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Research article

Anything for a quiet life: shelter from mobbers drives reproductive success in a top-level avian predator

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Understanding how habitat structure relates to reproductive performance of species can help identify what habitats are of the highest quality for a given species and thereby guide effective management. Here, we compared the influence of prey abundance and the amount of shelter area on the relationship between habitat and breeding performance. We focused on the forest-dwelling northern goshawk *Accipiter gentilis* in an agroforestry system. Using structural equation modelling, we tested the associations between reproductive performance and three explanatory factors: habitat structure, abundance of food resources or levels of mobbing disturbance, and prey supply to the nest. Our results suggest that habitat structure influences reproductive performance through shelter rather than through prey abundance. During the study period, forested habitats in the breeding territories provided shelter to the goshawk, reducing disturbance by carrion crows *Corvus corone*, which acted as large, aggressive, social mobbers. Decreased disturbance increased prey supply to the nest, probably because it favored food accessibility and male goshawk foraging efficiency. Habitat was not significantly associated with quality of the breeders, both in terms of body size and seniority in the territories. Our findings suggest that reproductive performance, and therefore habitat quality, may depend more on sheltered access to food resources than on the amount of food available. Our observation that mobbers decrease predator foraging efficiency highlights the possibility of designing effective, socially acceptable predator management strategies to protect sensitive domestic prey.

Keywords: *Accipiter gentilis*, biotic disturbances, breeding success, corvids, feeding ecology, hunting efficiency, prey accessibility, territory quality

Introduction

Understanding how habitat structure relates to reproductive performance of bird species can aid efforts to conserve, manage and restore species and habitats (Morrison et al. 2006, Gaillard et al. 2010). Managers could promote certain habitat characteristics to benefit species of concern. Before this is possible, much more needs to be learned about how habitat features influence species' performance.

Quality of breeding habitats relates to the abundance, quality and accessibility of food (Sergio and Newton 2003, Tapia and Zuberogoitia 2018). When considering food abundance, not all types of food should be considered equal: special weight should be assigned to a species 'preferred food', defined as food that maximizes energy intake (Sih and Christensen 2001). To be of good quality, a habitat should also offer shelter, especially during the breeding season (Zuberogoitia et al. 2019). The nest and surroundings should allow adults, eggs, nestlings and fledglings to remain concealed and protected (Orians and Wittenberger 1991). Protection from attackers allows adults devoting more time to tasks such as searching for food, cleaning the nest or grooming the nestlings (Tilgar et al. 2010, Tapia and Zuberogoitia 2018). Although the importance of food and shelter in the reproductive performance of species has already been recognized and demonstrated, the specific mechanisms that link these habitat resources with species' performance are still not fully understood. For example, the role of indirect antagonistic biotic interactions (e.g. mobbing) in habitat-driven reproductive performance of avian predators has received little attention.

The amount of food that can be delivered to a nest is an important determinant of the number of offspring that birds will raise (Ruffino et al. 2014). Researchers have generally focused on studying how the variation in the abundance of food in the environment affects nesting success (Tjemberg 1983, McKinnon et al. 2012). However, the amount of food delivered to a nest also depends on the ability of adults to acquire this food and transport it to their nests. The constraints on food acquisition and transportation will vary among bird species (e.g. handling time, travel distance, etc.) and environmental conditions such as weather (Dawson and Bortolotti 2000). Raptors may also face a limitation that is rarely experienced by other groups of birds: mobbing by other species that reduces the raptors' abilities to forage (Pettifor 1990). We do not know yet whether this interference can affect both the amount of food that is delivered to the nest and the number of offspring that raptor species can produce.

The present study analysed the relationship between habitat structure and reproductive performance of an avian predator in southern Europe. The overall objective was to determine the environmental variables (i.e. patch-specific vegetation structure, prey abundance and level of mobbing interference) that influence habitat quality for breeding northern goshawks *Accipiter gentilis* as measured by the hawk's nesting success and nesting phenology. We assessed the influence of habitat-determined prey abundance and amount of shelter area on reproductive performance while exploring the role of mobbers in the habitat–performance relationship. As a model for apex avian predator, we studied northern goshawks (hereafter goshawks). Goshawks are distributed extensively throughout the Holarctic region breeding in agroforestry systems and hunting prey in woodland and farmland patches and ecotones (Kenward 2006, Rebollo et al. 2017a). This raptor, like other forest-dwelling diurnal raptors, have been used as ecological indicators of changes that affect species' habitat quality in agroforestry systems (Burgas et al. 2016, García-Salgado et al. 2018, Reynolds et al. 2019). Several species of corvids, such as the carrion crow *Corone corone corone* (hereafter crow), regularly mob adult goshawks and other medium-sized raptors in the agroforestry systems of northern Spain. While crows are a frequent prey of goshawks in northern Europe (Hoy et al. 2017), they make up for less than 1% of the goshawk diet in our study area, both according to the number of prey items or their biomass (Rebollo et al. 2017a). In northern Spain cooperative breeding is frequent in crow populations and group members typically move and cooperate to attack avian predators (Baglione et al. 2002a, Canestrari et al. 2008), which could explain the low frequency of crows in the diet of the goshawk in our study area. Thus, the goshawk in northern Spain is a species suitable for testing whether mobbing might play a substantial role in determining the amount of food delivered to nests and the number of offspring that a pair can raise. We used two indicators of breeding performance (breeding success and breeding phenology) as proxies for breeding habitat quality. In this approach, greater fledgling production and earlier laying dates would be indicative of greater reproductive performance and thus, of good-quality habitats (Johnson 2007).

First, we tested the food resource hypothesis (Fig. 1a). We hypothesised that higher proportion of prey-rich habitats would feature higher prey abundance within the breeding territory, facilitating higher prey supply to the nest (i.e. prey delivery) and leading to higher reproductive performance (Newton 1998, Kenward 2006, Tapia and Zuberogoitia 2018, Reynolds et al. 2019). Second, we tested the shelter hypothesis (Fig. 1b). We hypothesised that higher proportion of forest habitats (shelter) within the breeding territory would reduce levels of mobbing disturbance by corvids therein, increasing prey supply to the nest, and ultimately enhancing reproductive performance (Kim and Monaghan 2005, Zuberogoitia et al. 2019). We also expected a direct effect of mobbing disturbance on reproductive performance, independently of prey supply: less mobbing disturbance should leave adults with more time to distribute food among the nestlings or to groom the nest (grey right path in Fig. 1b).

Reproductive performance of species in a given habitat depends not only on the food and shelter that it offers, but also on the quality of breeders (Balbontin and Ferrer 2008). Individual quality can depend on animal size or seniority (years breeding in the same territory) (Rutz et al. 2006, Pérez-Camacho et al. 2015, Reynolds et al. 2019). The association between seniority and individual quality of predators may be reflected in a correlation between seniority, and greater
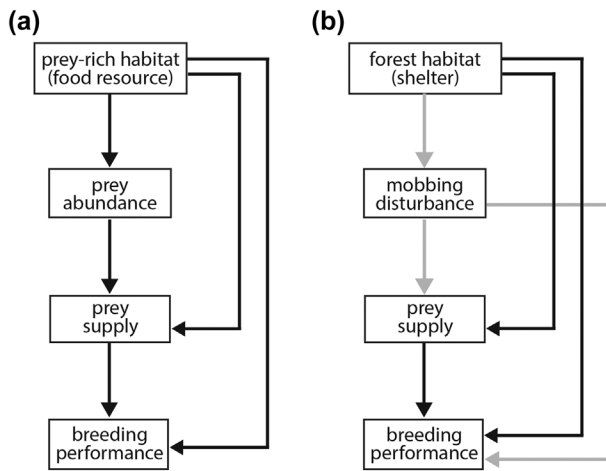
Figure 1. Two path diagrams representing factors potentially affecting the reproductive performance of raptors during the breeding season. (a) In the food resource hypothesis, reproductive performance depends mainly on the abundance of prey (total or preferred) in the breeding habitat. (b) In the shelter hypothesis, the reproductive performance depends mainly on the area of shelter, which reduces disturbance in the breeding habitat. Arrows show causal effects of one factor on another. Paths correspond to hypotheses, and directions of the effects are explained in the main text and path coefficients in Table 1. Black arrows represent positive effects and grey arrows negative effects.

experience and foraging efficiency in the predator's hunting territory. The reproductive performance is well known to vary directly with the quality of the adult individuals (Sasvári et al. 2000), but whether the quality of individual also varies directly with habitat quality is unclear (Germain and Arcese 2014). When evaluating both hypotheses, we expected that, if high quality breeders distributed preferably in good-quality habitats, then these habitats should lead to higher prey supply and higher reproductive performance than poor-quality habitats (two right black paths in Fig. 1a and b). We also expected under both hypotheses that good-quality habitats should be occupied more consistently over the years (higher territory occupancy) than poor-quality ones (Sergio and Newton 2003, Johnson 2007, Germain and Arcese 2014).

Once we knew the results of the two hypotheses (food resource and shelter hypotheses) we proposed to test a derived synthetic model that combined the parameters and links identified as key in the two hypotheses. Our analyses led us to identify the factors more important for determining habitat quality for these breeding predators, which may help guide interventions to reduce predation pressure on some domestic prey.

Material and methods

Study area and species

The study area is a 400-km² coastal area in northwestern Spain (Galicia region, 42°20′N, 8°47′E), which is comprised of a western and an eastern subzone of similar size (Supporting information). The climate is wet temperate oceanic (Cfb Köppen type) with annual average precipitation of 1402 mm and temperature of 14.2°C (Rodríguez-Lado et al. 2018). The landscape is mountainous, with an average altitude of 213 m a.s.l. (range 0–646 m a.s.l.). The human population density is high (480 inhabitants km⁻²). The habitat is heterogeneous at the landscape scale, arranged in a mosaic of woodland and farmland patches. More than half the study area (50.9%) is woodland, covered by either non-native pure eucalyptus plantations *Eucalyptus globulus* or mixed forest of eucalyptus with English oaks *Quercus robur* and maritime pines *Pinus pinaster*, which occupy mostly the upper halves of the hills. Valley bottoms and lowlands are farmland comprised of crops and scattered houses (35.5%) and urban areas and coastal habitats (13.6%). In our study area, goshawks nest close to the forest edges, at an average distance of 176.6 m away from them (García-Salgado et al. 2018).

Availability of suitable nest-trees and nest-sites is not a limiting factor because the study area features tall, mature, evenly distributed eucalyptus trees, the main nesting tree of goshawks in this region (García-Salgado et al. 2018).

Goshawks prey upon a wide variety of medium-sized birds and mammals. In the study area, 88% of prey by number and 82% of prey by biomass were birds that thrive in woodland, farmland and ecotones (Rebollo et al. 2017a). The main prey (domestic pigeon *Columba livia f. domestica*) and the 36.6% of prey by number and 44.2% of prey by biomass in our study systems are exclusively of non-forested environments, including Eurasian collared dove *Streptopelia decaocto*, Eurasian magpie *Pica pica*, yellow-legged gull *Larus michahellis*, domestic chicken *Gallus gallus domesticus* and spotless starling *Sturnus unicolor* (see Table 1 in Rebollo et al. 2017a). We assume that goshawks hunt more than half of their prey in farmland areas and woodland-farmland ecotones in our study area. The goshawk breeding population in the study area shows one of the highest densities and fecundities in the literature, with an annual average of 10.0 egg-laying pairs per 100 km² and a mean productivity of 2.3 fledged young per laying pair (García-Salgado et al. 2018). This high density means that even poor-quality habitats should be occupied in some years, since higher raptor density usually correlates with greater occupancy of poor-quality sites (Balbontin and Ferrer 2008). Goshawks are the dominant species of the diurnal and nocturnal raptor guild in the study area (Rebollo et al. 2017b). The guild of diurnal forest raptors in the study area is mainly composed of the goshawk, the common buzzard *Buteo buteo* and the Eurasian sparrowhawk *Accipiter nisus* (Rebollo et al. 2011, 2017, Pérez-Camacho et al. 2015). Other diurnal forest raptors, such as the European honey buzzard *Pernis apivorus* and the Eurasian hobby *Falco subbuteo*, are rare in this area. The nocturnal forest raptor guild is composed mainly of the tawny owl *Strix aluco* and the barn owl *Tyto alba*. Big eagles and the eagle owl *Bubo bubo*, predators of the aforementioned diurnal and nocturnal raptors, are not present in the study area.

Data collection

Spatial distribution of active goshawk nests and historic territories

Forest patches were systematically surveyed on foot for goshawk nests in order to locate active nests every year for the period 2008–2011 (see details in García-Salgado et al. 2018 and Martínez-Hesterkamp et al. 2018). These surveys are part of a long-term ecological research program focused on the diurnal raptor community since 2004 and continuing to the present (2022). We considered active nests to be those where incubation was observed (Reich et al. 2004). Historic goshawk territories contained several nests used alternately over the years. Based on the active nests, we estimated territory occupancy in 30 historic territories over the 2008–2011 period as the percentage of years the territory had active nests.

Breeding territories

In the set of 30 historic territories, we studied 58 different active nests. In the western subzone we studied 21 historic territories containing 44 different active goshawk nests and in the eastern subzone we studied 9 historic territories containing 14 different active goshawk nests (Supporting information). A breeding territory was defined as the area around the active nest defended by the breeding pair against other goshawks and showing relatively little overlap with neighbouring territories (Squires and Reynolds 1997, but see Blakey et al. 2020 for home range overlap). Breeding territories were considered to be circular with a radius of 1100 m around the nest tree, and we assumed that this area included the main hunting grounds of goshawk pairs during the breeding season (as done in our previously published work, García-Salgado et al. 2018). That radius corresponds to approximately half the average distance between neighbouring active nests in the study area (2234 ± 162 m; García-Salgado et al. 2018).

Next, we describe the methods to studying the 58 breeding territories (one breeding territory for each different active nest) following the hierarchical 4-level effects tested in each model: habitat structure, habitat-derived characteristics (prey abundance or mobbing disturbance), prey supply and breeding performance.

Habitat structure in the breeding territories

We used a GIS land cover layer that contained 11 land cover types (Table 1) based on historic orthophotos taken in 2008, which was produced by the Plan Nacional de Ortografia Aerea (https://centrodedescargas.cnig.es/CentroDescargas/; pixel size = 25 cm). The layers used were PNOA_ANUAL_2008_OF_ETRS89_HU29_h50_0184.ecw, _0185.ecw, _0186. ecw, _0222.ecw, _0223.ecw and _0224.ecw. Land cover

Table 1. Land cover types described in the study area and number of sampling transects and prey densities.

Land cover type	%	Description	Mean number of sampling transects per year	Total avian prey per km^2	Preferred avian prey per km^2
Forest classes					
Old mixed eucalyptus stands	10.7	Mixed eucalyptus plantations with large eucalyptus and high cover of oak and pine	21	111.8	65.8
Mixed eucalyptus stands	12.2	Mixed eucalyptus plantations with large eucalyptus and medium cover of oak and pine	21	79.9	52.1
Monospecific eucalyptus stands and burned eucalyptus stands	8.3	Monospecific and contemporary eucalyptus plantations. Mixed or monospecific eucalyptus stands, partially burned with large eucalyptus and variable cover of oak and pine	10	66.7	40.9
Native deciduous forest	3.3	Deciduous riparian forest of alder, willow and oak and forests dominated by oak, chestnut or cork oak	4	191.4	98.3
Other forests	2.8	Pine forests or plantations and Australian blackwood *Acacia melanoxylon* plantations	2	126.5	81.6
Non-forest classes (open uses)					
Shrublands and forests with scattered trees	19.9	Gorse and heath shrublands and coastal dune areas. Young tree plantation mainly of eucalyptus. Recently harvested patches without trees or with eucalyptus regrowth. Forest or plantations (mainly eucalyptus) with scattered trees.	11	203.0	85.0
Fields and meadows	12.8	Farmland. Open lands, mainly cornfields, orchards, vineyards and pasturelands	33	330.4	155.5
Fields with scattered buildings	22.7	Farmland. Open lands with scattered isolated buildings or small villages	22.5	441.1	246.8
Beaches and coastal rocky areas	0.9	Beaches, coastal cliffs and rocky areas	8	661.3	95.0
Urban areas	4.2	Towns or cities and large infrastructures (ports, industrial estates)	14.5	556.4	272.9
Other open uses	2.2	Marsh (low freshwater wetlands) and large roads (motorways, highways, expressways and their embankments)	1	193.9	101.6

types were digitised using a geographic information system (Arc-GIS 10, ESRI 2010). To verify the classification of land cover types, we surveyed all UTM (Universal Transverse Mercator) 1×1 km^2 grids in April–May 2011, covering 200 grid cells and spending an average of 36 min per grid cell checking and validating the land cover types and their spatial limits (Martínez-Hesterkamp et al. 2018). At a detailed spatial scale, farmland areas contain multiple small forest patches or are close to woodland-farmland ecotones. Goshawks can use many types of forest structures as perches, including the aforementioned small forest patches and woodland-farmland ecotones. We assumed negligible variation in land cover types during 2008–2011, the period over which we recorded most of the variables used in this work.

For evaluation of the food resource hypothesis, we estimated the area of prey-rich habitats (i.e. those with high prey density) as a surrogate of the habitat structure of the breeding territory, based on the three habitats showing, by far, the highest prey densities in the breeding territories: farmland, urban and coastal land (Table 1 and 'prey abundance' section below). These three non-forested habitats provided a mean of 225.1 prey per km^2 while the remaining habitats provided a mean of 77.5 prey per km^2 (Table 1). For evaluation of the shelter hypothesis, we estimated the total area covered by forests of all types as a surrogate of the habitat structure of the breeding territory because this habitat encompassed all the nests and provided complex vertical structures (~39.6 m high *Eucalyptus* trees), which have shown to act as shelter for this species (García-Salgado et al. 2018).

Prey abundance in the breeding territories

We estimated the abundance of avian prey in the breeding territories using two methods. Censuses for both methods were conducted between 15 May and 15 September (the period when we estimated prey supply in the goshawk nests with video cameras, below) during the first 4 h after sunrise or the last 3 h before sunset on days that were not windy or rainy, in order to ensure high bird detectability.

The first method (census by line transects) was indirect. We estimated the avian prey density (number of prey km^{-2}) in the different habitat types of the study area (Table 1). During the breeding seasons of 2013 and 2014, we estimated the abundance of avian goshawk prey by counting all diurnal birds larger than a house sparrow *Passer domesticus*. Every year, we surveyed 148 line transects that were 300 m long that were located both inside and outside goshawk breeding territories. We recorded all bird contacts within and beyond a distance of 30 m in forest habitats, and 50 m in open habitats in order to estimate the effective strip width when estimating bird densities. The effective strip width limits the area being surveyed only to that in which prey species had higher likelihoods of being detected. Details about this distance sampling method and the estimation of the absolute densities of avian species in each habitat type have been described in Carrascal et al. (2010) and Rebollo et al. (2017a). We averaged the densities by habitat type in 2013 and 2014 in order to obtain the mean prey density by habitat type (Table 1).

Absolute abundance of prey in each goshawk breeding territory was estimated as the sum of the products obtained by multiplying the average density of each prey species in each habitat by the area covered by that habitat in the orthophotos of 2008. We assume small changes in prey density in each habitat type in 2008 relative to the 2013–2014 period in our study area.

The second method (census by count stations) was direct. We estimated the avian prey abundance in 29 breeding territories in 2011 from 12-point count stations within each territory, with stations located in the four orientations and at 200, 400 and 600 m away from the nest. We sampled 29 breeding territories out of 58 for logistical reasons. We estimated an index of the density of avian prey-species in the breeding territories by counting all individuals detected in a circle of radius 50 m extending from each of the 12-point count stations.

From the two sampling methods (indirect by line transects and direct by count stations), we estimated two parameters of prey abundance per breeding territory: number of total avian prey and number of preferred avian prey. To assess goshawk prey preferences, we used Ivlev's selectivity index to relate the proportion of prey delivered to nests to the proportion of the same prey available to the environment (Rebollo et al. 2017a). The index ranges from −1 to +1. Positive values indicate that goshawks prey upon a species above its availability. We considered preferred prey to be prey species with an Ivlef selectivity index above zero (Rebollo et al. 2017a). We found that the abundances of avian prey obtained using the two methods (indirect by line transects and direct by count stations) correlated positively and significantly with each other in the 29 breeding territories ($r = 0.62$, $p < 0.05$ for total avian prey abundance; $r = 0.49$, $p < 0.05$ for preferred avian prey abundance). Therefore, in subsequent analyses, we used mean avian prey densities of the habitats (from the line transects) to estimate prey abundance in the 58 breeding territories according to the cover of each habitat in the territories.

Because habitat changed little between 2008–2011 and 2013–2014, we assumed that prey abundance variation between these two time periods would be negligible. As total avian prey abundance strongly correlated with preferred avian prey abundance in the breeding territories ($r = 0.99$, $p < 0.0001$), we used total avian prey abundance in subsequent analyses.

We note that since birds are the main component of the nestling diet by number of prey and biomass, we do not expect any relevant consequence derived from excluding mammals in the results and discussion.

Levels of mobbing disturbance by corvids in the breeding territories

The main disturbance to adult goshawks in the breeding territories is the crow that regularly mobs adult goshawks in the study area (pers. obs.). This large, territorially resident corvid is abundant in the study area. We estimated a density of 3.46–4.09 crows per km^2 in the western subzone in 2010 (unpubl.). This density increases to 9.89–11.69 crows

per km² if we consider only the area where crows nest. The crow builds its nest in the canopy of tall *Eucalyptus* trees in small forest patches on farmland areas and on the forest edge between farmland and woodland. During 2008–2011, we surveyed active crow nests following a similar method as for the survey of active goshawk nests, but only in the western subzone (Supporting information), where 44 of the total 58 active goshawk nests were located (a total of 21 historic territories). We visually detected mobbing disturbances by crows in the goshawk territories and registered active crow nests in 64.5% of them. We used the number of active crow nests in each goshawk breeding territory, defined as crow nests falling inside a circle of radius 1100 m from the center of the breeding territory, as a surrogate of levels of mobbing disturbance. We imputed the number of crow nests in the territories of the remaining 14 active goshawk nests (9 historic territories) based on the linear relationship existing between number of crow nests and the cover of fields, urban areas and beaches and coastal rocky areas ($r = 0.72$, p-value < 0.0001) (Table 1).

Prey supply in the active nests

We installed one digital trail-camera at each of the 58 nests to monitor the frequency and type of prey supplied to the nests by adult goshawks during 2008–2011 (García-Salgado et al. 2015, Rebollo et al. 2017a). Trail-cameras were installed once nestlings were able to thermoregulate and feed by themselves (16 days of age and older). The mean nestling age was 23.7 ± 3.4 SD days. The median time during which these cameras recorded prey deliveries to the nest was 14.2 days, ranging 8–26 days (García-Salgado et al. 2015). We multiplied the number of prey species by the mean mass of each species from Rebollo et al. (2017a) to estimate the mean mass of prey delivered daily to a nest.

Reproductive performance in the active nests

As indices of reproductive performance, for 2008–2011 we recorded the number of nestlings at the time of camera installation (hereafter 'breeding success') and laying date (a phenological measure). We did not account for nestling mortality after camera installation because not all cameras were in operation until the nestlings left the nest. The number of nestlings at the time of camera installation was considered as an indicator of breeding success, since nestling mortality is usually highest around hatching (Byholm 2005). As we indicated above, cameras were only installed in nests with live 16-day-old nestlings or older. We did not include in the study those active nests that failed with chicks younger than 16 days or that failed with eggs because we did not have data on prey supply to the nest, a key parameter in this study. We estimated breeding phenology at the time of trail-camera installation from the age of nestlings based on the lengths of seventh primary feathers (Mañosa 1994). Laying dates were estimated by subtracting the incubation time of a single egg (38 days) from the hatching date of the oldest nestling in each nest (Kenward 2006). Laying phenology was estimated in Julian days, with 1 January defined as day 1. The average

laying date was 11 April, ranging between 17 March and 19 May (Rebollo et al. 2017b).

Identification and features of adult goshawks in the breeding territories

We trapped 39 breeding individuals (19 males and 20 females). Trapped goshawks were measured, weighted and ringed with field-readable rings, allowing us to estimate individual size and mark individuals for future identification. We analysed the plumage of trapped individuals to identify one- and two-year-old breeding individuals based on the amount of juvenile feathers. By studying the photographs taken by the cameras installed in the nests, we also analysed the plumage of non-ringed breeders to detect juvenile feathers and any other characteristics that could identify the individuals. We identified ringed breeders in subsequent years either by recapturing those (11 identifications) or using data from the cameras placed in the nests (40 identifications). In the end, 90 identifications were made throughout the four years of the study (2008–2011) through captures, recaptures and the photographs taken with the cameras installed in the nests, allowing us to estimate male and female seniority in a fraction of the individuals. We did not use unbanded goshawks to estimate seniority except for five individuals with juvenile plumage indicating low seniority in the breeding territory. Seniority is a feature of the breeders and indicates the number of years that adults were nesting in the same historic territory during 2008–2011. We estimated seniority separately for males and females. We classified adults into five categories of seniority: 1: one year, 2: two years, 3: three years, 4: four years and 5: more than four years. We also considered the following intermediate categories: 1.5: minimum one and maximum two years, 2.5: minimum two and maximum three years, 3.5: minimum three and maximum four years. When the same nest was used in more than one year, we averaged the seniorities of the birds occupying that nest across all years.

We defined adult body size separately for males and females as the first axis of a principal component analysis (PC1, hereafter 'adult size') involving the following variables: wingspan, defined as the distance between the wing tips after the bird was laid on its back and the wings extended to form a straight line; head-to-bill length, measured from the base of the skull to the tip of the bill; and tarsus length (Pérez-Camacho et al. 2015). PC1 explained 63% of the size variation in males and 46% of that in females, and had high positive loadings for wingspan (males, $r = 0.77$; females, $r = 0.48$), head-to-bill length (0.83, 0.72) and tarsus length (0.78, 0.79) (Pérez-Camacho et al. 2015). When a goshawk was identified in photographs but not captured each year, we used its most recently recorded morphological measurements in the data analysis. Details about trapping, measurements and identification have been described in Pérez-Camacho et al. (2015).

Statistical analyses

Structural equation modelling

We used structural equation modelling (SEM) to test the food resource and shelter hypotheses (Fig. 1). SEM is a

powerful statistical technique when an a priori causal model is specified and both direct and indirect effects of predictors on response variables are of interest (Mitchell 1993). An indirect effect occurs when a causal link between two variables passes through a third intermediate variable. This approach can be useful for situations where experimentation is not feasible because of field conditions or the spatial or temporal scales involved (Olalla-Tárraga et al. 2019). The hypothetical causal model describes a priori how variables are causally linked in terms of their direct and indirect effects (McElreath 2020). We fit four models for the food resource hypothesis, corresponding to the combination of two response variables (breeding success and phenology) and two direct effects of habitat structure on prey supply and on breeding performance. We fit six models for the shelter hypothesis, corresponding to the combination of breeding success and phenology, two direct effects of habitat structure on prey supply and on breeding performance, and one direct effect of mobbing disturbance on breeding performance (Fig. 1). Given our relatively low sample size (final sample size in SEMs was n = 56 due to missing data for prey supply in two breeding territories) analysing the full set of relationships among factors in a single, all-encompassing model was not feasible. Further, the structure of our dataset (with collinearity among variables), and the ratio between the number of variables and links studied would advise against such an all-encompassing model. Instead, our 'deconstructive' approach (i.e. fitting and comparing smaller models representative of competing hypotheses) is suited to understand the underlying relationships among variables, similarly as done in previous ecological research using SEMs (Hawkins et al. 2007, Olalla-Tárraga et al. 2019).

We assessed the models in two steps. First, we tested each model as a whole using a chi-squared test to assess the null hypothesis. In this approach, if the probability of the null hypothesis is small ($p < 0.05$), then the observed data are unlikely to have been generated by the hypothesised causal processes, and the models should be rejected (Shipley 1999). Chi-squared tests may be less reliable with larger samples (Mitchell 1993), but they should be reliable for moderately small samples such as ours. Nevertheless, we also assessed the models using the comparative fit index (CFI), which ranges from 0 to 1 and serves as an index of deviation from a null model. CFI > 0.9 is considered indicative of good fit (Lefcheck 2016).

Second, we tested whether the hypothesised direct and indirect relationships among predictors and response variables were statistically significant (Z-test) and consistent with the predicted 'direction' (positive or negative). If not, we planned to reject the model, regardless of the chi-squared results and CFI. Thus, we planned to accept the food resource hypothesis only if the data showed significant direct or indirect positive associations between prey abundance and reproductive performance. We planned to accept the shelter hypothesis only if the data showed significant direct or indirect negative associations between mobbing disturbance and reproductive performance. Standardised partial regression coefficients were

calculated to estimate the sign and strength of individual paths in the model (Mitchell 1993).

Finally, we fitted two models synthetizing the results of the above hypotheses (food resource and shelter hypotheses) including only the factors showing significant and biologically relevant associations with prey supply. Synthetic models included simultaneously the factors directly related to prey supply (i.e. prey abundance and mobbing disturbance) and tested the existence of relationships between them (associations among the variables connected by causal links). Note that, beyond direct effects (i.e. direct links in the models), SEM have the advantage of allowing for straightforward calculation of indirect effects, simply by multiplying the coefficients of the links connecting two factors separated by more than one link.

Additional analyses

If breeders were distributed in a despotic settlement pattern (i.e. where high-quality individuals select for the best breeding territories), good-quality habitats would contain adults of higher quality. Lack of enough data about the quality of individuals prevented us from including effects of adult quality on reproductive performance in the SEM. Instead we performed simple Pearson regressions to test for linear relationships of indicators of adult quality (body size and seniority) with prey abundance in the food resource hypothesis, or with levels of disturbance in the shelter hypothesis. If good-quality habitats were those with more prey (food resource hypothesis) we would expect a significant positive relationship between prey abundance and adult body size or seniority in the breeding territories. If instead good-quality habitats were those with less disturbance (shelter hypothesis) we would expect a significant negative relationship between levels of disturbance by crows and adult size or seniority in the breeding territories. We also computed Pearson correlations to test for linear relationships between territory occupancy and levels of disturbance within the historic territories. Data were analysed using the packages 'semTools' (Jorgensen et al. 2020) and 'lavaan' (Rosseel 2012) in R 4.0.0 (www.r-project.org).

Results

As expected, our models under the food resource hypothesis showed a strong, significant effect of the structure of the habitat in the breeding territory (prey-rich habitat cover in the breeding territory) on prey abundance, and showed positive associations between prey supply to the nest and the two response variables, breeding success and early nesting (Table 1a–d, Fig. 2a–d). Surprisingly, however, prey supply to the nest decreased with increasing prey abundance in the breeding territory in all models. This negative relationship between prey abundance and prey supply contradicts the predictions of food resource hypothesis, which we therefore rejected despite the acceptable goodness-of-fit indices (Table 2).
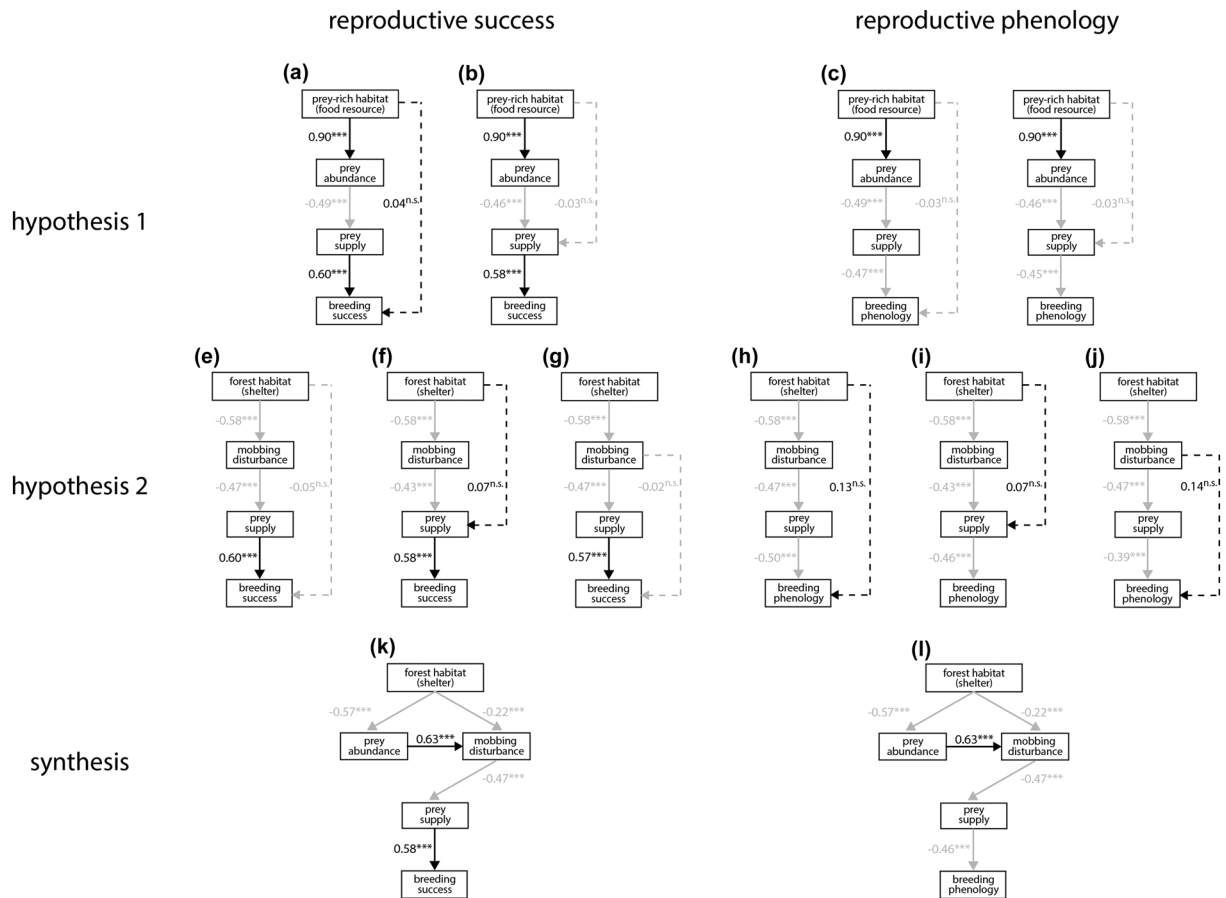
Figure 2. Results from structural equation modelling to test the food resource hypothesis (hypothesis 1: a–d), the shelter hypothesis (hypothesis 1: e–j) and the synthetic model that combines both hypotheses (synthesis: k–l). When testing each hypothesis, the response variable was either breeding success (a–b, e–g, k) or breeding phenology (c–d, h–j, l). Hierarchical, 4-level effects were tested in each model: habitat structure → habitat-derived characteristics (prey abundance or mobbing disturbance) → prey supply → breeding performance. The direct effects of habitat structure or habitat-derived characteristics (prey abundance or mobbing disturbance) on performance were also tested in the hypotheses 1 and 2. Black arrows represent positive effects; grey arrows, negative effects; solid arrows, significant effects; and dashed arrows, non-significant effects.

The models for the shelter hypothesis indicated a negative effect of shelter habitat on levels of mobbing disturbance and a negative effect of mobbing disturbance on prey supply to the nest (Fig. 2e–j, Table 2e–j). As expected, higher prey supply to the nest increased breeding success and shifted the breeding phenology of goshawks earlier in the year. The models under this hypothesis showed good chi-squared and CFI values (Table 2). We accepted the shelter hypothesis because model goodness of fit was supported by chi-squared and CFI values (first step) and because data showed significant negative (indirect) associations between mobbing disturbance and reproductive performance (both for breeding success and breeding phenology) (second step).

The models developed under the shelter hypothesis did not show significant direct associations between cover of forest habitats and reproductive performance (breeding success and breeding phenology) (Fig. 2e, h) or direct associations between cover of forest habitat and prey supply (Fig. 2f, i). They also failed to show significant direct effects of mobbing

disturbance on reproductive performance (breeding success and breeding phenology) (Fig. 2g, j). This suggests that mobbing disturbance affects reproductive performance indirectly by reducing the amount of prey that adults deliver to their nests. Similar results were obtained when either breeding success or breeding phenology was used as an indicator of reproductive performance.

Considering the results of the previous models we tested a new synthetic model that completed the shelter hypothesis and combined key parameters and links identified in the previous models (Fig. 2k, l). This new model emphasized the importance of the cover of forest habitats in the breeding performance (breeding success and breeding phenology) of this forest-dwelling predator. As in the shelter hypothesis, the cover of forest habitats had a positive indirect effect on prey supply to the nest (prey delivery) by negatively affecting to the levels of mobbing disturbance in the breeding territory. Prey abundance had a negative indirect effect on prey supply to the nest because breeding territories with more

Table 2. Structural equation modelling of the food resource hypothesis, shelter hypothesis and synthetic model that combined both models. Two response variables were used in models of breeding success (a–b, e–g, k) and models of breeding phenology (c–d, h–j, l). Standardised regression coefficients, their 95% confidence intervals, z-test significance and R^2 are reported for each variable of the models (Fig. 2). The goodness of fit was calculated for each model in terms of the chi-squared value and comparative fit index (CFI). In all models, n was 56 observations due to missing data for prey supply in two nests.

Hypothesis	Model	Predictor		Response	Est. SD	p-value	ci.lower	ci.upper	R^2	χ^2	p-value	CFI
Resources	a	Prey supply	→	Breeding success	0.599	0.000	0.400	0.799	0.340	0.351	0.839	1.000
		Prey-rich habitat	→	Breeding success	0.040	0.742	−0.197	0.277	0.241			
		Prey abundance	→	Prey supply	−0.491	0.000	−0.682	−0.300				
		Prey-rich habitat	→	Prey abundance	0.899	0.000	0.860	0.938	0.808			
	b	Prey supply	→	Breeding success	0.582	0.000	0.409	0.754	0.338	0.447	0.800	1.000
		Prey abundance	→	Prey supply	−0.466	0.072	−0.973	0.041	0.241			
		Prey-rich habitat	→	Prey supply	−0.028	0.915	−0.549	0.492				
		Prey-rich habitat	→	Prey abundance	0.899	0.000	0.860	0.938	0.808			
	c	Prey supply	→	Breeding phenology	−0.475	0.000	−0.709	−0.241	0.212	0.200	0.905	1.000
		Prey-rich habitat	→	Breeding phenology	−0.034	0.795	−0.293	0.225				
		Prey abundance	→	Prey supply	−0.491	0.000	−0.682	−0.300	0.241			
		Prey-rich habitat	→	Prey abundance	0.899	0.000	0.860	0.938	0.808			
	d	Prey supply	→	Breeding phenology	−0.459	0.000	−0.666	−0.253	0.211	0.256	0.880	1.000
		Prey abundance	→	Prey supply	−0.466	0.072	−0.973	0.041	0.241			
		Prey-rich habitat	→	Prey supply	−0.028	0.915	−0.549	0.492				
		Prey-rich habitat	→	Prey abundance	0.899	0.000	0.860	0.938	0.808			
Shelter	e	Prey supply	→	Breeding success	0.598	0.000	0.418	0.779	0.343	0.505	0.777	1.000
		Forest habitat	→	Breeding success	−0.055	0.628	−0.275	0.166	0.224			
		Mobbing disturbance	→	Prey supply	−0.473	0.000	−0.675	−0.271				
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			
	f	Prey supply	→	Breeding success	0.582	0.000	0.409	0.755	0.338	0.452	0.798	1.000
		Mobbing disturbance	→	Prey supply	−0.428	0.002	−0.693	−0.164				
		Forest habitat	→	Prey supply	0.076	0.596	−0.206	0.358	0.227			
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			
	g	Prey supply	→	Breeding success	0.572	0.000	0.364	0.781	0.339	0.704	0.703	1.000
		Forest habitat	→	Breeding success	−0.020	0.870	−0.262	0.222	0.224			
		Prey abundance	→	Prey supply	−0.473	0.000	−0.675	−0.271				
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			
	h	Prey supply	→	Breeding phenology	−0.500	0.000	−0.710	−0.290	0.231	3.643	0.162	0.967
		Mobbing disturbance	→	Breeding phenology	0.128	0.288	−0.108	0.365				
		Forest habitat	→	Prey supply	−0.473	0.000	−0.675	−0.271	0.224			
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			

(Continued)

Table 2. Continued.

Hypothesis	Model	Predictor	Response		Est. SD	p-value	ci.lower	ci.upper	R²	χ²	p-value	CFI
	i	Prey supply	→	Breeding phenology	−0.459	0.000	−0.666	−0.253	0.211	4.422	0.110	0.951
		Mobbing disturbance	→	Prey supply	−0.428	0.002	−0.693	−0.164				
		Forest habitat	→	Prey supply	0.076	0.596	−0.206	0.358	0.227			
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			
	j	Prey supply	→	Breeding phenology	−0.395	0.002	−0.641	−0.149		3.668	0.160	0.966
		Mobbing disturbance	→	Breeding phenology	0.136	0.304	−0.124	0.396	0.225			
		Mobbing disturbance	→	Prey supply	−0.473	0.000	−0.675	−0.271	0.224			
		Forest habitat	→	Mobbing disturbance	−0.581	0.000	−0.739	−0.423	0.338			
Synthesis	k	Prey supply	→	Breeding success	0.582	0.000	0.409	0.755	0.34	3.546	0.617	1.000
		Mobbing disturbance	→	Prey supply	−0.473	0.000	−0.675	−0.271	0.22			
		Forest habitat	→	Mobbing disturbance	−0.220	0.029	−0.418	−0.023	0.61			
		Prey abundance	→	Mobbing disturbance	0.631	0.000	0.457	0.805				
		Forest habitat	→	Prey abundance	−0.572	0.000	−0.733	−0.411	0.327			
	l	Forest habitat	→	Prey abundance	−0.572	0.000	−0.733	−0.411	0.327	8.970	0.110	0.961
		Prey supply	→	Breeding success	−0.459	0.000	−0.666	−0.253	0.21			
		Mobbing disturbance	→	Prey supply	−0.473	0.000	−0.675	−0.271	0.22			
		Forest habitat	→	Mobbing disturbance	−0.220	0.029	−0.418	−0.023	0.61			
		Prey abundance	→	Mobbing disturbance	0.631	0.000	0.457	0.805				
		Forest habitat	→	Prey abundance	−0.572	0.000	−0.733	−0.411	0.327			

prey abundance had higher levels of mobbing disturbance (Fig. 2k, l). Despite their low prey abundances, breeding territories with more cover of forest habitats had more prey supply to the nest because cover of forest habitats prevented from mobbing disturbance. Both chi-squared and CFI values supported this synthetic model (Table 2).

We did not detect any significant association between habitat quality and quality-related features of the adults. We found not significant relationships (Pearson correlations) between mobbing disturbance or cover of forest habitats (shelter habitats) and female seniority ($r = -0.3$, $p = 0.1$, $n = 31$ and $r = 0.24$, $p = 0.19$, $n = 31$, respectively) and male seniority ($r = -0.13$, $p = 0.5$, $n = 29$ and $r = -0.27$, $p = 0.12$, $n = 29$, respectively). We also found non-significant relationships between mobbing disturbance or cover of forest habitats (shelter habitats) and female body size ($r = 0.09$, $p = 0.65$, $n = 30$ and $r = -0.13$, $p = 0.49$, $n = 30$, respectively) and male body size ($r = -0.17$, $p = 0.41$, $n = 25$ and $r = 0.09$, $p = 0.68$, $n = 25$, respectively).

Finally, we found a negative association between occupancy of historic goshawk territories (i.e. the proportion of years during which a historic territory was occupied) and abundance of breeding corvids in those historic territories ($r = -0.587$, $p = 0.0051$, $n = 21$).

Discussion

We found an indirect relationship between habitat structure and reproductive performance in goshawks, supporting the shelter hypothesis as an explanation of the variation in reproductive performance of this top predator. Greater availability of shelter reduced disturbance by crows in the goshawk breeding territories, indirectly leading to an increase in prey supply to the nest. This increased prey supply improved reproductive performance, both in terms of breeding success and breeding phenology. Our findings suggest that higher habitat quality for raptors means greater possibility of sheltered hunting without mobbing. This finding may be particularly important for top-predators such as goshawks that hunt agile prey. The reported effects of density of active crow nests (as a surrogate for potential disturbance through mobbing) in controlling goshawk foraging efficiency might be of interest, for example, to design more effective, socially acceptable raptor management strategies in situations when the raptor hunts some sensitive domestic prey such as racing pigeons.

From habitat structure to reproductive performance

Understanding how habitat structure relates to habitat quality for raptors requires understanding the environmental conditions that influence prey supply to the nest (prey delivery) and reproductive performance (Johnson 2007). At our study site, greater forest cover in the breeding territory was associated with lower levels of mobbing disturbance, which in turn increased goshawk reproductive performance. Lower mobbing may help explain our previous findings that goshawk

nests in the present study area are located farther from forest edges and farmland than one would expect by chance (breeding sites: 176.6 m and random points: 133 m) (García-Salgado et al. 2018). Farmland areas and forest edges are the main nesting habitats of crows in the study area. Indeed, studies of woodland–farmland mosaics and fragmented forests have described an 'edge effect' in which the levels of disturbance are greater nearer forest edges (Murcia 1995, Tapia et al. 2007). Our findings point to an 'edge effect' on goshawks due to corvid mobbing, highlighting the role of biotic antagonistic interactions – i.e. disturbance by corvids – as a potential mediator of such edge-effect. However, we did not detect any important difference in diet composition between 'edge' and 'interior' goshawk breeding territories in the study area (unpubl.).

Although crows are abundant in the study area and can depredate on goshawk eggs and nestlings (Kenward 2006, Byholm and Nikula 2007), we found their effect on goshawk reproductive performance to be indirect (Table 2e–j, Fig. 2e–j): their presence decreased the delivery of prey to goshawk nests. Since primarily male goshawks provide prey to the nest during the breeding season (Kenward 2006), we suggest that crow disturbances decrease the hunting time and foraging efficiency of breeding male goshawks. Goshawks hunt mainly by waiting hidden on a perch where they remain undetected by their agile prey (birds and mammals) to ambush them (Widén 1997). From there the goshawks make a quick attack on their prey when the prey is close enough or is unaware. The short wings and long tail allow goshawks to obtain the speed and maneuverability that the attack needs to be successful (Kenward 2006). So we suspect, based on our own field observations and other studies (Consla and Mumme 2012, Marzluff et al. 2015), that crows discover, harass and mob the goshawks, thereby alerting their prey. This makes it difficult for the goshawk to hunt and transport prey to the nest. In fact, the mobbing calls of corvids, but not those of smaller passerines, induce stress and behavioural responses in raptors (Consla and Mumme 2012).

While crows are a frequent prey of goshawks in northern Europe (Hoy et al. 2017), they make up less than 1% of the goshawk diet in our study area, based either on number of prey items or their biomass (Rebollo et al. 2017a). This may reflect that southern male goshawks, with an average weight of only 670 g (Pérez-Camacho et al. 2015), are too similar in size to the crows (an average weight of 515 ± 7.2 g, Canestrari et al. 2007), making the capture and/or transport of such prey too costly. Another explanation may be that crows adopt a group defense strategy (flocking) against raptors in order to protect their nestlings, fledglings and adults (Cramp and Simmons 1980). Furthermore, in most European populations, crows breed as unassisted pairs, but cooperative breeding is frequent in populations of northern Spain (Baglione et al. 2002a). Cohesive groups of up to nine birds (average group size 3.2) hold territories year-round and unassisted pairs are found in about 25% of the territories. Group members typically move and forage together in the territory and cooperate to evict intruders and attack avian

predators. Thus, this cooperative breeding could improve the mobbing response by this corvid because larger groups are likely to perform better against predators and this might explain why crows that do not provision the chicks are tolerated in the breeding territories of crows (Canestrari et al. 2008).

We found that crow mobbing disturbances in the study area delayed the start of goshawk nesting. Delayed laying phenology is usually related to poor body condition and lower breeding success (Johnson 2007), so the observed delay in laying by goshawks suggests that crow disturbance harms goshawk reproductive performance before the breeding season begins, when their energy demand is lower than during the nesting stage. The fact that cohesive groups of crows hold territories year-round (Baglione et al. 2002a, b) agrees with this finding.

We found the area of high-density prey habitats to be a good predictor of the abundance of total and preferred prey in goshawk breeding territories (Table 2a–d, Fig. 2a–d). Surprisingly, though, we found that prey abundance correlated negatively with prey supply to the nest. A plausible explanation for this is that total and preferred goshawk prey occur most densely in open habitats, mainly farmlands (Table 1), in the study area, where the level of mobbing disturbance is also greater. This finding emphasises the need to define habitat quality not solely based on the amount of resources, but also based on access to those resources, which can be limited by antagonistic biotic interactions (Morrison et al. 2006, Tapia and Zuberogoitia 2018).

Indeed, more than 20 years ago, Widén (1997) already warned that forest management intensification and fragmentation in Fennoscandia was decreasing goshawk habitat quality by decreasing the raptor's foraging efficiency of certain prey species, not by decreasing the abundance of such prey or the availability of suitable nesting habitats. In North America, goshawks select foraging habitats based on prey accessibility (determined by habitat structure) rather than on prey abundance (Greenwald et al. 2005). Widén (1997) and Greenwald et al. (2005) argued that goshawk foraging efficiency depends largely on forest structure, which they quantified as stands of mature forest. Our study suggests that in addition to forest structure, mobber abundance should be taken into account when assessing habitat quality for goshawks. The present study, makes a much-needed contribution to the sparse literature on how antagonistic biotic interactions affect habitat quality by limiting access to resources (Johnson 2007, Marzluff et al. 2015). The literature on avian mobbing affecting habitat quality of predators is even sparser, despite the adaptive importance of this behaviour (Curio 1978). In our study area mobbers reduced foraging efficiency of predators in areas with higher density of prey. Breeding territories with more prey abundance had a lower prey supply to the nest and worst breeding performance because their higher levels of mobbing disturbance. We assume that the amount of food in the environment will affect nesting success in birds; however, our study shows that

this effect of availability of food is acting in combination with mobbing-related limits to the amount of food that is actually delivered to the raptor nest.

Aside from mobbing, other antagonistic interactions can reduce foraging efficiency of predators in areas with higher density of prey. For example, habitats with more food resources may attract more competitors, reducing per capita feeding rates due to inter- or intra-specific competition for trophic resources (Vance-Chalcraft and Soluk 2005, López-Bao et al. 2011 and see Chakarov et al. 2010, Solonen 2011, Byholm et al. 2012, Fedyń et al. 2021 for specific examples with goshawks). However, the goshawk is the dominant raptor in the study area (Rebollo et al. 2017b), so inter-specific competition with other raptors seems unlikely. In addition, other diurnal raptors capable of hunting similar agile avian prey in this biogeographic region are either absent (e.g. *Hieratus pennatus*) or present at very low density (e.g. *Falco peregrinus*). Intra-specific competition among breeding goshawk individuals may not be relevant either. The distance between two active goshawk nests did not correlate with abundance of total prey (n=30, r=0.15, p=0.438) or preferred prey (n=30, r=0.05, p=0.780) in our study area. This suggests that breeding territories are not aggregated in areas of high prey density, which would lead to high intra-specific competition. Non-breeding conspecifics ('floaters') have been shown to influence the breeding performance of some raptors (Bretagnolle et al. 2008), so future study should investigate whether this may also occur with goshawks in our study area.

The small number of adults in our dataset prevented us from including individual adult parameters such us body size and seniority in the SEM. Instead we explored bivariate relationships between individual parameters and habitat quality, with the latter expressed as forest cover and crow abundance in the breeding territories. We did not detect any significant association between habitat quality and features of the adults in terms of both body size and seniority in the territories. Our analysis of individual quality and reproductive performance, although limited, suggests that reproductive performance in more forested habitats depends on habitat quality (more and better shelter from mobbing disturbance) more than individual breeder quality (body size or adult seniority). We cannot entirely eliminate alternative explanations associated with habitat quality and features of adults, such as for example, the age or the body condition of the breeders. Thus, 'lower quality' goshawks may be both nesting within closer proximity to crows, and simultaneously having lower nesting success that is not caused by the proximity to crows. This topic deserves further research.

We found that the historic goshawk territories that were occupied longer, tended to contain fewer breeding crows in our study area. This is an important result of the present study. Given that good-quality habitats should be occupied more consistently over the years than poor-quality habitats (Johnson 2007), our finding suggests this biotic antagonistic negative interaction can heavily influence habitat quality for

goshawks. On a landscape scale, goshawks have likely adapted to avoid the presence of breeding crows and to prevent crows from reducing goshawk's reproductive performance.

Speculations

Our study has intriguing implications for controlling predation of some sensitive domestic prey. In our study system, the presence of breeding crows seems to negatively affect goshawks by decreasing their occupancy of historic territories, delaying their laying phenology, and decreasing their prey supply to the nest and reproductive success. These observations open an interesting research avenue: monitoring how mobber species limit hunting efficiency of diurnal raptors that depredate on some agile domestic prey in southern Europe. Over the last decades, we have observed how goshawks increasingly prey on racing pigeons, which is a lucrative activity within the study area (Rebollo et al. 2017a). In recent years, we have detected illegal trap killing of goshawks in the study area, which coincided with a decrease in the number of goshawk breeding pairs (Martínez-Hesterkamp et al. 2018). The pigeon-raptor conflict is in fact a worldwide human-raptor conflict that requires effective yet socially acceptable solutions (Parrott et al. 2008). Our results suggest that negative effects of raptors on human activities such as pigeon racing could be controlled by reducing raptor foraging efficiency, such as by increasing crow mobbing against raptors near pigeon lofts.

Better understanding of bird behaviour and function, especially in agrarian environments, may allow us to promote bird ecosystem services, such as provisioning, regulating, cultural and supporting services (Whelan et al. 2008). More research is needed to quantify bird functions and services in agrarian systems as well as evaluate their effectiveness and economic value (Wenny et al. 2011). Our findings suggest that mobbing, an anti-predator strategy seen mostly in birds (Caro 2005, Pawlak et al. 2019), can be a research avenue for bird services, and that avian mobbers can be exploited to protect some sensitive domestic prey from raptor attacks.

Author contributions

Salvador Rebollo: Conceptualization (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead). **Lorenzo Pérez-Camacho**: Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Sara Martínez-Hesterkamp**: Investigation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (supporting). **Luis Tapia**: Investigation (supporting); Methodology (supporting); Writing – review and editing (equal). **José M. Fernández-Pereira**: Data curation (lead); Investigation (equal); Methodology (equal). **Ignacio Morales-Castilla**: Formal analysis (lead); Software (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available in: https://github.com/MoralesCastilla/RaptorHabitat/tree/main/data (Rebollo et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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