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CAVITY-ENTRANCE ORIENTATION AND NEST-SITE USE BY SECONDARY HOLE-NESTING BIRDS

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Abstract.—If cavity-entrance orientation confers some benefit (e.g., thermoregulation of eggs and young) to secondary hole-nesting birds, individuals should use cavities with certain entrance orientations, and the orientation of a cavity's entrance should influence reproductive success. During a 2-yr study conducted at natural cavity populations in southeastern Ontario, Tree Swallows (*Tachycineta bicolor*) were found to prefer cavities whose entrances faced S–SE, but the orientations of cavity entrances did not differ between pairs that fledged young and those whose breeding attempts failed. European Starlings (*Sturnus vulgaris*) did not show a preference for cavities whose entrance faced a specific compass direction. The conclusions of other similar studies are reviewed and several reasons why research concerned with the influence of cavity-entrance orientation on nest-site use by secondary hole-nesting birds has yielded inconsistent conclusions are discussed.

ORIENTACIÓN DE LA ENTRADA DE CAVIDADES Y USO SECONDARIO DE LAS MISMAS POR AVES QUE NO LAS EXCAVAN

Sinopsis.—Si la orientación de la entrada de una cavidad, le confiere ventajas al que la utiliza de forma secundaria (ej. termoregulación más apropriada para huevos y pichones) dichas aves deben utilizar cavidades con cierta orientación particular y por ende esto debe tener su efecto en el éxito reproductivo de la especie. Durante un estudio de dos años llevado a cabo en el sureste de Ontario se encontró que la golondrina arbórea (*Tachicineta bicolor*) prefería cavidades cuya entrada estuviera dirigida hacia el sur-sureste. Sin embargo la orientación de la entrada de la cavidad no influyó entre parejas que produjeron pichones y las que fracasaron. El estornino (*Sturnus vulgaris*) no tiene preferencia por una orientación particular de la entrada de la cavidad. Las conclusiones de otros trabajos similares se revisan, y se discuten las razones por las cuales estudios relacionados con el uso secondario de cavidades han tenido conclusiones tan inconsistentes.

Many characteristics of cavities affect nest-site use and reproductive success in secondary hole-nesting birds, such as the location of nest sites within a habitat (e.g., Rendell and Robertson 1990) and cavity size (e.g., Rendell and Robertson 1993). Another characteristic that could affect nest-site use and reproductive success in these birds is the compass orientation of a cavity's entrance. Studies of several bird species, including those that construct open (Bergin 1991, Högstedt 1978, Verbeek 1981, Walsberg 1981), flask-shaped (Austin 1974, Facemire et al. 1990, Ricklefs and Hainsworth 1969), and domed nests (Austin 1976), as well as those that excavate nest cavities (Dennis 1969, 1971; Inouye et al. 1981; Korol and Hutto 1984), show that some birds orient nest entrances or nest cups in a preferred direction. Generally, the explanation for this behavior is that birds derive thermoregulatory benefit(s) from specific nest-site ori-

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entations, e.g., by avoiding direct exposure to wind or sun, although other explanations have been suggested (Conner 1975, Dennis 1971, Högstedt 1978, Korol and Hutto 1984, Stauffer and Best 1982). If cavity-entrance orientation confers some benefit to secondary hole-nesting birds, species should exhibit a preference for cavities with a specific entrance orientation, and the orientation of a cavity's entrance should influence reproductive success. Some studies have provided evidence of preferred cavity orientation in secondary hole nesters (e.g., Lumsden 1986), but many have not (e.g., Stauffer and Best 1982), and no study to date has demonstrated that cavity-entrance orientation influences reproductive success.

We present cavity-entrance orientation data for Tree Swallows (*Tachycineta bicolor*) and European Starlings (*Sturnus vulgaris*), collected during a study of the breeding ecology of Tree Swallows nesting in natural cavities (Rendell and Robertson 1989, Robertson and Rendell 1990). We also determine whether the orientation of a cavity's entrance affected the reproductive success of Tree Swallows, and we review the evidence from this and other studies concerning the effect of cavity-entrance orientation on nest-site use by secondary hole-nesting birds.

METHODS

Data were collected at Allan's Pond and Osprey Marsh located within 12 km of the Queen's University Biological Station in southeastern Ontario, Canada (44°34'N, 76°20'W). Both sites are beaver ponds on stream courses in deciduous woodland, and each site has hundreds of dead trees standing in 0.5–1.5 m of water (Rendell and Robertson 1989). Data on breeding success for Tree Swallows, and nest-site use by both Tree Swallows and European Starlings, were collected in 1986 and 1987 at both ponds. Cavities where birds nested were identified with numbered aluminum tags that were nailed to the snags.

Measurements of cavity-entrance orientation were made in February and March 1989 when the ponds were frozen. We sampled 130 of the approximately 170 total number of cavities available at both ponds combined during 1986–1987 (Allan's Pond: $n = 65$ used by Tree Swallows and European Starlings, $n = 15$ available, but not used; Osprey Marsh: $n = 44$ used, $n = 6$ unused). Eight characteristics (e.g., cavity size) of 19 of the 21 (90%) unused cavities, other than cavity-entrance orientation, had previously been compared with cavities that were used by Tree Swallows and other species of hole nesters at our study sites in 1986 (Rendell and Robertson 1989). The unused cavities were found to be similar to occupied cavities in all respects.

To measure cavity-entrance orientation we faced the entrance to a cavity, took a bearing which bisected the entrance using a hand-held Silva® Ranger compass, and recorded the back-bearing. Data were corrected to true north.

We used circular statistics to analyze the data (Batschelet 1981, Zar 1984). Data were combined across sites and years where possible based on two-sample statistical comparisons. We present mean angle (ϕ) and mean vector length (r) for samples. Mean vector length is a measure of concentration of data; it is unitless and ranges from 0 (low concentration) to 1 (high concentration). All samples were tested for uniformity of distribution (randomness) using Rao's spacing test (Batschelet 1981, Bergin 1991). Rejection of the null hypothesis means that a sample exhibits nonrandom orientation with respect to the compass as a whole. To determine if two samples differed significantly from one another we used Watson's U^2 test. When applying this test we randomly allocated tied observations between samples by flipping a coin (Batschelet 1981). We used significance level 0.05 for all tests.

For Tree Swallows, some cavities were used in succession by more than one pair within a season, so we included only one observation for each cavity during the analysis of used and available nest sites. To analyze the reproductive success data of Tree Swallows, we grouped cavities as those from which young fledged and those where a breeding attempt failed (e.g., nestlings died, or were depredated). When the same nest was used repeatedly within a season, we included only the outcome of the first attempt in our analysis.

RESULTS

Cavity-entrance orientation.—The entrances of available cavities were randomly distributed with respect to compass direction for both sites and years combined (Rao's U = 136.2, n = 130, r = 0.16, $P > 0.10$). The mean angle was approximately SSE (ϕ = 151°), and the low r value indicates that the data were widely dispersed about the compass.

Similarly, the distribution of entrance orientations for cavities used by Tree Swallows and European Starlings combined was random for both sites and years combined (Rao's U = 133.7, n = 109, r = 0.17, $P > 0.10$). The mean angle of cavity entrances faced SSE (ϕ = 159°), and the data were widely dispersed about the compass.

The orientations of the entrances to cavities that were not occupied by either species were also randomly distributed about the compass for both sites and years combined (Rao's U = 133.8, n = 21, r = 0.21, $P > 0.10$, ϕ = 106°). The orientations of cavity entrances for cavities that were not used (nu) did not differ from those for cavities that were used (u) by Tree Swallows and European Starlings (Watson's U^2 = 0.117, n_u = 102, n_{nu} = 19, P = 0.20).

Although both Tree Swallows and European Starlings collectively showed no preference for cavity-entrance orientation, Tree Swallows alone exhibited a significant preference for cavities with entrances facing S–SE for both years combined at Allan's Pond and Osprey Marsh (Table 1, Fig. 1). The orientations of entrances to cavities used by European Starlings were random with respect to compass direction at both sites for both years combined (Table 1, Fig. 1). The orientations of entrances to cavities used by Tree Swallows differed significantly from those used by European Starlings at Osprey Marsh, but not at Allan's Pond (Table 1).

Reproductive success for Tree Swallows.—Cavity-entrance orientation

TABLE 1. Mean angle (ϕ), mean vector length (r), and results of Rao's spacing and Watson's U^2 tests for cavities used by Tree Swallows and European Starlings.

Site	Species	ϕ (°)	r	n	Rao's U	Watson's U^2
Allan's	Swallows	187	0.26	46	176.5**	0.129[a]
Pond	Starlings	46	0.10	28	152.8[b]	
Osprey	Swallows	134	0.34	41	191.8**	0.236*
Marsh	Starlings	288	0.17	18	148.0[a]	

[a] $P > 0.10$.
[b] $P > 0.05$.
* $P < 0.02$.
** $P < 0.01$.

did not influence the reproductive success of Tree Swallows (Table 2). The significant Rao's U values for both the fledged and failed groups indicate that the entrances of cavities for both groups exhibited nonrandom orientation with respect to the compass as a whole, but the orientations of cavity entrances for both groups did not differ from each other (Watson's U^2 test, Table 2). The entrances of cavities to both successful and failed nests faced S–SE on average.

DISCUSSION

If cavity-entrance orientation confers some benefit(s) (e.g., reduced thermoregulatory costs) to secondary hole-nesting birds, then a preference for cavities with beneficial entrance orientation should be exhibited by these species, and cavity-entrance orientation should influence reproductive success. The conclusions of previous studies and our data, however, provide contradictory evidence that cavity-entrance orientation is important to these species. Tree Swallows exhibited a preference for south-facing holes, but European Starlings exhibited no orientation preference. Table 3 summarizes the general conclusions of previous research regarding the importance of cavity-entrance orientation on nest-site selection in secondary hole-nesting birds. Of 16 studies involving 19 species across 11 families, nine (56%) concluded that cavity-entrance orientation was not important during nest-site selection, four (25%) concluded the opposite, and the remaining three (19%) studies provide evidence both for and against its importance. Nest-site use by four species (White-breasted

TABLE 2. Mean angle (ϕ), mean vector length (r), and results of Rao's spacing and Watson's U^2 tests for Tree Swallow cavities where young fledged and where breeding attempts failed.

Success	ϕ (°)	r	n	Rao's U	Watson's U^2
Fledged	185	0.37	30	183.0*	0.151[a]
Failed	136	0.24	57	164.9*	

[a] $P > 0.10$.
* $P < 0.01$.

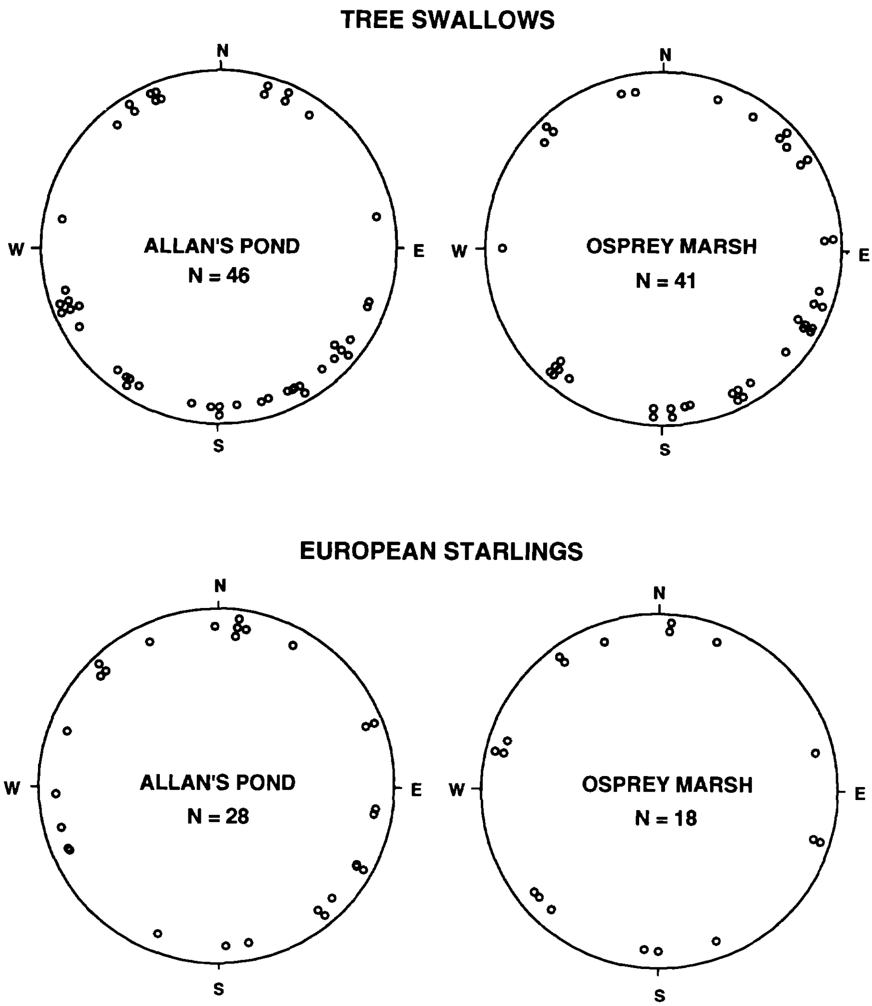

FIGURE 1. Distributions of the compass orientations of cavity-entrances for Tree Swallows and European Starlings at Allan's Pond and Osprey Marsh, 1986–1987. Where two or more cavity-entrance orientations are the same, the points are arranged perpendicular to the boundary of the circle.

Nuthatch, *Sitta carolinensis,* American Kestrel, *Falco sparverius,* Tree Swallow, European Starling) was found to both be affected, and not affected, by cavity-entrance orientation in different studies (Table 3).

In addition to our results, two other studies present conflicting results for different species in the same project. Lumsden (1986) showed that Tree Swallows exhibited a preference for south facing nest boxes, whereas House Wrens (*Troglodytes aedon*) did not. Van Balen et al. (1982) found

TABLE 3. Summary of the conclusions of previous research concerned with the importance of cavity-entrance orientation on nest-site use by secondary hole-nesting birds.

Species	Study[a]
Entrance orientation affects nest-site use	
Pygmy Nuthatch (*Sitta pygmaea*)	9
White-breasted Nuthatch (*S. carolinensis*)	9
American Kestrel (*Falco sparverius*)	1, 12
Tree Swallow (*Tachycineta bicolor*)	7, 13
European Starling (*Sturnus vulgaris*)	15, 16
Entrance orientation does not affect nest-site use	
White-breasted Nuthatch	5, 14
American Kestrel	4
Tree Swallow	5, 10
European Starling	4–5, 10, 13–14
Eastern Bluebird (*Sialia sialis*)	11
Mountain Bluebird (*S. currucoides*)	10
Bufflehead (*Bucephala albeola*)	10
Eastern Screech-Owl (*Otus asio*)	2
Flammulated Owl (*O. flammeolus*)	8
Barred Owl (*Strix varia*)	6
Elf Owl (*Micrathene whitneyi*)	3
House Wren (*Troglodytes aedon*)	4–5, 7, 14
Great Tit (*Parus major*)	15
Blue Tit (*P. caeruleus*)	15
Mountain Chickadee (*P. gambeli*)	5
Black-capped Chickadee (*P. atricapillus*)	14
Great Crested Flycatcher (*Myiarchus crinitus*)	14
House Sparrow (*Passer domesticus*)	14

[a] Studies: 1. Balgooyen 1976; 2. Belthoff and Ritchison 1990; 3. Goad and Mannan 1987; 4. Gutzwiller and Anderson 1987; 5. Ingold and Ingold 1984; 6. Johnson 1987; 7. Lumsden 1986; 8. McCallum and Gehlbach 1988; 9. McEllin 1979; 10. Peterson and Gauthier 1985; 11. Pinkowski 1976; 12. Raphael 1985; 13. this study; 14. Stauffer and Best 1982; 15. van Balen et al. 1982; 16. Verheyen 1969.

that European Starlings avoided W–NNW facing holes in natural populations, while Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) showed no preference.

Evidence of a preference for cavity-entrance orientation that has been observed in some secondary hole-nesting species may be the result of nest-site availability (Raphael 1985). For example, although a significant proportion of natural cavities occupied by Eastern Bluebirds (*Sialia sialis*) faced SE, Pinkowski (1976) concluded that bluebirds were randomly using available sites, most of which faced that direction. This, however, does not explain preferences by Tree Swallows for south-facing holes in Lumsden's (1986) study, or ours (cf. Raphael 1985). Contrary to Pinkowski's (1976) results, available cavities at our sites were randomly distributed with respect to compass direction.

It is possible that Tree Swallows in our study preferred south-facing holes because this orientation improved cavity microclimate, although cavity orientation did not appear to affect reproductive success as we measured it. We do not have data concerning local rainfall, wind direction or wind speeds during the breeding season, but south-facing cavities are exposed to sun for a longer period during the day, and this may help to warm young and keep the cavity dry. Lumsden (1986) suggested that Tree Swallows nested facing south to avoid wind chill. This may also be the case at our sites. Considering all studies in which a species has exhibited a preference for cavity-entrance orientation (Table 3), the preferred orientation was always observed to lay between E–NE (Raphael 1985) and SW (McEllin 1979), reinforcing the suggestion that there are thermoregulatory benefits derived from using an approximately east- or south-facing cavity.

There are several possible explanations for the inconsistent conclusions regarding the influences of cavity-entrance orientation on secondary hole-nesting birds. For example, cavity-entrance orientation may affect nest-site use by all of these species, but researchers fail to detect patterns because of competition for nest sites. As these species are mostly incapable of excavating their own nest sites, there can be intense intra- (e.g., Leffelaar and Robertson 1985, Robertson et al. 1986) and interspecific (e.g., Rendell and Robertson 1990, 1991) competition for cavities, and individuals may be forced to settle for what is available. Thus, although individuals may seek cavities with specific entrance orientations, these preferences may be obscured by the simultaneous settlement of many individuals of several species in a study area, all of which are seeking nest sites with certain characteristics. Moreover, cavity-entrance orientation may not be important in all habitats, or to all species. Cavity microclimate likely varies greatly from habitat to habitat, e.g., depending on whether a cavity is exposed or in cover, and because different species of hole nesters build nests that differ greatly in size and in the types of materials used. In species such as the House Wren, which typically nest in cover and fill their cavity with nesting material, the relatively stable thermal environment that results (Kendeigh 1963) may preclude the need to seek nest sites with specific entrance orientations. In contrast, for species such as Tree Swallows, which nest in exposed locations, cavity orientation may have a large influence on the energy balance of both the cavity and its occupants. Finally, there are several other cavity characteristics in addition to entrance orientation that affect nest-site use in secondary hole-nesting birds. For example, cavity size (Rendell 1992; Rendell and Robertson 1989, 1993), entrance size (Rendell and Robertson 1989), the distance of a nest site from forest edge (Rendell and Robertson 1990) and possibly the number of ectoparasites in nest sites (Rendell 1992) affect nest-site choice in Tree Swallows, and similar results have been found for many other hole nesters (e.g., van Balen et al. 1982). Thus, individuals consider several characteristics of a cavity during nest-site selection, and depending on the species, habitat and individual, the actual importance of cavity orientation during cavity choice relative to other characteristics may be extremely variable.

Given the complex nature of the nest-site selection process, the degree of competition for nest sites, limited evidence for preferred directionality of cavity entrances exhibited by most species studied to date, and no evidence of significant benefits for species that have shown preferences for certain cavity-entrance orientations, the influence of cavity-entrance orientation on hole-nesting birds remains ambiguous. Detailed studies of several hole-nesting species, their cavity microclimate and studies using more precise measures of reproductive success will be necessary to reveal the importance of cavity-entrance orientation on the breeding ecology of these species.

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