

COMPETITION BETWEEN EUROPEAN STARLINGS AND NATIVE WOODPECKERS FOR NEST CAVITIES IN SAGUAROS

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ABSTRACT.—European Starlings (*Sturnus vulgaris*) have recently invaded Arizona and breed in some areas but not in similar areas nearby. In Arizona, European Starlings commonly nest in cavities in saguaro cacti (*Carnegiea gigantea*) but do not excavate these cavities. To examine whether European Starlings compete with native woodpeckers for nest cavities in saguaros, we studied Gila Woodpeckers (*Melanerpes uropygialis*) and Northern Flickers (*Colaptes auratus*) in areas with European Starlings and in similar, nearby areas with no European Starlings. We determined which factors explained the variation in the number of nests of each species present on fifteen 10-ha plots. We also compared the location and dimensions of nest cavities used by each species to determine whether European Starlings use Gila Woodpecker nest cavities, Northern Flicker nest cavities, or both.

We found that European Starlings compete with Gila Woodpeckers but not with Northern Flickers. This competition decreases the number of Gila Woodpeckers that nest in areas where European Starlings nest. European Starlings used Gila Woodpecker nest cavities, and there was a negative relationship between the number of European Starling nests and the number of Gila woodpecker nests that explained 46.7% of the variation in the number of Gila Woodpecker nests on the plots. European Starlings did not use Northern Flicker nest cavities, and we found no relationship between the number of European Starling nests and the number of Northern Flicker nests.

In addition, the number of Gila Woodpecker nests was positively related to the number of large saguaros and negatively related to the slope of the plot. The number of Northern Flicker nests was positively related to the volume of ironwood (*Olneya tesota*). The number of European Starling nests was negatively related to the distance to agriculture and large lawns. Received 29 June 1989, accepted 4 December 1989.

EUROPEAN Starlings (*Sturnus vulgaris*) were introduced into North America in 1890 and rapidly spread throughout most of the United States (Kessel 1953). They were not observed in Arizona until ca. 1946 (Monson 1948). In Arizona, European Starlings commonly nest in cavities in saguaro cacti (*Carnegiea gigantea*), but they do not excavate these cavities (Kessel 1957). Gila Woodpeckers (*Melanerpes uropygialis*) and Northern Flickers (*Colaptes auratus*) excavate these cavities in saguaros for nest sites (Gilman 1915, Bent 1939), and the nesting season of the European Starling overlaps that of the Gila Woodpecker and the Northern Flicker (Gilman 1915, Bent 1939, Royall 1966).

Brenowitz (1978) observed European Starlings usurp nest cavities from three pairs of Gila

Woodpeckers. One pair of Gila Woodpeckers lost three successive cavities to European Starlings. European Starlings have been observed usurping nest cavities from Northern Flickers in New Hampshire (Shelly 1935), Maryland (Howell 1943), and Massachusetts (Bent 1950). European Starlings have also usurped nest cavities from many other species including Purple Martins (*Progne subis*) in Michigan (Allen and Nice 1952), Red-bellied Woodpeckers (*Melanerpes carolinus*; Kilham 1958) and Wood Ducks (*Aix sponsa*; McGilvrey and Uhler 1971) in Maryland, Acorn Woodpeckers (*Melanerpes formicivorus*) in California (Troetschler 1976), Eurasian Nuthatches (*Sitta europaea*) in Sweden (Nilsson 1984), and Buffleheads (*Bucephala albeola*) in British Columbia (Peterson and Gauthier 1985). Van Balen et al. (1982) concluded that by competing for nest cavities European Starlings decreased the number of Great Tits (*Parus major*) nesting in their study area in the Netherlands.

Our objective was to determine whether Eu-

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ropean Starlings competed with Gila Woodpeckers and Northern Flickers for next cavities in saguaro cacti, and if so, to evaluate the effects of this competition. European Starlings presently breed in some areas of Arizona but not in similar areas nearby. Therefore, we were able to study Gila Woodpeckers and Northern Flickers in areas with no European Starlings and in similar, nearby areas with various densities of European Starlings. To assess the effect of competition, we studied the relationship between the number of European Starlings nesting in an area and the number of Gila Woodpeckers and Northern Flickers nesting in that area. We examined the relationships between habitat variables and the numbers of nesting Gila Woodpeckers, Northern Flickers, and European Starlings to separate the effects of habitat and competition. We also compared the location and dimensions of nest cavities used by each species to determine whether European Starlings use Gila Woodpecker nest cavities, Northern Flicker nest cavities, or both.

METHODS

We established 15 square plots (10-ha each) in a 1,557-km² area in and around the Picacho Mountains, Pinal County, Arizona, and the Tucson Mountains, Pima County, Arizona. Saguaros in the study area usually occur in large patches that reflect microclimatic differences. We conducted preliminary surveys at each accessible area of saguaro habitat to determine whether European Starlings were present. We located randomly 7 plots in areas of saguaro habitat with European Starlings and 8 plots in areas of saguaro habitat with no European Starlings. All plots were at least 600 m from any other plot, and the mean minimum distance between plots was 1,579 m.

We intensively searched each plot for several days until we were sure we had located all the European Starling, Gila Woodpecker, and Northern Flicker nests. The visibility in saguaro cacti forests allowed us to see birds fly to and from their nests, and we could often hear nestlings calling from a nest. Only cavities with eggs or nestlings were considered nests. When we were uncertain if a cavity was a nest, we climbed the saguaro with a ladder and looked into the cavity with a mirror and light. If we could not reach a suspect nest cavity with a ladder, we checked the cavity every week until nestlings could be heard, a bird was observed feeding nestlings, or the nesting season ended. The number of days each plot was censused varied, depending on the number of saguaros and cavities we needed to examine. We finished censusing one plot before we started another.

Between 8 April and 4 June, when all three species

were nesting, we censused nests on 8 plots in 1983 and 7 plots in 1984. Approximately 50% of the plots censused each year contained European Starling nests. Of the 7 plots censused in 1984, 4 were censused again in 1985 for a pairwise comparison of the number of nests present in 1984 and 1985. The 1985 census data were not used in any other analysis because they were not independent of the 1984 census data.

For each nest we found on or near the plots, we measured the height and orientation of the cavity entrance, the height of the saguaro in which the nest was located (the nest saguaro), and the number of arms on the nest saguaro. For nests that could be reached with a 7.6-m ladder, we measured the vertical and horizontal diameters of the cavity entrance, the horizontal depth of the cavity, and the vertical depth of the cavity (Fig. 1).

To sample the vegetation, we selected randomly 10 points in every plot, and recorded all saguaros within 30 m of each point. For each saguaro, we estimated height, and we counted the number of arms and holes that, from the ground, appeared to be possible nest cavities. A 60-m-long and 3-m-wide transect was centered on each point and randomly oriented. We estimated the height and width of the foliage of all trees, shrubs, and cacti (except triangle-leaf bursage [*Franseria deltoidea*]), which each transect intersected. Only the number of triangle-leaf bursage intersected by a transect was recorded because of the relatively uniform size of triangle-leaf bursage. We practiced estimating the heights and widths of vegetation until we were accurate to within 30 cm, and we continually checked our estimates throughout the study to maintain this accuracy.

The volume of each plant intersected by the transects was calculated from the estimated height and width of the plant. The shape of all plants except ocotillo (*Fouquieria splendens*) was estimated as a hemi-ellipsoid. For ocotillo, the plant shape was estimated as a cone. The volume estimates for individual plants were summed to provide an index of the volume of each plant species on each plot.

The plots were delineated on 1:2400 U.S. Geological Survey topographic maps. From these maps we measured the elevation, slope, aspect, and distance to nearest agriculture for each plot. *Agriculture* was defined as any area ≥ 1 acre that was irrigated for the growth of vegetation not typical of the Sonoran Desert. We defined agriculture to include areas of lawn (such as golf courses, parks, and housing developments) because they are used by European Starlings for foraging much like farm fields (Dunnet 1955, Royall 1966, Troetschler 1976, Feare 1984, T. A. Kerpez pers. obs).

For all statistical tests, the alpha level was 0.05. The alpha levels for multiple pairwise tests were calculated as described by Neu et al. (1974) to maintain an alpha of 0.05 across experiments. Means are given with standard errors.

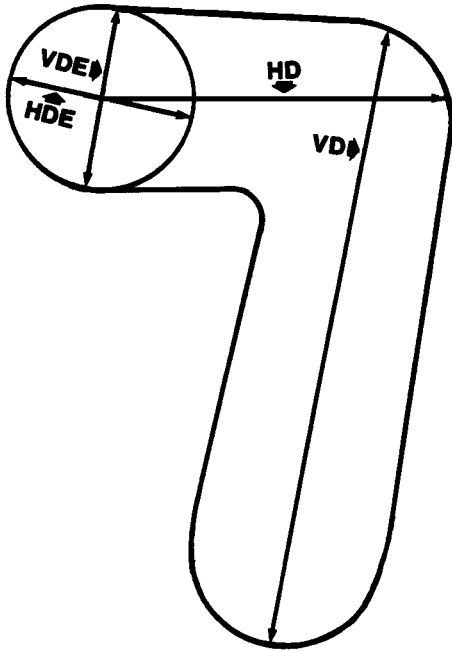


Fig. 1. Measurements of cavity dimensions: vertical diameter of entrance (VDE), horizontal diameter of entrance (HDE), horizontal depth (HD), and vertical depth (VD).

Analysis of factors affecting the number of nests.—We tested with the Mann-Whitney test differences in the number of Gila Woodpecker and Northern Flicker nests on the plots with European Starlings and the plots without European Starlings. However, these tests did not account for habitat variables that may affect the number of nests; therefore, we used multiple linear regression analysis with forward stepwise inclusion of variables (Dixon 1985, computer program BMDP-2R, F -to-enter = 4.0, F -to-remove = 3.9) to simultaneously examine the effects of European Starlings and habitat variables. Three regression models (one for each species) were developed. The dependent variables were the number of nests of each species present on each plot. To include a measure of the saguaros on the plots as a possible explanatory variable, saguaros were categorized into four classes that were approximately equal in number and easily distinguished (Table 1), and the number of saguaros in each class was calculated for each plot. The possible explanatory variables were the following plot characteristics: the number of saguaros in each of the four saguaro classes; the volume index for each of the 30 tree, shrub, and cacti species found on the plots; the total volume of all plant, tree, shrub, and cacti species on each plot; the distance from the plot to the nearest agriculture; the slope of the plot; the elevation of the plot; the year the plot was censused; and the mean

TABLE 1. Heights and number of arms of saguaro classes.

| Class | Description |
|-------|--|
| 1 | Height < 2.5 m |
| 2 | 2.5 m ≤ height < 4.5 m |
| 3 | 4.5 m ≤ height < 7.0 m & no. of arms < 6 |
| 4 | Height ≥ 7.0 m or no. of arms ≥ 6 |

date the plot was censused. The number of European Starling nests on the plot also was used as a possible explanatory variable for the Gila Woodpecker and Northern Flicker regressions. The number of saguaro holes that appeared to be possible nest cavities was also used as a possible explanatory variable for the European Starling regression.

Before the regression analysis, the dependent variables were transformed with the square root transformation ($\sqrt{x + 0.375}$) to cause the dependent variables' means to be independent of their variances and to make the dependent variables more normally distributed (Draper and Smith 1981). Plots of the regression residuals against the predicted values and the independent variables were analyzed for each regression (as described by Draper and Smith 1981) and met the assumptions for multiple linear regression analysis.

To examine the relationship of plot aspect to the number of nests present, each plot was classified into one of four 90° quadrats centered on North, South, East, and West. We tested differences among quadrats with the Kruskal-Wallis test and a nonparametric multiple comparison (Gibbons 1976). The effect of southern aspect could not be tested because only one plot had a southern aspect. Differences between 1984 and 1985 in the number of nests present for each species on the four plots censused both these years were tested with the paired-sample t -test.

Analysis of nest-cavity dimensions and location.—We tested whether the dimensions of Gila Woodpecker, Northern Flicker, and European Starling nest cavities differed by multivariate analysis of variance (overall differences), analysis of variance (differences in each dimension), and the Student-Newman-Keuls test (differences between species). Differences in the nest-cavity heights among the three species were tested with analysis of variance. Nest-cavity height was not included in the multivariate analysis of variance, because the nests for which cavity dimensions were measured were lower than the nests for which cavity dimensions could not be measured. No variable's distribution differed significantly from the normal distribution ($P > 0.05$, Kolmogorov-Smirnov goodness-of-fit tests; Zar 1984). Variables with significantly unequal variances ($P < 0.05$, Bartlett-Box F -test; Nie et al. 1975) were transformed with the logarithmic transformation [$\ln(x)$] to equalize their variances.

We tested with the Rayleigh test (Batschelet 1981)

whether the orientation of nest cavities was nonrandom for each species. Differences between species in their use of saguaro classes were tested with the binomial test for two proportions (Zar 1984).

RESULTS

In 1983, 15 Gila Woodpecker nests, 15 Northern Flicker nests, and 10 European Starling nests were found on the 8 plots censused; and in 1984, 19 Gila Woodpecker nests, 6 Northern Flicker nests, and 11 European Starling nests were found on 7 plots.

Factors affecting the number of Gila Woodpecker nests.—The number of Gila Woodpecker nests on the plots with European Starling nests ($\bar{x} = 0.86 \pm 0.404$, $n = 7$) was significantly less than the number of Gila Woodpecker nests on the plots without European Starling nests ($\bar{x} = 3.5 \pm 0.707$, $n = 8$) ($P = 0.01$). This was confirmed by the regression analysis. Of all the explanatory variables examined, the number of European Starling nests explained the most variation in the number of Gila Woodpecker nests. The relationship of European Starling nests to Gila Woodpecker nests was negative and alone explained 46.7% of the variation in the number of Gila Woodpecker nests ($P = 0.0012$, $b = -0.1704$). The number of class 4 saguaros, the largest saguaros (Table 1), was positively related to the number of Gila Woodpecker nests. After the relationship to European Starling nests was determined, the number of class 4 saguaros explained an additional 18.1% of the variation in the number of Gila Woodpecker nests ($P = 0.0167$, $b = 0.1593$). The slope of the plot was negatively related to the number of Gila Woodpecker nests and explained an additional 16.2% of the variation in the number of Gila Woodpecker nests ($P = 0.0109$, $b = -0.0434$). Together, these three variables explained 81.0% of the variation in the number of Gila Woodpecker nests ($P = 0.0003$, intercept = 1.643).

There were no significant differences in the number of Gila Woodpecker nests on plots with different aspects ($P = 0.917$). There was no significant difference between 1984 and 1985 in the number of Gila Woodpecker nests on the four plots censused both years ($P = 0.240$). However, one of the plots contained 3 Gila Woodpecker nests and 0 European Starling nests in 1984. This plot contained 2 European Starling nests and only 1 Gila Woodpecker nest in 1985. The 2 nest cavities used by European Starlings

in 1985 had been used by Gila Woodpeckers in 1984.

While censusing one of the plots, we observed a pair of Gila Woodpeckers fight with a pair of European Starlings for a nest cavity (Kerpez 1986). When we returned to this plot a week later, the nest cavity was occupied by European Starlings and no Gila Woodpeckers were nesting on the plot.

Factors affecting the number of Northern Flicker nests.—The number of Northern Flicker nests on the plots with European Starling nests ($\bar{x} = 1.38 \pm 0.324$, $n = 7$) was not significantly different from the number of Northern Flicker nests on the plots without European Starling nests ($\bar{x} = 1.43 \pm 0.571$, $n = 8$) ($P = 0.530$). This was confirmed by the regression analysis. Throughout the stepwise inclusion of variables in the Northern Flicker regression, the number of European Starling nests was never significant in explaining the number of Northern Flicker nests ($P \geq 0.927$).

The year the plot was censused explained 25.0% of the variation in the number of Northern Flicker nests ($P = 0.0151$, $b = -0.5436$). Because year was coded as 1 = 1983 and 2 = 1984, the negative coefficient in the regression equation means that there were fewer Northern Flicker nests in 1984 than in 1983. There also were significantly fewer Northern Flicker nests in 1984 than in 1985 on the four plots censused both years ($P = 0.007$). Examination of winter precipitation recorded at two weather stations near the study area (Tucson and Eloy) showed that there was much less precipitation in the period December–March before the 1984 breeding season (5.1 cm) compared with the precipitation before the 1983 (22.0 cm) and 1985 (17.2 cm) breeding seasons (National Oceanic and Atmospheric Administration 1982, 1983, 1984, 1985).

The volume of ironwood (*Olneya tesota*) was positively related to the number of Northern Flicker nests. After the effect of year was determined, ironwood volume explained an additional 20.7% of the variation in the number of Northern Flicker nests ($P = 0.0539$, $b = 0.0483$). The volumes of the following plants found on the plots were significantly correlated with the volume of ironwood: gray-thorn (*Condalia lycioides*) ($r = 0.917$, $P = 0.001$), desert hackberry (*Celtis pallida*) ($r = 0.932$, $P = 0.001$), burro-bush (*Hymenoclea salsola*) ($r = 0.940$, $P = 0.001$), cane cholla (*Opuntia spinosior*) ($r = 0.944$, $P = 0.001$),

TABLE 2. Dimensions (cm) and height (m) of Gila Woodpecker, European Starling, and Northern Flicker nest cavities. Differences among species were tested with ANOVA and the Student-Newman-Keuls test. Means followed by the same letter did not differ significantly ($P > 0.05$).

| Nest cavity variable | Gila Woodpecker ($\bar{x} \pm SE$) | European Starling ($\bar{x} \pm SE$) | Northern Flicker ($\bar{x} \pm SE$) | P^1 |
|---|---|---|--|---------|
| Entrance vertical diameter ² | 5.7 \pm 0.18 A | 5.7 \pm 0.22 A | 7.0 \pm 0.46 B | 0.0023 |
| Entrance horizontal diameter ² | 6.3 \pm 0.21 A | 6.6 \pm 0.25 A | 8.3 \pm 0.42 B | <0.0001 |
| Cavity vertical depth ² | 27.8 \pm 0.99 A | 31.8 \pm 2.02 A | 37.6 \pm 1.45 B | 0.0001 |
| Cavity horizontal depth ² | 15.7 \pm 0.63 A | 14.0 \pm 0.93 AB | 12.5 \pm 0.97 B | 0.0252 |
| Height of nest ³ | 5.8 \pm 0.14 A | 6.0 \pm 0.19 A | 6.2 \pm 0.23 A | 0.3036 |

¹ From ANOVA.

² $n = 32$ for Gila Woodpeckers, $n = 19$ for European Starlings, and $n = 15$ for Northern Flickers.

³ $n = 64$ for Gila Woodpeckers, $n = 26$ for European Starlings, and $n = 28$ for Northern Flickers.

and honey mesquite (*Prosopis juliflora*), ($r = 0.533$, $P = 0.041$). Together, the year the plot was censused and the volume of ironwood explained 45.7% of the variation in the number of Northern Flicker nests ($P = 0.0257$, intercept = 1.958).

There were no significant differences in the number of Northern Flicker nests on plots with different aspects ($P = 0.726$).

Factors affecting the number of European Starling nests.—The mean number of European Starling nests on the plots with European Starlings was 3.00 ± 0.926 ($n = 7$). The distance from the plot to the nearest agriculture was negatively related to the number of European Starling nests and alone explained 29.2% of the variation in the number of European Starling nests ($P = 0.0078$, $b = -0.2260$). The mean date the plot was censused was negatively related to the number of European Starling nests and explained an additional 26.3% of the variation in the number of European Starling nests ($P = 0.0208$, $b = -0.2319$). Together, these two variables explained 55.5% of the variation in the number of European Starling nests ($P = 0.0078$, intercept = 2.220).

Plots with northern aspects had significantly fewer European Starling nests than did plots with eastern aspects ($P = 0.027$). All three plots with northern aspects had no European Starling nests; however, this was probably not caused by their northern aspect but instead by their distance from agriculture. The three plots with northern aspects were all >4 km from agriculture. The farthest plot from agriculture with a European Starling nest was ca. 4 km from agriculture.

There was no significant difference between 1984 and 1985 in the number of European Starling nests on the four plots censused both years ($P = 0.392$).

Nest-cavity dimensions and location.—Throughout the study, 64 Gila Woodpecker, 28 Northern Flicker, and 26 European Starling nests were found on or near the plots. We measured the cavity dimensions of 32 Gila Woodpecker, 15 Northern Flicker, and 19 European Starling nests. European Starlings and Gila Woodpeckers did not significantly differ in nest-cavity dimensions ($P = 0.3840$). European Starlings and Gila Woodpeckers both significantly differed from Northern Flickers in nest-cavity dimensions ($P = 0.0182$ and $P = 0.0001$, respectively). European Starling and Gila Woodpecker nest cavities had significantly smaller entrances (vertical and horizontal diameters), and the cavities were significantly shallower in the vertical plane of the saguaro than Northern Flicker nest cavities (Table 2). The three species did not significantly differ in nest-cavity height (Table 2).

European Starlings and Gila Woodpeckers did not differ significantly in their use of saguaros for nest sites ($P = 0.511$) (Fig. 2). European Starlings and Gila Woodpeckers nested in class 3 saguaros significantly less and in class 4 saguaros significantly more than Northern Flickers ($P \leq 0.013$) (Fig. 2). The orientation of nest cavities did not significantly differ from random for Gila Woodpeckers ($r = 0.02$, $P > 0.90$), Northern Flickers ($r = 0.16$, $P > 0.47$), and European Starlings ($r = 0.21$, $P > 0.30$). For more information on Gila Woodpecker and Northern Flicker nest-site selection and nest-cavity characteristics see Kerpez and Smith (1990).

DISCUSSION

Competition between European Starlings and Gila Woodpeckers.—European Starlings compete with Gila Woodpeckers for nest cavities in saguaros and this competition decreases the number of

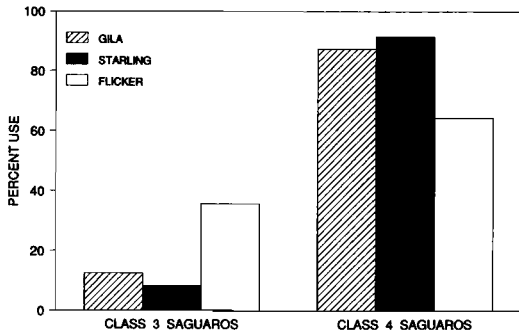


Fig. 2. Use of saguaros for nest sites by Gila Woodpeckers ($n = 64$), Northern Flickers ($n = 28$), and European Starlings ($n = 26$). Class 1 and class 2 saguaros were not used for nest sites by any of the species.

Gila Woodpeckers that nest in areas where European Starlings nest. European Starlings nest in Gila Woodpecker nest cavities, and no other factors examined could explain the negative relationship between the number of European Starling nests and the number of Gila Woodpecker nests.

European Starlings use cavities in saguaros only when they nest and are rarely seen in saguaro habitat during the rest of the year (T. A. Kerpez pers. obs.). Plots that had many European Starling nests and no Gila Woodpecker nests during the breeding season had no European Starlings and several Gila Woodpeckers present during the rest of the year. Apparently, at the beginning of the nesting season European Starlings move into areas that Gila Woodpeckers inhabit the rest of the year and usurp nest cavities from the Gila Woodpeckers.

Gila Woodpeckers that lose their nest cavities to European Starlings did not excavate another cavity and nest in the same area. If they did, there would be more Gila Woodpeckers that nest in areas where European Starlings nest. There are several possible reasons why Gila Woodpeckers do not excavate another cavity in the same area. There may be a lack of suitable sites for cavities. Many of the holes in saguaros are only a few inches deep (T. A. Kerpez pers. obs.). Woodpeckers may begin excavating cavities only to find that the site is unsuitable. It is also possible that European Starlings harass Gila Woodpeckers if the woodpeckers remain in the area.

Another possibility is that Gila Woodpeckers

excavate cavities only during winter and the loss of a nest cavity during spring may not trigger them to excavate another one. Soule (1964) saw Gila Woodpeckers excavate cavities in February. There are no other published reports on the time of Gila Woodpecker cavity excavation. The Museum of Ornithology at the University of Arizona and the Tucson Audubon Society receive almost all of their calls complaining about Gila Woodpeckers excavating cavities in buildings during winter (S. M. Russell pers. comm.). For three years we observed Gila Woodpeckers almost daily during the breeding season (April–June), and we never saw them excavate cavities. Because Gila Woodpeckers nest in the same cavity for several years (Bendire 1892, Gilman 1915, S. M. Russell pers. comm., Kerpez 1986), they may excavate a new cavity only when necessary. European Starlings were absent during winter; therefore, Gila Woodpeckers may not be stimulated to excavate more cavities during winter.

Competition between European Starlings and Gila Woodpeckers could affect the entire cavity-nesting community. The two plots with the most European Starling nests had no Gila Woodpecker nests. Communities with many European Starlings may no longer have Gila Woodpeckers, and communities with intermediate numbers of European Starlings may have fewer Gila Woodpeckers. If Gila Woodpeckers cannot nest in an area, they may not excavate new cavities in that area. If this is true, as the saguaros with existing cavities die, the number of cavities available will decrease in areas where Gila Woodpeckers are excluded or reduced in number by European Starlings. This decrease in the number of available cavities would be large because Gila Woodpeckers and Northern Flickers are the only common excavators of cavities in saguaros, and except where European Starlings were present, Gila Woodpeckers were much more numerous in the areas we studied than Northern Flickers. A decrease in the number of cavities available could have a profound effect. There are six other species of native birds that regularly nest in cavities in saguaros: Elf Owls (*Micrathene whitneyi*), Brown-crested Flycatchers (*Myiarchus tyrannulus*), Ash-throated Flycatchers (*M. cinerascens*), Purple Martins, Western Screech-Owls (*Otus kennicottii*), and American Kestrels (*Falco sparverius*) (Bent 1937, 1942; Allen and Nice 1952). These birds do not

excavate cavities but depend on the woodpecker's cavities. Also, if there are fewer Gila Woodpecker cavities available, European Starlings may compete with Northern Flickers for nest cavities. Also, European Starlings may compete with the other secondary cavity nesters, if they do not already.

European Starlings and Northern Flickers.—European Starlings compete with Gila Woodpeckers and not with Northern Flickers probably because European Starlings may be able to displace Gila Woodpeckers more easily than Northern Flickers. Northern Flickers are larger than Gila Woodpeckers (Ridgeway 1914, Dunning 1984), and they may also be more aggressive. Northern Flickers usurp nest cavities from Gila Woodpeckers (Brenowitz 1978, Martindale 1982), but the reverse situation has not been reported.

Habitat factors affecting the number of Gila Woodpecker nests.—The number of class 4 saguaros positively affects the number of Gila Woodpeckers that nest in an area because Gila Woodpeckers use them for nesting and foraging. Gila Woodpeckers nest almost exclusively in class 4 saguaros (Fig. 2; Kerpez and Smith 1990). During the nesting season, Gila Woodpeckers spend more than half their foraging time on saguaros, feeding their nestlings pollen, fruit, and insects gleaned from saguaros (Martindale 1983). Class 4 saguaros have the most flowers and fruits, are the tallest saguaros, and have the most arms (Steenbergh and Lowe 1977). Also, class 4 saguaros have the most surface area from which Gila Woodpeckers glean insects and may have more insects per unit area because class 4 saguaros are older.

Slope is negatively related to the number of Gila Woodpeckers that nest in an area possibly because it affects the vegetation. Differences in the total volume of all plant, tree, shrub, or cacti species, or the volume of any single plant species could not explain the relationship that slope had to the number of nesting Gila Woodpeckers. Steep slopes may cause differences in the amount of several plant species that are not obviously related. These differences may affect the availability of insects that Gila Woodpeckers eat and feed their nestlings. Also, steep slopes may increase the energy required to forage and deliver food to a nest.

Factors affecting the number of Northern Flicker nests.—Fewer Northern Flickers nested on the

study area in 1984 than in 1983 and 1985. This was probably caused by the lack of precipitation during the months preceding nesting (December–March) in 1984 compared with 1983 and 1985. Northern Flickers in the Sonoran Desert forage primarily for insects on the ground and in annual foliage <10 cm high (Tomoff 1974, Vander Wall 1980). In deserts the timing and quantity of precipitation plays an important role in the germination and growth of annuals (MacMahon and Schimpf 1981). The germination and growth of annuals along with soil moisture probably affect the production of insects that Northern Flickers eat and feed their nestlings.

Gila Woodpeckers were not affected by the lack of precipitation in 1983 because during the nesting season they forage primarily on saguaro cacti (Martindale 1983). Seasonal drought does not affect the production of flowers and fruits by saguaros because saguaros store water reserves in their succulent stem tissue (Steenbergh and Lowe 1977). European Starlings were not affected by the lack of precipitation in 1983 because, during the nesting season in the Sonoran Desert, they forage primarily for insects in irrigated agricultural areas (Royall 1966, T. A. Kerpez pers. obs.), which produce insects relatively independent of seasonal precipitation.

The volume of ironwood was related positively to the number of Northern Flickers that nest in an area probably because the presence of ironwood indicates a warmer microclimate (Kearny and Peebles 1960) and a different vegetation community. The volumes of five plant species were correlated significantly with the volume of ironwood. The warmer microclimate and the vegetation community indicated by ironwood may produce more insects that Northern Flickers eat and feed their nestlings.

The number of class 4 saguaros did not affect the number of Northern Flickers nesting on the plots because all the plots had some class 4 saguaros. Northern Flickers rarely use saguaros for foraging (Tomoff 1974, Vander Wall 1980), and one large saguaro is probably sufficient for each nesting pair. Further, Northern Flickers often use class 3 saguaros for nest sites (Fig. 2; Kerpez and Smith 1990).

Factors affecting the number of European Starling nests.—The distance to agriculture was correlated negatively with the number of nesting

European Starlings in an area. European Starlings that nest in the Sonoran Desert obtain most of their food from agricultural areas (Royall 1966, T. A. Kerpez pers. obs.). During our census, we saw no European Starlings forage on the plots. European Starlings always flew off, usually toward agriculture, to forage. When we were close enough to see agricultural areas, we saw European Starlings repeatedly leave their nest, fly to the agriculture, land on the ground, and return to the nest with insects. Other reports confirm that during the nesting season European Starlings forage primarily in agricultural areas (Dunnet 1955, Royall 1966, Troetschler 1976, Feare 1984). Feare (1984) found that agricultural areas supported the highest densities of breeding European Starlings in Europe.

European Starlings nested on the plots throughout the census period, but fewer European Starlings nested toward the end of the census period. In Arizona, many European Starlings have two broods and begin their second brood in May (Royall 1966). Usually fewer European Starlings have second broods than have first broods (Kessel 1957). The decrease in the number of European Starlings nesting on the plots may be due to single broods.

Future implications.—Competition between European Starlings and Gila Woodpeckers will probably become more severe and more widespread. From 1968 to 1976, the number of European Starlings in the southwestern United States has more than doubled (Dolbeer and Stehn 1979). European Starlings are probably still increasing in the Sonoran Desert, but it is difficult to tell if they will increase only near agriculture. We did not find European Starling nests on plots farther than 4 km from agriculture. However, if European Starlings are increasing, they may be using only their preferred habitat (i.e. areas near agriculture) now. Once the preferred areas are full, European Starlings may invade areas farther from agriculture. Also, human activity has decreased the amount of desert that is far from large lawns and agriculture. If European Starlings continue to increase and spread, the survival of Gila Woodpeckers could be threatened. A decline in Gila Woodpeckers could profoundly affect the unique community of birds that nest in saguaro cavities and could also affect the survival of saguaros because Gila Woodpeckers may be important pollinators of saguaros (S. Martindale pers. comm.).

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LITERATURE CITED

- ALLEN, R. W., & M. M. NICE. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). *Am. Midl. Nat.* 47: 606-665.
- BATSCHLEET, E. 1981. *Circular statistics in biology*. New York, Academic Press Inc.
- BENDIRE, C. E. 1892. Life histories of North American birds with special reference to their breeding habits and eggs. *U.S. Natl. Mus. Bull.* 1.
- BENT, A. C. 1937. Life histories of North American birds of prey, part 2. *U.S. Natl. Mus. Bull.* 170.
- . 1939. Life histories of North American woodpeckers. *U.S. Natl. Mus. Bull.* 174.
- . 1942. Life histories of North American flycatchers, larks, swallows and their allies. *U.S. Natl. Mus. Bull.* 179.
- . 1950. Life histories of North American wagtails, shrikes, vireos and their allies. *U.S. Natl. Mus. Bull.* 197.
- BRENEWITZ, G. L. 1978. Gila Woodpecker agonistic behavior. *Auk* 95: 49-58.
- DIXON, W. J. (Ed.). 1985. *BMDP statistical software*, 1985 ed. Berkeley, Univ. California Press.
- DOLBEER, R. A., & R. A. STEHN. 1979. Population trends of blackbirds and starlings in North America 1966-1976. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl.* 214.
- DRAPER, N. R., & H. SMITH. 1981. *Applied regression analysis*, 2nd ed. New York, John Wiley & Sons.
- DUNNET, G. M. 1955. The breeding of the Starling *Sturnus vulgaris* in relation to its food supply. *Ibis* 97: 619-662.
- DUNNING, J. G., JR. 1984. Body weights of 686 species of North American birds. *West. Bird Band. Assoc. Monogr.* 1.
- FEARE, C. 1984. *The starling*. New York, Oxford Univ. Press.
- GIBBONS, J. D. 1976. *Nonparametric methods for quantitative analysis*. New York, Holt, Rinehart, & Winston.
- GILMAN, M. F. 1915. Woodpeckers of the Arizona lowlands. *Condor* 17: 151-163.
- HOWELL, A. B. 1943. Starlings and woodpeckers. *Auk* 60: 90-91.

- KEARNEY, T. H., & R. H. PEEBLES. 1960. Arizona flora, 2nd ed. Berkeley, Univ. of California Press.
- KERPEZ, T. A. 1986. Competition between European Starlings and native woodpeckers for nest cavities in saguaros. M.S. thesis, Tucson, Univ. Arizona.
- , & N. S. SMITH. 1990. Nest-site selection and nest cavity characteristics of Gila Woodpeckers and Northern Flickers. *Condor* 92: 193-198.
- KESSEL, B. 1953. Distribution and migration of the European Starling in North America. *Condor* 55: 49-67.
- . 1957. A study of the breeding biology of the European Starling (*Sturnus vulgaris*) in North America. *Am. Midl. Nat.* 58: 257-331.
- KILHAM, L. 1958. Pair formation, mutual tapping and nesthole selection of Red-bellied Woodpeckers. *Auk* 75: 318-325.
- MACMAHON, J. A., & D. J. SCHIMPF. 1981. Water as a factor in the biology of North American desert plants. Pp. 114-171 in *Water in desert ecosystems* (D. Evans and J. Thames, Eds.). U.S./I.B.P. Synth. Series 12.
- MARTINDALE, S. 1982. Nest defense and central place foraging: a model and experiment. *Behav. Ecol. Sociobiol.* 10: 85-89.
- . 1983. Foraging patterns of nesting Gila Woodpeckers. *Ecology* 64: 888-898.
- MCGILVREY, F. B., & F. M. UHLER. 1971. A starling deterrent Wood Duck nest box. *J. Wildl. Manage.* 35: 793-797.
- MONSON, G. 1948. The starling in Arizona. *Condor* 50: 45.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1982, 1983, 1984, 1985. Climatological data: Arizona, annual summary. Asheville, North Carolina, Natl. Climatic Ctr.
- NEU, C. W., C. R. BYERS, & J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541-545.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BRENT. 1975. SPSS, statistical package for the social sciences, 2nd ed. New York, McGraw-Hill.
- NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica* 15: 167-175.
- PETERSON, B., & G. GAUTHIER. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. *Wilson Bull.* 97: 319-331.
- RIDGEWAY, R. 1914. The birds of North and Middle America. U.S. Natl. Mus. Bull. 50.
- ROYALL, W. C., JR. 1966. Breeding of the starling in central Arizona. *Condor* 68: 196-205.
- SHELLY, L. O. 1935. Flickers attacked by starlings. *Auk* 52: 93.
- SOULE, O. 1964. The saguaro tree-hole microenvironment in southern Arizona. II: Summer. M.S. thesis, Tucson, Univ. Arizona.
- STEENBERGH, W. F., & C. H. LOWE. 1977. Ecology of the saguaro II. Natl. Park Serv. Sci. Monogr. Series 8.
- TOMOFF, C. S. 1974. Avian species diversity in desert scrub. *Ecology* 55: 396-403.
- TROETSCHLER, T. G. 1976. Acorn Woodpecker breeding strategy as affected by starling nest-hole competition. *Condor* 78: 151-165.
- VAN BALEN, J. H., C. J. H. BOOY, J. A. VAN FRANKEK, & E. R. OSIECK. 1982. Studies on hole-nesting birds in natural sites: 1. availability and occupation of natural nest sites. *Ardea* 70: 1-24.
- VANDER WALL, S. B. 1980. The structure of the Sonoran Desert bird communities: effects of vegetation structure and precipitation. Ph.D. dissertation, Logan, Utah State Univ.
- ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.