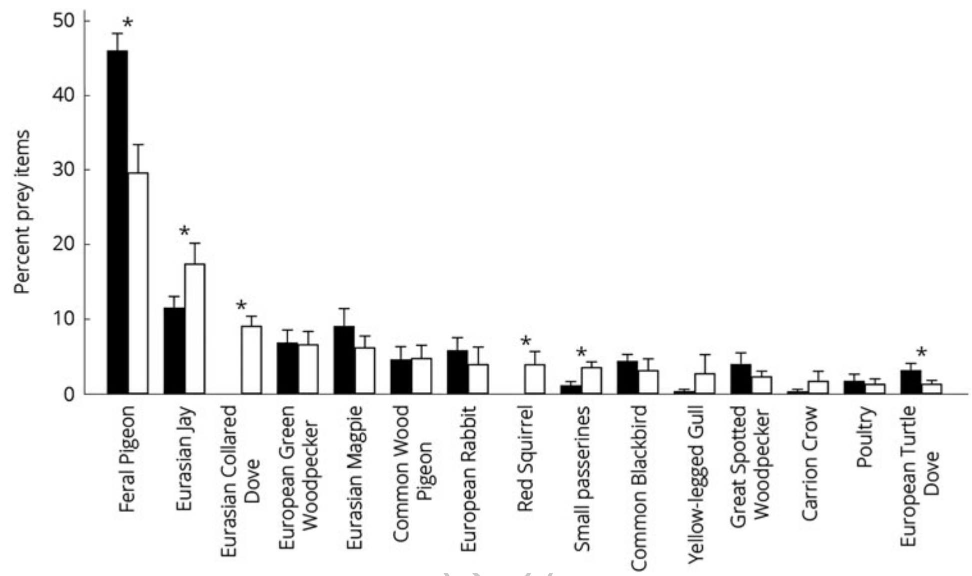

Figure 1. Percentage by number of different prey species in the diet of breeding Goshawks for the period 1980–84 (black bars) and for the period 2008–11 (white bars) estimated from prey remains from seven nesting territories studied in both periods. Only species with >1% abundance during either of the two periods are shown. The following species with <1% abundance in the current diet were not detected in prey remains from the 1980s: Song Thrush, Mistle Thrush, Spotless Starling, Eurasian Sparrowhawk, European Nightjar, Tawny Owl, Pssittacine sp. and micromammals. The following species at <1% abundance in the 1980s were not detected in the current diet: Common Cuckoo, Eurasian Scops Owl, Black-headed Gull *Chroicocephalus ridibundus*, Eurasian Hoopoe *Upupa epops*, and Ocellated lizard. * indicates significant differences ($P < 0.1$) based on the Wilcoxon matched pairs test.

Prey abundance and current Goshawk avian prey preferences

Absolute density of avian prey was estimated to be 3152 individuals (90% CI 2323–4074) within Goshawk territories (online Table S2). Goshawk nesting territories showed high abundance of Common Blackbird (30%), Yellow-legged Gull (13%), and Wood Pigeon (12%). Abundance of avian prey regarding prey size had the following proportions: <100 g (41%), 100–400 g (26%) and >400 g (33%).

The four most frequent avian prey species in the Goshawk diet were captured above their abundance (preferred species, Figure 2). Relative preference followed the order: European Green Woodpecker (Ivlev's index 0.7) > Feral Pigeon (0.6) > Eurasian Jay (0.6) > Eurasian Collared Dove (0.5). Four prey species were captured in proportion to their abundance (thrushes, Eurasian Magpie, Great Spotted Woodpecker and Wood Pigeon), and five species were caught below their abundance (Eurasian Turtle Dove, Common Blackbird, Carrion Crow, Spotless Starling and Yellow-legged Gull). Within the pigeons-and-doves prey group, Goshawks preferred species typical of open, more man-made habitats (Feral Pigeon, Eurasian Collared Dove) to species more likely to use forests (Wood Pigeon and Eurasian Turtle Dove). Goshawks preferred the larger Green Woodpecker (175 g) to the smaller Great Spotted Woodpecker (65 g). Within corvids, Goshawks rejected the largest species (Carrion Crow, 500 g) and, between the medium-sized corvids, preferred the forest species Eurasian Jay to the non-forest Eurasian Magpie. Within the thrushes-and-starlings prey group, Goshawks preferred species with more forest habits (Song and Mistle Thrushes) to species typical of open, man-made habitats (Common Blackbird and Spotless Starling).

GAM analyses showed a significant effect of prey body mass and prey habitat on Ivlev's index (Table 3), indicating that Goshawks preferred species with body masses between 100 and 400 g to species with more extreme weights (Figure 3), as well as forest prey species to non-forest species. In contrast, GAM analyses failed to show a general relationship between Ivlev's index and prey abundance or between Ivlev's index and the percentage of nestlings + fledglings among prey species in the diet (Table 3). Of the preferred prey, e.g. Eurasian Jay appeared with a high percentage of nestlings + fledglings, while Feral Pigeon appeared with a low percentage (Table 2).

Discussion

The Goshawks in the study area mainly preyed upon birds and behaved like generalist predators with marked prey preferences. Avian prey preferences were

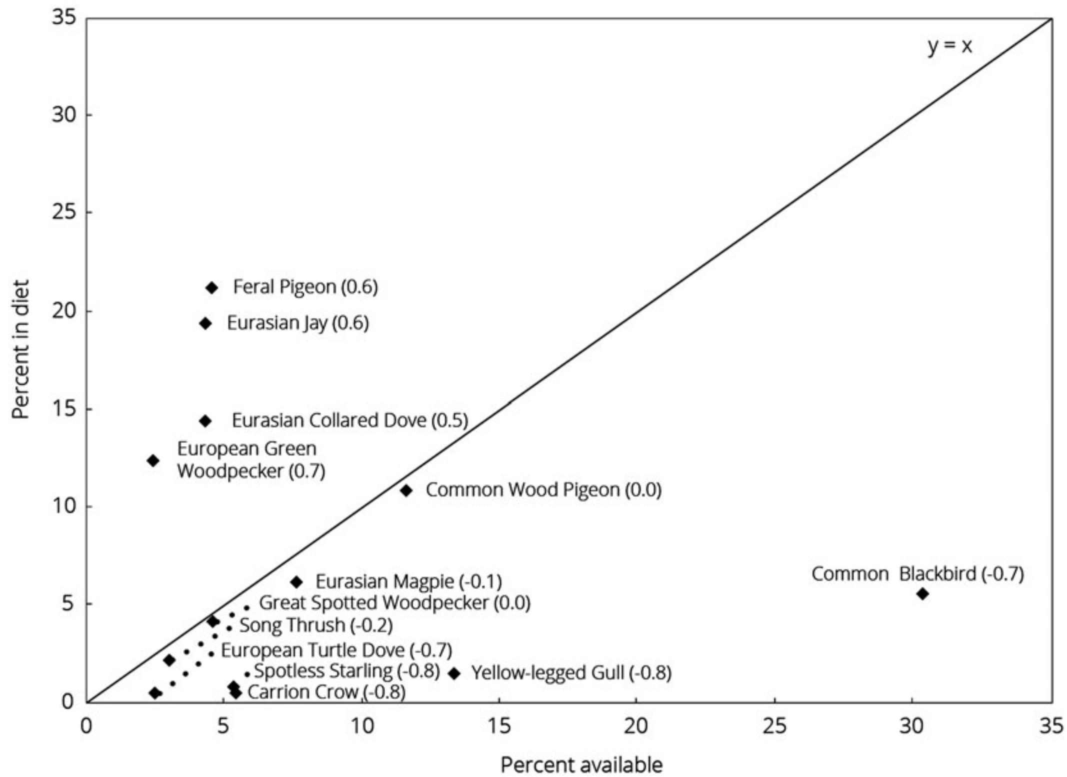

Figure 2. Percentage by number of different prey species in the Goshawk diet plotted against their relative abundance in the nesting territories. Ivlev′′s selectivity index is shown in brackets. Species above the diagonal line were hunted above their abundance, and so were preferred prey.

mainly determined by prey body mass and habitat. We found significant changes in the Goshawk diet between the periods 1980–84 and 2008–11. We suggest that they were due to changes in the abundance of preferred prey species (100–400 g) between both periods. These changes in the Goshawk diet would have been driven by factors such as changes in land use, colonization by new prey species, and changes in the abundance and management of domestic prey. Despite diet changes, Goshawk breeding density increased and its reproductive success remained unchanged.

Current (2008–11) Goshawk diet

The Goshawk is a versatile predator whose diet shows marked regional differences in Europe (Rutz *et al.* 2006). In our study area, the Goshawk was markedly ornithophagous, with birds accounting for 88% of prey by number. Feral Pigeon, Eurasian Jay, Eurasian Collared Dove, Green Woodpecker and Wood Pigeon were the most important prey, accounting for 64% of prey by number and 66% by biomass. Overall, diet composition was more similar to that of central European Goshawk populations than to that of other

Table 3. GAM analysis of the effects of prey body mass, prey abundance, proportion of inexperienced individuals (nestlings + fledglings) in the diet, and habitat of prey species on Goshawk prey preferences (Ivlev′′s selectivity index).

	Approx. significance of smooth terms			Significance of parametric terms			Parametric coefficients			
Bivariate models	df	*F*	*P*-value	df	*F*	*P*-value	Intercept	Forest prey	R^2(adj.)	GCV
Ivlev′′s index ~ s(prey body mass)	2.861	4.302	0.037				−0.122		0.46	0.27065
Ivlev′′s index ~ s(prey abundance)	6.028	1.331	0.371				−0.122		0.33	0.51256
Ivlev′′s index ~ s(inexperienced individuals in diet)	1	1.776	0.209				−0.122		0.06	0.39217
Ivlev′′s index ~ prey habitat[a]				1	4.149	**0.067**	−0.286	0.709	0.21	0.33073
Final model										
Ivlev′′s index ~ s(prey body mass) + prey habitat[a]	2.88	5.361	**0.024**	1	5.732	**0.043**	−0.260	0.596	0.64	0.20386

Note: Smoothed predictors are indicated with 's()'. Since the variable 'habitat' is a two-level factor, it was included in GAM models as a non-smoothed linear predictor. The adjusted version of R^2 used for this analysis adjusts for small sample size and model complexity. The generalized cross validation score (GCV) is an estimate of the mean square prediction error that can be used to choose among different models in a manner similar to Akaike's information criterion. Lower GCV scores indicate a better fit. Significant effects ($P < 0.1$) are shown in bold.
[a]The intercept of these models is the mean Ivlev′′s index estimated by the model for non-forest prey.

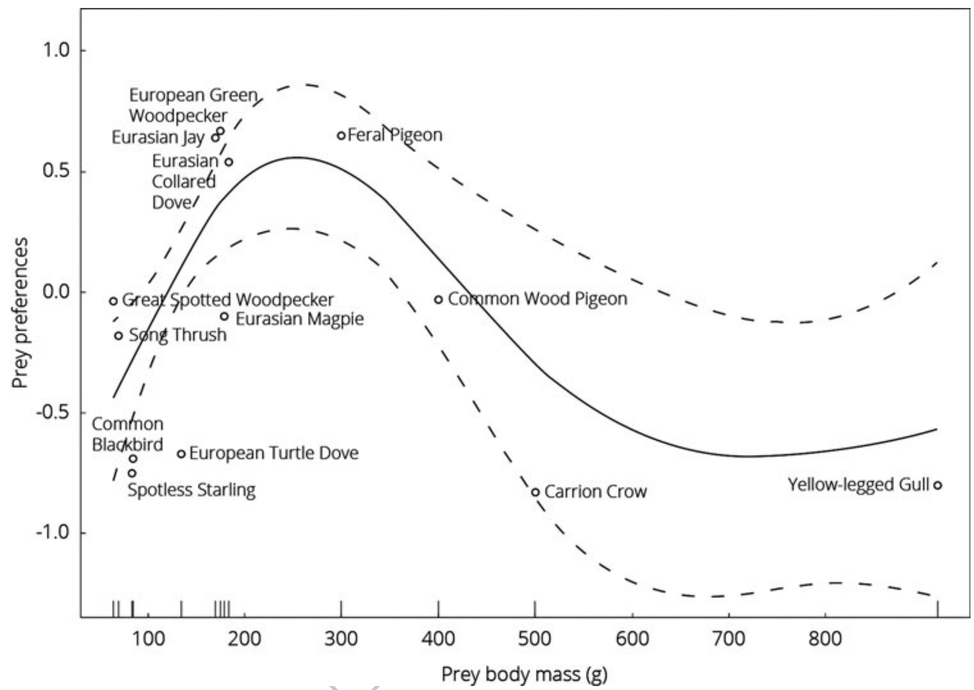

Figure 3. GAM plot for the final model showing the effect of prey species body mass on Ivlev's index (solid curve). The dashed curves show approximate 95% confidence intervals around the prediction. *Prey preferences* (*y*-axis) represents the effect of the smoothing function on the average value of the response variable (Ivlev's index) estimated by the model. The average value of the response is the intercept of the model.

Iberian populations of Mediterranean climate, where diet contains a higher proportion of European Rabbits and reptiles and a lower proportion (76%) of birds (Mañosa 1994). In our study area, characterized by a humid, oceanic climate and high forest cover, the abundance of European Rabbit is low (Tapia *et al.* 2010) and Red Squirrel, a typical forest species, was the main mammalian prey for the Goshawk.

In terms of prey biomass, the proportion of avian prey decreased slightly from 88% to 82% in favour of mammals, and the relative importance of Feral Pigeon increased from 17% to 25%, highlighting its status as the main prey. However, overall diet composition was similar regardless of whether relative prey abundance was calculated in terms of number or biomass, since the most frequent prey species, both birds and mammals weighed between 100 and 400 g.

Changes in Goshawk diet between the periods 1980–84 and 2008–11

The composition and dominance of prey species in the Goshawk diet in our study area has changed significantly over the past few decades. The contribution of Feral Pigeons has decreased, probably due to a decline in its abundance (by more than 70% in the study area since the 1980s) and its vulnerability has probably decreased since the relative increase in the proportion of racing Pigeons to the total number of Feral Pigeons.

Eurasian Collared Dove and Red Squirrel were new prey species in the current diet. These species were not present in the study area in the 1980s (personal observation) but have recently colonized the study area: Eurasian Collared Dove by spreading from Turkey throughout Europe during the twentieth century (Marti & Del Moral 2003, Eraud *et al.* 2007), and Red Squirrel from the nearby Cantabrian Mountains (Palomo & Gisbert 2002).

Other changes in the diet between 1980–84 and 2008–11 can also be interpreted in terms of changes of prey abundance. The decrease of Eurasian Turtle Doves in the Goshawk diet was probably due to a sharp decline in its abundance across western Europe (Boutin 2001) and specifically by 50–80% in northern Spain between 1980 and 2013 (SEO/BirdLife 2013). Conversely, the proportion of forest species such as Eurasian Jay increased in the Goshawk diet in our study area, likely reflecting their habitat and population increase in northern Spain due to declining livestock farming and agriculture, as well as increasing afforestation (SEO/BirdLife 2013).

Current (2008–11) Goshawk avian prey preferences and hunting strategy

The Goshawk is often considered to be a generalist and opportunistic predator, hunting a broad range of prey types and sizes (see also Tornberg 1997, Kenward 2006, Rutz *et al.* 2006 for other areas). However, based on distinctive avian prey preferences, the Goshawks in this population did not seem to behave as true opportunists (*sensu* Jacksic 1989). They did not hunt each bird species according to their relative abundances within the prey size range taken in Europe (51–500 g, Rutz & Bijlsma 2006). Instead, the Goshawk strongly preferred certain species as prey.

Goshawk food preferences were best explained by prey size which accounted for up to 46% of the variability in Ivlev's index. Bird species weighing between 100 and 400 g made up 75% of the Goshawk diet but represented only 36% of prey abundance in the field. Optimal diet theory predicts that breeding raptors should prefer the most profitable prey, that is, prey that provides more energy per unit time (Sih & Christensen 2001), taking into account the costs to locate, capture, handle and carry the prey to the nest.

As potential prey species of all sizes were generally abundant, there was unlikely to be any significant difference in locating preferred versus non-preferred prey. We suggest that male Goshawks, which take on the bulk of the nestling provisioning during the breeding season (Newton 1979), provide fewer small birds (<100 g) because they incur relatively higher capture and transportation costs in comparison to larger prey species (Andersson & Norberg 1981, Korpimäki *et al.* 1994). Another explanation is that male Goshawks may have consumed small prey at the capture site (Sonerud 1992, Rutz 2003). The avoidance of very large avian prey, such as crows and gulls weighing over 400 g, may also be associated with higher costs of capture; large, social and aggressive prey could be difficult to hunt for small southern Goshawks weighing on average only 670 g (Pérez-Camacho *et al.* 2015). Moreover, gulls and crows exhibit mobbing behaviour and adopt a group defence strategy against raptors, which probably protects nestlings and fledglings against Goshawk attacks, possibly explaining why they rarely appeared in the diet.

The short wings and long tail of the Goshawk make it an extremely manoeuvrable hunter that is well adapted to hunting within forest habitats. Nestlings and fledglings of forest birds found immediately near the Goshawk's nest are profitable prey. Feral Pigeons, as open habitat dwellers, however, formed an exception. Preference for them is likely due to their optimal size and concentrations near pigeon lofts, villages and buildings, often near forest edges where Goshawks can make ambush attacks. Diet preference analyses were limited to avian prey so inferences apply only to birds. Including mammals in the analyses might have changed some of the inferences, but since avian prey provides the main component of the Goshawk diet, we expect that our general conclusions would remain much the same. The fact that the main mammal in the Goshawk diet was the Red Squirrel, a typical forest species between 100 and 400 g, supports this statement.

Relationship between prey preferences and changes in Goshawk diet between the periods 1980–84 and 2008–11

Our findings suggest that Goshawks showed a different functional response to preferred prey species (100–400 g) and non-preferred species (<100 or >400 g). Goshawks responded to abundance changes of preferred prey (Feral Pigeon, Eurasian Collared Dove, Eurasian Turtle Dove, Eurasian Jay and Red Squirrel) accordingly, while it did not significantly alter its predation behaviour for less preferred species (<100 g, e.g. thrushes, Blackbird and European Starling; and >400 g, e.g. Common Woodpigeon and gulls) despite their increasing abundance (Marti & Del Moral 2003, SEO/BirdLife 2013). These results are consistent with prey selection models, which predict that generalist predators do not react to changes in the abundance of non-preferred prey species if the density of preferred profitable prey remains sufficient (Sih & Christensen 2001). In our study, Goshawks compensated for declining abundance and vulnerability of its main prey (Feral Pigeon) by increasing its predation on alternative preferred species such as Eurasian Jay, Eurasian Collared Dove and Red Squirrel. Note that prey-level estimates of diet composition are sensitive to changes in overall diet. For example, as one species becomes proportionately less important, others will inevitably increase in relative importance (values always add up to 100%), which points to the need to interpret our results with caution.

One could expect that the long-term changes detected in the diet and the decline in abundance and availability of the main prey (Feral Pigeon) might impact on Goshawk population status in terms of lowered breeding density and reproductive success. Conversely, we observed that from 1980–84 to 2008–11 the number of Goshawk nesting territories in the western subzone of the study area almost doubled (from 14 to 26 nesting territories) and that the number of nestlings per nest at the time of ringing (chicks of 20–30 days old) was exactly the same in both periods (2.42 nestlings; $n = 24$ for the period 1980–84, and $n = 40$ for the period 2008–11). The increase in breeding density may suggest that the total availability of prey increased from the 1980s to the present, to the extent that the decline in abundance and availability of the main prey, Feral Pigeon, might have been overcompensated with the increase in abundance of other preferred prey species, such as Eurasian Jay, Eurasian Collared Dove and Red Squirrel. The fact that the Goshawk has successfully incorporated these new preferred prey species in the diet would emphasize the high adaptability of Goshawks to changes in prey species abundance. Nevertheless, other factors could also have contributed to the increase in Goshawk breeding density, such as the increase in forest area since 1950s (as a result of declining livestock and farming activities and increasing afforestation) or the decline in illegal plundering of raptor nests (pers. obs.).

The adaptability of the Goshawk to changes in prey species abundance without declining breeding parameters is consistent with the hunting behaviour of a generalist predator and makes studies of Goshawk diet potentially informative as ecological indicators of changes in the food webs of European agroforest systems. These changes have presumably been driven by factors occurring at different spatial and temporal scales in our study area: (a) changes in land use that increased forest cover; (b) colonization by new prey species, both native and exotic and (c) changes in the abundance and management of domestic pigeons. Our diet analysis suggests that the major transformations occurring in such ecosystems are affecting the preferred prey of important forest predators, which may have consequences for conservation. For example, we observed increasing pressure of Goshawk predation on racing pigeons, which is a lucrative activity within our study region. Nowadays, banded racing pigeons represent 4.3% of Goshawk prey by number in the breeding season. Fifty-two per cent of the racing pigeons came from non-local pigeon lofts, mainly Portuguese lofts. The study area lies along the return route of thousands of racing pigeons that annually participate in international competitions (Petronilho & Vingada 2002). Although only about half of racing pigeons actually come from local pigeon lofts, pigeon breeders tend to overestimate the effect of the Goshawk on their pigeon losses. This generates conflict between the top predator and local racing pigeon breeders. In the last few years, we have detected illegal killing of Goshawks in the study area and this has coincided with a decrease in the number of Goshawk breeding pairs (Martínez-Hesterkamp *et al.* 2015).

Acknowledgements

We are indebted to E. de la Montaña, M. Rebollo, P. Rebollo, J. Meltzer, M. Zurita and S. Morcelle for extensive assistance with field and laboratory work, and C. Sobreira for assistance with prey identification in photographs. D. Álvarez and J.A. Cuevas provided body masses of prey species. O. Martín edited the figures, and A. Chapin Rodríguez revised the English and provided valuable comments on the manuscript. We acknowledge the Dirección Xeral de Conservación da Natureza of the Xunta de Galicia for granting permission to carry out the study.

Funding

This work was supported by funds from CICYT projects of the Spanish Ministerio de Educación y Ciencia [CGL2007–60533/BOS, CGL2010–18312/BOS] and Ministerio de Economía y Competividad [CGL2014–53308–P], the REMEDINAL network [S–0505/AMB/0335, S2009 AMB–1783 and S2013/MAE–2719] and University of Alcalá project [CCG2014/BIO–002]. GGS and SMH were supported, respectively, by an FPU fellowship [AP2006–00891] and an FPI fellowship [BES–2008–006630] from the Ministerio de Educación y Ciencia.

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