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**Is there competition between exotic and native cavity-nesting
birds in the Sonoran Desert: An experiment**

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The University of Arizona, 1992

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IS THERE COMPETITION BETWEEN EXOTIC AND NATIVE
CAVITY-NESTING BIRDS IN THE SONORAN DESERT: AN EXPERIMENT

by

Brent Dean Bibles

A thesis Submitted to the Faculty of the
SCHOOL OF RENEWABLE NATURAL RESOURCES
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE
In the Graduate College
THE UNIVERSITY OF ARIZONA

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ACKNOWLEDGEMENTS

I wish to thank Dr. Bill Mannan for his help during all stages of this study. I also thank Dr. Norm Smith for the original suggestion of an experimental approach for the study and for serving as a committee member. I thank Dr. Bill Shaw for serving as a committee member.

I am grateful to all those who helped with field work during this study: Vicki Meretsky, Keith Hughes, Mark Maghini, and members of Dr. Bill Mannan's avian management class in 1988 and 1989. Lastly, special thanks go to Jim Dawson for his support and friendship throughout the study, and to my wife, Erin, for her love and support in the later stages of the study.

This study was funded by the United States National Park Service.

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ABSTRACT

I examined the relationship between exotic and native cavity-nesting birds in the Sonoran desert near Tucson, Arizona during 1988 and 1989. I attempted to limit cavity availability in 1989 by plugging cavities that were unused, or used by exotics, in 1988 with rubber test tube stoppers. Numbers of nests of any species did not significantly change between 1988 and 1989. Control plots showed similar results. I found no significant negative correlations between number of nests of European starlings (Sturnus vulgaris) and any other cavity-nesting species. Of the cavity characteristics examined, species only differed in size of cavity openings. My data indicate that exotic and native cavity-nesting birds were not competing for nest cavities. An excess of available nest cavities is the probable reason for this lack of competition. Temporal differences in cavity use among species may have helped contribute to the abundance of cavities.

The idea that two or more species that use identical resources cannot coexist in the same area for long is a primary basis for theories on competition among animals (Schoener 1974, Jackson 1981). A logical consequence of this idea is that if two or more species coexist and use a common resource they must somehow differ in their use of the resource, or the resource must be superabundant. Therefore, studying competition in natural assemblages of species is difficult because mechanisms to reduce the intensity of competition generally are operating, or environmental variability prevents competition from occurring for long enough for competitive exclusion to occur (Wiens 1977). In either case, observing ongoing competitive interactions in coevolved assemblages is unlikely. Any resource partitioning observed among species often is attributed to the past effects of competition or "the ghost of competition past" (Connell 1980).

The introduction of exotic species may provide the opportunity to measure competition because exotic and native species are not likely to have evolved mechanisms for resource partitioning (Kerpez 1986). The presence of European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) in the Sonoran Desert provides an opportunity to study competition for nest cavities for 3 reasons. First, European starlings and house sparrows both

nest in cavities and both are capable of usurping nest holes from other cavity-nesting birds. Numerous authors have described European starlings usurping nest holes from native North American birds (Shelly 1935, Howell 1943, Allen and Nice 1952, Kilham 1958, McGilvrey and Uhler 1971, Troetschler 1976, Brenowitz 1978, Zeleny 1978, Brown 1981, Ingold 1989). Second, cavities frequently are considered a limiting resource for cavity-nesting birds (von Haartman 1957, Alerstam and Hogstedt 1981, van Balen et al. 1982), although some studies have documented situations where cavities were not limiting (Brush 1983, Brawn and Balda 1988, Waters et al. 1990). Third, neither the European starling nor the house sparrow forage in Sonoran Desert vegetation. Rather they forage in areas associated with human development (Royall 1966). Because they forage in areas unlike those used by native cavity-nesting birds, competition for food between native and exotic birds in the Sonoran Desert is not likely. Any competition observed between species in these groups should be for nest cavities.

Competition with European starlings for nest cavities has been proposed as an explanation for declines in abundance and nesting success in several species, including the eastern bluebird (Sialia sialia) in North America

(Yoakum et al. 1980), parrot populations in Australia (Long 1981), and the nuthatch (Sitta europeae) in Sweden. In the Sonoran Desert, Kerpez and Smith (1990), found a negative correlation between the breeding densities of European starlings and gila woodpeckers (Melanerpes uropygialis) and believed competition for cavities was responsible for this correlation. House sparrows also have been observed usurping nests of other cavity-nesting birds, and may be responsible for population declines of cliff swallows (Samuel 1969, Stoner 1939) and purple martins (Progne subis) (Jackson and Tate 1974) in North America, and several finch and sparrow species worldwide (Long 1981).

No information exists about the influence of exotic cavity-nesting birds on native secondary cavity-nesting birds in the Sonoran desert. Kerpez and Smith (1990) proposed that if European starlings are outcompeting gila woodpeckers for nest cavities in saguaros, the availability of cavities for native secondary cavity-nesting birds may be reduced. Exotic species also could directly influence secondary cavity-nesting birds by usurping their nest cavities.

I was interested in determining if European starlings and house sparrows negatively influenced the abundance of native cavity-nesting birds in the Sonoran Desert. I had 3 research objectives. First, determine if there was a

negative relationship between the abundance of the exotic species (European starlings and house sparrows) and native cavity-nesting birds. Second, determine if cavities in saguaro cacti were limiting cavity-nesting birds. Lastly, evaluate the use of cavities by cavity-nesting birds after cavities were experimentally reduced.

STUDY AREA AND METHODS

I conducted the study in 1988 and 1989 near Tucson, Arizona. I established six 10-ha plots (316 m X 316 m). Two plots were in the Rincon Mountain Unit, Saguaro National Monument on the north end of the interior loop road. Two plots were adjacent to Arthur Pack golf course in northern Tucson. The remaining 2 plots were at the University of Arizona Tumamoc Hill Desert Laboratory. I positioned plots to contain potential nest sites for cavity-nesting birds. All plots contained at least 21 (range 21-37) saguaros with what appeared to be cavities. Vegetation in the plots was relatively undisturbed and was in the paloverde-cacti-mixed scrub series of the Sonoran Desert (Turner and Brown 1982). Dominant plants on the plots included saguaro cacti, foothill paloverde (Cercidium microphyllum), triangle-leaf bursage (Ambrosia deltoidea), mesquite (Prosopis velutina), and various species of Opuntia.

The 2 plots on Saguaro National Monument (SNM Exclosure and Wash) did not support exotic cavity-nesting birds. I used these plots as controls. I positioned the 4 experimental plots near potential foraging areas for European starlings and house sparrows so that these species would likely nest on the plots. The 2 plots at Tumamoc Hill

(Tumamoc Hill North and South) were adjacent to each other and were bordered on the west by a housing subdivision at the Laboratory boundary, and by undisturbed desert on the remaining sides. The Arthur Pack plots (Arthur Pack North and South) were contiguous and were bounded by the golf course on the east, a housing subdivision on the west, and undisturbed desert on the remaining sides.

I surveyed cavity-nesting birds on the plots from 18 April to 14 July in 1988. I marked the location of all saguaro cacti on aerial photographs (Tumamoc Hill 1:1200, remaining plots 1:2400). During diurnal surveys, I observed saguaros with cavities and plotted the location of all cavity-nesting bird activity on copies of the aerial photos. I surveyed plots until I had found all nests; this usually required 4 to 9 diurnal visits. I considered a cavity a nest, when adult, diurnal, cavity-nesting birds were attending the cavity on at least 2 visits or when I heard nestlings in the cavity.

I surveyed elf owls and western screech owls by playing tape-recorded calls of these species (no more than 9 plays per plot) to elicit responses (Johnson et al. 1981). I recorded the location of all responses on maps of the plots. I roughly delineated potential nest areas after 2 to 7 nocturnal visits to each plot. I located nest cavities of owls by listening for begging calls of

nestlings during mid- to late June. I only considered as nests those cavities from which I heard nestlings calling.

I measured the height, location (arm or main stem), and opening size (large or small, see Fig. 1) of all cavities on experimental plots and of nest cavities on control plots. I also measured, with a clinometer, the heights of all saguaros that contained cavities. I recorded the number of real cavities and unfinished holes on experimental plots. I used a 7.6 m ladder to inspect visually all apparent cavities to distinguish real cavities from unfinished holes. Cavities not within reach of the ladder were "inspected" using a telescoping pole with a plummet.

In January and February 1989, I attempted to limit cavity availability on experimental plots by plugging cavities that were either unused, or used by exotics during 1988 (95 cavities plugged, range 16 to 42 plugs per plot). I plugged cavities with rubber test tube stoppers. Cavities excavated during the 1989 breeding season were not plugged. I resurveyed plots from 27 March to 14 July in 1989 using the methods previously described.

I compared the difference in number of nests of each species between years using the sign test (Gibbons 1985). Experimental plots were considered sampling units in these

tests. I used an alpha level of 0.10 to determine significance because of the small sample of plots. I also compared numbers of nests of each species with the number of nests of European starlings among plots using Spearman's rank correlation (Gibbons 1985). Correlations were calculated separately for each year. Probability values for the sign test and Spearman's rank correlations were based on a one-sided test.

I analyzed differences in cavity height and height of nest saguaros among species using the Kruskal-Wallis test (Gibbons 1985). I used data from all plots in 1988 and the control plots in 1989. For comparisons involving unused cavities in 1988, I only used data from the experimental plots. Comparisons involving unused cavities in 1989 included data only from cavities known to be real cavities (i.e., cavities used as nests in 1988 but not in 1989). I used the G-test of Independence (Sokal and Rohlf 1981) to compare the opening size and location of used and unused cavities for each year. I used the G-test for goodness-of-fit to compare differences in size of cavity openings and cavity location among species. If the tests showed significant differences among species, I used the unplanned test for homogeneity of replicates (Sokal and Rohlf 1981) to test which species' pairs created the difference. An alpha level of 0.05 was used to determine significance in

all cavity analyses.

RESULTS

COMPETITION BETWEEN NATIVE AND EXOTIC CAVITY-NESTING BIRDS

Experimental Plots. The number of nests did not significantly change between 1988 and 1989 on the experimental plots for any species (Table 1). Most of the differences in abundance of nests between years were relatively small (species with no change = 39%; ± 1 nest = 46%; ± 2 nests = 11%; $\pm > 2$ nests = 4%). The only large change recorded was the decrease in house sparrows on Arthur Pack South (Table 1).

Direction of changes in nest abundance was inconsistent within species among plots (Table 1). Five of the 7 species increased on some plots and decreased on others. Only the northern flicker and the elf owl were consistent in direction of change. On the experimental plots, the number of northern flicker nests decreased or stayed the same whereas the number of elf owl nests increased or stayed the same.

Control Plots. The small sample of control plots prevented statistical analysis of changes in the abundance of nests between years. However, the changes recorded were similar in magnitude to those on the experimental plots: two (20.0%) involved no change in nest abundance, 6 (60.0%) involved changes of ± 1 nest, and the remaining 2 (20.0%)

involved changes of ± 2 nests (Table 2).

Correlations. No correlation between the number of European starling nests and number of nests of other cavity-nesting birds was significant (Table 3). Only the house sparrow, in 1988, and ash-throated flycatcher, in 1989, had negative correlation coefficients. However, neither species was negatively correlated with European starling numbers during both years (Table 3).

ANALYSIS OF DIFFERENCES IN CAVITY CHARACTERISTICS

Cavity Height. Height of nest cavity did not significantly vary among species ($p = 0.1749$, $n = 109$) (Table 4). However, cavity height was significantly different between used and unused cavities in 1988 ($p = 0.0001$, $n = 131$), but not in 1989 ($p = 0.4597$, $n = 51$) (Table 5).

Saguaro Height. Height of nest saguaros did not vary significantly among species ($p = 0.1982$) (Table 4), or between used and unused cavities in 1988 ($p = 0.0581$), or 1989 ($p = 0.4716$) (Table 5).

Opening Size. Species exhibited differences in the opening size of their nest cavities ($p < 0.001$, $n = 110$) (Table 4) (Fig. 1). Northern flickers used proportionately more cavities with large openings than all other species except ash-throated flycatchers (Fig. 1). Ash-throated flycatchers used proportionately more cavities with large

openings than purple martins and European starlings (Fig. 1). Used and unused cavities did not significantly differ in opening size in 1988 ($0.5 < p < 0.7$, $n = 137$), or in 1989 ($0.5 < p < 0.7$, $n = 51$) (Table 5).

Cavity Location. Species did not vary in their selection of nest cavity location (i.e., arm or main stem of a saguaro cactus) ($0.8 < p < 0.9$, $n = 117$). Used and unused cavities did not differ in location in 1988 ($0.7 < p < 0.8$, $n = 137$), or 1989 ($0.3 < p < 0.5$, $n = 51$).

Cavity Use. Only 32.8% of the available cavities on the experimental plots were used as nests during 1988 (137 available, 45 used). Use increased to, at most, 72.5% of known cavities on the experimental plots in 1989 (51 available, 37 used). Of 38 cavities available during both years, 18 were used during both years, 14 were used in 1988 but not in 1989, and 6 were used in 1989 but not in 1988. The latter were cavities that I either could not plug or that became unplugged during the 1989 breeding season. In addition, 12 new cavities were excavated and used as nests during 1989. I observed 2 species nesting simultaneously in different cavities in the same saguaro on 15 occasions.

In general, the exotic and primary cavity-nesting species nested earlier in the year than the native secondary cavity-nesting species. Exotic and native

primary cavity-nesting species are year-round residents in the Tucson area and were observed on the plots throughout the breeding season. However, the period during which they exhibited breeding behaviors was more restricted. I observed European starlings and northern flickers using cavities for nesting from mid-March to the end of May (Table 6). I observed gila woodpeckers using cavities for nesting from the end of March through mid-July (Table 6). I only noted house sparrows at their nest cavities from late March to early April (Table 6), however, I observed them near cavities, apparently breeding, as late as 25 May.

The native secondary cavity-nesting species are migratory and usually were not observed on the plots until April. Elf owls called on the plots from mid-April to July, but I observed them in cavities from the end of May to late June (Table 6). Ash-throated flycatchers used cavities for nesting from mid-May to mid-July (Table 6). Purple martins bred from early June through mid-July (Table 6).

The difference in time of breeding between resident and migratory species is exemplified by the fact that some cavities (2 in 1988 and 5 in 1989) were used by woodpeckers or exotic species early in the year and by migratory species later in the same year.

Table 1. Number of nests on experimental plots for each year and one-sided sign test p-values for tests of declines in nest numbers between years.

| SPECIES ^a | TUMAMOC HILL | | | | ARTHUR PACK | | | | P-VALUE |
|----------------------|--------------|------|-------|------|-------------|------|-------|------|---------|
| | NORTH | | SOUTH | | NORTH | | SOUTH | | |
| | 1988 | 1989 | 1988 | 1989 | 1988 | 1989 | 1988 | 1989 | |
| COAU | 3 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 0.5000 |
| MEUR | 5 | 6 | 4 | 3 | 4 | 3 | 1 | 2 | 0.6875 |
| MIWH | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1.0000 |
| MYCI | 2 | 1 | 3 | 3 | 1 | 0 | 0 | 1 | 0.5000 |
| PRSU | 2 | 3 | 0 | 0 | 1 | 0 | 2 | 1 | 0.5000 |
| STVU | 4 | 3 | 1 | 1 | 1 | 2 | 0 | 2 | 0.5000 |
| PADO | 0 | 1 | 0 | 0 | 1 | 1 | 8 | 1 | 0.7500 |
| TOTAL | 16 | 17 | 9 | 8 | 10 | 8 | 12 | 8 | |

^aCOAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, Gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin; STVU = Sturnus vulgaris, European starlings; PADO = Passer domesticus, house sparrow.

Table 2. Number of nests on control plots in 1988 and 1989.

| SPECIES ^a | SAGUARO NATL. MON., RINCON MTN. UNIT | | | |
|----------------------|--------------------------------------|------|---------|------|
| | PLOT #1 | | PLOT #2 | |
| | 1988 | 1989 | 1988 | 1989 |
| COAU | 1 | 0 | 0 | 0 |
| MEUR | 4 | 6 | 2 | 3 |
| MIWH | 3 | 4 | 4 | 6 |
| MYCI | 3 | 2 | 2 | 1 |
| PRSU | 1 | 2 | 0 | 0 |
| TOTAL | 12 | 14 | 8 | 10 |

^aCOAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin.

Table 3. Spearman's rank correlation coefficients for comparisons between the number of nests of European starlings and other cavity-nesting birds in 1988 and 1989, near Tucson, Arizona.

| CORRELATIONS OF STARLINGS WITH: | 1988 | | 1989 | |
|------------------------------------|---------|---------|---------|---------|
| | r_s | P-VALUE | r_s | P-VALUE |
| COAU ^a | 0.6325 | 0.816 | 0.5000 | 0.750 |
| MEUR | 1.0000 | 1.000 | 0.5000 | 0.750 |
| MIWH | 0.0000 | 0.500 | 0.3333 | 0.667 |
| MYCI | 0.6325 | 0.816 | -0.5000 | 0.250 |
| PRSU | 0.0000 | 0.500 | 0.8333 | 0.917 |
| PADO | -0.8333 | 0.083 | 0.8165 | 0.908 |

^aCOAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin; PADO = Passer domesticus, house sparrow.

Table 4. Characteristics of saguaro cacti and cavities used as nest sites by native and exotic species of cavity-nesting birds near Tucson, Arizona. Data from all plots in 1988 and control plots in 1989.

| SPP ^b | MEAN SAGUARO HEIGHT (in m.) | | MEAN CAVITY HEIGHT (in m.) | | OPENING SIZE OF CAVITY ^a (%) | | | CAVITY LOCATION (%) | | |
|------------------|-----------------------------|------|----------------------------|------|---|-------|-------|---------------------|------|------|
| | M | (N) | M | (N) | SMALL | LARGE | (N) | STEM | ARM | (N) |
| | COAU | 7.5 | (7) | 5.5 | (7) | 0.0 | 100.0 | (7) | 75.0 | 25.0 |
| MEUR | 7.9 | (34) | 5.4 | (35) | 83.3 | 16.7 | (36) | 60.5 | 39.5 | (38) |
| MIWH | 8.0 | (25) | 5.5 | (25) | 76.0 | 24.0 | (25) | 61.5 | 38.5 | (26) |
| MYCI | 7.4 | (15) | 6.2 | (15) | 40.0 | 60.0 | (15) | 75.0 | 25.0 | (16) |
| PRSU | 8.4 | (14) | 6.5 | (14) | 92.9 | 7.1 | (14) | 64.3 | 35.7 | (14) |
| STVU | 7.1 | (5) | 6.3 | (4) | 100.0 | 0.0 | (4) | 83.3 | 16.7 | (6) |
| PADO | 8.8 | (9) | 6.0 | (9) | 77.8 | 22.2 | (9) | 55.6 | 44.4 | (9) |

^aCavities were placed into 2 size classes based on size of opening: small - those excavated by gila woodpeckers (average vertical diameter of entrance = 5.7 cm, average horizontal diameter of entrance = 6.3 cm); and large - those excavated by northern flickers (average vertical diameter of entrance = 7.0 cm, average horizontal diameter of entrance = 8.3 cm; Kerpez and Smith 1990).

^bCOAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin; PADO = Passer domesticus, house sparrow.

Table 5. Characteristics of cavities used and not used as nest sites by native and exotic species of cavity-nesting birds near Tucson, Arizona. Data from experimental plots in 1988 and 1989.

| USE | MEAN SAGUARO HEIGHT (in m.) | | MEAN CAVITY HEIGHT (in m.) | | OPENING SIZE OF CAVITY ^a (%) | | CAVITY LOCATION (%) | | |
|-------------|-----------------------------|------|----------------------------|------|---|-----------|---------------------|------|------|
| | M | (N) | M | (N) | SMALL | LARGE (N) | STEM | ARM | (N) |
| <u>1988</u> | | | | | | | | | |
| USED | 7.4 | (39) | 5.4 | (39) | 65.0 | 35.0 (40) | 71.1 | 28.9 | (45) |
| UNUSED | 6.9 | (90) | 4.5 | (92) | 72.8 | 27.3 (92) | 73.9 | 26.1 | (92) |
| <u>1989</u> | | | | | | | | | |
| USED | 7.4 | (37) | 5.4 | (37) | 73.0 | 27.0 (37) | 64.9 | 35.1 | (37) |
| UNUSED | 7.1 | (13) | 5.0 | (14) | 64.3 | 35.7 (14) | 78.6 | 21.4 | (14) |

^aCavities were placed into 2 size classes based on size of opening: small - those excavated by gila woodpeckers (average vertical diameter of entrance = 5.7 cm, average horizontal diameter of entrance = 6.3 cm); and large - those excavated by northern flickers (average vertical diameter of entrance = 7.0 cm, average horizontal diameter of entrance = 8.3 cm; Kerpez and Smith 1990).

| | | | | | | | |
|----------------------|------|------|------|------|------|------|-------|
| % Nests ^a | 0.00 | 40.0 | 76.0 | 77.8 | 83.3 | 92.9 | 100.0 |
| Species ^b | COAU | MYCI | MIWH | PADO | MEUR | PRSU | STVU |

Figure 1. Percentage of nest cavities with small openings^a by species. Lines indicate species groups not significantly different ($\alpha = 0.05$) in opening size. Data from all plots in 1988 and control plots in 1989.

^a Percent of nest cavities with small openings. Cavities were placed into 2 size classes based on size of opening: small - those excavated by gila woodpeckers (average vertical diameter of entrance = 5.7 cm., average horizontal diameter of entrance = 6.3 cm.); and large - those excavated by northern flickers (average vertical diameter of entrance = 7.0 cm., average horizontal diameter of entrance = 8.3 cm.; Kerpez and Smith 1990).

^b COAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin; STVU = Sturnus vulgaris, European starling; PADO = Passer domesticus, house sparrow.

Table 6. Dates combined, during which each species was observed utilizing a specific cavity for nesting. Data is from all plots and for 1988 and 1989 combined.

| SPECIES ^a | EARLIEST DATE | LATEST DATE |
|----------------------|---------------|-------------|
| COAU | 29 MARCH | 28 APRIL |
| MEUR | 30 MARCH | 11 JULY |
| MIWH | 30 MAY | 21 JUNE |
| MYCI | 24 MAY | 13 JULY |
| PRSU | 9 JUNE | 14 JULY |
| STVU | 30 MARCH | 1 JUNE |
| PADO | 30 MARCH | 3 APRIL |

^aCOAU = Colaptes auratus, northern flicker; MEUR = Melanerpes uropygialis, Gila woodpecker; MIWH = Micrathene whitneyi, elf owl; MYCI = Myiarchus cinerascens, ash-throated flycatcher; PRSU = Progne subis, purple martin; STVU = Sturnus vulgaris, European starlings; PADO = Passer domesticus, house sparrow.

DISCUSSION

I found little evidence for competition between exotic and native cavity-nesting birds on my study sites. There are at least 4 factors which potentially could have reduced competition between exotic and native cavity-nesting birds: 1) an excess of cavities suitable for nesting, 2) differences among species in time of cavity use, 3) differences in characteristics of cavities used by native and exotic cavity-nesting birds, and 4) lack of interspecific territoriality among the cavity-nesting species.

Cavity Availability. Brush (1983) found that cavity-nesting birds used 73.9% of the cavities on riparian woodland plots. He believed that the availability of unused cavities combined with the ability of gila woodpeckers to excavate new cavities prevented competition for nest sites. Troetschler (1976) observed that acorn woodpeckers (Melanerpes formicivorus) excavated new cavities in response to losing nest cavities to European starlings. She believed that this was one of several ways acorn woodpeckers avoided competition with European starlings. In British Columbia, Peterson and Gauthier (1985) found use of only 57% of cavities and could not show that European starlings were competing with native cavity-

nesting birds.

Van Balen et al. (1982) found that 54 - 93% of available holes were occupied and that used and unused cavities differed significantly for 6 of 8 cavity attributes measured. They interpreted these results as demonstrating cavity limitation. Gustafsson (1988) found almost 100% occupation of nest boxes when they were provided at less than 10 per ha. Minot and Perrins (1986) found the breeding density of blue and great tits was dependent on nest box densities up to 8 per ha, at which 41% were occupied.

Cavities did not limit cavity-nesting bird densities on the experimental plots in my study in either year. This was probably the result of both the low use of existing cavities and the ease with which new cavities were constructed. Birds nested in only 32.8% of the cavities available on experimental plots in 1988. However, because height of cavities used as nests in 1988 was significantly higher than height of cavities not used as nests, it is possible that not all cavities classified as available were suitable as nest sites. There also appeared to be an excess of cavities during the 1989 breeding season (i.e., after plugging) primarily because woodpeckers excavated and used 12 new cavities, and because I could not plug or plugs

fell out of 6 cavities that were used in 1989 but not in 1988.

Vander Wall (1980) believed the availability of suitable nest sites was the primary influence on the abundance of cavity-nesting birds in the Sonoran desert. My results suggest that cavities are not limiting in areas with abundant large saguaros. Cavities could be limiting, however, in areas with few saguaros.

Temporal partitioning. Ingold (1989) and Troetschler (1976) believed that asynchrony in breeding was responsible for reducing competition between European starlings and the species they were studying. Cavity-nesting bird species on my study plots used cavities at different times during the breeding season. This "temporal partitioning" even further reduced the likelihood that cavities were limiting. At any one time during the breeding season only a fraction of the available cavities contained active nests.

The existence of temporal differences in breeding between the exotic and native secondary cavity-nesting species is of interest from a theoretical viewpoint. If I had examined this assemblage of cavity-nesting birds without knowing that the exotics were recently established, it is possible that I would have inferred that past competition had led to the temporal partitioning. Clearly, the partitioning between the exotic species and the native

secondary cavity-nesting species was coincidental. This illustrates the need for caution in evaluating the causes of observed resource partitioning.

Spatial partitioning. Several authors have reported simultaneous nesting of European starlings and other cavity-nesting species within the same nesting substrate (Royall 1966, Gutzwiller and Anderson 1986, Ingold 1990). The latter 2 authors also noted low aggression among nesting species. Kerpez (1986), however, reported an unsuccessful attempt by a pair of gila woodpeckers to usurp a European starling nest cavity. Troetschler (1976) observed European starlings taking nest cavities from acorn woodpeckers but never saw them initiate an attack on a heterospecific.

Interspecific territoriality can reduce cavity availability. During this study, I observed some interspecific aggression, but I did not find interspecific territoriality. Of the 15 occasions on which I observed 2 species simultaneously nesting in different cavities in the same saguaro, 7 involved gila woodpeckers and European starlings. In agonistic interactions that occurred at nest saguaros between these 2 species, gila woodpeckers were dominant over European starlings. For example, I observed gila woodpeckers supplanting European starlings from perch

sites on numerous occasions. I did not observe either species attempt to take a nest from the other species.

Resource Partitioning. Some cavity-nesting bird species appear to partition nest cavities based on cavity size or location. East and Perrins (1988) believed that differences in cavity use were partially responsible for the limited interspecific competition observed between great tits (Parus major) and blue tits (P. caeruleus). However, Nilsson (1984), when examining a community of 6 cavity-nesting birds, concluded that the observed differences in cavity use appeared primarily due to differences in preference.

I found some partitioning of cavities based on opening size. However, because cavities of both sizes were available for nesting, I interpret differences in use of cavities based on size as preferences and not as the result of competition.

CONCLUSIONS

Exotic cavity-nesting birds did not compete for nest cavities with native cavity-nesting birds on my experimental plots. The abundance of cavities and nesting substrate, as well as temporal differences in breeding, appeared to prevent nest site competition between exotic and native cavity-nesting birds in the Sonoran desert. Large saguaros were abundant on my study areas and provided ample substrate for cavity excavation by woodpeckers. Waters et al. (1990) concluded that in areas not manipulated by man, factors other than cavity availability likely limit cavity-nesting bird populations. My study plots likely represent such areas. However, cavity competition between exotic and native species may occur in areas where few saguaros occur. Intraspecific territoriality is the most likely limiting influence on this avifauna at this time.

As urbanization occurs adjacent to areas of saguaro desert habitat, populations of exotic cavity-nesting birds probably will increase. My data indicate that competition with native species for nest cavities is unlikely as long as saguaros are abundant. In areas where saguaros are sparse or have been "thinned" by development it is possible that competition for nest cavities may occur. Management recommendations based on the findings of this research are

presented in Mannan and Bibles (1990).

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