Nest-site selection by the European roller (*Coracias garrulus*) in southern France.

Simon J. Butler

Department of Biology, University of York, York, YO10 5YW, UK

Summary

1. Between 18th June 2001 and 23rd July 2001, the nests of 10 pairs of European roller (*Coracias garrulus* L.) were located at the Marais de L'Ilon, a partially drained marsh in the Bouches-du-Rhône, France. All nests were in abandoned green woodpecker (*Picus viridis* L.) cavities in live white poplar (*Populus alba* L.) trees.

2. The breeding density of 11.75 pairs km^{-2} represents the highest recorded breeding density of rollers in western Europe. Seven out of ten pairs bred in the narrow strip of riparian vegetation along the Canal de la Vallée des Baux. The minimum nest separation was 14 m and three pairs bred within a 40 m section of the canal bank.

3. To determine nest-site selection, the characteristics of nest-cavities were compared to those of potential but unoccupied nest-sites. It was assumed that characteristics contributed to nest-site selection if their means differed significantly between the two groups or if the occupied cavities exhibited significantly reduced variance.

4. Cavity selection was based on entrance width, hole height and the diameter at breast height (DBH) of the tree. Rollers also exhibited a strong preference for cavities with south-westerly or north-westerly aspects. There was no selection for tree height, diameter at hole height (DHH), cavity height, cavity depth, entrance height or entrance depth.

5. Cavity availability was determined by the activities of green woodpeckers, the excavator species, and by intra- and inter-specific competition, particularly for nest-sites. Nest box installation is recommended to consolidate the breeding population of rollers at the Marais de L'Ilon.

Key words: cavity characteristics; cavity-entrance orientation; entrance size; nest boxes; secondary cavity-nester.

Introduction

The European roller (*Coracias garrulus* L.) breeds throughout temperate, steppe and Mediterranean zones from north-west Africa to the western Himalayas (Cramp & Simmons 1988). In the western Palearctic region, their breeding populations are highly fragmented and generally declining (Tucker & Heath 1994). Over the past century, rollers have become extinct in Denmark, Finland, Sweden and Germany (Glutz von Blotzeim & Bauer 1980; Samwald & Štumberger 1997; Avilés *et al*. 1999) and their populations are seriously threatened in Poland (Sosnowksi & Chmielewski 1996) and Austria (Samwald & Samwald 1989). As a consequence, the species is currently listed under Annex 1 of the EC Birds Directive (EC 79 / 409).

Information relating to the breeding biology and ecology of the roller in Europe is scarce, with only general descriptions of their principle habitats available (e.g. Glutz von Blotzeim & Bauer 1980; Cramp & Simmons 1988). The loss of suitable habitat as a consequence of agricultural intensification has been highlighted as the main cause of the roller's decline (Tucker & Heath 1994; Bousquet 1999). However, it is unclear whether it is the loss of foraging habitats or suitable nest-sites that has had a greater impact on breeding populations.

Research has shown that the breeding density of many insectivores is related to food availability and the presence of suitable foraging habitat (e.g. Li & Martin 1991; Valido, Telleria & Carrascal 1994; Robertson, Jarvis & Day 1995). Recent studies have suggested that rollers select nest location on the basis of prey availability, prey size and the presence of natural perches from which to hunt (Centre Ornithologique du Gard 1994; Avilés & Costillo 1998; Avilés, Sánchez & Parejo 2000). The roller's decline in western Europe parallels widespread changes in agricultural practices, where the conversion of original steppe into cereal fields, market gardens and orchards and an increased use of pesticides has led to a reduction in prey availability (Samwald and Štumberger 1997).

However, Avilés *et al.* (2000) propose that it is the loss of natural nest-sites, as a consequence of agricultural intensification and woodland management, that has been the major cause of the roller's decline. Rollers are obligate, secondary hole-nesters, i.e. cavity-nesters that do not excavate their own cavity (Tucker & Heath 1994). Although they will make use of sandy banks and walls in their southern range (Samwald & Štumberger 1997), rollers nest primarily in natural tree cavities or the nest-holes of black woodpecker (*Drycopus martius* L.) or green woodpecker (*Picus viridis* L.) (Cramp & Simmons 1988; Bousquet

1999). The majority of tree cavities are located in dead wood, so the number of available holes increases with the age of the trees (Peace 1962). However, woodland management typically involves the removal of dead or damaged trees and many mature trees have been lost from hedgerows. Natural nest-site availability throughout much of Europe has therefore been substantially reduced (Waters, Noon & Verner 1990; Newton 1994). There is both circumstantial and experimental evidence to support the theory that the breeding range and population size of cavity-nesting birds can be limited by nest-site availability (e.g. Slagsvold 1978; Munro & Rounds 1985; Li & Martin 1991; Smith 1997).

In many situations where natural nest-site availability limits a breeding population, the installation of artificial nest boxes can lead to population increases (East & Perrins 1988; Avilés & Sánchez 2000). However, it is important that the breeding ecology of the target species is understood. Several cavity characteristics, such as cavity size (van Balen *et al*. 1982), entrance size (van Balen *et al*. 1982; Rendell & Robertson 1989) and cavity-entrance orientation (Raphael 1985; Rendell & Robertson 1994), have been shown to influence nest-site selection by cavity-nesters. Since different species select for different characteristics in natural cavities, they also show preferences for boxes with different dimensions, hole sizes, aspect and surrounding habitat (Newton 1994). Consequently, to maximise the benefits of nest boxes, their design and positioning must reflect the preferences of the target species. Although rollers will make use of artificial nest-sites (Sosnowksi & Chmielewski 1996; Avilés *et al*. 2000), little is known about the importance of different cavity characteristics for nest-site selection and therefore the most appropriate design and location of nest boxes.

The first aim of this study was to determine the breeding density of rollers at the Marais de L'Ilon in the Bouches-du-Rhône, France. The second aim was to identify the important cavity characteristics used in nest-site selection to determine the most appropriate design and location of nest boxes.

Study site

This research was undertaken at the Marais de L'Ilon, a partially drained marsh in the Vallée des Baux (43°41' N, 4°46' E), southern France. The valley is bounded by the Alpilles hills to the north and the semi-desert plain of La Crau to the south. The study site covers 85 ha, including 63 ha of open pasture and 22 ha of woodland. The wooded area is composed primarily of holm oak (*Quercus rotundifolia* L.) 60.5% and poplar (*Populus* spp.) 25.5% with smaller amounts of pine (*Pinus* spp.), elm (*Ulmus* spp.) and willow (*Salix* spp.).

Methods

Breeding density

The study site was visited daily between 18th June 2001 and 23rd July 2001, with surveys being completed between 0700 and midday or between 1600 and 1900. The first stage involved a combination of line transects and territory mapping, using a mapping technique similar to that advocated by the International Bird Census Committee (1969). The study site was surveyed evenly and the positions and activities of all rollers were plotted on a 1:5000 map (Marchant *et al*. 1990; Bibby, Burgess & Hill 1992). This map was then analysed to identify the location of roller breeding territories. Within each territory, the area with the highest intensity of display flights and territorial vocalisations was identified as the most likely nest location (Sosnowski & Chmielewski 1996).

Having located all the breeding territories, the areas identified as probable nest-sites were visited to pinpoint nest-cavity location. Cavity use was confirmed by the observation of an adult entering a cavity or of a food pass to an incubating bird or chicks. Nests were visited regularly through the season to monitor their progress. Breeding activity was assumed to have ceased when no activity at the nest-site was observed during a three-hour watch.

Cavity characteristics

Once the rollers had left their nest-sites, the cavities were accessed and a number of measurements taken. Firstly, tree species, height and diameter at breast height (DBH) were recorded. Cavity dimensions measured were (1) hole height, (2) cavity-entrance orientation (recorded in 45^o octants), (3) diameter at hole height (DHH), (4) entrance height, (5) entrance width, (6) entrance depth, (7) cavity height and (8) cavity depth (Fig. 1). Cavity height was measured using a plumb bob lowered into the cavity. The distance to the nearest nest-cavity was also measured.

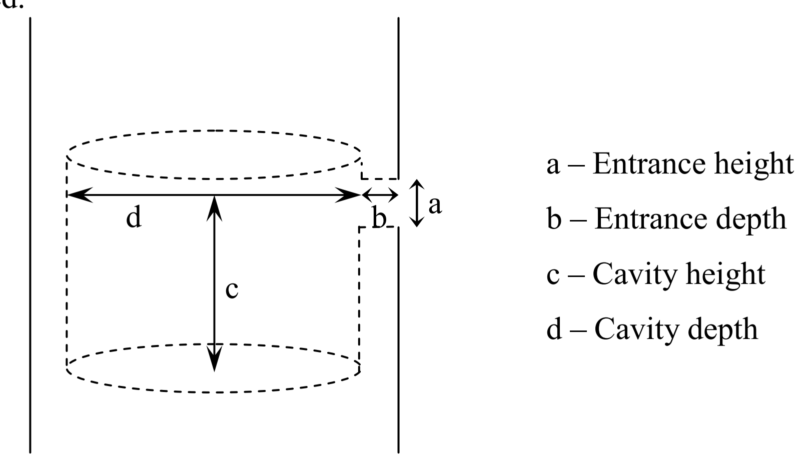

Figure 1. Schematic representation of a tree cavity showing some of recorded measurements.

An intensive survey of the study site was then completed to locate all potential but unoccupied roller nest-sites. Using the data collected from the occupied nest-cavities, only cavities with an entrance height and width greater than 4.5 cm were assumed to be potential sites. For cavities that could be reached with an 8 m ladder, the tree and cavity measurements listed above were recorded. If the cavity could not be accessed, trees species and height, DBH, hole height and entrance orientation were recorded. Finally, the DBH and height of 50 randomly selected trees, without cavities, were recorded.

DATA ANALYSES

To evaluate nest-site selection, the characteristics of occupied and unoccupied cavities were analysed using SPSS software (Norusis 1993). Data were tested for normality using the Kologomorov-Smirnov test. Measurements of tree height, entrance height, entrance depth, cavity height and cavity depth were compared using one-way analysis of variance (ANOVA). Data for DBH, hole height and entrance width did not meet the assumptions of this test concerning homogeneity of variance (Levene's test, $P < 0.05$) and were therefore analysed using the equivalent, non-parametric Mann-Whitney *U* test. The relationships between tree and cavity characteristics were tested using Spearman's rank coefficient tests. The entrance orientations of occupied and unoccupied cavities were analysed using the chi-squared test, with a random distribution between each 45^{o} octant taken as the expected value.

Results

Between 18th June 2001 and 23rd July 2001 the nest-cavities of ten pairs of rollers were located on the study site, giving a breeding density of approximately 11.75 pairs km^{-2}. Seven out of ten pairs bred in the narrow strip of riparian vegetation along the southern edge of the Canal de la Vallée des Baux that borders the study site. This represented a linear density of 5.6 pairs km^{-1}.

All nest were in abandoned green woodpecker holes in live white poplar (*Populus alba* L.) trees. The mean nest-cavity height (± SD) was 5.33 ± 1.41 m, with the lowest at 2.25 m and the highest at 7.50 m. The mean distance between nest-sites was 166.4 ± 204.1 m. The minimum separation was 14 m and three pairs bred within a 40 m section of the canal bank. Additional cavity characteristics are summarised in Table 1.

Table 1. Summary of tree and cavity characteristics for occupied and unoccupied sites. Values represent mean ± SD.

Variable	Occupied cavities (n = 10)	Unoccupied cavities (n = 37)	Total (n = 47)
Tree height (m)	15.00 ± 3.69	14.39 ± 3.66	14.52 ± 3.63
Hole height (m)	5.33 ± 1.41	5.70 ± 2.45	5.62 ± 2.26
DBH (cm)	49.22 ± 10.42	50.31 ± 19.06	50.08 ± 17.49
DHH (cm)	37.78 ± 8.04	35.41 ± 9.31	35.98 ± 8.99
Entrance height (cm)	5.39 ± 0.51	5.32 ± 0.65	5.34 ± 0.62
Entrance width (cm)	5.88 ± 0.42	5.54 ± 0.70	5.62 ± 0.65
Entrance depth (cm)	7.24 ± 2.05	7.14 ± 2.64	7.16 ± 2.49
Cavity height (cm)	23.18 ± 19.67	22.90 ± 19.38	22.97 ± 19.37
Cavity depth (cm)	22.50 ± 6.67	18.73 ± 6.35	19.67 ± 6.55

DBH – diameter at breast height; DHH – diameter at hole height

A further 37 unoccupied cavities, which met the assumptions relating to entrance hole size for potential nest-sites, were also found. There were therefore 47 available cavities at the Marais de L'Ilon, with an occupancy rate of 21.3 %. The characteristics of the unoccupied cavities are also summarised in Table 1.

There were a number of significant relationships between tree and cavity characteristics. As expected, there were strong positive correlations between DBH and tree height ($r_s = 0.465$, $n = 47$, $P < 0.001$), DHH ($r_s = 0.495$, $n = 42$, $P < 0.001$) and hole height ($r_s = 0.421$, $n = 47$, $P = 0.003$). Tree DBH was negatively correlated with entrance height ($r_s = -0.472$, $n = 42$, $P = 0.002$). There were also strong correlations between entrance height and entrance width ($r_s = 0.467$, $n = 41$, $P = 0.002$) and between DHH and cavity depth ($r_s = 0.505$, $n = 40$, $P < 0.001$).

The mean DBH of all trees with suitable cavities, 50.08 ± 17.49 cm, and those with occupied cavities, 49.22 ± 10.42 cm, were both significantly greater than the mean DBH of trees without cavities, 29.80 ± 8.90 cm (Mann-Whitney *U* test, $U = 295$, $P < 0.001$ and $U = 31$, $P < 0.001$ respectively; Fig. 2). The mean height of trees with suitable cavities, 14.52 ± 3.63 m, and those with occupied cavities, 15.00 ± 3.69 m, were both significantly higher than that of trees without cavities, 13.22 ± 2.23 m (one-way ANOVA, $F_{1,95} = 4.584$, $P < 0.05$ and $F_{1,58} = 37.59$, $P < 0.001$ respectively).

There were no significant differences between occupied and unoccupied cavities for either DBH (Mann-Whitney *U* test, $U = 166$, $P = 0.636$) or tree height (one-way ANOVA, $F_{1,45} = 0.215$, $P = 0.645$). The variance in the DBH of trees with unoccupied cavities was significantly greater than that of trees with occupied cavities (Levene's test, $F_{1,45} = 5.09$, $P = 0.03$; Fig. 2).

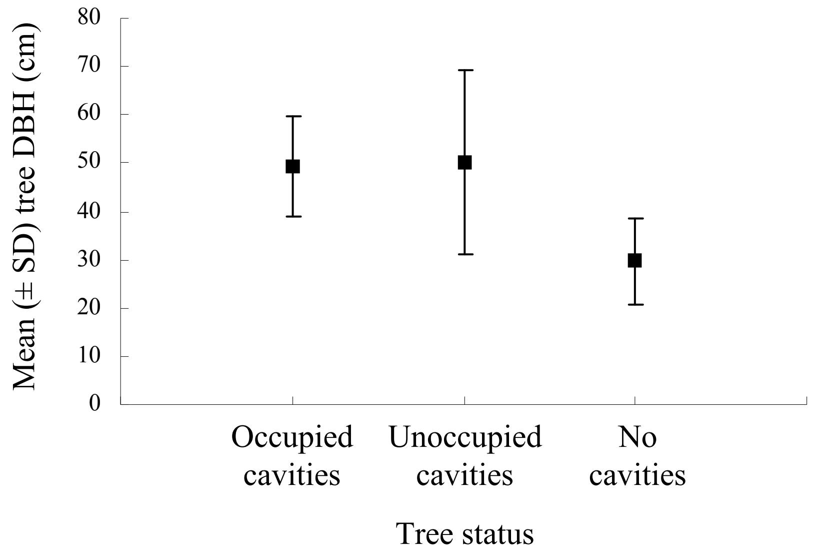

Figure 2. Mean diameter at breast height (DBH) of trees with occupied or unoccupied cavities and those with no cavities.

There were no significant differences between the DHH, entrance height, entrance depth, cavity height or cavity depth of occupied and unoccupied cavities (Table 2). There were also no significant differences between either the hole height or entrance width of occupied and unoccupied cavities (Mann-Whitney U test, $U = 184$, $P = 0.990$ and $U = 107$, $P = 0.151$ respectively). However, the variance in the measurements of these two characteristics was significantly lower in occupied cavities than in unoccupied cavities (Levene's test; hole height, $F_{1,45} = 7.106$, $P = 0.01$ and entrance width, $F_{1,39} = 4.591$, $P = 0.04$; Fig. 3).

Table 2. Results of one-way ANOVA on cavity characteristics of roller nest-sites and potential but unoccupied sites.

Variable	*F*	d.f.	*P*
DHH	0.523	1,40	0.474
Entrance height	0.097	1,39	0.757
Entrance depth	0.012	1,39	0.912
Cavity height	0.002	1,38	0.969
Cavity depth	2.587	1,38	0.116

DHH – diameter at hole height

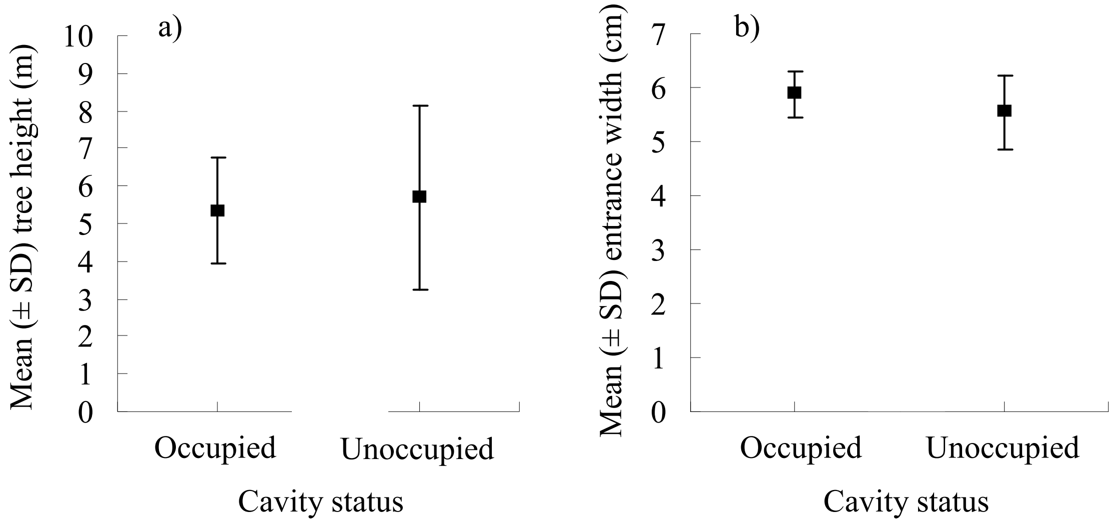

Figure 3. Comparison of a) tree height and b) entrance width between occupied cavities and unoccupied cavities.

The entrance orientations of available cavities were randomly distributed between the 45° octants of compass direction (χ^2 = 9.53, d.f. = 7, P = 0.220). This suggests that green woodpeckers, the cavity excavators, exhibit no preference for cavity-entrance orientation. However, the entrance orientations of the cavities chosen by rollers were not randomly distributed with respect to compass direction (χ^2 = 17.51, d.f. = 7, P = 0.014). Rollers exhibited a strong preference for cavities with either a south-westerly or north-westerly aspect (Table 3, Fig. 4).

Table 3. Distribution of cavity-entrance orientation between the 45° octants for available and occupied cavities.

Cavity aspect	Available cavities (n = 47)	Expected occupation (n = 10)	Observed Occupation (n = 10)	Percentage available cavities occupied (%)
N	5	1.064	1	20
NE	5	1.064	1	20
E	9	1.915	0	0
SE	6	1.277	1	16.7
S	6	1.277	0	0
SW	4	0.851	4	100
W	5	1.064	0	0
NW	7	1.489	3	42.86

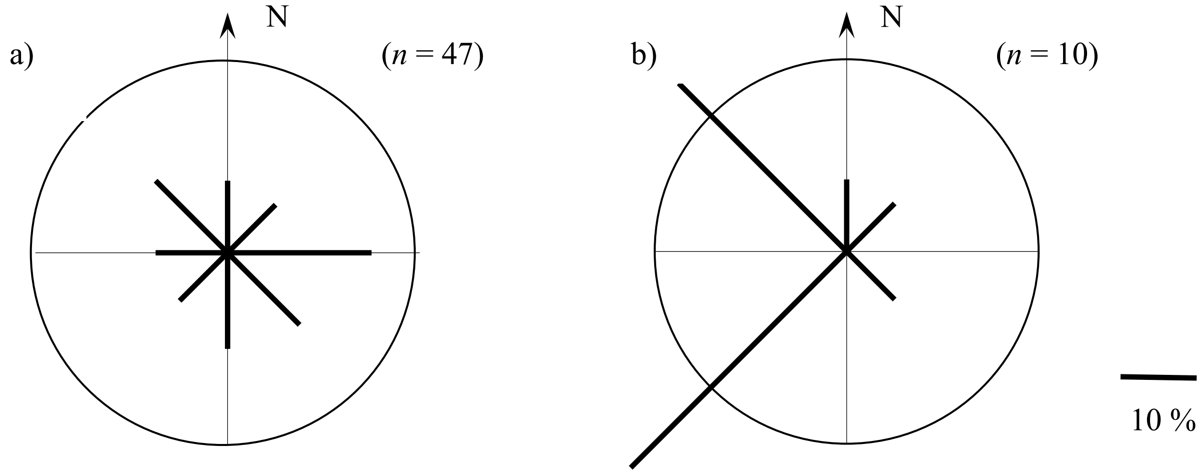

Figure 4. Distribution of cavity-entrance orientation between 45° octants for a) all available cavities and b) occupied cavities.

Discussion

A total of ten roller breeding pairs were recorded at the Marais de L'Ilon between 18th June and 23rd July 2001. This represented a breeding density of 11.75 pairs km^{-2}. Since the majority of nests were located in the narrow strip of riparian vegetation along the bank of the Canal de la Vallée des Baux, this figure can also be represented in terms of a linear density of 5.6 pairs km^{-1}. All nests were located in abandoned green woodpecker holes in live white poplar trees. A number of cavity characteristics appeared to influence nest-site selection by rollers. Measurements of DBH, hole height and entrance width all showed significantly reduced variation at occupied sites compared to unoccupied sites whilst cavity-entrance orientation at nest sites was not randomly distributed. Although green woodpeckers showed no preference for entrance orientation during excavation, rollers exhibited a strong preference for cavities with either a south-westerly or north-westerly aspect.

BREEDING DENSITY

The European roller is one of 85 bird species on France's Red list of endangered, vulnerable or rare breeding birds (Yeatman-Berthelot & Rocamora 1999). The breeding population in France is believed to be between 500 and 600 pairs, with 100-150 of these in the Bouches-du-Rhône department (Bousquet 1999). However, the breeding density of rollers at this study site represents the highest density recorded in western Europe. Previously, the highest known densities were 6 pairs km^{-2} at Vergière, also in the Bouches-du-Rhône (Frisch

1966) or, more recently, 5 pairs in one linear kilometre in the Gare department (Bousquet 1999). The main stronghold of the roller in western Europe is in the Iberian peninsula, with 6600 breeding pairs (Samwald & Štumberger 1997). Yet, even in the Extrmadura region of Spain where the population has benefited from the installation of a large number of wooden nest boxes, a breeding density of just 1.23 pairs km^{-1} has been recorded (Avilés & Costillo 1998).

Rollers hunt from exposed perches such as electricity wires and fence posts and are therefore highly visible at their foraging sites (Tucker & Heath 1994). Breeding population estimates of rollers are frequently calculated from surveys of hunting birds, often made from vehicles. The Marais de L'Ilon is not easily accessed by vehicle and the breeding population here has not been previously surveyed. The discovery of ten pairs has therefore increased the known breeding population of the Bouches-du-Rhône department by approximately 10 %. It may be that estimating breeding populations from sightings of foraging birds, rather than through the detection of nest-sites, has led to a substantial under-estimation of the roller population in the Bouches-du-Rhône and perhaps even in France as a whole.

Cavity characteristics

It is difficult to compare the cavity characteristics of nest-sites in this study to data published on breeding populations in other regions of Europe. Since rollers are non-excavator species, the characteristics of potential nest-sites will depend on the excavator species. At the Marais de L'Ilon, the only excavator species large enough to create potential nest-cavities for rollers are green woodpeckers. In contrast, in their study of rollers in the Puszcza Pilicka Forest, central Poland, Sosnowski and Chmielewski (1996) found that 79 % of roller nests were in abandoned black woodpecker nests, with only 11 % in green woodpecker nests. Black and green woodpeckers vary considerably in size and breeding ecology (Cramp & Simmons 1988) and this will clearly influence the characteristics of cavities available to rollers. The measurements of hole height, entrance size and cavity size for the roller nests in this study are closely comparable to those described for green woodpecker nests (Cramp & Simmons 1988) but differ considerably to those in Sosnowski and Chmielewski's study (1996). For instance, the mean hole height, 5.62 ± 2.26 m, of available cavities at the Marais de L'Ilon was significantly lower than the mean hole height of 9.0 ± 3.4 m in the Polish study. Similarly, in this study the entrance holes had mean dimensions of 5.34 x 5.62 cm whilst in Poland the mean entrance dimensions were 8 x 12 cm (Sosnowski and Chmielewski 1996).

In addition to this problem, much of the recently published data on roller breeding ecology is based on studies of birds using nest boxes (e.g. Avilés & Costillo 1998; Avilés *et al.* 1999; Avilés *et al.* 2000) and is not easily comparable to data from natural nest-sites. This paper therefore focuses on the factors influencing cavity selection at the Marais de L'Ilon by comparing the characteristics of occupied and unoccupied cavities. It is acknowledged that the conclusions and recommendations derived from this research will be most appropriate for conservation action at this study site but it is hoped that the principles can be applied more widely.

Although rollers do not show any attachment to water, they are known to regularly nest in riparian vegetation, particularly lines of poplars (Cramp & Simmons 1988; Isenmann 1993). Since all available cavities at the study site were found in poplar trees, the fact that the nest-cavities were all located in this tree species does not demonstrate a positive selection by rollers. Instead, it appears that white poplars offer preferable conditions for nesting green woodpeckers, the excavator species. The correlations found between tree and cavity characteristics also arise as consequences of green woodpecker activity rather than roller activity.

Given that both the DBH and height of trees with available cavities were significantly greater than those of trees without cavities, it is evident that green woodpeckers excavate their nests in the larger, older trees. The selection of mature trees by cavity excavators has been widely reported (e.g. Newton 1994; Joy 2000) and has been explained as an attempt to maximise nest space and thermal insulation or to minimise predation risk. Perhaps more important in this selection is the fact that decayed heartwood is essential for most cavity-nesting, excavator species (Harestad & Keisker 1989).

Measurements of DBH, hole height and entrance width all showed significantly reduced variation at sites chosen by rollers, indicating that these characteristics are involved in nest-site selection. However, given the strong correlations between entrance dimensions, between hole height and tree DBH and between entrance height and tree DBH, it may be that only one of these characteristics was important. For instance, selection for entrance width would also manifest itself as an apparent selection for DBH and hole height. Both hole height and entrance size have been shown to influence nest-site selection by other secondary cavity-nesters (e.g. van Balen *et al*. 1982; Rendell & Robertson 1989). Belthoff and Ritchison (1990) found a significantly reduced variation in the hole heights of sites used by Eastern screech-owls (*Otus asio* L.). They proposed that this was a consequence of opposing selective forces, with predation risk favouring the use of cavities above a minimum height and increased exposure and energy requirements favouring the use of lower cavities. Similar selective forces may also act on rollers although data on predation risk at nest-sites is unavailable.

Rollers must exhibit some degree of selectivity for entrance size since there must be a minimum size to permit entry. There is also likely to be a selection against cavities with entrances much larger than necessary, to reduce the likelihood of predation or to avoid competition with other secondary cavity-nesters. Potential nest-site competitors include starlings (*Sturnus vulgaris* L.), hoopoes (*Upupa epops* L.) and jackdaws (*Corvus monedula* L.) (Sosnowski and Chmielewski 1996). Recent research has shown that jackdaws require a minimum cavity-entrance size of 6.5 cm (Pilard & Brun 1998). There is a breeding population of jackdaws at the Marais de L'Ilon and inter-specific competition may limit the maximum entrance size for roller nests here.

There were no significant differences between occupied and unoccupied sites in either cavity height or cavity depth. Again, some degree of selectivity should be evident since nest-cavities must be large enough to accommodate a brood of 3 – 5 young (the normal brood size; Cramp & Simmons 1988). It should be noted that measurements of cavity depth were taken once breeding activity at the nest-site had ceased. Rollers do not expel their faeces from the nest-cavity (Sosnowski and Chmielewski 1996) and cavities will therefore fill during the breeding season. Research with marked birds has also shown that rollers display site fidelity for a number of years (Sosnowski and Chmielewski 1996). Cavity depth at the time of nest-site selection will have been greater than at the time these measurements were taken. The rate at which a cavity fills will depend on the number of young raised and also on cavity use by other bird species outside the breeding season. It is therefore possible that rollers do exhibit a preference for cavity depth when selecting new nest-sites but that, to a point, this preference is outweighed by the strength of site fidelity.

It is also possible that the absence of significant differences between some of the measured characteristics of occupied and unoccupied cavities is an artefact of small sample size, rather than a lack of selectivity by rollers. Similar problems of small sample size potentially obscuring significant differences between occupied and unoccupied cavities were acknowledged by Belthoff and Ritchison (1990) in their study of nest-site selection by Eastern screech-owls.

Rollers exhibited a strong preference for cavities with a south-westerly or north-westerly aspect. This selection was not influenced by nest-site availability, since available cavities were distributed randomly with respect to compass direction. In their study of rollers in Poland, Sosnowski and Chmielewski (1996) found that the nest-hole entrance most often faced east or north-east. However, since they did not survey all the available cavities, they could not conclude whether this was a consequence of selection by rollers or because woodpeckers orientate their holes in such a way.

Cavity-entrance orientation affects the microclimate within a cavity, particularly when the cavity tree is situated on the forest edge or in open habitat (Belthoff & Richison 1990). If birds derive certain thermoregulatory benefits from specific nest-site orientations, e.g. by avoiding direct exposure to wind or sun, hole-nesting species should exhibit a positive selection for nest-sites with that orientation (Rendell & Robertson 1994). Orientation selection by rollers at the Marais de L'Ilon is likely to be influenced by two main factors.

Firstly, the conditions at the site are strongly influenced by the Mediterranean climate. Hole-nesting birds in this region are more prone to over-heating than chilling and would therefore be expected to select cavities with shaded entrances, avoiding direct sunlight. Since cavities with east- or south-facing entrances are generally exposed to the sun for the longest periods during a day (Rendell & Robertson 1994), one would expect them to be avoided. The climate of the study site is also heavily influenced by the Mistral, a cold northerly wind that funnels down the Rhône valley from the Alps. The Mistral often blows for many days at a time and can lower the air temperature by a number of degrees. Hole-nesting birds in the region would therefore also be expected to avoid cavities with northerly aspects, to reduce the risk of wind chill.

There have been a number of other studies to investigate the influence of cavity-entrance orientation on nest-site selection by secondary hole-nesting species. Rendell and Roberton (1994) summarise the findings of this research. Of 16 studies involving 19 species across 11 families, nine concluded that cavity-entrance orientation did not influence nest-site selection, four concluded the opposite and the remaining three provided evidence both for and against its importance. In addition, the evidence of a preference for cavity-entrance orientation that has been recorded for some secondary hole-nesters may well be a consequence of nest-site availability (Raphael 1985). Thus, the cavities occupied by secondary hole-nesters are randomly selected from available sites, most of which face in a particular direction.

. The importance of cavity-entrance orientation for secondary hole-nesters in general remains unclear. Although rollers do appear to exhibit a preference for cavity-entrance orientation, nest-site selection is unlikely to be influenced by one cavity characteristic alone. In addition, the preferences of individual species for particular cavity characteristics may be obscured by inter-specific competition for nest sites (Rendell & Robertson 1994). In this study, a cavity was included as a potential nest-site if the entrance height and width were greater than 4.5 cm. However, many of these sites may not actually have been available due to other site and habitat characteristics or the presence of competitor species. Rollers are considered a species of limited effectiveness in fights for nest-sites with starlings, hoopoes and jackdaws (Cramp & Simmons 1988), and therefore may have been prevented from occupying many of the potential cavities.

Nest-site availability may also have been limited by the uneven distribution of cavities. Like most woodpeckers, green woodpeckers usually excavate a new nest-cavity each year (Cramp & Simmons 1988). However, given the limited availability of mature trees at the study site and the relatively large territory size of green woodpeckers, available cavities were clustered across the site. Thus the 47 available cavities were distributed between just 38 trees, with many of these adjacent to each other. Rollers are described as aggressively territorial, solitary breeders (Samwald & Štumberger 1997) so it is highly unlikely that more than one pair would nest in the same tree. Indeed, given the results of this research, a nest separation of less than 14 m would not be expected.

Since nest-site availability may be a limiting factor, the breeding population of rollers at the Marais de L'Ilon may benefit from the installation of artificial nest boxes. The installation of nest boxes is a technique widely used to consolidate breeding populations and encourage range expansion into previously unoccupied areas (Bousquet 1999). The results of this study suggests that the most appropriate nest boxes would have an entrance size of approximately 5.5 x 5.5 cm, large enough to permit entry by rollers but small enough to prevent nest-site competition by jackdaws. Rollers do not appear to show any preference for cavity size but the boxes must be large enough to accommodate a brood of 3 –5 young. Based on the design of nest boxes used by rollers elsewhere (e.g. Bolund 1987; Sánchez & Sánchez 1991), and the results of this study, a nest box width, depth and height of 25 x 25 x 25 cm would be sufficient.

Boxes should be installed at a height of between 4 m and 8 m, with a south-westerly or north-westerly aspect. It is necessary to ensure that the boxes are in a sheltered position but that the entrance is not obstructed by any leaves or branches. When returning from foraging, each pair of rollers made use of dead branch near their cavity to perch on before entering the nest (pers. obs.). It is therefore recommended that nest boxes are positioned close to a suitable perch or that one is constructed near the box. To reduce intra-specific competition and territorial conflict, a minimum nest box separation of 50 m is also recommended. In addition to consolidating the breeding population, the installation of nest boxes will facilitate further studies of roller ecology. If access hatches are incorporated into the nest box design, reproductive success can be more easily monitored and both adults and chicks can be caught and colour-banded, allowing the recognition of individual birds in the field.

In conclusion, this research has identified a strong breeding population of rollers at the Marais de L'Ilon. Nest-site distribution is determined by cavity availability which, in turn, is determined by the activities of green woodpeckers, the excavator species, and by intra- and inter-specific interactions, particularly competition for cavities. This study also highlights the importance of protecting mature trees in roller conservation. Hole height, entrance size and cavity-entrance orientation all appear to influence nest-site selection. Given that nest-site availability may be limiting the population in this area, the installation of nest boxes is recommended.

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