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

The University of Arizona

M.S. 1986

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

by

Theodore Alfred Kerpez

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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ACKNOWLEDGMENTS

I am especially grateful to Dr. Norm Smith, my major advisor, for his advice and guidance throughout this study. I thank Dr. Bill Mannan for his advice during the study and for serving as a committee member and critically reviewing the manuscript. I also thank Dr. Bill Matter for serving as a committee member and critically reviewing the manuscript.

I am very grateful to Drs. Bruce Leopold and Bob Kuehl for their invaluable help with the statistical analysis.

Special thanks go to my wife, Barbara Sunshine, for her support and help throughout this study and especially for typing the manuscript.

This study was funded by the Arizona Cooperative Wildlife Research Unit, the University of Arizona, and the Arizona Game and Fish Department.

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ABSTRACT

I examined the relationship between the number of European Starlings (*Sturnus vulgaris*), and Gila Woodpeckers (*Melanerpes uropygialis*) and Northern Flickers (*Colaptes auratus*) nesting on 15, 10 ha plots in saguaro cacti habitat. I also examined the relationship between habitat variables and the number of each species nesting. European Starlings used Gila Woodpecker nest cavities and negatively affected the number of Gila Woodpeckers nesting. European Starlings did not use Northern Flicker nest cavities and did not affect the number of Northern Flickers nesting. Nesting Gila Woodpeckers were positively affected by the number of large saguaros and negatively affected by the slope of the plot. Nesting Northern Flickers were positively affected by the volume of ironwood. Nesting European Starlings were negatively affected by the distance to agriculture and large lawns. The dimensions of Gila Woodpecker and Northern Flicker nest cavities differed and both selected the larger saguaros for nest sites.

INTRODUCTION

For a quarter of a century most ecologists viewed competition as the dominant ecological interaction (Schoener 1982). However, recently there has been controversy about the importance and prevalence of interspecific competition (Conner and Simberloff 1979, Schoener 1982, Connell 1983, Roughgarden 1983). A major part of this controversy concerns the importance of interspecific competition in structuring communities. This controversy exists, at least in part, because effects of interspecific competition are difficult to study. Throughout this paper competition refers to interspecific competition.

Examination of even the simplest case in which 2 sympatric species use the same limited resource reveals the difficulty of studying the effects of competition on the structure of present communities. If both species depend on this resource, and the resource is limited enough so that each species has a substantial negative effect on the other species abundance, competition theory and evolutionary theory predict that eventually 1 of 3 things should happen. One of the species may gain an advantage at exploiting the resource, and the other go extinct. The 2 species may diverge in resource use enough that competition is minimal and they can coexist. Or the 2 species may become allopatric, each having an advantage at exploiting the resource in their respective areas. In all 3 instances competition would have had a large impact on the structure of the communities involved. However, in all 3 instances

it would be difficult to determine in retrospect what role competition played in structuring the present community.

Once a species is extinct, it is very difficult, if not impossible, to determine what caused its extinction. If 2 species have diverged in resource use to avoid competition, it is difficult to determine if they competed in the past. Even if the fossil record shows that 2 species were once morphologically similar and then diverged, we don't know if the divergence was caused by competition. The only outcome we can examine in the present is allopatry caused by competition, and even this is difficult. If we remove from an area 1 of 2 allopatric species (species A) which utilize the same resource and the other species (species B) expands into that area, we can conclude that the 2 species allopatric distribution was caused by competition. However, if species B does not expand into an area where species A was removed, we can not safely conclude that competition was not involved in causing their allopatry. The 2 species' allopatry could have been caused by competition, but once separated 1 or both of the species may have evolved adaptations to their particular area which make them unable to occupy their entire original range (i.e. their range before competition caused the allopatric distribution). Also, colonization of new areas can take many years, and most studies of competition last less than 1 or 2 years (Schoener 1983).

The major problem with studying the effects of competition on the structure of present communities is all we usually have to study are the results of a process, not the process itself. Ideally, we would

like to study communities while they are changing because of competition. Recently introduced exotic species provide this opportunity. Native species in a community to which an exotic species is introduced have not evolved with the exotic species. Therefore, if an exotic species uses the same resource as 1 or more native species, and that resource is limited enough to cause competition, we can study the effects of this competition on the community while the community is changing. Whether a species invades a new area because it was introduced by humans or because of a breakdown in isolation barriers, the processes which follow and the results should be the same. Although such studies may not resolve the controversy over the importance of interspecific competition in structuring communities, they can add much to our understanding of competition and the way it affects community structure. I am not suggesting that exotic species be introduced so that we can study competition, but rather that those exotic species already introduced be used to increase our understanding of competition.

European Starlings (*Sturnus vulgaris*) in Arizona are a good example of a recently introduced exotic species which may be competing with native species. Although European Starlings were introduced into North America in 1890 and rapidly spread throughout the United States (Kessel 1953), they did not invade Arizona until about 1946 (Monson 1948). European Starlings compete successfully with some native species for nest cavities (Feare 1984). Because the invasion of Arizona by European Starlings is so recent, if they are competing with native

species, we should be able to examine the effects of this competition on the structure of the community.

European Starlings nest in cavities but do not excavate them (Kessel 1957). In Arizona, European Starlings commonly nest in cavities in saguaro cacti (Carnegiea gigantea). Gila Woodpeckers (Melanerpes uropygialis) and Northern Flickers (Colaptes auratus) excavate these cavities in saguaro cacti for nest sites (Gilman 1915, Bent 1939). The nesting season of the European Starling overlaps that of the Gila Woodpecker and Northern Flicker (Gilman 1915, Bent 1939, Royall 1966).

Brenowitz (1978) observed European Starlings take nest cavities from 3 pairs of Gila Woodpeckers. One pair of Gila Woodpeckers lost 3 successive cavities to European Starlings. European Starlings have been observed taking nest cavities from Northern Flickers in New Hampshire (Shelly 1935), Maryland (Howell 1943), and Massachusetts (Bent 1950). European Starlings have also taken 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), Nuthatches (Sitta europaea) in Sweden (Nilsson 1984), and Buffleheads (Bucephala albeola) in British Columbia (Peterson and Gauthier 1985). Van Balen et al. (1982) found that by competing for nest cavities European Starlings decreased the number of Great Tits (Parus major) nesting in their study area in the Netherlands.

My objective was to determine whether European Starlings are competing with Gila Woodpeckers and Northern Flickers for nest cavities in saguaro cacti, and if so, to evaluate the effects of this competition. Presently European Starlings breed in some areas of the Sonoran Desert but not in other areas. These areas with and without European Starlings are often very similar and very close to each other. Therefore, I was able to study Gila Woodpeckers and Northern Flickers in areas with no Starlings and in areas with various densities of Starlings. To assess competition and its effects, I examined 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. I 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. I also compared the location and dimensions of nest cavities used by each species to determine whether Gila Woodpeckers use different nest cavities than Northern Flickers, and if so, which types of nest cavities European Starlings use.

METHODS

During 1983 and 1984 I established 15 square, 10 ha plots in saguaro cacti habitat in and around the Picacho Mountains, Pinal Co., Arizona, and the Tucson Mountains, Pima Co., Arizona. These plots were randomly located within areas with various densities of European Starlings and similar areas with no European Starlings. All plots contained some large saguaros.

Within each plot I located all European Starling, Gila Woodpecker, and Northern Flicker nests. On each plot, I searched intensively for nests for several days until I had found all the nests. The visibility in saguaro cacti forests allowed me to see birds flying to and from their nests. Nest sites were especially evident when the birds were feeding their young. I could also hear the nestlings calling from the nest. When I was not sure whether a cavity was a nest, I checked by climbing the saguaro with a ladder and looking into the cavity with a mirror and light.

I located nests on (censused) eight plots in 1983 and 7 plots in 1984. Approximately half of the plots censused each year contained European Starling nests. Four of the plots censused in 1984 were censused again in 1985. All plots were censused between 8 April and 4 June, when all 3 species were nesting. The dates that each plot was censused were recorded. Winter precipitation during 1983, 1984, and 1985 was examined at 2 weather stations near the study area.

For each nest located, I 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. Nest cavity orientation was measured with a compass to the nearest degree. For nests which I was able to reach with a 7.6 m ladder, I 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, I randomly located 10 points in every plot. To ensure that all vegetation recorded was on the plot, and that no plant was recorded more than once, point locations were restricted so that all points were at least 30 m from the plot boundary and at least 60 m from any other point. At each point I recorded all saguaros within a 30 m radius. For each saguaro I estimated its height and counted the number of arms and holes which, from the ground, appeared to be possible nest cavities. At each point I also located a transect which was 60 m long and 3 m wide, centered on the point, and randomly oriented. I estimated the height and width of the foliage of all trees, shrubs, and cacti, except triangle-leaf bursage (Franseria deltoidea), which the transect intersected. For triangle-leaf bursage, only the number intersected by the transect was recorded because of triangle-leaf bursage's relatively uniform size. I practiced estimating heights and widths until I was accurate to within 30 cm and I checked my accuracy throughout the study.

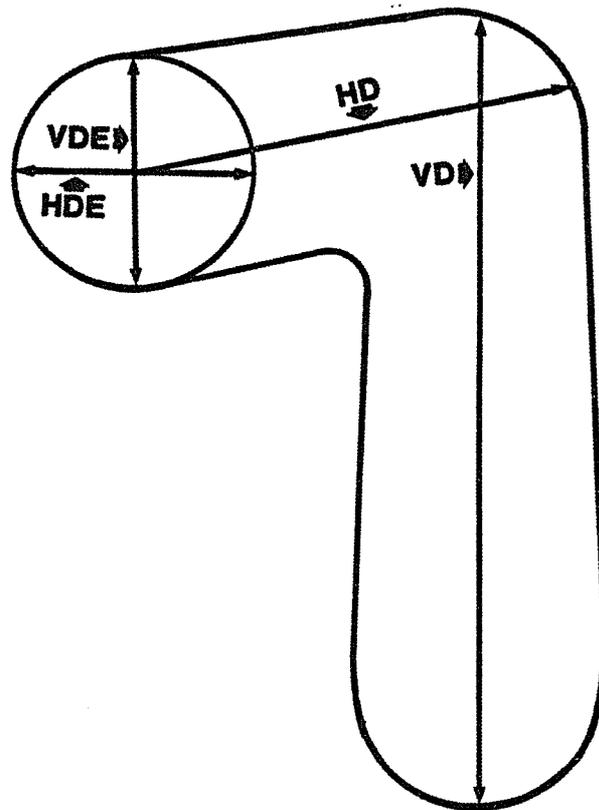


Fig. 1 Measurements of cavity dimensions: vertical diameter of entrance (VDE), horizontal diameter of entrance (HDE), horizontal depth (HD), and vertical depth (VD).

From the estimated height and width of each plant intersected by the transects I calculated that plant's volume. For all species except octillo (Fouquieria splendens), I estimated the plant shape to be a hemiellipsoid. For octillo, I estimated the plant shape to be a cone. The volume estimates for all individual plants of each species, that were intersected by the transects on a plot, were summed. This provided an index of the volume of each plant species on each plot.

All plots were delineated on 1:2400 U.S. Geological Survey topographic maps. From these maps I measured the elevation, slope, aspect, and distance to nearest agriculture for each plot. Throughout this paper the usual definition of agriculture is expanded to include large areas of lawn, such as golf courses, parks, and housing developments, because they are used by European Starlings for foraging much like agricultural areas (Dunnet 1955, Royall 1966, Troetschler 1976, Feare 1984, pers. obs.).

For all statistical tests the alpha for significance was 0.05.

Analysis of Factors Affecting the Number of Nests

For the analysis of factors affecting the number of nests on the plots, saguaros were categorized into 4 classes based on their probable value to the birds (Table 1). The number of saguaros recorded in each class was calculated for each plot. This was a better characterization of the saguaros on each plot than any other variable, such as total number of saguaros or average saguaro height. For example, 2 plots can have the same number of saguaros and average saguaro height, but one might have mostly tall and short saguaros while the other has mostly

Table 1. Description of saguaro classes.

Saguaro class	Description
1	Height < 2.5 m
2	2.5 m \leq Height < 4.5 m
3	4.5 m \leq Height < 7.0 m and number of arms < 6
4	Height ≥ 7.0 m or number of arms ≥ 6

mid-sized saguaros. There is less ambiguity about a plot with a certain number of saguaros in each class.

To examine whether the number of nests found on a plot was affected by the date the plot was censused, I coded the dates that each plot was censused as the number of days after 8 April (the date the first plot was censused). The mean date (mean number of days after 8 April) that each plot was censused was calculated by averaging the coded dates. This provided an ordinal measure of when a plot was censused in relation to when other plots were censused.

I determined which factors affected the number of each species' nests present on the plots with multiple linear regression analysis with stepwise inclusion of variables (Draper and Smith 1981). I used the computer program BMDP-2R (Dixon 1985). Three regression models were developed, one for each species. The dependent variables were the number of nests of each species present on each plot. The possible independent variables were the following measures of each plot's characteristics: the number of saguaros in each of the 4 saguaro classes; the volume index for each of the 30 tree, shrub, and cacti species found on the plots; 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 date the plot was censused. The number of European Starling nests on the plot was also used as a possible independent variable for the Gila Woodpecker and Northern Flicker regressions. The number of holes in saguaros, which appeared to

be possible nest cavities, was also used as a possible independent variable for the European Starling regression.

Before the regression analysis, the dependent variables were transformed with the square root transformation ($\sqrt{X + 0.375}$) because plots of the regression residuals against the predicted values indicated that the square root transformation caused the dependent variables means to be independent of their variances. Plots of the dependent variables observed values against values expected from a normal distribution (normal probability plots) (Dixon 1985) showed that the square root transformation caused the dependent variables to be more normally distributed.

Pearson correlation coefficients were calculated for all pairs of variables. Multicollinearity was not a problem in the regression analysis because all the independent variables that were significant in each regression were uncorrelated with each other ($r < 0.27$, $P > 0.34$). Plots of the regression residuals against the predicted values and the independent variables were analyzed for each regression (Draper and Smith 1981) and met the assumptions for multiple linear regression analysis.

To examine the effect of plot aspect on the number of nests present, each plot was classified into 1 of 4, 90° quadrats centered on North, South, East, and West. I tested differences among quadrats in the number of each species nests present per plot with the Kruskal-Wallis test because I could not assume normality or equality of variances among quadrats. For species with a significant difference

among quadrats, differences between each pair of quadrats were tested with the nonparametric multiple comparison discussed by Gibbons (1976). The effect of southern aspect could not be tested because only 1 plot had a southern aspect.

Differences between 1984 and 1985, in the number of each species nests present on the 4 plots censused both these years were tested with the paired-sample t test. Before testing, the nest counts were transformed with the square root transformation ($\sqrt{X + 0.375}$) (Zar 1984).

Analysis of Differences in Nest Cavity Location and Dimensions

Differences in the location and dimensions (Fig. 1) of nest cavities among Gila Woodpeckers, Northern Flickers, and European Starlings were tested with analysis of variance (ANOVA). Before testing with ANOVA, the distributions of all variables were tested for normality with the Kolmogorov-Smirnov goodness of fit test (Zar 1984). Variables with distributions that differed significantly from the normal distribution were transformed with the square root transformation so that their distributions did not differ significantly from the normal distribution. All variables were tested for equality of variances among groups with the Bartlett-Box F-test (Nie et al. 1975). Variables with significantly unequal variances were transformed with the logarithmic transformation ($\ln(x)$) which equalized the variances of all variables transformed except height of nest saguaros. Therefore, differences in the height of nest saguaros were tested with the Kruskal-Wallis test which does not assume equality of variances (Zar 1984).

For variables that were significantly different among the 3 species, I tested differences between each pair of species with the Student-Newman-Keuls test.

I tested whether the orientation of nest cavities was nonrandom for each species with the Rayleigh test (Batschelet 1981). For the Rayleigh test, the mean vector length (r) of the nest orientations was calculated for each species. The mean vector length (r) is a measure of the concentration of nest orientations around the mean nest orientation. The mean vector length (r) can vary from 0 to 1, with 0 indicating the nest orientations were so dispersed there was no mean orientation, and 1 indicating that all nests were oriented in the same direction (Batschelet 1981).

Analysis of Use of Saguaros for Nest Sites

The use of each saguaro class by each species was calculated from all the nests found while censusing the randomly located plots. The availability of each saguaro class for Gila Woodpeckers and Northern Flickers was calculated from the random sample of saguaros recorded while sampling plot vegetation.

Overall differences between the use and availability of saguaro classes were tested for Gila Woodpeckers and Northern Flickers with the G test (Zar 1984). Differences between the use and availability of each saguaro class and differences between species in their use of saguaro classes were tested with the binomial test for 2 proportions (Zar 1984). To maintain an overall alpha of 0.05, the alpha for significance of

individual tests was calculated as described by Neu, Byers, and Peek (1974).

RESULTS

Factors Affecting the Number of Gila Woodpecker Nests

The number of European Starling nests had the greatest effect on the number of Gila Woodpecker nests (Table 2). The effect of European Starling nests was negative (Table 2) and alone explained 46.7% of the variation in the number of Gila Woodpecker nests present ($r^2 = 0.467$, $P = 0.0050$). The number of class 4 saguaros, the largest saguaros (Table 1), positively affected the number of Gila Woodpecker nests (Table 2). After the effect of 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 present ($R^2 = 0.648$, $P = 0.0019$). The slope of the plot negatively affected the number of Gila Woodpecker nests and explained an additional 16.2% of the variation in the number of Gila Woodpecker nests present (Table 2).

The slope of the plot only affected the number of Gila Woodpeckers nesting on the 3 plots with the steepest slopes. Six plots had slopes of 0%, 6 plots had slopes of 2.7%, and the other 3 plots had slopes of 10.8%, 16.0%, and 19.0%. Before the effect of slope was added to the regression, all 3 plots with steep slopes had predicted numbers of Gila Woodpecker nests greater than their observed number of Gila Woodpecker nests. For the other 2 slopes (0% and 2.7%), half of the plots had predicted values greater than their observed values and the other half had predicted values less than their observed values.

Table 2. Multiple regression equation explaining the number of Gila Woodpecker nests present on the plots. $R^2 = 0.810$, $P = 0.0003$ for total regression, $n = 15$, intercept = 1.643.

Independent variable	Regression coefficient	P
Number of European Starling nests	- 0.1704	0.0012
Number of class 4 saguaros	0.1593	0.0176
Slope of the plot	- 0.0434	0.0109

Together, the number of European Starling nests, the number of class 4 saguaros, and the slope of the plot explained 81.0% of the variation in the number of Gila Woodpecker nests present (Table 2). No other variables significantly increased the ability of the regression model to explain the variation in the number of Gila Woodpecker nests present.

The aspect of a plot did not significantly affect the number of Gila Woodpecker nests present ($P = 0.917$).

There was no significant difference between 1984 and 1985 in the number of Gila Woodpecker nests present on the 4 plots censused both years ($P = 0.240$). However, 1 of the plots contained 3 Gila Woodpecker nests and no European Starling nests in 1984. This same plot contained 2 European Starling nests and only 1 Gila Woodpecker nest in 1985. The 2 nest cavities used by European Starlings in 1985 were 2 of the nest cavities used by Gila Woodpeckers in 1984.

Factors Affecting the Number of Northern Flicker Nests

The number of European Starling nests did not significantly affect the number of Northern Flicker nests. 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 present ($p \geq 0.927$). Furthermore, the number of Northern Flicker nests was not significantly correlated with the number of European Starling nests ($r = 0.043$, $P = 0.879$).

The year the plot was censused explained 25.0% of the variation in the number of Northern Flicker nests present ($r^2 = 0.250$, $P =$

0.0576). Because year was coded as 1 = 1983 and 2 = 1984 the negative coefficient in the regression equation (Table 3) means that there were fewer Northern Flicker nests present in 1984 than in 1983. The volume of ironwood (Olneya tesota) positively affected the number of Northern Flicker nests (Table 3). After the effect of year was determined, ironwood volume explained an additional 20.7% of the variation in the number of Northern Flicker nests present (Table 3). The volume 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) ($r = 0.944$, $P = 0.001$), 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 present (Table 3). No other variables significantly increased the ability of the regression model to explain the variation in the number of Northern Flicker nests present.

The aspect of a plot did not significantly affect the number of Northern Flicker nests present ($P = 0.726$).

There were significantly fewer Northern Flicker nests present in 1984 than in 1985 on the 4 plots censused both years ($P = 0.007$).

There was no precipitation during February and March of 1984 and much less precipitation during December of 1983 and January of 1984 than during December of 1982 and 1984 and January of 1983 and 1985 (Table 4).

Table 3. Multiple regression equation explaining the number of Northern Flicker nests present on the plots. $R^2 = 0.457$, $P = 0.0257$ for total regression, $n = 15$, intercept = 1.958.

Independent variable	Regression coefficient	P
Year plot was censused	- 0.5436	0.0151
Volume index for ironwood	0.0483	0.0539

Table 4. Winter precipitation (cm) at Tucson and Eloy
(Natl. Oceanic and Atmos. Adm. 1982, 1983, 1984,
1985).

Month	Tucson ^a			Eloy		
	1982- 1983	1983- 1984	1984- 1985	1982- 1983	1983- 1984	1984- 1985
Dec	5.72	2.82	8.41	9.55	4.85	11.4
Jan	4.01	1.24	4.47	3.40	1.24	3.23
Feb	5.31	0.00	4.60	3.53	0.00	1.02
Mar	3.58	0.00	0.69	8.53	0.00	0.64

^aCampbell Avenue Experimental Farm.

Factors Affecting the Number of European Starling Nests

The distance from the plot to the nearest agriculture negatively affected the number of European Starling nests (Table 5) and alone explained 29.2% of the variation in the number of European Starling nests present ($r^2 = 0.292$, $P = 0.0375$). The mean date (mean number of days after 8 April) the plot was censused negatively affected the number of European Starling nests and explained an additional 26.3% of the variation in the number of European Starling nests present (Table 5). Together these 2 variables explained 55.5% of the variation in the number of European Starling nests present (Table 5). No other variables significantly increased the ability of the regression model to explain the variation in the number of European Starling nests present.

Plots with northern aspects had significantly fewer European Starling nests than did plots with eastern aspects ($P = 0.027$). All 3 plots with northern aspects had no European Starling nests. However, the lack of European Starling nests on these plots was probably not caused by their northern aspect but instead by their distance from agriculture. The 3 plots with northern aspects were all more than 4,000 m from agriculture. The farthest plot from agriculture with a European Starling nest present was about 4,000 m from agriculture.

There was no significant difference between 1984 and 1985 in the number of European Starling nests present on the 4 plots censused both years ($P = 0.392$).

Table 5. Multiple regression equation explaining the number of European Starling nests present on the plots. $R^2 = 0.555$, $P = 0.0078$ for total regression, $n = 15$, intercept = 2.220.

Independent variable	Regression coefficient	P
Distance to agriculture	- 0.2260	0.0078
Mean date plot was censused	- 0.2319	0.0208

Differences in Nest Cavity Location and Dimensions

The dimensions of Gila Woodpecker and Northern Flicker nest cavities significantly differed (Table 6). Gila Woodpecker nest cavities had significantly smaller entrances (cavity entrance vertical and horizontal diameters), were significantly shallower in the vertical plane of the saguaro (cavity vertical depth), and were significantly deeper in the horizontal plane of the saguaro (cavity horizontal depth) than Northern Flicker nest cavities (Table 6).

European Starlings and Gila Woodpeckers did not significantly differ in nest cavity location or dimensions (Table 6). European Starling nest cavities had significantly smaller entrances (cavity entrance vertical and horizontal diameters) and were significantly shallower in the vertical plane of the saguaro (cavity vertical depth) than Northern Flicker nest cavities (Table 6).

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 ($r = 0.21$, $P > 0.30$).

Use of Saguaros for Nest Sites

Gila Woodpeckers and Northern Flickers selected class 4 saguaros, the largest saguaros (Table 1), for nest sites ($P < 0.001$) (Fig. 2). Gila Woodpeckers nested in all other classes of saguaros significantly less than expected from their availability ($P \leq 0.001$) (Fig. 2). Northern Flickers nested in class 1 saguaros significantly less than expected from their availability ($P < 0.001$) (Fig. 2).

Table 6. Differences in Gila Woodpecker, Northern Flicker, and European Starling nest cavity location and dimensions. Differences among species were tested with ANOVA except for saguaro height, which was tested with the Kruskal-Wallis test. The species which differed from each other were determined with the Student-Newman-Keuls test. Means with the same superscript did not significantly differ ($P > 0.05$). Standard errors of the means are presented in Appendix A.

Nest variable	Means			P
	Gila Woodpecker	European Starling	Northern Flicker	
Entrance vertical diameter (cm) ¹	5.66 ^a	5.68 ^a	6.98 ^b	0.0023
Entrance horizontal diameter (cm) ¹	6.28 ^a	6.58 ^a	8.30 ^b	<0.0001
Cavity vertical depth (cm) ¹	27.83 ^a	31.75 ^a	37.57 ^b	0.0001
Cavity horizontal depth (cm) ¹	15.69 ^a	14.02 ^{ab}	12.50 ^b	0.0252
Height of nest (m) ²	5.80 ^a	6.00 ^a	6.18 ^a	0.3036
Height of nest saguaro (m) ³	8.16 ^a	8.19 ^a	7.49 ^a	0.115
Number of arms on nest saguaro ³	4.81 ^a	5.96 ^a	4.21 ^a	0.1343

¹n = 32 for Gila Woodpeckers, n = 19 for European Starlings, and n = 15 for Northern Flickers.

²n = 64 for Gila Woodpeckers, n = 26 for European Starlings, and n = 28 for Northern Flickers.

³n = 64 for Gila Woodpeckers, n = 24 for European Starlings, and n = 28 for Northern Flickers.

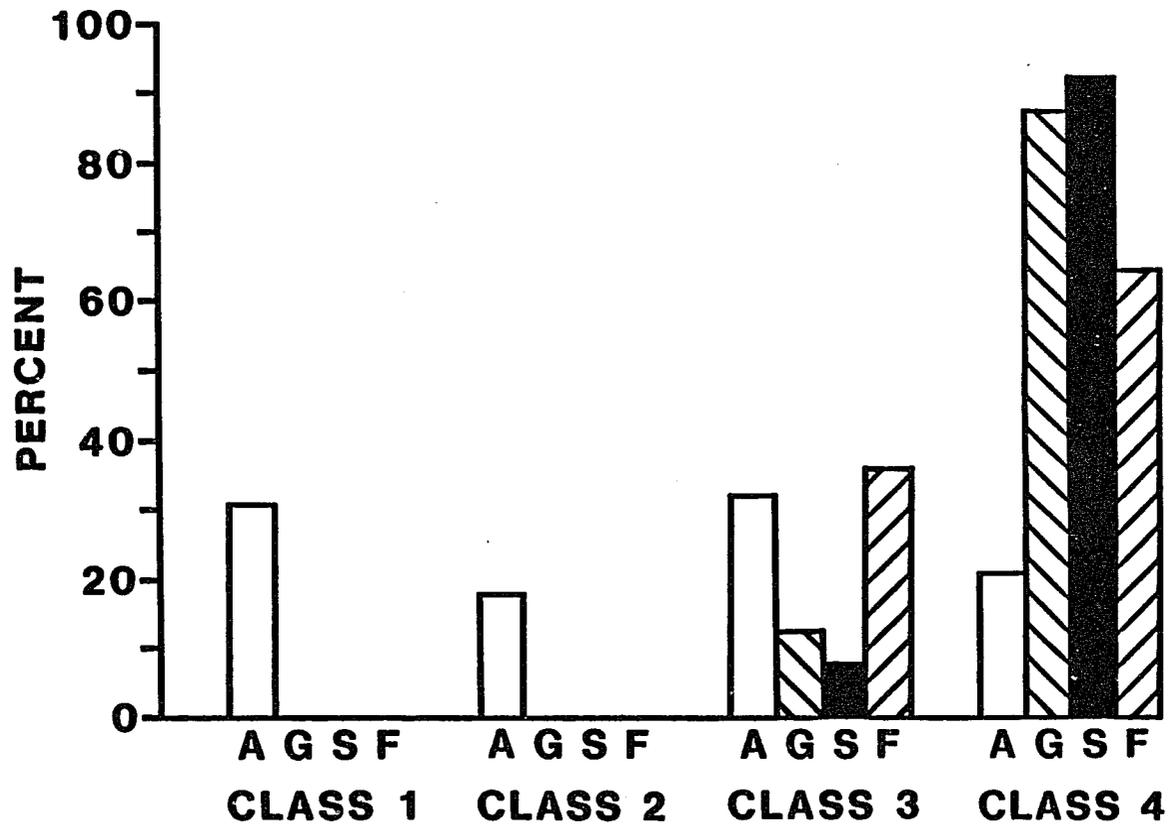


Fig. 2. Use of saguaros for nest sites by Gila Woodpeckers (G) (n = 64), Northern Flickers (F) (n = 28), and European Starlings (S) (n = 26), and availability (A) (n = 1,235) of saguaros for Gila Woodpeckers and Northern Flickers.

European Starlings and Gila Woodpeckers did not significantly differ 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 ($P < 0.013$) (Fig. 2).

Nest Cavities Used More Than One Year

Several of each species' nest cavities located in 1984 were checked for nesting activity in 1985. Three out of 10 Gila Woodpecker nest cavities located in 1984 were used again by Gila Woodpeckers in 1985. Two out of 4 Northern Flicker nest cavities located in 1984 were used again by Northern Flickers in 1985. One out of 2 European Starling nest cavities located in 1984 were used again by European Starlings in 1984.

Observation of Gila Woodpecker - European Starling Interaction

While censusing 1 of the plots, I observed a pair of Gila Woodpeckers fight with a pair of European Starlings for a nest cavity. When I first arrived, the nest cavity was occupied by a pair of European Starlings. Then a pair of Gila Woodpeckers landed on the nest saguaro and the European Starlings chased them away. Later in the day, while the European Starlings were away from the nest cavity, a pair of Gila Woodpeckers landed on the nest saguaro and inspected the nest cavity. The female Gila Woodpecker started removing material from the cavity, which may have been placed there by the European Starlings. European Starlings line their nest cavities with grass and other material (Kessel

1957, pers. obs.) and Gila Woodpeckers use bare nest cavities (Bent 1939, pers. obs.). Later that day, the European Starlings returned to the nest cavity and chased the Gila Woodpeckers away. I returned to this plot a week later and the nest cavity was occupied by European Starlings. Gila Woodpeckers were not nesting on the plot.

DISCUSSION

Competition Between European Starlings and Gila Woodpeckers

European Starlings are competing with Gila Woodpeckers for nest cavities in saguaros and this competition is decreasing the number of Gila Woodpeckers nesting in areas where European Starlings are nesting. No other factor I examined could explain the negative relationship of European Starlings to the number of nesting Gila Woodpeckers.

The Gila Woodpeckers which lose their nest cavities to European Starlings are not excavating another cavity and nesting in the same area. If they were, there would not be fewer Gila Woodpeckers nesting in areas where European Starlings are nesting. When European Starlings take nest cavities from Gila Woodpeckers whatever triggers Gila Woodpeckers to excavate a new cavity may be missing, possibly because Gila Woodpeckers may not excavate cavities during the nesting season. Soule (1964) saw Gila Woodpeckers excavate cavities in February. There are no other reports in the literature 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 the winter (S. M. Russell pers. comm.). For 3 years I observed Gila Woodpeckers almost daily during the breeding season (April - June) and I never saw them excavate cavities during this time. If Gila Woodpeckers normally only excavate cavities during the winter, losing

their nest cavity during the spring may not trigger them to build another one. Also, because Gila Woodpeckers nest in the same cavity for several years (Bendire 1895, Gilman 1915, S. M. Russell pers. comm., pers. obs.) they may not excavate a new cavity each year. They may excavate 1 cavity for nesting and use it for several years, possibly for life.

Competition between European Starlings and Gila Woodpeckers has already affected the community structure in some areas. The 2 plots with the most European Starling nests had no Gila Woodpecker nests. All the plots which did not have European Starling nests had at least 1 Gila Woodpecker nest. Communities with many European Starlings no longer have Gila Woodpeckers and communities with intermediate numbers of European Starlings have fewer Gila Woodpeckers.

If Gila Woodpeckers do not 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 cavities available would be large because Gila Woodpeckers and Northern Flickers are the only animals which commonly excavate cavities in saguaros, and except where European Starlings were present, Gila Woodpeckers were much more numerous than Northern Flickers in the areas I studied. A substantial decrease in the number of cavities available would have a profound effect on the bird community. There are 6 other species of native birds, Elf Owls (Micrathene whitneyi), Brown-crested Flycatchers

(Myiarchus tyrannulus), Ash-throated Flycatchers (M. cinerascens), Purple Martins, Western Screech-Owls (Otus kennicotti), and American Kestrels (Falco sparverius) which regularly nest in cavities in saguaros (Bent 1937, 1942; Allen and Nice 1952). These birds do not excavate cavities so they depend on the woodpecker's cavities. Therefore, competition between European Starlings and Gila Woodpeckers could indirectly affect the entire secondary cavity nesting community. In addition, if there are fewer Gila Woodpecker cavities available, European Starlings may start competing with Northern Flickers for nest cavities. Also, European Starlings may start competing with the other secondary cavity nesters, if they do not already.

European Starlings and Northern Flickers

European Starlings are not competing with Northern Flickers for nest cavities in saguaros. European Starlings are not affecting the number of Northern Flickers nesting and do not nest in the same type of cavities that Northern Flickers use for nesting. European Starlings are competing 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. Northern Flickers in Arizona have an average length of about 268 mm (Ridgeway 1914) and an average weight of 111 g (Dunning 1984), and Gila Woodpeckers have an average length of about 220 mm (Ridgeway 1914) and an average weight of 65 g (Dunning 1984). European Starlings are about 200 mm in length and weigh about 88 g (Feare 1984). Also, Northern Flickers may be more aggressive than Gila Woodpeckers.

Northern Flickers have been observed taking nest cavities from Gila Woodpeckers (Brenowitz 1978, Martindale 1982), but the reverse situation has not been reported in the literature.

Habitat Factors Affecting the Number of Gila Woodpecker Nests

The number of class 4 saguaros positively affects the number of Gila Woodpeckers nesting in an area because Gila Woodpeckers use them for nesting and foraging. Gila Woodpeckers nest almost exclusively in class 4 saguaros (Fig. 2). During the nesting season, Gila Woodpeckers spend over half their total foraging time on saguaros (Martindale 1983). Gila Woodpeckers feed their nestlings pollen from the saguaro flowers, saguaro fruit, and insects gleaned from saguaros (Martindale 1983). Class 4 saguaros have the most flowers and fruits because they are the tallest saguaros and have the most arms (Steenbergh and Lowe 1977). Also, class 4 saguaros have the most surface area for Gila Woodpeckers to glean insects from and may have more insects per unit area because class 4 saguaros are older.

Steep slopes negatively affect the number of Gila Woodpeckers nesting in an area probably by affecting the vegetation. Differences in the amount of any one plant species could not explain the effect that steep slopes had on the number of nesting Gila Woodpeckers. Steep slopes probably cause a difference in the amount of several plant species which may affect the availability of insects which Gila Woodpeckers eat and feed their nestlings.

Factors Affecting the Number of Northern Flicker Nests

There were fewer Northern Flickers nesting on the study area in 1984 than in 1983 and 1985. This was probably caused by the lack of precipitation on the study area during the months preceding nesting (December - March) in 1984 compared to 1983 and 1985 (Table 4). Northern Flickers in the Sonoran Desert forage primarily for insects on the ground and in annual foliage less than 10 cm high (Tomoff 1974, Vander Wall 1980). In deserts the timing and quantity of precipitation plays an important role in triggering the germination and growth of annuals (MacMahon and Schimpf 1980). 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 agricultural areas (Royall 1966, pers. obs.). Irrigated agricultural areas produce insects relatively independent of seasonal precipitation.

The volume of ironwood positively affects the number of Northern Flickers nesting 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 5 plant species were significantly correlated with the volume of ironwood. The warmer microclimate and the vegetation community indicated by ironwood may produce more insects which 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. Because Northern Flickers rarely use saguaros for foraging (Tomoff 1974, Vander Wall 1980), 1 large saguaro to provide a nest site for each nesting pair is probably sufficient. The nest saguaro does not even need to be a class 4 saguaro because Northern Flickers often use class 3 saguaros for nest sites.

Factors Affecting the Number of European Starling Nests

The distance to agriculture negatively affects the number of European Starlings nesting in an area because European Starlings nesting in the Sonoran Desert obtain most of their food from agricultural areas (Royall 1966, pers. obs.). While I was censusing, I never saw European Starlings forage on the plots. European Starlings always flew off the plot, usually toward agriculture, to forage. When I was close enough to see agricultural areas, I saw European Starlings repeatedly leave their nest, fly to the agriculture, land on the ground and return to the nest with insects. Several authors have reported that during the nesting season European Starlings forage primarily for insects in agricultural areas (Dunnet 1955, Royall 1966, Troetschler 1976, Feare 1984). Feare

(1984) found that agricultural areas support the highest densities of breeding European Starlings in Europe.

There were European Starlings nesting on the plots throughout the census period, but there were fewer European Starlings nesting toward the end of the census period. In Arizona, many European Starlings have 2 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 toward the end of the census period was caused by European Starlings which finished their first brood and did not have a second brood.

Differences in Nest Cavity Dimensions

Northern Flicker nest cavities have larger entrances and are deeper in the vertical plane of the saguaro than Gila Woodpecker nest cavities because Northern Flickers are larger than Gila Woodpeckers (see section on European Starlings and Northern Flickers). Gila Woodpecker nest cavities are deeper in the horizontal plane of the saguaro than Northern Flicker nest cavities possibly because Gila Woodpeckers may be more adapted to nesting in saguaros than Northern Flickers. Areas deeper in the horizontal plane of the saguaro have lower maximum daily temperatures (Soule 1964). Nesting deeper in the cross-sectional plane of the saguaro may be an adaptation to avoid the extremely high temperatures in the Sonoran Desert during the nesting season. Northern Flickers are not as dependent on saguaros as are Gila Woodpeckers. Where saguaros are available, Northern Flickers nest in them, but in

most other areas Northern Flickers nest in trees (Bent 1939). Nesting deep in the horizontal plane of trees may not be as feasible or as beneficial as nesting deep in the horizontal plane of saguaros.

European Starling nest cavities are the same as Gila Woodpecker nest cavities and different from Northern Flicker nest cavities, because European Starlings are using Gila Woodpecker nest cavities and are not using Northern nest cavities.

Random Orientation of Nest Cavities

If there is an advantage to nesting in cavities oriented in a particular direction, it is outweighed by other factors. Two other studies; Inouye, Huntly, and Inouye (1981); and Korol and Hutto (1984); claim to have investigated the orientation of Gila Woodpecker nest cavities in saguaro cacti. In both studies any hole in a saguaro was assumed to be a Gila Woodpecker nest cavity, however Northern Flickers also excavate cavities in saguaros and all cavities excavated in saguaros are not necessarily used as nest cavities. In fact, many holes which appear to be possible nest cavities from the ground only go into the saguaro a small distance (pers. obs.). Obviously, these studies have investigated the orientation of holes in saguaros and not the orientation of Gila Woodpecker nest cavities.

Inouye et al. (1981) assigned holes to 1 of 4, 90° quadrats centered on North, South, East, and West, and using the chi-square test found a significant difference among quadrats in the number of holes. Although they reported the test statistic (χ^2) used in the Rayleigh test (see section on analysis of differences in nest cavity location and

dimensions), they did not report the results of this test. I tested for nonrandom orientation with the Rayleigh test and the r they reported and found that the orientations of the holes were not significantly different from random ($P > 0.055$, $r = 0.24$, $n = 49$). The low value of r indicates the orientations of the holes were dispersed. Korol and Hutto (1984) using the Rayleigh test found that the orientations of holes in saguaros were significantly different from random. However, they noted that the orientations of the holes were dispersed ($r = 0.21$) and concluded that the nonrandom orientation was a statistical phenomenon.

Use of Saguaros for Nest Sites

Gila Woodpeckers and Northern Flickers select class 4 saguaros for nesting because they nest in cavities about 6 m high (Table 6). Only class 4 saguaros and the tallest class 3 saguaros are 6 m tall, and the diameter of most class 3 saguaros at 6 m is probably not large enough for a suitable cavity. Shorter saguaros have smaller diameters (McAuliffe and Janzen in press), and the top portion of a saguaro is usually smaller in diameter than lower on the saguaro (pers. obs.). Northern Flickers nest in class 3 saguaros more than Gila Woodpeckers (Fig. 2) possibly because their nest cavities are not as deep in the horizontal plane of the saguaro as Gila Woodpecker nest cavities. Therefore, Northern Flickers may not require a saguaro with as large a diameter as Gila Woodpeckers to excavate a suitable nest cavity. Gila Woodpeckers and Northern Flickers prefer to nest about 6 m high probably because nest predation and ambient temperatures may be greater closer to the ground.

European Starlings and Gila Woodpeckers do not differ in their use of saguaros for nest sites because European Starlings are using Gila Woodpecker nest cavities. European Starlings and Northern Flickers differ in their use of saguaros for nest sites because European Starlings are not using Northern Flicker nest cavities.

Future Implications

In the future, competition between European Starlings and Gila Woodpeckers will probably become more severe and more widespread. Dobeer and Stehn (1979) examined the North American breeding bird surveys from 1968 to 1976 and found that the number of European Starlings in the southwestern United States more than doubled during that time. The number of European Starlings in Arizona is probably still increasing and may continue to increase for many years. Presently, it is impossible to tell whether European Starling populations in the Sonoran Desert will continue to increase only within a certain distance from agriculture. The number of European Starling nests were greater near agriculture, and I did not find European Starling nests on plots further than 4,000 m from agriculture. However, if European Starlings are still increasing in numbers, presently they may only be using their preferred habitat (i.e. areas near agriculture). Once these preferred areas are full, European Starlings may start invading areas further from agriculture, possibly the entire desert. Also, as more housing developments, parks, and golf courses are built throughout the desert, the amount of desert that is far from large lawns and agriculture will decrease. If European Starlings continue to

increase and spread throughout the desert, the survival of Gila Woodpeckers could be threatened. In the future it is important that we monitor European Starling populations in Arizona and their effect on native cavity nesting species; not only to learn more about competition and it's effects on community structure, but also to insure the survival of the native species.

APPENDIX A

STANDARD ERRORS OF THE MEANS OF NEST CAVITY LOCATIONS AND DIMENSIONS

Nest variable	Standard errors		
	Gila Woodpecker	European Starling	Northern Flicker
Entrance vertical diameter (cm)	0.184	0.219	0.455
Entrance horizontal diameter (cm)	0.207	0.247	0.424
Cavity vertical depth (cm)	0.985	2.023	1.446
Cavity horizontal depth (cm)	0.627	0.932	0.965
Height of nest (m)	0.142	0.186	0.230
Height of nest saguaro (m)	0.197	0.179	0.242
Number of arms on nest saguaro	0.499	0.781	0.769

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