RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Natural cavity restoration as an alternative to nest box supplementation

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Nest box supplementation is widely used to increase nest-site availability for cavity nesting animals but the analysis of its effects on individuals breeding in natural cavities is often neglected. This study offers a novel restoration technique to revert abandonment of natural breeding sites by a secondary cavity avian bird, the European roller (*Coracias garrulus*), and other ecologically similar species. We found that, after a program of nest box supplementation with ensuing monitoring, rollers gradually abandon nesting in natural and seminatural cavities in favor of nest boxes because the latter are of higher quality. We examine whether reducing the entrance size of natural and seminatural cavities improves their suitability for rollers. A 6-year program reduced the diameter of the entrance of sandstone cavities and cavities in bridges. This led to a high occupancy (59%) of manipulated nest-sites. Manipulated sites were most frequently occupied by rollers and little owls (*Athene noctua*) (31 and 18% of sites, respectively). Manipulation did not affect clutch size or fledgling success. We suggest that nest-site diversity and nesting in natural cavities should be preserved to reduce nest box dependence. Our study illustrates the value of nest boxes when used alongside restoration of natural breeding sites and provides insights for the management of natural cavities.

Key words: natural cavity, nest box, nest hole size, nest-site limitation, restoration technique

Implications for Practice

- The negative effects of nest box programs can be difficult to detect over the short term.
- Identification of key features of nest-site suitability may improve the attractiveness of natural and seminatural cavities for secondary cavity nesters.
- The restoration technique proposed here can be implemented in a range of human-altered landscapes where nest-site limitation for cavity nesting birds is usually severe.
- Nest box programs alongside restoration of natural cavities promotes nest-site diversity and reduces nest box dependence.

Introduction

Wild animals require from their habitats food and water resources, shelter from weather and predators, and space to breed. A body of evidence emphasizes that the availability of safe nest-sites is a limiting factor for many populations of cavity-using organisms, mainly mammal and bird species (Newton 1994, 1998; Bunnell 2013) but also reptiles and insects (Souter et al. 2004; Friedrich & Philpott 2009). Human activity, e.g. land clearance and managed tree removal, frequently results in the decline of large old trees and the subsequent decrease of nesting sites (Gibbons et al. 2008; Le Roux et al. 2014; Plieninger et al. 2015). As a result, many cavity-using vertebrates are currently threatened (Bunnell 2013; Lindenmayer et al. 2017). Not surprisingly, nest-site supplementation by addition of nest boxes has become an increasingly common restoration strategy in modified landscapes, mainly in forested areas (Franzreb 1997; Harper et al. 2005; Goldingay et al. 2015; Le Roux et al. 2016*a*). Nest box supplementation has been reported to have economic, sociological, and scientific benefits (Møller 1989; Jedlicka et al. 2011) as well as population increases of threatened species (e.g. Václav et al. 2011; Berthier et al. 2012; Kiss et al. 2017). However, a number of shortfalls have also been reported: nest boxes are sometimes regarded as ecological traps (Schlaepfer et al. 2002; Klein et al. 2007; Rodríguez et al. 2011) and, at the population scale, nest box programs may segregate spatially birds of various quality (Rodríguez et al. 2011), leading to negative changes in local demography (Gauthier & Smith 1987; Petty et al. 1994). The local responses of cavity-nesting fauna to nest box addition are not well-known (Beyer & Goldingay 2006; Goldingay & Stevens 2009). To date, only limited research has tested

Author contributions: FV conceived the idea; all authors collected the data and conducted the research; FV, RV, JV wrote the paper; RV analyzed the data; MAC-T, TM contributed substantial resources.

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doi: 10.1111/rec.12841
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12841/suppinfo

empirically how habitat supplementation efforts affect wildlife responses at the local and landscape scales (but see Von Post & Smith 2015; Lindenmayer et al. 2016). A preference for artificial nest-sites over natural ones has been reported (Newton 1994; Llambías & Fernández 2009; Rodríguez et al. 2011; Singh et al. 2016). This could lead to abandonment of natural nest-sites after nest box installation. A need for alternative techniques has therefore been stressed to improve the quality of artificial cavities (e.g. Klein et al. 2007; Rueegger 2017).

Innovative alternatives to nest box supplementation replicating natural habitat structures could prove advantageous, e.g. artificial tree cavity creation. Although their side effects are largely unknown, methods such as chainsaw cavity creation may be more ecologically sustainable and cost-effective over the long term, and may also offer important advantages for wildlife (Rueegger 2017 and references therein). These methods also need to be guided by a proper understanding of which fine-scale, local, and landscape-level attributes bear an influence on nest-site selection (Le Roux et al. 2016*b*). Nest entrance size is an important feature. Selection pressures, like predation and competition over limited nest-sites, may prime cavities where the entrance is just large enough for entry (Goldingay & Stevens 2009; Le Roux et al. 2016*b*). Most alternatives to nest box supplementation focus on forest fauna (Rueegger 2017 and references therein) whereas organisms breeding in other habitats are more poorly known.

Burrow-dwelling animals are distinct types of cavity users for their particular nest-site requirements (e.g. soil composition, see Heneberg 2009). Many of them frequently rely on other species—ecological engineers (Casas-Crivillé & Valera 2005)—for suitable roosting or breeding places. This is because natural cavities are rare and, like forests, are badly altered by human activity (Valera et al. 2011). Artificial nest-sites for burrow-nesting species must meet both these species' requirements and also specific criteria such as resistance to collapse. Most of the research in this field is about burrow-nesting seabird and owl species nesting in artificial nest-sites (Collins & Landry 1977; Priddel & Carlile 1995; Smith & Belthoff 2001; Bolton et al. 2004; Sutherland et al. 2014; Bourgeois et al. 2015). The efforts for the conservation of burrow-dwelling animals mainly address habitat changes like slope management (Moffatt et al. 2005; Heneberg 2009, 2012; Wang et al. 2009). These changes benefit excavating birds, secondary burrow users, and their associated fauna (Heneberg 2012). Whereas some burrow-nesting bird species can also use nest boxes, natural cavities potentially offer greater thermoregulatory benefits (Ar & Piontkewitz 1992; Lill & Fell 2007; Amat-Valero et al. 2014). This may be crucial for some species, considering interspecific differences in heat tolerance (Catry et al. 2015). Yet, we do not know of any specific actions for secondary cavity burrow-nesting birds aiming at preserving the diversity of nest-site types.

Avian communities in southeastern Spain are more diverse in dry watercourses than in shrub steppes due to the presence of certain cavity-nesting species (Valera et al. 2011). The distribution and abundance of these species depends on the availability of sandstone nest cavities carved by other birds (European bee-eaters, *Merops apiaster*) (Casas-Crivillé & Valera 2005). The scarcity of suitable nest-sites increases both intra and interspecific competition for these cavities (Václav et al. 2011). Nest-site scarcity is particularly severe for trans-Saharan migrants, such as the European roller, *Coracias garrulus* (hereafter roller), as it arrives relatively late in the breeding season. Nest box supplementation confirmed nest-site limitation for this species, and resulted in a population increase by 56% after 5 years (Václav et al. 2011).

This paper builds on previous research to explore the impact of a 13-year nest box supplementation program on nest-site use by rollers. We study whether other factors than nest-site limitation may account for nest-site selection and apparent desertion of otherwise suitable natural breeding sites. We hypothesize that nest entrance size is a critical feature of nest-site suitability for rollers, such that large entrances make cavities less attractive than entrances of the size of the bird. We also suggest a method for an enhanced use of natural cavities by rollers and other burrow-nesting species based on smaller entrance sizes in natural cavities. If rollers desert natural cavities according to nest-site suitability (e.g. in nest boxes), use of natural cavities should increase after increasing their attractiveness by means of nest entrance manipulation. To ascertain whether this has any effect on breeding performance, we examine the breeding parameters of rollers nesting in manipulated and nonmanipulated nest-sites over the course of 6 years.

Methods

Study Site and Species

The study area (approximately 50 km^2) lies in the Desert of Tabernas (Almería, SE Spain, 37.08°N, 2.35°E). The landscape is mostly open shrubland with olive and almond groves interspersed among numerous dry riverbeds. The climate is semiarid Mediterranean with a strong water deficit in the summer months. The mean annual rainfall is approximately 230 mm, with high interannual and intra-annual variability (Lázaro et al. 2001). The average annual temperature is 18°C, with mild interannual oscillations and significant intra-annual fluctuations (Lázaro et al. 2004).

The European roller is a migratory bird that arrives at its breeding grounds in the study area in the second fortnight of April, when resident, secondary cavity nesting birds like jackdaws (*Corvus monedula*), little owls, or common kestrels (*Falco tinnunculus*) are already settled. Rollers rear one brood per year (Cramp 1998). Only jackdaws have been observed evicting rollers from natural cavities in the study area. In contrast, rollers were observed expelling from nest boxes house sparrows (*Passer domesticus*), spotless starlings (*Sturnus unicolor*), and scops owls (*Otus scops*). The species is evaluated as "least concern", even if the population is thought to be declining (BirdLife International 2017), mainly due to the loss of suitable breeding habitats (Tokody et al. 2017). The little owl (*Athene noctua*) and the jackdaw are single-clutch, resident cavity nesters. Both are evaluated as least concern (BirdLife International 2017).

Figure 1. Manipulation of natural cavities in sandstone cliffs (left) and cavities in bridges (right) with plaster squares (left) and wooden frames (right).

Manipulation of Nest-Site Availability for Rollers and Occupancy Monitoring

Long-term manipulation of nest-site availability for rollers increased the number of nest boxes in the study area at 2-year intervals from 2005 until 2009 (2005 and 2006: 13 nest boxes; 2007 and 2008: 23 nest boxes; 2009: 54 nest boxes) (see Václav et al. 2011). The number of nest boxes available varied slightly between 2010 and 2017 (54–63 nests).

Nest boxes, sandstone cavities, and stone cavities in three bridges (50, 100, and 100 m long) used by rollers, kestrels, jackdaws, feral pigeons (*Columba livia*), little owls, and scops owls were monitored each year for occupancy by rollers and any other species.

Natural and Human-Made Cavity Manipulation

Nest-site availability limits the population of rollers in our study area (Václav et al. 2011, see also Avilés & Sánchez 2000 for open habitat areas). Many of the abundant cavities available in sandstone cliffs are too shallow or collapsed. Other cavities appear to be suitable but the appropriateness of natural cavities for rollers and other secondary cavity nesting birds is difficult to assess, as breeding was also recorded in suboptimal natural cavities (e.g. unstable cliffs, small breeding chambers, or large entrances that allowed harassing by jackdaws). Otherwise, rollers breed in natural cavities with a range of significant features (e.g. height aboveground: 2.0–6.1 m, length of the burrow: 0.4–2.1 m, entrance size–shortest diameter: 9–20 cm). Entrance size can be a particularly important nest attribute to reduce the likelihood of predation and to avoid competition with other secondary cavity nesters. The entrance of natural and human-made cavities was covered with a plate (hereafter lid) bearing a 6-cm diameter hole (i.e. the same diameter as used for nest boxes in this and other studies, see Bohuš 2007; Kiss et al. 2014). Cavities thus were of two entrance size classes: 6 cm and above 6 cm. We used two lid types: (1) 15 × 15 × 5 cm plaster squares with a central 6-cm diameter hole, fitted into the entrance of natural cavities and fixed with polyurethane foam, plaster, and stones (Fig. 1), and (2) 41 × 31 × 4 cm wooden frames with a door and a 6-cm diameter hole, attached to sandstone or bridge walls so the cavity entrance was the hole in the lid (Fig. 1), and sealed to the wall with polyurethane foam. The former allowed partial inspections of the cavity through the entrance hole, the latter allowed full nest content monitoring.

Cavities to be manipulated were selected according to two criteria: (1) they were located within usual breeding areas; and (2) they were potential nest-sites given their main features (cavity height, burrow, and breeding chamber dimensions). Among the cavities in sandstone cliffs meeting these requirements, 18 were selected at random. Some were abandoned cavities that had been used previously by rollers or little owls, others had never been used in the period 2005–2009.

Unlike sandstone cliffs, cavities in bridges are abundant (20–40 per bridge), easy to quantify, and all have similar physical properties and dimensions (entrance diameter > 15 × 20 cm, Fig. 1). Based on our dataset, the cavities used by any bird species 1 or 2 years before our manipulations were discarded to avoid any effect of inter or intraspecific habitat copying (Stamps 1988; Danchin et al. 1998; Doligez et al. 2003). We selected at random 12 of the remaining cavities in three different bridges (three, four, and five cavities) during the period 2013–2017.

Overall, lids were placed on 30 different cavities during the study period. Twelve plaster lids were placed in 2012 in sandy cliffs. In 2013, we replaced some plaster lids with wooden lids and 10 more wooden lids were installed both in cliffs and bridges. The lid was kept for 1 year in nine cavities, and for 2–6 years in the rest. Use of lids for several years allowed to see if the occupancy of handled cavities changed over time. In summary, 30 different cavities were manipulated in several years, that is 120 manipulated cavity-years. No artificial measures were used to attract rollers to cavities.

Breeding Parameter Monitoring

The study was conducted for six breeding seasons (2012–2017). Manipulated cavities, nest boxes, and nonmanipulated bridge cavities and sandstone cavities were inspected periodically (approximately every 2–6 days) for nest occupancy and breeding success. Nests were considered occupied if one egg was recorded. Cavities and nest boxes occupied by rollers were inspected more frequently (approximately every 2–4 days). The breeding parameters recorded were clutch size, and the number of nestlings and fledglings. Some breeding parameters (mainly clutch size) could not be monitored in some roller nests, particularly in nests with plaster lids. Detrimental effects on reproduction were measured compared to the breeding performance of rollers breeding in nest boxes, manipulated natural and seminatural cavities, and nonmanipulated natural and seminatural cavities.

Data Analysis

Temporal trends in roller breeding abundance for three nest types were built with generalized additive models (GAM) with Gaussian distribution (Zuur et al. 2009). Multivariate time series data were examined so that roller breeding abundance (number of breeding pairs) per each nest type was examined as the response variable, nest type was a categorical predictor, and abundance time series for each nest type were examined as smooth terms (Zuur et al. 2009). Temporal autocorrelation in abundance data was addressed by implementing the residual first-order autoregressive (AR-1) correlation structure. We also addressed differences in variances between nest types by considering the varIdent variance structure in additive models.

Frequency data of occupancy were examined with the *G* (likelihood ratio) test for occupancy patterns of manipulated nest-sites. In particular, we assessed interannual differences in overall manipulated nest-site occupancy and manipulated nest-site occupancy by the two most frequent occupant species, that is roller and little owl.

Nest-site occupancy of manipulated and nonmanipulated bridge cavities by rollers was examined with the *G* test. The test was done on pooled frequency data for all the bridges in order to increase sample sizes for individual categories. This is justified by the consistent pattern in nest-site occupancy across the bridges (see below).

We used linear mixed model (LMM) and generalized linear mixed model (GLMM) to examine differences in roller clutch size and fledging success (fledgling number to clutch size ratio) in the period 2012–2017 according to nest type: nest box, manipulated, and nonmanipulated natural and seminatural nest-site. In models for both response variables, we controlled for the random effect of nest identity and the random effect of year nested in cavity type (cavity type had three categories: nest boxes, sandstone cavities, and bridge cavities). LMM for clutch size was fitted by REML and the *t*-tests were conducted using Satterthwaite approximation to degrees of freedom. We assessed the distribution of clutch size data with a Cullen and Frey graph (Delignette-Muller & Dutang 2015). Gaussian distribution was found to be more appropriate than Poisson distribution. Fledgling success was assessed assuming binomial distribution and examined as the fledgling number to clutch size ratio with GLMM. GLMM was fitted by ML via Laplace approximation. The *p* values associated with post hoc comparisons for clutch size and fledging success were adjusted by the Tukey method.

All data were analyzed with R software (R Core Team 2016), binomial and Gaussian mixed models with the lme4 1.1–12 package (Bates et al. 2015), and *G* tests with the RVAideMemoire 0.9–62 package (Hervé 2016).

Results

The Effect of Nest Box Supplementation on Nest Occupancy

The number of roller pairs breeding in nest boxes increased sharply until 2011, where the increase decelerated (GAM, $p < 0.001$, Table S1, Fig. 2A). In contrast, both the number of roller pairs breeding in sandstone cavities and bridge cavities without wooden/plaster lids decreased significantly in the same period (GAM, $p < 0.001$ in both cases, Fig. 2B and 2C, Table S1). The decrease in breeding abundance would be slightly less pronounced in sandstone cavities and bridge cavities, even if still highly significant, if natural and seminatural cavities with wooden/plaster lids were included in the analysis (Table S2).

Occupancy of Manipulated Nest-Sites, 2012–2017

Five species occupied manipulated nest-sites (Table 1). The total occupancy of manipulated nest-sites by all species was 59% (71/120 manipulated nest-site-years; occupancy range for 6 years = 36–73%). The occupancy of manipulated nest-sites did not differ among years ($G_5 = 8.48$, $p = 0.13$). Eight out of 30 manipulated nest-sites were never used (four, one, two, and one of the unused nest-sites being available for 1, 3, 4, and 5 years, respectively). Four manipulated nest-sites were occupied for five running years. The rest of used manipulated nest-sites were occupied intermittently.

Manipulated nest-sites were occupied mainly by rollers and little owls (Table 1). The total occupancy of manipulated nest-sites by rollers was 31% (37/120 manipulated nest-site-years; occupancy range for 6 years = 17–36%), with the species occupying 15 out of 30 different manipulated nest-sites at least once. The occupancy of manipulated nest-sites by rollers did not differ among years ($G_5 = 2.03$, $p = 0.84$). Little owls occupied 18% of the manipulated nest-sites (Table 1) (22/120 manipulated nest-site-years; occupancy range for 5 years = 9–23%). As with rollers, the occupancy of manipulated nest-sites by little owls did not differ among years ($G_5 = 2.94$, $p = 0.71$). Alternate occupancy between years of the same manipulated nest-site by rollers and little owls occurred in six manipulated nest-sites.

The total occupancy of manipulated nest-sites by jackdaws was low (7/120 manipulated nest-site-years) and occurred mainly in nest-sites with plaster lids after enlarging entrance holes by pecking (6/7 cases).

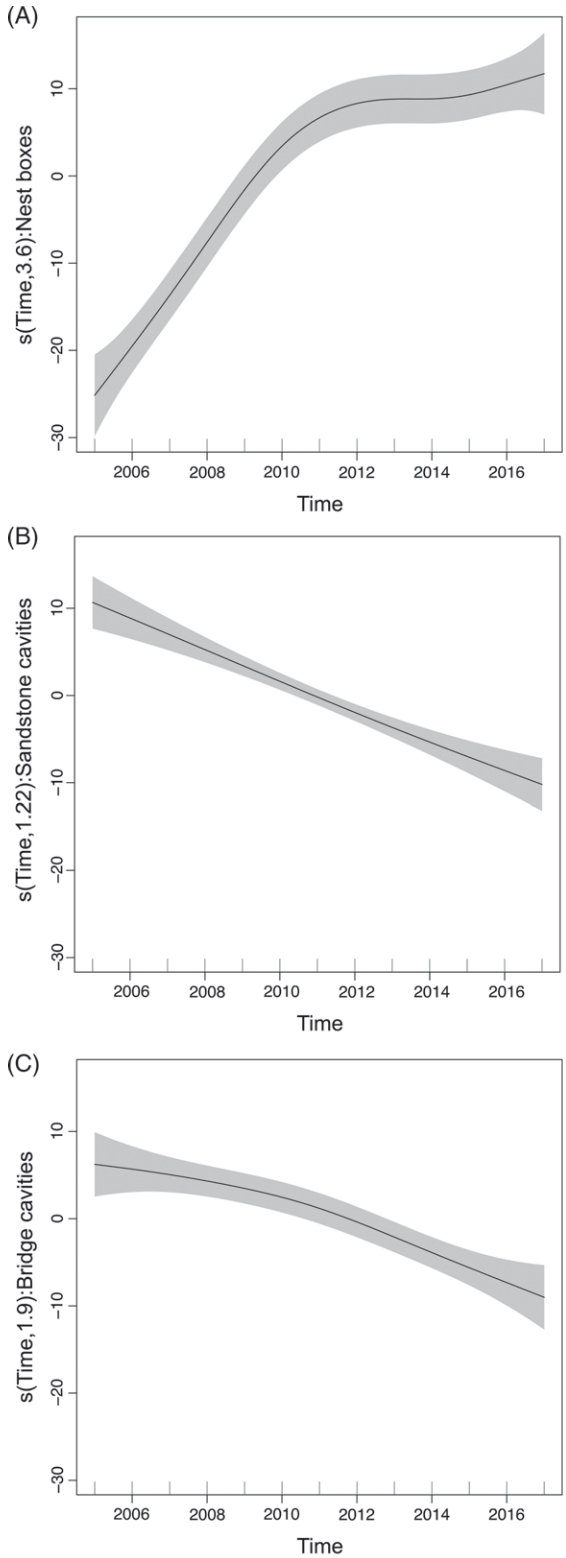

Figure 2. Generalized additive models on the breeding abundance of European roller *Coracias garrulus* pairs nesting in three different cavity types: (A) nest boxes, (B) sandstone cavities, and (C) bridge cavities over the period of 13 years in SE Spain. Lines represent fitted values for smooth terms with shaded regions showing areas delimited by ±95% CI.

Table 1. Occupancy of manipulated nest-sites during 2012–2017. During this period, 30 cavities were manipulated, resulting in 120 manipulated nest-site-years. Both the total number of manipulated nest-sites occupied (nest-site-years) and the total number of different manipulated nest-sites occupied are shown.

Bird Species	*No. of Manipulated Nest-Site-Years Occupied*	*No. of Manipulated Nest-Sites Occupied*
European roller (*Coracias garrulus*)	37	15
Little owl (*Athene noctua*)	22	9
Jackdaw (*Corvus monedula*)	7	5
Scops owl (*Otus scops*)	4	3
Black wheatear (*Oenanthe leucura*)	1	1

Table 2. Percentage of breeding attempts by European roller at manipulated and nonmanipulated cavities of three bridges (data pooled for the years when manipulated cavities were available in the bridges).

Bridge ID	*% (No. of Breeding Attempts in Nonmanipulated Cavities/No. of Available Nonmanipulated Cavities)*	*% (No. of Breeding Attempts in Manipulated Cavities/No. of Available Manipulated Cavities)*
Bridge 1	3.5 (4/114)	36.4 (4/11)
Bridge 2	0.0 (0/77)	47.8 (11/23)
Bridge 3	13.1 (25/191)	66.6 (6/9)
Total	7.6 (29/382)	48.8 (21/43)

Patterns of Cavity Occupancy in Bridges by European Rollers, 2012–2017

The total occupancy of manipulated bridge cavities by rollers was significantly higher than that of nonmanipulated cavities (21/43 vs. 29/382; $G_1 = 43.02$, $p < 0.001$; Table 2). None of the eight manipulated bridge cavities used by rollers had been occupied by the species in the two breeding seasons before cavity manipulation. Six out of eight manipulated bridge cavities used by rollers were occupied the first year following cavity manipulation.

The Effect of Nest-Site Manipulation on the Breeding Performance of the European Roller, 2012–2017

Clutch size did not differ among cavities with and without manipulated entrance and nest boxes (type-3 test: $F_{[2, 19.21]} = 2.23$, $p = 0.13$, Table S3A). Post hoc comparisons revealed that natural and seminatural cavities with a manipulated entrance tended to show larger clutches than such cavities without a manipulated entrance (manipulated vs. nonmanipulated cavities: estimate ± SE = 0.50 ± 0.24, $t_{114.22} = 2.08$, $p = 0.098$; manipulated cavities vs. nest boxes: estimate ± SE = 0.38 ± 0.24, $t_{22.65} = 1.55$, $p = 0.29$; nonmanipulated cavities vs. nest boxes: estimate ± SE = −0.12 ± 0.21, $t_{13.87} = -0.58$, $p = 0.83$). Finally, fledgling success (fledglings number to clutch size ratio) did not differ significantly among nest boxes, manipulated cavities, and nonmanipulated cavities (type-3 test: $\chi^2 = 2.47$, $p = 0.29$; Table S3B).

Discussion

Unvalidated conservation techniques can cause serious damage (Martínez-Abraín et al. 2004), especially for threatened species. Nest box supplementation is the most common technique for increasing breeding opportunities of cavity-nesting organisms. Its effectiveness, pros, and cons are currently under debate (Goldingay et al. 2015; Le Roux et al. 2015; Lindenmayer et al. 2016, 2017; Goldingay 2017; Rueegger 2017) but some of their effects are admittedly poorly known, e.g. wildlife responses at local and landscape scales (Von Post & Smith 2015).

Václav et al. (2011) suggested that nest-site limitation could explain the success of nest box supplementation in the study area. Here we analyze the effects of a long-term nest box installation program. During the first 5 years of the program, the use of natural cavities did not apparently decrease in absolute terms (Václav et al. 2011). From then onwards, the absolute number and the proportion of rollers breeding in natural cavities and in human constructions has decreased, leading to most of the population breeding in nest boxes. This study adds to our previous research that the success of the nest box scheme may not only reflect nest-site limitation but also a generally lower suitability of available natural nest-sites.

Our results support the hypothesis that nest entrance size is a critical feature of nest-site suitability for rollers and that natural cavities increase their attractiveness after entrance manipulation. Reduction of the entrance size of natural and seminatural cavities resulted in rapid and continuous occupancy by rollers (and other species), therefore slowing down the interannual decrease in the number of rollers breeding in natural and seminatural cavities. Moreover, occupancy was higher in manipulated cavities in bridges than in nonmanipulated cavities. These results suggest that nest boxes are preferred to natural and seminatural cavities because the latter are perceived as inferior nest-sites. Adequate entrance size (proportional to the body size of the target species) is a critical feature of nest-site suitability (Le Roux et al. 2016*b*). Nest boxes and cavities with small entrances can be seen as more suitable breeding sites because they provide increased protection against competitors and predators, which are the main cause of nest failure among birds (Martin 1993), including cavity nesters (Martin & Li 1992).

Except for some seabirds and owls (Smith & Belthoff 2001; Bourgeois et al. 2015), techniques aimed at cavity-nesting birds breeding in sandstone cavities and burrows involve mainly habitat management (e.g. sandy slope restoration, Moffatt et al. 2005; Heneberg 2009; Wang et al. 2009). We are not aware of any management schemes to encourage cavity-nesting species to use nest-sites other than nest boxes. Here, we suggest a method to promote persistence and diversification of nesting habitats by manipulating the entrance size of natural and human-made cavities. This method can prove a useful, alternative cavity-provision tool because: (1) it may promote the use of diverse cavity types. Nest-site choice may be affected by previous experience (Newton 1994; White et al. 2002), so the increased number of birds breeding in nest boxes could reduce the probability of occupancy of other cavity types; (2) manipulation did not affect reproductive performance and rollers nesting in manipulated cavities even tended to produce larger clutches compared to those from nonmanipulated cavities; (3) it has important advantages compared to nest box schemes. Nest boxes may have shortcomings, e.g. short lifespan (e.g. Bender & Irvine 2001; Lindenmayer et al. 2002, 2009), unfavorable microclimate (Amat-Valero et al. 2014; Maziarz et al. 2017), and unsuitable designs for the cavity requirements of the target species (Lindenmayer et al. 2016, 2017; Le Roux et al. 2015; Rueegger 2016, but see Goldingay et al. 2015). Overall, use of natural cavities (with the smallest possible addition of artificial parts) allows lid-manipulated nest-sites to offer a better microclimate (Amat-Valero et al. 2014), lower ectoparasite loads (Calero-Torralbo et al. 2013), higher attractiveness for various cavity-dependent species (e.g. little owl), and low conspicuousness to predators (soil sedimentation sealed gaps around the lids that more closely resembled a natural cavity).

Availability of natural nests, and thus of a range of breeding sites, is important because it reduces the dependence of birds on human-made structures. This technique could be implemented to a variety of human-altered landscapes where nest-site limitation for cavity nesting birds is usually severe (Wiebe 2011) and to specific species to manage or reclaim their breeding habitats (see, e.g. Cockle et al. 2008 for a case involving parrots in Argentinian Atlantic forests).

Our knowledge of the consequences of nest box programs is incomplete, partly because, as shown here, they can be difficult to identify based on short-term programs. Even if successful, they should not be considered a permanent solution. Animal populations depending on nest boxes are not self-sustainable because they require continuous investment in personnel and operating expenses. The unavailability or decay of these nesting-sites may make their depending populations decline drastically (Taylor 1994; Mainwaring 2015). The causes of nest-site limitation must therefore be simultaneously addressed by means of habitat restoration (Sutherland et al. 2014; Lindenmayer & Laurance 2017). Nesting habitat restoration and a higher nesting habitat diversity should be a priority for breeding habitat management. Nest boxes can play a major role when used alongside restoration of natural breeding sites. Besides their immediate practical value, nest boxes can also reveal habitat selection patterns for adequate management or restoration of natural cavities.

Acknowledgments

We thank J. Avilés, J. Rodríguez, and D. Parejo for fruitful comments and M. Amat for fieldwork assistance. L. Manresa contributed to lid design. We thank Dr. D. Lindenmayer and an anonymous referee for their valuable suggestions. F.V. received financial support from the Spanish Ministry of Science and Innovation (CGL2008-00562), the Spanish Ministry of Economy, Industry and Competitiveness (CGL2014-55969), and the European Regional Development Fund. R.V. was supported by a VEGA grant of the Ministry of Education of the Slovak Republic (No. 2/0008/16). J.V. was funded by the Spanish Ministry of Economy, Industry and Competitiveness (predoctoral grant BES-2015-075951). None of these agencies had input into the content of this manuscript or required approval of the manuscript before submission or publication. All trapping and handling undertaken in this study was approved by the Consejería de Medio Ambiente, Junta de Andalucía.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Generalized additive model examining breeding abundance time series for three nesting cavity types (sandstone cavities, bridge cavities, nest boxes) in European roller *Coracias garrulus* in SE Spain excluding the pairs nesting in sandstone cavities and bridge cavities fitted with wooden lids.

Table S2. Generalized additive model examining breeding abundance time series for three nesting cavity types (sandstone cavities, bridge cavities, nest boxes) in European roller *Coracias garrulus* in SE Spain including the pairs nesting in sandstone cavities and bridge cavities fitted with wooden lids.

Table S3. Linear (LMM) and generalized (GLMM) mixed models on differences in clutch size and fledging success among three nest types.

Coordinating Editor: Peter Cale

Received: 18 March, 2018; First decision: 5 May, 2018; Revised: 8 June, 2018; Accepted: 8 June, 2018; First published online: 4 July, 2018