
Bird Study

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tbis20

# Nesting associations and breeding output of Barn Owls *Tyto alba* and Red-billed Choughs *Pyrrhocorax pyrrhocorax* sharing nest boxes

**Diego Villanúa, Juan Arizaga, Alberto Artázcoz, Daniel Alonso, Alberto Lizarraga, Juan M. Barbarin & Guillermo Blanco**

**To cite this article:** Diego Villanúa, Juan Arizaga, Alberto Artázcoz, Daniel Alonso, Alberto Lizarraga, Juan M. Barbarin & Guillermo Blanco (2022) Nesting associations and breeding output of Barn Owls *Tyto alba* and Red-billed Choughs *Pyrrhocorax pyrrhocorax* sharing nest boxes, Bird Study, 69:3-4, 90-96, DOI: 10.1080/00063657.2022.2160696

**To link to this article:** https://doi.org/10.1080/00063657.2022.2160696

Published online: 09 Jan 2023.

BIRD STUDY
2022, VOL. 69, NOS. 3–4, 90–96
https://doi.org/10.1080/00063657.2022.2160696

Check for updates

# Nesting associations and breeding output of Barn Owls *Tyto alba* and Red-billed Choughs *Pyrrhocorax pyrrhocorax* sharing nest boxes

Diego Villanúa[a,b], Juan Arizaga[a], Alberto Artázcoz[c], Daniel Alonso[a], Alberto Lizarraga[a], Juan M. Barbarin[a] and Guillermo Blanco[d]

[a]Departamento de Ornitología, Sociedad de Ciencias Aranzadi, Donostia-S. Sebastián, Spain; [b]Gestión Ambiental de Navarra (GAN-NIK), Navarra, Spain; [c]Pamplona, Spain; [d]Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

**ABSTRACT**

**Capsule:** Barn Owls *Tyto alba* and Red-billed Choughs *Pyrrhocorax pyrrhocorax* show differential breeding outputs as a consequence of sharing nest boxes.
**Aims:** To describe for the first time a commensal relationship between the Red-billed Chough and the Barn Owl during the breeding period.
**Methods:** During systematic monitoring of 90 nest boxes installed for Barn Owls in Navarre, northern Spain, it was found that in some boxes, Barn Owls and Red-billed Choughs nested simultaneously (inside and on top of the box, respectively). The clutch size, breeding success, and the number of fledglings of each species were compared when nesting together versus separately during the breeding period of 2015 and 2017.
**Results:** About one-third of the nest boxes observed during the study were simultaneously used by both Barn Owls and Red-billed Choughs. No relationship was found between the composition of the habitat around the boxes and the degree of occupancy for either species. Nest box sharing had no significant effect on the breeding output of Barn Owls, but improved the breeding performance of Red-billed Choughs by increasing the number of fledglings in relation to clutch size.
**Conclusion:** Barn Owls can provide benefits to Red-billed Choughs by controlling the populations of rodents, which could act as nest predators. Given that Barn Owls apparently do not obtain benefits nor incur any costs by the association with Red-billed Choughs, this interaction may be defined as commensalism. To our knowledge, this is the first documented nesting association between a corvid and an owl species.

**ARTICLE HISTORY**
Received 8 September 2021
Accepted 8 September 2022

Predation during the breeding season is one of the most important factors affecting breeding success in birds (Ricklefs 1969, Lima 2009). A broad range of strategies to reduce breeding failure through predation have evolved in different avian species, including cryptic colouration in eggs and breeders (Blanco & Bertellotti 2002, Troscianko *et al.* 2015), nesting colonially with conspecifics (Brown & Brown 2001), and interspecific associations with aggressive neighbouring species, such as raptors (Haemig 2001, Quinn & Kokorev 2002, Quinn & Ueta 2008). The latter strategy may be governed by trade-offs between the advantages of breeding near a predator that will exclude other potential predators, and the risk of predation by the potentially protective species, although not all protectors predate on their associates (Quinn & Kokorev 2002, Quinn & Ueta 2008).

Populations of cavity-nesting birds are generally limited by the availability of nesting sites, as has been extensively demonstrated experimentally through the provision of nest boxes to increase breeding opportunities and reproductive success, and to reduce the impact of nest predation and ectoparasitism (Newton 1994, Fargallo *et al.* 2001). This management action is often applied to increase the number of predatory birds in programmes aimed at controlling pest species, such as rodents in farmed environments (Meyrom *et al.* 2009, Paz-Luna *et al.* 2020). The provision of nesting sites can also contribute to increasing the regional abundance and diversity in the community of cavity nesters (Newton 1994), thus promoting or relaxing interactions between competing species depending on environmental conditions and community composition (Dhondt 2012). Symbiotic interactions between different species nesting in nearby cavities (Blanco & Tella 1997, Campobello *et al.* 2012), and between hole- and open-nesting species (Hernández-Brito *et al.* 2020), have been

**CONTACT** Diego Villanúa diegovillanua@yahoo.es

recorded less frequently (Haemig 2001, Quinn & Kokorev, 2002, Quinn & Ueta 2008). These nesting associations have included mutualistic or commensal interactions, in which respectively both or a single species benefitted, and other complex relationships with conditional outputs within interaction continuums (Quinn *et al.* 2003).

Here, we evaluated whether the provision of large nest boxes targeting diurnal and nocturnal raptors can be used by other medium-sized species, and whether this can promote interspecific nesting associations. Specifically, we tested whether nest boxes aimed at increasing a population of Barn Owls *Tyto alba* and Common Kestrels *Falco tinnunculus* could be used by Red-billed Choughs *Pyrrhocorax pyrrhocorax*, a corvid species with fragmented and declining populations in Europe (BirdLife International 2020). We also assessed whether the occupation of nest boxes may be promoted by nesting interactions between different species, and how these associations might influence the breeding output of each species through mutual or asymmetric protector-protected relationships. Red-billed Choughs do not predate the contents of nests of other bird species yet could be susceptible to such predation themselves (Blanco & Tella 1997), so the nature of these potential interactions may range across a continuum between mutually beneficial or commensal (beneficial for the protected species) or antagonistic (detrimental to at least one of the associated species). Therefore, asymmetric reproductive outputs were expected between and within species depending on their association at the nesting sites.

## Methods

### Study species

The Red-billed Chough (hereafter Chough) is a medium-sized corvid for which three different nesting strategies have been described: (i) nesting in exclusive territories, (ii) nesting in small aggregations with conspecifics, and (iii) nesting in association with more aggressive species, such as Lesser Kestrels, *Falco naumanni* (Blanco *et al.* 1997, 1998, Blanco & Tella 1997). Choughs nest in cavities of various sizes which often represent a relatively scarce resource, so nest site availability and distribution largely influence breeding output (Blanco *et al.* 1998, Banda & Blanco 2009). The availability of nesting sites greatly depends on nesting substrate on cliffs or buildings and other artefacts that mimic the conditions of caves and crags (Blanco *et al.* 1997, 1999, Banda & Blanco 2009).

The Barn Owl is a widely distributed nocturnal raptor associated with open environments, especially those devoted to traditional agriculture (Martínez & Zuberogoitia 2004, Bunn *et al.* 2010). Barn Owls are exclusively territorial and nest in a range of cavities in cliffs and buildings and, unlike Choughs, in holes in trees (Mikkola 1983, Bunn *et al.* 2010). The provision of nest boxes on poles, trees, and buildings has been used as a management measure to increase populations of Barn Owls (Meyrom *et al.* 2009, Paz-Luna *et al.* 2020).

### Study area and data collection

The study was carried out in a pseudo-steppe area of approximately 2400 km$^2$ in the Ebro Valley, Navarre, northern Spain. The study area is comprised of a mosaic of arable land dominated by cereal crops with some small patches of natural steppe-like vegetation. In this area, several bird species nest in cavities and inside abandoned or collapsed farmhouses and corrals, which have increased in number during the last few decades (Tella *et al.* 1993, Blanco *et al.* 1997, Banda & Blanco 2009). From 2007 to 2015, the regional administrative authority (Government of Navarra) installed a large number of nest boxes in order to improve the conservation status of some raptors nesting in these traditional farms, and as a form of biological rodent pest control (see Montoya *et al.* 2021 for details). Of these, 90 were designed to be occupied by Barn Owls. Owl nest boxes were made of wood (size: $60 \times 40 \times 35$ cm, with and entrance hole $13 \times 13$ cm) and had an internal partition dividing the box into two spaces. Nest boxes were always installed inside farmhouses, at heights of 2–3 m, and placed to reduce access by terrestrial predators.

In 2015 and 2017, the nest boxes were visited as part of a breeding monitoring survey. The protocol consisted of two visits per season, the first in April, to determine the occupation of nest boxes (egg laying) by each species, and the second 45 days later, to determine the output of reproduction at each box. Within the study area, these dates cover the reproductive periods for both the Barn Owl (Zuberogoitia 2000) and the Chough (Banda & Blanco 2017). For each breeding attempt, we recorded clutch size, breeding success and the number of fledglings (productivity), and a breeding failure index was obtained from the difference between clutch size and the number of fledglings.

### Statistical analysis

To determine whether the clutch size and productivity of Barn Owls and Choughs varied between nest boxes with one (single) or two (associated) species, we conducted generalized linear mixed models (GLMM; Conway–Maxwell Poisson error distribution with log-link function). As most breeding pairs raised at least one fledgling, instead of using breeding success as a dichotomous variable we calculated a breeding failure index for each breeding attempt as the number of fledglings out of the total number of eggs laid. This index was then used as a dependent variable to assess the influence of the kind of nesting attempt (single/associated; fixed factor) using a GLMM (binomial error distribution, logit link function; nest box ID as a random term).

The occupation of nest boxes by the Choughs (0 = no, 1 = yes) was analysed with a GLMM (binomial error distribution, logit link function; nest box ID as a random term). Explanatory variables were the occupation of each nest box by a Barn Owl (fixed factor), and habitat features, estimated as the three first principal components (PC1 to PC3; eigenvalues > 1) from a principal component analysis (PCA) on soil cover around boxes. Land use variables included in the analyses were human-made surfaces (buildings, landfills, etc.), water points (small lagoons and cattle troughs), cereal crops, woody crops (mainly vineyards and Almond *Purnus dulcis* plantations), grassland, scrub and forest (mainly *Quercus ilex* and *Pinus halepensis*) obtained from the 2018 Corine Land Cover layer and calculated for a 500 m buffer around each box and expressed in $m^2$. Models were run using the *glmmTMB* package and model fit was checked using the *DHARMa* package (Hartig 2018).

Model selection was performed using the Akaike Information Criterion corrected for small sample sizes (AICc; Sugiura 1978). Within each set of models obtained after running each possible combination of covariates (which includes the null model but not models that did not converge), we calculated the ΔAICc as the difference between the AICc of model i and that of the best model, and the Akaike weight (w) of each model using AICcmodavg (Mazerolle 2020). The resulting models with ΔAICc < 2 were considered as equally supported, and thus were averaged (model averaging) using the MuMIn package (Barton 2020). We considered that a given effect received support when the 95% confidence intervals (CI) did not overlap with zero. All analyses were performed in R 4.1.0 (R Core Team 2022).

## Results

Overall, 126 breeding attempts were monitored (Table 1). Pooling both study years, these attempts included a single ('solitary') species (n = 62) or associated species sharing the same nest box (n = 64) (Figure 1). Barn Owls always nested inside the boxes, while the Choughs built their nests either on top of the box or inside the box, though never inside when breeding in association with a Barn Owl (Table 1). Other species, such as the Common Kestrel, Western Jackdaw *Coloeus monedula*, and Feral Pigeon *Columba livia* also occupied nest boxes, but in much lower numbers ($n = 8$, 2, and 5 breeding attempts, respectively) and never in association with Barn Owls or Choughs.

The analysis revealed that the Barn Owls did not experience any significant change in their breeding performance in relation to breeding with or without associated Choughs (Table 2). Instead, Choughs nesting in association with Barn Owls showed a higher productivity and lower breeding failure index (higher number of fledglings after controlling for clutch size) than those nesting solitarily, without the association with Barn Owls (Table 2). The occupation of nest boxes by Choughs as a binary variable showed no effect of the occupation by Barn Owls nor of surrounding land cover variables (Table 3).

**Table 1.** Number and frequency of solitary and associated nests of the Red-billed Chough (RBC) and Barn Owl (BO), in 2015 and 2017, in Navarre, northern Spain.

| Strategy | Nest location | BO, *n* (%) | | RBC, *n* (%) | |
|---|---|---|---|---|---|
| | | 2015 | 2017 | 2015 | 2017 |
| Solitary | Inside box | 13 (44.8%) | 13 (44.8%) | 10 (29.4%) | 11 (32.4%) |
| | Over box | 0 | 0 | 8 (23.6%) | 7 (20.5%) |
| Associated | Inside box | 16 (55.2%) | 16 (55.2%) | 0 | 0 |
| | Over box | 0 | 0 | 16 (47.1%) | 16 (47.1%) |

**Figure 1.** Example of a nest box occupied simultaneously by Barn owls (inside the box) and Red-billed Choughs (on top of the box).

**Table 2.** Mean ± sd of breeding parameters of Barn Owls and Red-billed Choughs nesting solitarily (a single species in each box) or associated (sharing nest boxes), and estimates (±se) obtained for the effect of each kind of nesting attempt (single/associated; fixed factor) on measures of reproductive success. Sample sizes are shown in Table 1.

| | Breeding parameters | | Statistical test (GLMM) | | |
|---|---|---|---|---|---|
| Dependent variable | Solitary | Associated | Estimate ± se | *z* | *P* |
| **Barn Owl** | | | | | |
| Clutch size | 5.80 ± 0.58 | 5.81 ± 0.74 | −0.002 ± 0.03 | −0.06 | 0.95 |
| Productivity | 4.27 ± 0.67 | 4.47 ± 0.92 | 0.04 ± 0.05 | 0.76 | 0.45 |
| Breeding failure | 1.52 ± 0.71 | 1.33 ± 0.96 | 0.17 ± 0.27 | 0.631 | 0.53 |
| Breeding success | 100% | 100% | | | |
| **Red-billed Chough** | | | | | |
| Clutch size | 5.02 ± 0.69 | 4.81 ± 0.60 | −0.07 ± 0.04 | 1.77 | 0.08 |
| Productivity | 3.18 ± 1.27 | 3.72 ± 0.81 | 0.32 ± 0.10 | 3.28 | 0.001 |
| Breeding failure | 2.02 ± 1.39 | 1.17 ± 0.86 | 1.09 ± 0.32 | 3.43 | 0.0006 |
| Breeding success | 88.89% | 100% | | | |

## Discussion

Nesting associations between bird species generally represent a strategy to reduce the impact of predation on breeding adults and their nest contents (Haemig 2001, Quinn & Kokorev 2002, Quinn & Ueta 2008). As for other ecological interactions, the outcomes of interspecific nesting associations might range from mutually beneficial to progressively detrimental, depending on the species involved, the ecological context, and individual traits (Quinn & Kokorev 2002, Quinn & Ueta 2008, Dall *et al.* 2012). In this study, we describe for the first time a nesting association between a corvid and an owl species, with asymmetric breeding outcomes for each interacting species.

About one-third of the nest boxes examined were simultaneously used by Barn Owls and Choughs. This sharing of particular nest boxes could be a consequence of the local scarcity of nesting sites for each species, rather than an active association between them. However, the fact that Choughs nested inside and on top of the box, while the Barn Owls nested only inside the box suggests different requirements and plasticity regarding nest placement (Tella *et al.* 1993). In the absence of nest boxes, Barn Owls almost exclusively nest inside relatively large and dark cavities, while Choughs can nest on a variety of placements and substrates, including ledges, shelves, beams, columns, and cavities of variable size inside and outside walls of buildings (Tella *et al.* 1993, Banda & Blanco 2017). This suggests a higher availability of suitable nesting sites for Choughs than for Barn Owls, thus supporting an active nesting association sought after by Choughs rather than by Barn Owls. However, this can depend on the availability of suitable farm buildings and cliffs for nesting at a regional scale (Blanco *et al.* 1997, Martínez & Zuberogoitia 2004), and especially on the availability of suitable nesting places for each species in each building (Tella *et al.* 1993, Banda & Blanco 2017). Barn Owls and Choughs may prefer the same nesting buildings rather than the same nest boxes, due to specific features of the buildings in terms of location, state of conservation, perceived abundance of shared predators, and the level of disturbance inside and around these places (Tella *et al.* 1993, Banda & Blanco 2009). In addition, Choughs and Barn Owls might nest in the same boxes because of the apparent limitation of suitable nest sites, forcing both species to share the single available location that fulfils their nesting requirements (see Banda & Blanco 2017 for Choughs, and Martínez & Zuberogoitia 2004 for Barn owls). The apparent lack of an effect of the surrounding land cover on the occupation of the nest boxes by Choughs could be a consequence of relatively high homogeneity of habitat composition, and of the scarcity of places to nest in the area, which could be forcing these species to

**Table 3.** Models to assess the effects of the occupation of each nest box by a Barn Owl and habitat features (estimated as PC1, PC2, and PC3) on the occupation of each nest box by Red-billed Choughs (only alternative models with ΔAICc ≤ 2 are shown). Estimates and 95% confidence intervals were assessed after model averaging for variables included in alternative models with ΔAICc < 2. All models were run including nest box identity as a random term. A null model was included in our set of models. df: degrees of freedom; AICc: Akaike Information Criterion corrected for small sample sizes; ΔAICc: difference between the AICc of model *i* and that of the best model (i.e. the model with the lowest AICc); W: Akaike weight.

| Model selection | | | | |
|---|---|---|---|---|
| Model | df | AICc | ΔAICc | W |
| null | 2 | 98.31 | 0.00 | 0.28 |
| PC2 | 3 | 100.10 | 1.80 | 0.12 |
| Occupied by Barn Owl | 3 | 100.26 | 1.95 | 0.11 |
| PC1 | 3 | 100.29 | 1.98 | 0.10 |
| PC3 | 3 | 100.37 | 2.06 | 0.10 |
| Model averaging | | | | |
| Variable | Estimate | 2.5% CI | 97.5% CI | |
| Intercept | −11.50 | −14.82 | −8.18 | |
| PC2 | 0.46 | −1.25 | 2.17 | |
| occupied by *T. alba* | 0.73 | −3.38 | 4.84 | |
| PC1 | −0.23 | −1.87 | 1.41 | |

occupy any suitable place to nest, regardless of the features of the surrounding habitat.

In general, corvids and owls are traditionally considered as enemies, because owls can prey upon corvids (Donázar 1989, Serrano 1998), while corvids often mob owls (Marzluff & Angell 2007, Cunha *et al.* 2017). Although, the Barn Owl rarely preys on birds heavier than 130 g (Negro *et al.* 1989, Szep *et al.* 2019) they actually can predate nestling Choughs, as demonstrated by the presence of young (unfeathered) nestlings as unconsumed prey in Barn Owl nests (Banda & Blanco 2009, 2017; author's pers. obs. in the study area). Obviously, nestling predation by Barn Owls may be enhanced when both species coincide in the nesting sites, and further when they share the same nest box. Whether these circumstances can increase or decrease the breeding success of each species would explain the nature of this nesting association.

Our results indicate that sharing nest boxes had no significant effect on the breeding output of Barn Owls. However, this association was related to a slightly improved breeding performance of the Chough by increasing the number of fledglings (i.e. productivity) and the proportion of fledglings in relation to clutch size. In the study area, up to 27 actual and potential predatory species have been recorded preying upon breeding Choughs and their nest contents (Blanco & Tella 1997). Among them, the most frequent nest predators are nocturnal species against which Choughs cannot actively defend themselves or their nests (Banda & Blanco 2009). These predator species include carnivorous mammals, against which Barn Owls can likely not actively defend themselves and, therefore, neither indirectly defend Choughs. Nevertheless, Barn Owls could protect their nests, and thus passively also the nests of associated Choughs, by preying upon Black Rats *Rattus rattus*, Garden Dormice *Eliomys quercinus*, and other potential predators (Blanco & Tella 1997). These represent a relatively high proportion of the diet of Barn Owls in the study area (Torre *et al.* 1997). These rodents nest in the same farm houses, often in high abundance, and frequently prey on the nest contents of Choughs and other bird species (Blanco & Tella 1997, Serrano *et al.* 2004). Therefore, Choughs could benefit by nesting in association with Barn Owls if they act as protectors against rodents by preying upon them in the nesting sites and their surroundings. A cascading protective effect can also arise in this case, because carnivorous mammals actively searching for rodents as prey in the farm houses can also act as incidental or opportunistic predators of both Barn Owls and Choughs (Banda & Blanco 2009, 2017). Barn Owls could, therefore, also indirectly defend their nests and those of associated Choughs by reducing and eventually locally depleting the rodent populations inside and around farm houses used for nesting, as occurred around nest boxes (Paz-Luna *et al.* 2020). Similar results were reported for Choughs nesting in association with colonial Lesser Kestrels, through an active defence by the kestrels against predators and through a dilution effect of predation risk (Blanco & Tella 1997). Given that Barn Owls apparently do not obtain benefits nor incur a cost by association with Choughs, this interaction may be defined as commensalism, a form of ecological facilitation in which one species benefits and the other is unaffected (Mathis & Bronstein 2020). Since Barn Owls can prey on nestling Choughs, the output of this relationship could eventually vary within the mutualism-antagonism continuum depending on changing environmental conditions, for instance, due to the availability of rodents as food for nestling Barn Owls, and due to the abundance of these and other predators of Chough nests. However, Choughs might only associate with owls in places where no alternative nest sites exist, and where the presence and abundance of predatory rodents can be pre-emptively perceived (Banda & Blanco 2017). In this way, they could adjust the costs and benefits of their association with the owl. Nevertheless, a possible benefit for the owl may be derived from early warning against predators due to sentinel behaviour by Choughs during daylight (Blanco & Tella 1997). This activity might be assessed by Barn Owls breeding inside the box through Chough activity above and around the nest box, and through Chough alarm calls as a reaction to the presence of diurnal predators (Gill & Bierema 2013). To test this possibility, further research would be required. Whatever the actual nature of nesting associations, understanding the ecological context of interspecific protective interactions is paramount for its implications in the composition and functioning of avian communities and predator-prey systems (Quinn & Kokorev 2002, Quinn & Ueta 2008, Lima 2009, Ibáñez-Álamo *et al.* 2015).

The results of this study have implications for our understanding of the factors governing the regional and local use of farm buildings by the community of cavity nesters. Our study also has relevance for the management and conservation projects aimed at improving the populations of declining Barn Owls and Choughs. We encourage the provision of nest boxes inside abandoned farm buildings in an attempt to increase the nesting populations of both species, the breeding success of Choughs, and the role of Barn

Owls in controlling rodent pests also acting as nest predators of Choughs and other endangered species (Serrano *et al.* 2004). Moreover, given the increasing collapse of traditional farm buildings in the study area, and other Spanish regions, during recent decades (Tella *et al.* 1993, Blanco *et al.* 1997, Banda & Blanco 2017; authors' unpubl. data), and the fact that both species mostly use roofed buildings, the restoration of buildings is also encouraged for the long-term conservation of these species and Spain's architectural heritage.

## Acknowledgements

The Government of Navarra provided the necessary permits and paid for the installation of the nest boxes through technical assistance in biological pest control, implemented by Navarra Environmental Management (GAN-NIK). The rest of the work was carried out without any financial support. The authors want to thank Mark den Toom for reviewing the English version of the manuscript, and to Martina Carrete for help with statistical analysis. Both the anonymous reviewer and the editor made insightful comments that improved the final version of the article.

## References

**Banda, E. & Blanco, G.** 2009. Implications of nest-site limitation on density-dependent nest predation at variable spatial scales in a cavity-nesting bird. *Oikos* **118:** 991–1000.

**Banda, E. & Blanco, G.** 2017. Does nest placement in buildings influence nest predation in Red-billed Choughs? *Ethol. Ecol. Evol.* **29:** 436–448.

**Barton, K.** 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

**BirdLife International** 2020. Species factsheet: *Pyrrhocorax pyrrhocorax*. http://www.birdlife.org (Accessed 6 October 2020).

**Blanco, G. & Bertellotti, M.** 2002. Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. *Biol. J. Linn. Soc.* **75:** 137–146.

**Blanco, G., Cuevas, J.A. & Fargallo, J.A.** 1999. Breeding density and distribution of Choughs (*Pyrrhocorax pyrrhocorax*) nesting in river cliffs: the roles of nest-site availability and nest-site selection. *Ardea* **86:** 237–244.

**Blanco, G., Fargallo, J.A., Cuevas, J.A. & Tella, J.L.** 1998. Effects of nest-site availability and distribution on density-dependent clutch size and laying date in the Chough *Pyrrhocorax pyrrhocorax*. *Ibis* **140:** 252–256.

**Blanco, G., Fargallo, J.A., Tella, J.L. & Cuevas, J.A.** 1997. Role of buildings as nest-sites in the range expansion and conservation of choughs Pyrrhocorax pyrrhocorax in Spain. *Biol. Conserv.* **79:** 117–122.

**Blanco, G. & Tella, J.L.** 1997. Protective association and breeding advantages of Choughs nesting in lesser kestrel colonies. *Anim. Behav.* **54:** 335–342.

**Brown, C.R. & Brown, M.B.** 2001. *Avian Coloniality*. Springer, Boston, MA.

**Bunn, D.S., Warburton, A.B. & Wilson, R.D.** 2010. *The Barn Owl*. T & AD Poyser, London.

**Campobello, D., Sarà, M. & Hare, J.F.** 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. *Behav. Ecol.* **23:** 425–433.

**Cunha, F.C.R.D., Fontenelle, J.C.R. & Griesser, M.** 2017. Predation risk drives the expression of mobbing across bird species. *Behav. Ecol.* **28:** 1517–1523.

**Dall, S.R.X., Bell, A.M., Bolnick, D.I. & Ratnieks, F.L.W.** 2012. An evolutionary ecology of individual differences. *Ecol. Lett.* **15:** 1189–1198.

**Dhondt, A.A.** 2012. *Interspecific Competition in Birds* (Vol. **2**). Oxford University Press, Oxford.

**Donázar, J.A.** 1989. Variaciones geográficas y estacionales en la alimentación del Búho Real (*Bubo bubo*) en Navarra. *Ardeola* **36:** 25–39.

**Fargallo, J.A., Blanco, G., Potti, J.A. & Viñuela, J.A.** 2001. Nestbox provisioning in a rural population of Eurasian Kestrels: breeding performance, nest predation and parasitism. *Bird Study* **48:** 236–244.

**Gill, S.A. & Bierema, A.M.K.** 2013. On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology* **119:** 449–461.

**Haemig, P.D.** 2001. Symbiotic nesting of birds with formidable animals: a review with applications to biodiversity conservation. *Biodivers. Conserv.* **10:** 527–540.

**Hartig, F.** 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models; R Package, Version 0.2.0. https://cran.r-project.org/package=DHARMa.

**Hernández-Brito, D., Blanco, G., Tella, J.L. & Carrete, M.** 2020. A protective nesting association with native species counteracts biotic resistance for the spread of an invasive parakeet from urban into rural habitats. *Front. Zool.* **17:** 1–13.

**Ibáñez-Álamo, J.D., Magrath, R.D., Oteyza, J.C., Chalfoun, A.D., Haff, T.M., Schmidt, K.A., Thomson, R.L. & Martin, T.E.** 2015. Nest predation research: recent findings and future perspectives. *J. Ornithol.* **156:** 247–262.

**Lima, S.L.** 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev.* **84:** 485–513.

**Martínez, J.A. & Zuberogoitia, I.** 2004. Habitat preferences and causes of population decline for Barn Owls *Tyto alba*: a multi-scale approach. *Ardeola* **51:** 303–317.

**Marzluff, J.M. & Angell, T.** 2007. *In the Company of Crows and Ravens*. Yale University Press, London.

**Mathis, K.A. & Bronstein, J.L.** 2020. Our current understanding of commensalism. *Annu. Rev. Ecol. Evol. Syst.* **51:** 167–189.

**Mazerolle, M. M.** 2020 AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. https://cran.r-project.org/package=AICcmodavg.

**Meyrom, K., Motro, Y., Leshem, Y., Aviel, S., Izhaki, I., Argyle, F. & Charter, M.** 2009. Nest-Box use by the barn Owl *Tyto alba* in a biological pest control program in the Beit She'an Valley, Israel. *Ardea* **97:** 463–467.

**Mikkola, H.** 1983. *Owls of Europe*. T & A.D. Poyser, London.

**Montoya, A., Cabodevilla, X., Fargallo, J.A., Biescas, E., Mentaberre, G. & Villanúa, D.** 2021. Vertebrate diet of the common kestrel (*Falco tinnunculus*) and barn owl (*Tyto alba*) in rain-fed crops: implications to the pest control programs. *Eur. J. Wildl. Res.* **67:** 79.

**Negro, J.J., Ferrer, M., Santos, C. & Regidor, S.** 1989. Selección de aves-presa por la lechuza. *Ardeola* **36:** 206–210.

**Newton, I.** 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Conserv.* **70:** 265–276.

**Paz-Luna, A., Bintanel, H., Viñuela, J. & Villanúa, D.** 2020. Nest-boxes for raptors as a biological control system of vole pests: High local success with moderate negative consequences for non-target species. *Biol. Control* **146:** 104267.

**Quinn, J.L. & Kokorev, Y.** 2002. Trading-off risks from predators and from aggressive hosts. *Behav. Ecol. Sociobiol.* **51:** 455–460.

**Quinn, J.L., Prop, J., Kokorev, Y. & Black, J.M.** 2003. Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum. *Anim. Behav.* **65:** 297–307.

**Quinn, J.L. & Ueta, M.** 2008. Protective nesting associations in birds. *Ibis* **150:** 146–167.

**R Core Team**. 2022. *R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing*. Vienna, Austria.

**Ricklefs, R.E.** 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9:** 1–48.

**Serrano, D.** 1998. Diferencias interhábitat en la alimentación del Búho Real (*Bubo bubo*) en el valle medio del Ebro: efecto de la disponibilidad de Conejo (*Oryctolagus cuniculus*). *Ardeola* **45:** 35–46.

**Serrano, D., González-Forero, M., Donázar, J.A. & Tella, J.L.** 2004. Dispersal and social attraction affect colony selection and dynamics of lesser kestrels. *Ecology* **85:** 3438–3447.

**Sugiura, N.** 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. *Commun. Stat. Theory Methods* **7:** 13–26.

**Szep, D., Klein, A. & Purger, J.** 2019. Investigating the relationship between the prey composition of Barn Owls (*Tyto alba*) and the habitat structure of their hunting range in the Marcal Basin (Hungary), based on pellet analysis. *Ornis Hungarica* **27:** 32–43.

**Tella, J.L. & Blanco, G.** 1993. Possible predation by little Owl *athene noctua* on nesting Red-billed choughs *pyrrhocorax pyrrhocorax*. *Bult. G.C.* **10:** 55–57.

**Tella, J.L., Pomarol, M., Muñoz, E. & López, R.** 1993. Importancia de la conservación de los mases para las aves en los Monegros. *Alytes* **6:** 335–350.

**Torre, I., Tella, J.L. & Ballestero, T.** 1997. Tendencias tróficas de la Lechuza Común (*Tyto alba*) en la Depresión Media del Ebro. *Hist. Animal* **3:** 34–44.

**Troscianko, J., Wilson-Aggarwal, J., Stevens, M. & Spottiswoode, C.N.** 2015. Camouflage predicts survival in ground-nesting birds. *Sci. Rep* **6:** 19966.

**Zuberogoitia, I.** 2000. La influencia de los factores meteorológicos sobre el éxito reproductor de la Lechuza común. *Ardeola* **47:** 49–56.