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DETERMINANTS OF THE VERTICAL DISTRIBUTIONS OF WOODPECKER NEST CAVITIES IN THE SAHUARO CACTUS[1]

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Abstract. In the Sonoran Desert, Gilded (Northern) Flickers (*Colaptes auratus chrysoides*) and Gila Woodpeckers (*Melanerpes uropygialis*) excavate nest cavities within the giant sahuaro cactus. Vertical distributions of nest cavities excavated by the two woodpecker species differ in height and breadth. Flicker cavities are usually restricted to within 3 m of the stem apex. Nest cavities excavated by Gila Woodpeckers are found over a considerably broader vertical range of heights; their average height is also lower. Competitive preemption of potential excavation sites cannot fully explain this differential utilization of vertical space. Rather, the initial positioning of nest cavities is constrained by cactus anatomy. Different nest-cavity sizes and wood-chiseling capabilities of the two woodpecker species limit the vertical range over which nest cavities can be excavated. In addition, an excavation by a flicker often results in death of the sahuaro. With this mortality, a long-running record of flicker nest-cavity heights is not preserved. In sahuaros containing only Gila Woodpecker cavities, the original heights of old excavations are preserved as the sahuaro continues to grow, thus contributing to the greater vertical range of observed cavity heights.

Key words: Carnegiea gigantea; Colaptes auratus; *Gila Woodpecker; Gilded Flicker;* Melanerpes uropygialis; *resource partitioning; sahuaro; Sonoran Desert; woodpeckers.*

INTRODUCTION

In the Sonoran Desert, Gila Woodpeckers (*Melanerpes uropygialis*) and Gilded (Northern) Flickers (*Colaptes auratus chrysoides*) excavate nest cavities within the giant sahuaro cactus, *Carnegiea gigantea.* Patterns of distribution of nest cavities within stems have only recently been reported (Inouye et al. 1981, Korol and Hutto 1984). The above two studies were primarily concerned with compass orientation of nest-cavity entrance holes. The vertical positioning of nest cavities has not been studied in detail.

Aside from the anecdotal reports of Gilman (1915) and Brandt (1951), patterns of nest-cavity excavation within internal tissues of the sahuaro have not been described. Constraints imposed by internal anatomy may provide an important key to understanding patterns such as the height distributions of nest cavities. Furthermore, the effects of tissue removal during nest-cavity excavation on survival of sahuaros have not been examined in depth, although Steenbergh and Lowe (1976, 1977, 1983) commented that woodpecker nest-cavity excavation can result in death of sahuaros.

The purpose of our paper is threefold: (1) to present comparative data on the vertical heights of nest cavities excavated in sahuaros by Gila Woodpeckers and Gilded Flickers, (2) to determine morphological characteristics of sahuaros that may influence the location of nest-cavity excavations, and (3) to examine the impacts of nest-cavity excavation on sahuaros.

MATERIALS AND METHODS

Information on nest-cavity locations was collected in Organ Pipe Cactus Monument (ORPI), Pima County, Arizona, in March 1983. The study area was located on an alluvial fan approximately 1 km west of the mouth of Alamo Canyon on the west side of the Ajo Mountains (32.1°N, 112.8°W).

The Gilded Flicker is the larger of the two woodpecker species; the species responsible for excavation of a nest cavity could easily be determined by the size of the cavity entrance hole (Gilman 1915, Brandt 1951) (Table 1). The presence of wear around the perimeter of the hole indicated repeated entry to the cavity and was used to distinguish actual nesting cavities from shallow holes.

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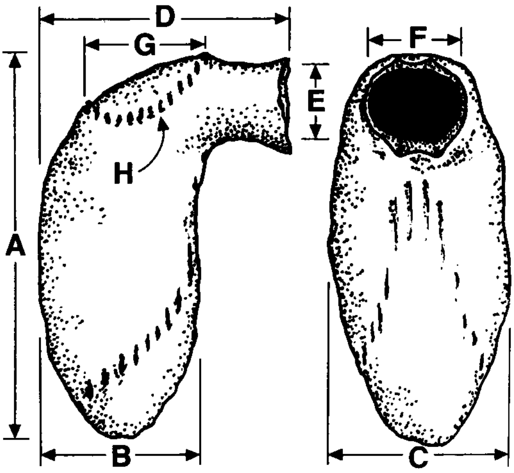

FIGURE 1. Diagram of a nest-cavity boot excavated by a Gilded Flicker. Descriptions of dimensions A–F are listed in Table 1. The letter G refers to the diameter of the severed woody skeleton; H refers to the proportion of individual woody skeletal rods that were severed.

For sahuaros containing entrance holes to nest cavities within the main stem, the nest-hole type (small for Gila Woodpeckers or large for Gilded Flickers) was identified. Heights of both the entrance hole and the sahuaro were measured by standing 25 m from the base of the sahuaro and measuring the apparent height of the entrance hole and the stem apex on a vertical scale held 1 m from the observer's eye. The apparent heights and actual heights represent sides of similar triangles. Apparent heights were converted to actual heights by multiplying by 25, the ratio of the distance from the eye to the cactus and from the eye to the base of the scale.

In response to excavation by a woodpecker, a sahuaro seals off the cavity with hard, suberin-impregnated layers of cork. These durable encasements of nesting cavities (hereafter descriptively referred to as nest-cavity "boots") can be found on the ground long after sahuaros containing them have died and the soft tissues have decayed. We determined the dimensions and structure of nest cavities excavated by each woodpecker species from measurements of these nest-cavity boots (Fig. 1). Occasionally, boots were partially destroyed or decayed, permitting only a partial set of measurements. Between 1983 and 1987 we collected and measured cavity boots whenever we found them at sites throughout the Sonoran Desert.

Details of the internal anatomy of sahuaros were determined from cross sections of seven individuals that were toppled in storms in 1986 and 1987. Total height was measured and cross sections were cut with a saw at distances of 25, 50, 100, 200, and 300 cm from the apex of the main stem. Measurements taken at cross sections included (1) average diameter, (2) the maximum and minimum thickness of the outer cortex measured from the outside surface of the internal skeletal rods to the ridges of the external pleats, (3) the diameter of the ring of woody skeletal rods, and (4) the average radial thickness of individual skeletal rods.

In June 1987, the possible contribution of nest-cavity excavation by flickers to sahuaro mortality was examined at a site located on an alluvial fan on the south side of the Tortolita Mountains, approximately 40 km northwest of Tucson, Pima County, Arizona (32.5°N, 111.1°W). The occurrence of flicker nest-cavity boots in the remains of dead sahuaros was compared with the occurrence of flicker nest cavities in live sahuaros. Only the remains of dead sahuaros that still possessed remnants of the epidermis were measured. Sahuaros in more advanced states of decay were not included. This insured that a more decay-

TABLE 1. Dimensions of nest-cavity boots originally excavated by Gila Woodpeckers and Gilded Flickers. Letter codes designating various measurements are pictured in Figure 1. All linear measurements are in centimeters.

		Gila Woodpeckers			Gilded Flickers		
Code	Description	n	$\bar{x}$	SD	n	$\bar{x}$	SD
A.	Vertical cavity length	13	26.5	5.83	31	36.2	6.56
B.	Chamber depth	13	9.2	1.58	34	13.9	2.10
C.	Chamber width	13	13.3	3.49	37	15.7	2.31
D.	Horizontal depth	9	12.2	3.03	29	19.2	2.82
E.	Vertical entrance diameter	6	5.1	0.45	20	6.8	0.92
F.	Horizontal entrance diameter	15	5.5	0.76	42	8.6	1.01

resistant cavity boot would be found with the skeletal remains if the cactus actually contained a nest cavity at the time of death. Because of eventual decay of cavity boots, inclusion of dead cacti in extreme states of decay could result in an underestimate of the original frequency of nest cavities. For each dead sahuaro, evidence of possible causes of mortality, including lightning strikes and internal tunneling by packrats (*Neotoma albigula*) was recorded. Sahuaros in which branches or portions of the stem were haphazardly scattered in several different compass directions were classed as possible lightning strike victims. The original heights of fallen, dead sahuaros were measured directly when the entire stem was intact. For dead sahuaros whose heights could not be measured directly, the diameter of the woody skeleton was measured 1 m above the base. This skeletal measurement was used to estimate original height since there is a tight linear relationship between these two variables ($Y = -62.3 + 41.04X$; $r^2 = 0.90$; X and Y are the skeleton diameter and sahuaro height, respectively, in centimeters). This relationship was derived from data collected between 1984 and 1987 on 35 fallen sahuaros in the vicinity of Tucson, Arizona.

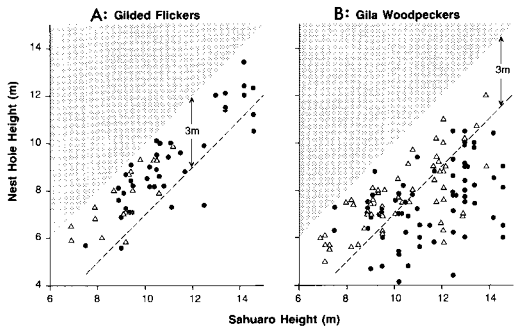

FIGURE 2. Height distributions of nest cavities within the main stems of sahuaros. The boundary between the shaded and unshaded regions indicates the maximum height of the stem, the stem apex. The broken lines indicate the upper 3 m of stem apexes for cacti of different sizes. Open triangles indicate locations of individual nests of respective species when the other species is absent from the same sahuaro. Solid circles indicate nest heights when nest cavities of the other species are located in the same sahuaro.

RESULTS

DISTRIBUTION OF NEST-CAVITY HEIGHTS

Cavities excavated in the main stem by Gilded Flickers are almost always located within 3 m of the stem apex, regardless of sahuaro height (Fig. 2A). Throughout nearly the entire range of sahuaro sizes, the average height of Gila Woodpecker nest cavities is less than the average height of Gilded Flicker nest cavities (Fig. 2B). In addition, the vertical range in the location of Gila Woodpecker nest cavities increases with increasing cactus height. In sahuaros 6 to 8 m tall, Gila Woodpecker nest cavities are found only within the top 3 m of the main stem. However, in 12- to 15-m tall sahuaros, the vertical range of nest locations extends from within 2 m of the cactus apex to as much as 8 m below the apex (Fig. 2B). This pattern is statistically significant: there is a positive correlation between the absolute values of residuals about a regression fit through the data in Figure 2B and sahuaro height (Spearman's rank correlation, $r_s = 0.353$, $P < 0.0001$). This contrasts sharply with the invariant vertical range over which Gilded Flicker nest cavities are located—almost exclusively within the upper 3 m of the stem, regardless of cactus height. There is no correlation between the absolute values of residuals about a regression fit through the data shown in Figure 2A and sahuaro height ($r_s = 0.096$, $P > 0.45$).

COMPETITIVE RESTRICTION OF NEST-CAVITY LOCATIONS?

We initially hypothesized in 1983 that interspecific competition for nest-site locations along the vertical stems of sahuaros was an important determinant of nest-cavity distributions. The presence of nest cavities excavated by Gila Woodpeckers in lower sections of sahuaro stems could potentially preempt the excavation of cavities by Gilded Flickers and restrict Gilded Flickers to upper sections of the stem. Conversely, the occupation of the apical region by cavities excavated by Gilded Flickers might displace Gila Woodpecker excavation activities to lower parts of the stem. Such interactions could also potentially restrict the vertical range over which cavities of both species are found.

To test these hypotheses, we subdivided the data collected at ORPI in 1983 into three groups: (1) sahuaros containing only the nest cavities of Gilded Flickers, (2) sahuaros containing only the cavities excavated by Gila Woodpeckers, and (3) sahuaros in which cavities excavated by both species were present. For each woodpecker species, we compared heights of nest cavities in sahuaros containing cavities of only that species with nest-cavity heights from sahuaros in which both species had excavated (i.e., for Gilded Flickers, group 1 vs. group 3; for Gila Woodpeckers, group 2 vs. group 3). Since nest-cavity height is dependent on sahuaro height for both species (Figs. 2A, B), we compared slopes and intercepts of the regressions of nest-cavity heights on sahuaro heights for the pairs listed above. For each regression, the residual variance ($s^2_{Y/X}$) is an estimate of the variance about the fitted regression line (Kleinbaum and Kupper 1978:49–50). These variances were considered as measures of the breadth of resource utilization along the vertical stem axis. Equality of these variance estimates was tested with F-tests for the above pairs.

GILDED FLICKERS

The regression describing Gilded Flicker nest-cavity height in sahuaros containing only flicker nest cavities is indistinguishable with respect to slope and intercept from the regression describing Gilded Flicker nest-cavity heights in sahuaros containing both species (regression equations describing Gilded Flicker nest height [Y] as a function of cactus height [X]: when Gila Woodpeckers are absent, $Y = 0.2126 + 0.8278X$; when Gila Woodpeckers present, $Y = 0.0004 + 0.8301X$; comparison of slopes: $t = 0.11$, df = 53, $P > 0.90$; comparison of intercepts: $t = 0.102$, df = 53, $P > 0.90$). Likewise, residual variances about the two regressions were not significantly different (Group 1: $s^2_{Y/X} = 0.748$, Group 2: $s^2_{Y/X} = 0.996$, $F = 1.33$, $P > 0.05$). We therefore concluded that the average height and vertical range of Gilded Flicker nest-cavity locations were unrelated to the presence of Gila Woodpecker nest cavities.

GILA WOODPECKERS

Since the variability in Gila Woodpecker nest-cavity heights (Y) increases directly with X (Fig. 2B), $\log_{10}$-transformed values of nest-cavity heights were used in comparisons of regressions. The $\log_{10}$ transformations stabilized variances and resulted in no departures from linearity. The slope of the nest-cavity height–stem-height regression for cacti containing only Gila Woodpeckers was slightly greater than the slope for Gila Woodpecker nest-cavity heights in cacti containing nests of both species, but this difference was only marginally significant (regression equations describing Gila Woodpecker nest-cavity height [Y] as a function of cactus height [X]: when Gilded Flickers are absent, $\text{Log } Y = 0.5659 + 0.0305X$; when Gilded Flickers are present, $\text{Log } Y = 0.6495 + 0.0183X$; $t = 1.03$, df = 119, $0.05 < P < 0.10$). There was no evidence for distinct intercepts for the two regressions ($t = 1.03$, df = 119, $P > 0.30$).

Although a conclusion that slopes of the two regressions are distinct is equivocal, a further examination of pattern more clearly indicates a difference between the two groups. In sahuaros containing only the nest cavities of Gila Woodpeckers, 69.1% of 56 nest cavities are found within 3 m of the apexes of cacti. In sahuaros containing nest cavities of both species, a significantly smaller proportion (32.4%) of 68 Gila Woodpecker nest cavities is found in the upper 3-m zone ($\chi^2 = 20.7$, $P < 0.001$).

Residual variances for the two regressions were significantly different (Group 2: $s^2_{Y/X} = 0.0039$; Group 3: $s^2_{Y/X} = 0.0074$, $F = 1.90$, $P < 0.05$). This difference, however, is opposite in direction from that originally hypothesized. Residual variance of Gila Woodpecker cavity heights was greater when nest cavities of both species were present. In summary, a slight downward shift in average nest-cavity height accompanied by a small increase in the vertical range of Gila Woodpecker nest-cavity locations is related to the presence of Gilded Flicker nest cavities.

Despite the slight downward shift of Gila Woodpecker nest cavities with the presence of Gilded Flicker cavities, Gila Woodpeckers nevertheless excavate a greater proportion of nests in lower portions of the stem than do Gilded Flickers, even when Gilded Flickers are absent. Only 10.7% of 56 Gilded Flicker nest cavities were located in areas below the apical 3-m section. For sahuaros containing only the nest cavities of Gila Woodpeckers, 30.9% of these cavities were located beneath this upper zone ($\chi^2 = 6.88$, $P < 0.01$). Similarly, in sahuaros containing only Gila Woodpeckers (Group 1), the range over which nest cavities are found greatly exceeds the vertical range over which Gilded Flicker nest cavities are found. These differences suggest the two species prefer different parts of the stem for nest-cavity excavation.

CONSTRAINTS ON NEST-CAVITY EXCAVATION IMPOSED BY SAHUARO STEM ANATOMY

The main stem as well as the branches of a sahuaro contain two soft tissues for water storage—

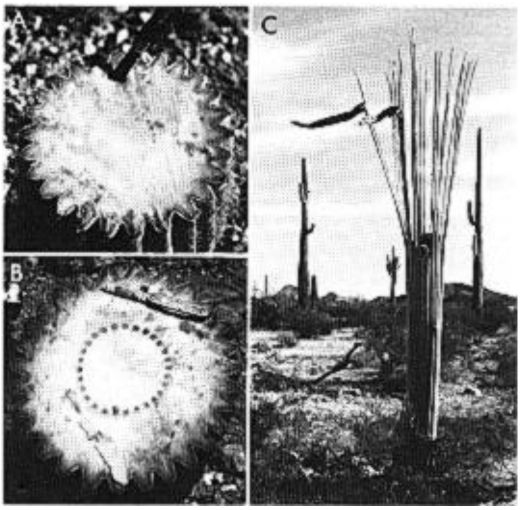

FIGURE 3. A. Cross section of a sahuaro approximately 50 cm from the stem apex. Note extremely thin, indistinct woody skeleton. B. Cross section taken approximately 2 m below the stem apex. C. Standing skeleton of a sahuaro. Small horizontal processes on upper left side are skeletal remains of small branches.

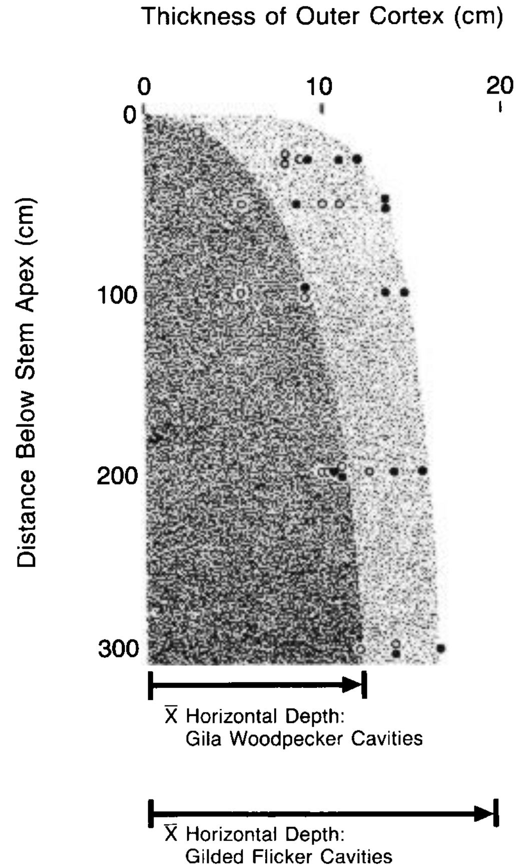

FIGURE 4. Thickness of outer cortex of sahuaros as a function of distance below the stem apex. The left margin indicates the boundary of the outer cortex and the woody skeleton. The dark shaded region shows the approximate minimum thicknesses measured for the outer cortex; the right-hand margin of the light shaded region denotes maximum cortical thicknesses measured from the same sections. Open circles are actual data on minimal cortex thickness; solid circles are measurements on maximal thickness.

an outer cortex and a central pith. The pith is surrounded by a skeleton consisting of a ring of parallel woody rods (Fig. 3). Near the base of the cactus, the skeletal rods can be several centimeters thick. Moving upward from the base, these woody rods become thinner and weaker. At 0.5 m below the stem apex, individual skeletal rods ranged between 5 and 6 mm in diameter. In the same cacti, the skeletal rods were 9 to 14 mm in diameter 2 m below the stem apex. The succulent layer of the outer cortex is also thinnest near the stem apex and attains a maximum thickness of approximately 16 cm with increasing distance below the apex (Fig. 4).

Nest cavities excavated by the two woodpecker species differ in size and shape. These differences apparently affect the ability of each species to excavate cavities in various parts of the stem. Nest cavities excavated by Gila Woodpeckers are considerably smaller than Gilded Flicker nest cavities (Table 1, Figs. 5A, B). The average horizontal depth of Gila Woodpecker cavities is approximately 12 cm; average horizontal depth of Gilded Flicker cavities is approximately 19 cm. The smaller nest cavities of Gila Woodpeckers are somewhat flattened; the inner chamber has greater width than depth (Table 1, Figs. 5A–C). Gila Woodpecker cavity boots usually bear vertical, linear scars on the back side that indicate contact with the woody skeleton (Fig. 5D). However, horizontal depth of cavity excavation by Gila Woodpeckers usually halts when the woody skeleton is encountered and typically none of the woody rods are severed (Table 2). Occasionally (two of 14 nest-cavity boots examined), Gila Woodpeckers will chisel a 5- to 6-cm hole through the cortex and two or three skeletal rods, and then excavate the larger chamber entirely within the confines of the woody skeleton in the soft pith. However, by excavating nest cavities in lower portions of the stem, especially more than 2 m from the stem apex, Gila Woodpeckers can

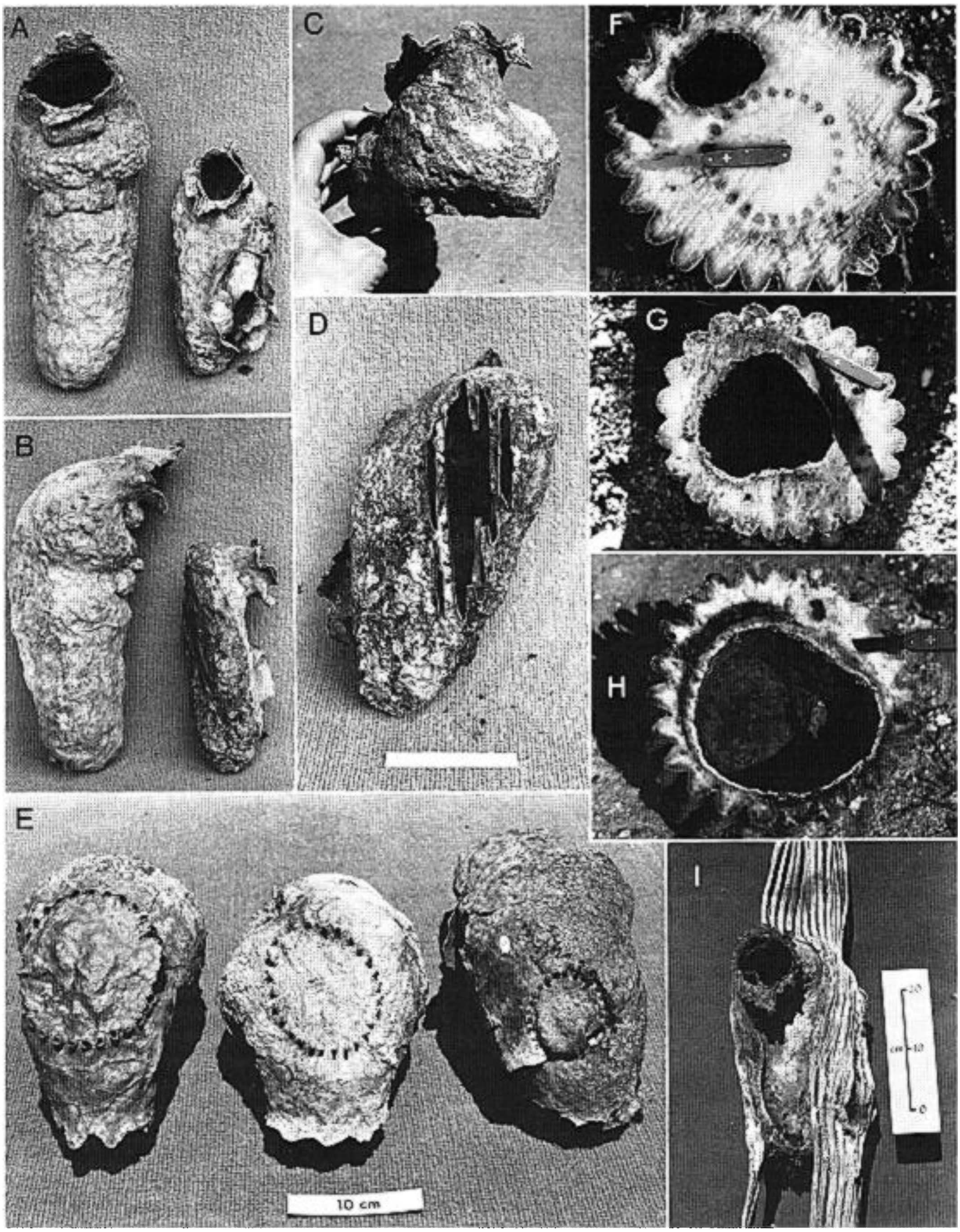

FIGURE 5. A, B. Front and side views, respectively, of Gilded Flicker (left) and Gila Woodpecker (right) nest-cavity boots. See Table 1 for average dimensions. C. Top view of a Gila Woodpecker nest-cavity boot. Notice the flattened back of the boot (lower side of photo) and the compressed cross-sectional shape of the nesting chamber. D. Rear view of the same nest-cavity boot. Parallel lines indicate the former contact with, but not penetration of, the sahuaro skeleton. Scale bar = 10 cm. E. Top view of three Gilded Flicker nest-cavity boots. Circular patterns on tops of the boots are the scars due to complete severing of the woody skeleton. F. Cross

TABLE 2. Extent of severing of skeletal rods by Gila Woodpeckers and Gilded Flickers during nest excavation. Data taken from nest-cavity boots associated with remains of dead sahuaros.

	Percentage of skeletal rods severed by nest-cavity excavation				
	0	1–25	26–50	51–75	76–100
Gila Woodpecker nest cavities	9	4	0	0	1
Gilded Flicker nest cavities	2	2	5	5	27

apparently avoid the necessity of chiseling through any part of the woody skeleton (Fig. 4).

The considerably greater horizontal depth of Gilded Flicker nest cavities precludes their excavation entirely within the outer cortex. Nowhere along the stem is the outer cortex thick enough to entirely accommodate a nest cavity much over 15 cm in horizontal depth (Fig. 4). Gilded Flickers must therefore chisel through the skeleton. By excavating nest cavities near the cactus apex, only relatively thin, soft woody rods would require removal. Flickers excavating nest cavities at increasing distances from the stem apex would encounter increasingly larger and impenetrable skeletal rods.

Flicker nest-cavity boots bear distinct scars that reveal their original proximity to the stem apex as well as the number of woody rods that were completely severed during excavation. These scars can be clearly seen on the upper side of a nest-cavity boot (Fig. 5E). If the entire woody skeleton was severed, the scar will have a ring-like pattern on the top of the nest chamber. If only a portion of the woody skeleton was severed, the scar will have a semicircular or crescent pattern when viewed from above. Out of the 35 nest cavities examined, 66% possessed scars revealing the entire skeleton was severed during excavation (Table 2). In live sahuaros, the diameter of the woody skeletal ring increases linearly with distance from the stem apex (Fig. 6B). Therefore, the approximate distance between the site of original cavity excavation and the stem apex can be estimated from the diameter of the scar present on the top of the nest-cavity boot. In most boots, the diameters of these scars is less than 12 to 14 cm (Fig. 6A), indicating that these nests were originally excavated very near the stem apex. The closer a Gilded Flicker excavates its cavity near the apex (as indicated by the diameter of the skeletal scar on top of a cavity boot), the greater is the likelihood that all of the skeletal rods will be cut. The estimated percentage of woody rods severed is negatively correlated with the diameter of the skeletal scar measured on the top of cavity boots ($r_s = -0.53$, $n = 35$, $P = 0.001$).

Only rarely do Gilded Flickers exhibit other ways of dealing with the barrier imposed by the woody skeleton. Out of 35 nest-cavity boots collected, only one was positioned entirely within the outer cortex. The nest chamber was considerably flattened. From the same sample of nest cavities, one was constructed by chiseling a small, 7- to 8-cm diameter hole through the cortex and three woody rods. This long throat extended horizontally to the pith. The entire chamber was excavated within the soft pith on the interior of the woody skeleton. The nest cavity was considerably smaller in diameter than others, indicating the probable restriction on internal diameter imposed by such positioning.

IMPACTS OF NEST-CAVITY EXCAVATION ON SAHUAROS

The two woodpecker species differ considerably in the damage they inflict on sahuaros during nest excavation. The typical Gila Woodpecker nest cavity located entirely within the soft outer cortex apparently causes little harm. The excavation heals over with the same response as to any wound. The main damage inflicted is the loss of a relatively small amount of water-storing cortex along with a small amount of photosynthetic surface at the site of the nest-cavity opening (Fig. 5F).

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section through a relatively small nest cavity excavated by a Gila Woodpecker. None of the skeletal rods are severed. This section was taken approximately 200 cm below the stem apex. G, H. Cross sections through nest cavities excavated by Gilded Flickers. In each, all of the woody rods were severed. I. Nearly complete healing of woody tissue around a Gilded Flicker nest cavity that originally severed all of the skeletal rods.

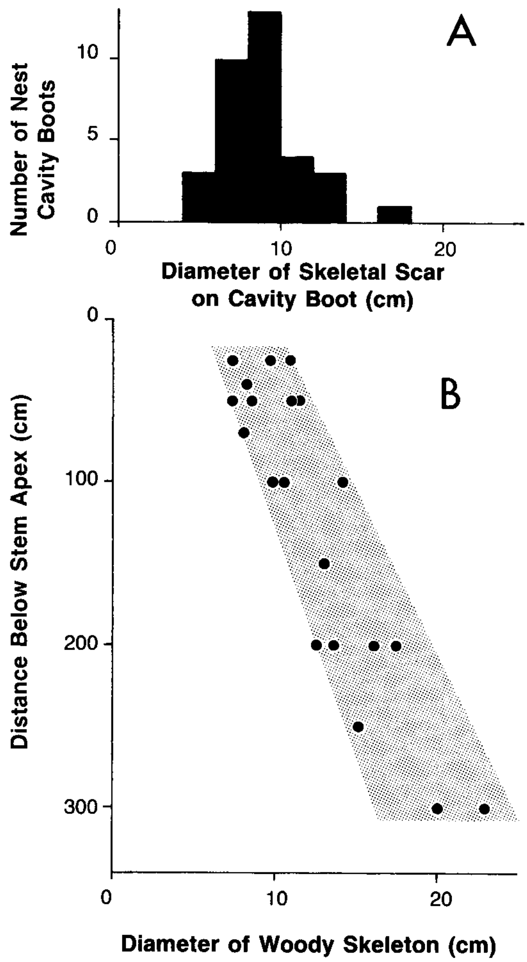

FIGURE 6. A. Diameters of the skeletal scars found on tops of Gilded Flicker nest-cavity boots. B. Data taken from cross sections of fallen sahuaros showing the diameter of the ring of woody skeletal rods at different distances below the stem apex. Individual solid symbols indicate actual measurements; the shaded region indicates the approximate range of values (fitted by eye).

The complete or even partial severing of the woody skeleton by Gilded Flickers has more detrimental impacts. One consequence is the loss of skeletal support. Cross sections made at the location of Gilded Flicker cavities in fresh, windthrown sahuaros show that only a relatively thin layer of soft outer cortex and epidermis may remain to support the stem apex if all of the woody skeletal rods are cut (Figs. 5G, H). Complete regeneration of severed skeletal rods rarely occurs. Of all the 35 flicker nest-cavity boots examined, only one showed a nearly complete healing and regrowth of woody tissue around the nest cavity (Fig. 5I). Sahuaros weakened by Gilded Flicker nest cavities may be especially subject to decapitation during violent storms. We have commonly observed decapitated sahuaros with the decaying remains of the apex near the base. It is far more rare to encounter living, decapitated sahuaros in which the fallen apex has completely decayed (a process that probably takes about 10 to 20 years at most in the Sonoran Desert near Tucson (Ebert and Zedler 1984). This suggests that once decapitation occurs, death of the cactus is common within the period of time required for complete decay of the fallen apical section.

In addition to providing skeletal support, the woody rods comprise the principal vascular tissue. The apical portions of cacti located above Gilded Flicker nest cavities are commonly shrunken with considerably smaller cross-sectional diameters than normal. This indicates the diminished transport of water to the apex due to the severing of the vascular tissue. The exterior of the cactus is covered with accordion-like pleats that allow for expansion or contraction of internal volume without changing external surface area. The loss of internal volume greatly increases the surface area to volume ratio which could accelerate the rate of unavoidable evaporative water loss on a per unit volume basis. It is possible that extreme water deficits could directly cause death of the apex.

Increased surface area/volume ratios of the apex can have another serious result. Tissue death due to freezing is a principal source of mortality in northern and eastern portions of the range of the sahuaro (Steenbergh and Lowe 1977, 1983). An increase in the surface/volume ratio would increase the rate of heat loss from internal tissues, thereby increasing the susceptibility to freezing. While a nest cavity may not be the direct cause of mortality in all cases, the interaction of the effects of the excavation with the effects of freezing may bring about increased mortality (see Steenbergh and Lowe 1976, fig. 23; 1983, p. 128).

Data collected from dead sahuaros at the Tortolita Bajada site provided information on the extent of mortality that may be attributed to nest-cavity excavation by Gilded Flickers. Of the 55 dead sahuaros examined, 21.8% contained Gilded Flicker nest cavities. No Gila Woodpecker nest-cavity boots were found associated with any of the dead sahuaros. Destruction by lightning was an apparent source of mortality in 30.9% of the dead sahuaros examined. Extensive internal tunneling by the woodrat, *Neotoma albigula,* may have been a principal cause of death in only one of the 55 cacti examined. A possible cause of death could not be determined in 45.5% of the dead sahuaros.

When live and dead sahuaros were compared, Gilded Flicker nest cavities were more commonly found in dead cacti than in live cacti. Flicker nest-cavity boots were found in the remains of 21.8% of dead sahuaros whose original height was estimated at more than 5 m. Flicker nest cavities were found in only 5.3% of living sahuaros taller than 5 m ($\chi^2 = 10.4$, $P < 0.01$). The greater incidence of flicker nest cavities in dead sahuaros indicates that once Gilded Flickers excavate cavities in sahuaros, these damaged cacti are recruited into the population of dead sahuaros at a faster rate than are cacti undamaged by flickers. Small sahuaros are apparently more prone to mortality as a result of flicker nest-cavity excavation than are older sahuaros. For sahuaros between 5 and 8 m tall, 20% of the dead individuals contained nest cavities, whereas nest cavities were never found in living sahuaros. In the larger size classes of sahuaros, the presence or absence of Gilded Flicker nest cavities was evenly distributed among live and dead sahuaros (Table 3).

TABLE 3. Distribution of Gilded Flicker nest-cavity boots among live and dead sahuaros.

Sahuaro condition	Sahuaros 5 to 8 m tall: Nest cavities Present	Sahuaros 5 to 8 m tall: Nest cavities Absent	Sahuaros taller than 8 m: Nest cavities Present	Sahuaros taller than 8 m: Nest cavities Absent
Live	0	91	6	15
Dead	7	28	5	15
	$\chi^2 = 18.96$, $P < 0.001$		$\chi^2 = 0.07$, $P > 0.10$	

DISCUSSION

Two processes not involving competition for nest sites can account for much of the difference in the vertical distributions of Gila Woodpecker and Gilded Flicker nest cavities. These are (1) constraints imposed by sahuaro anatomy on initial nest-cavity excavation and (2) differences in survival of sahuaros following excavation of nest cavities by the two species.

The two woodpecker species experience different constraints imposed by sahuaro anatomy because of their different body sizes (and hence requirements for different sizes of nest cavities) and wood-chiseling abilities. The woody skeleton of a sahuaro is undoubtedly the structure most resistant to removal by the chiseling efforts of either species. Gila Woodpeckers are capable of chiseling through wood considerably tougher than the skeletal rods of sahuaros. Along river floodplains in Arizona, Gila Woodpeckers commonly excavate nest cavities within trunks of cottonwoods and willows (Gilman 1915, Bent 1939). Yet, nest cavities excavated by Gila Woodpeckers are small enough that they can be positioned entirely within soft tissues of sahuaros without ever penetrating the woody skeleton. The typical flattening of Gila Woodpecker nest cavities against the inner skeletal rods (Figs. 5C, D) suggests an avoidance of chiseling on the skeleton.

The larger nest cavities of Gilded Flickers cannot fit entirely within the soft outer cortex of sahuaros. Hence the woody skeleton must be penetrated. This presents a dilemma for Gilded Flickers because their wood-chiseling capabilities are considerably less than those of Gila Woodpeckers. The Gilded Flicker forages almost exclusively on the ground; much of its diet consists of ants (Bent 1939, Short 1982, Vander Wall and MacMahon 1984). Accompanying the evolutionary specialization of ground feeding is a commensurate loss of wood-chiseling ability (Short 1982). Flickers possess narrow, pointed bills as opposed to the stouter, chisel-tipped bills of Gila Woodpeckers and other woodpecker species more capable of wood excavation. Gilded Flickers apparently minimize the difficulty of chiseling through the woody skeletons of sahuaros by excavating nest cavities near the stem apex. In this location, the skeletal rods are extremely thin and present the least resistance to removal. But by excavating near the cactus apex, usually all of the thin skeletal rods are severed, resulting in much more severe damage. This damage apparently is often directly or indirectly responsible for death of sahuaros.

Even if Gilded Flickers and Gila Woodpeckers constructed new nest cavities in the same relative location near the stem apex, differential mortality of cacti containing nest cavities of different species would eventually produce dissimilar distributions of nest-cavity heights. A newly excavated nest cavity leaves an external scar on the cactus whose absolute height remains the same over time—just like initials carved in the bark of a tree. All vertical growth occurs at the meristem tissue at the apex of the main trunk or arms. If nest cavities do not lead to death, a record of original heights of older excavations will be preserved as a cohort of sahuaros grows in height. Simultaneously, growth of the cacti will increase the vertical range available for the excavation of new nest cavities. The vertical distribution of Gila Woodpecker nest cavities therefore represents a long recorded history of recent and old nest-cavity excavations. This accumulation of nest cavities over time is probably largely responsible for the increasing range of Gila Woodpecker nest-cavity heights with increasing sahuaro height (Fig. 2B). For Gilded Flickers, however, excavation of new nest cavities occurs near the stem apex and these excavations commonly lead to death of the sahuaro. In this case, old nest cavities would rarely, if ever, be found in lower sections of the stem, regardless of cactus height, because only a relatively brief span of time elapses between the time of cavity excavation by a Gilded Flicker and death of the sahuaro. This mortality of sahuaros (and of the Gilded Flicker nest cavities they contain) explains the triangular zone in the lower right section of Figure 2A in which Gilded Flicker nest cavities are completely absent.

Patterns of sahuaro use by Gila Woodpeckers observed by other authors can be explained by the accumulation of nest cavities over time. Korol and Hutto (1984) reported that taller sahuaros more frequently contained Gila Woodpecker nest cavities than did smaller sahuaros. In addition, among sahuaros containing at least one Gila Woodpecker nest cavity, the number of nest cavities per sahuaro was positively correlated with sahuaro height. Korol and Hutto suggested that these patterns may be the result of problems such as excavation difficulties, increased predation rates, or thermal stress associated with nesting in shorter sahuaros. An alternative explanation is simply that younger sahuaros have been available for nest-cavity excavation for only a relatively short period of time, whereas large, older sahuaros possess an accumulated record of past nest excavations that may be as much as a century older (see data on age–height relationships for sahuaros in Steenbergh and Lowe [1977, 1983]).

INFLUENCES OF COMPETITION

Our initial interpretation of the different vertical distributions of nest cavities excavated by Gila Woodpeckers and Gilded Flickers was that competition was a major factor determining this pattern. Competition may actually have very little, if anything, to do with it. Although a slight shift in Gila Woodpecker nest-cavity heights was associated with the presence of Gilded Flicker nest cavities, it is impossible to clearly separate cause and effect with these data. This is because information on the sequence of nest-cavity excavations is unknown. Rather than Gila Woodpeckers shifting their excavation activities in response to the original presence of a Gilded Flicker cavity, Gilded Flickers may actually choose to excavate cavities in sahuaros where the average height of Gila Woodpecker nest cavities is lower. Either scenario could produce the same pattern.

Observations of agonistic behavior of Gila Woodpeckers toward Gilded Flickers and the eviction of a pair of Gila Woodpeckers by a Gilded Flicker (Martindale 1982) indicate that these two woodpecker species do compete. However, these types of interactions may not have much effect on the overall vertical distributions of nest cavities excavated by the two species. One competitive effect that may conceivably occur is a negative association of nest cavities of the two species in the same sahuaro. Evidence for this kind of competitive displacement could be obtained by collecting data on the numbers of sahuaros in a population that fall within four discrete categories: (1) those with only Gila Woodpecker cavities, (2) those containing only Gilded Flicker cavities, (3) those containing cavities excavated by both species, and (4) cacti lacking nest cavities altogether. The observed numbers of sahuaros contained in each category could be compared with the null expectation, given a random distribution of the observed number of nest cavities of each species among sahuaros.

Although our initial hypothesis based on competition-induced resource partitioning was appealing to us, it also temporarily shackled us with observational "blinders" that may have actually delayed the observation and consideration of constraints imposed by sahuaro skeletal anatomy and the implications of flicker-induced sahuaro mortality. Understanding the woodpecker nest-height distributions, and possibly other patterns of differential resource utilization requires detailed knowledge of the natural histories of the component species. Without such knowledge, the uncritical acceptance of a given pattern as prima facie evidence for a theoretically expected set of ecological interactions is far more likely, simply because of the lack of alternative explanations.

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