PATTERNS OF CAVITY-ENTRANCE ORIENTATION BY GILDED FLICKERS (*COLAPTES CHRYSOIDES*) IN CARDÓN CACTUS

PATRICK W. ZWARTJES[1] AND SHAWN E. NORDELL[2]

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, USA

ABSTRACT.—We studied patterns of cavity placement and orientation by the Gilded Flicker (*Colaptes chrysoides*) in the cardón cactus (*Pachycereus pringlei*) of Mexico, a columnar cactus characterized by a complex branching pattern. Overall, Gilded Flicker cavity entrances were oriented significantly toward the north–northwest, and they tended to face away from the rest of the cactus structure. There were more cavities proportional to the number of arms in the northwest quadrant, and these cavities had the strongest tendency to be oriented to the northwest and to face away from other arms. Cavities in the northeast quadrant were oriented slightly east of north, maintaining a strong pattern of orientation away from other cactus arms. Southwest quadrant cavity orientations were similar to those in the northwest quadrant but deviated from the trend of facing directly away from the bulk of the cactus structure. The fewest cavities proportional to number of arms were in the southeast quadrant, and these showed no significant orientations, instead having the greatest variation in directional orientation as well as orientation with respect to other cactus arms. *Received 24 March 1997, accepted 20 June 1997.*

THE EXCAVATIONS OF PRIMARY CAVITY-NEST-ING BIRDS provide a record from which the ecological factors that influence cavity placement may be inferred. Several studies have used this historical record to examine the patterns of cavity location and/or hole orientation in a variety of bird species (e.g. Conner 1975, Conner and Adkisson 1977, Stauffer and Best 1982). Previous analyses have examined vertical distribution, nest height (e.g. Nilsson 1984, Li and Martin 1991, Albano 1992), and nest orientation for thermoregulation, either in terms of facing toward the sun in cold environments, or away from the sun and/or toward prevailing winds in hotter environments (Ricklefs and Hainsworth 1969, Austin 1974, Inouye 1976, Inouye et al. 1981, Finch 1983, Facemire et al. 1990, Rendell and Robertson 1994).

Several studies have examined cavity dimensions, nest placement, and entrance orientation by Gilded Flickers (*Colaptes chrysoides*) and Gila Woodpeckers (*Melanerpes uropygialis*) in the saguaro cactus (*Carnegiea gigantea*) in southern Arizona (Inouye et al. 1981, Korol and Hutto 1984, McAuliffe and Hendricks 1988, Kerpez

¹ Present address: Department of Biological Sciences, Humboldt State University, Arcata, California 95521, USA. E-mail: zwartjes@humboldt1.com
² Present address: Department of Biology, California State University Northridge, Northridge, California 91330, USA.

and Smith 1990). The saguaro is one of several long-lived species of columnar cacti within the subfamily Cactoideae (Gibson and Nobel 1986). It has a relatively simple morphological structure, remaining a single unbranched column until approximately 40 to 50 years of age, after which it may develop one to five lateral branches that grow upward (Gibson and Nobel 1986). Farther south in Baja California and Sonora, Mexico, the cardón (*Pachycereus pringlei*) becomes the dominant columnar cactus (Wiggins 1980). The structure of the cardón on the eastern coast of the Gulf of California is more complex than that of the saguaro. Cardóns commonly have many branches that grow from a central trunk at the base, often with no single central stem, and they exhibit pronounced secondary branching on the longer primary branches (Borg 1956, Earle 1980, Wiggins 1980). The region of the Sonoran Desert dominated by the cardón also makes up a major portion of the breeding range of both woodpecker species that previously have been studied in saguaros in Arizona.

Studies of woodpecker nest-entrance holes in saguaro cacti have revealed that woodpeckers tend to orient their cavities toward the north and northwest (e.g. Inouye et al. 1981, Korol and Hutto 1984; but see Kerpez and Smith 1990). In addition, Korol and Hutto (1984) reported that cavity orientation was influenced in part by cac-

tus architecture. Specifically, when adjacent branches were present on a saguaro stem, cavities were oriented in the direction of least obstruction. If a specific direction and avoidance of obstructions are important factors influencing cavity placement and orientation, then the greater architectural complexity of the cardón cactus relative to the saguaro may force tradeoffs among preferred orientation characteristics. The various locations of the cardón arms, radially distributed around a center point, will not be equally suitable for a woodpecker attempting to achieve an optimal cavity orientation. For example, in the northwest region of a cardón cactus with respect to its center, orientation of the cavity toward the northwest automatically places the bulk of the cactus architecture opposite the entrance to the cavity. In parts of the cardón that do not correspond to a preferred compass direction, woodpeckers must make tradeoffs between maintaining a preferred direction and orienting the cavity entrance to avoid obstruction by the surrounding structure of the cactus (sensu Korol and Hutto 1984).

We quantified the architecture of cardón cacti in Sonora, Mexico, and examined the pattern of distribution and orientation of nest cavities of Gilded Flickers within the structure of these cacti. We tested the hypothesis that compass orientation of cavity entrances and orientation with respect to cactus structure differ among cavities located in the four quadrants defined by north-south and east–west axes through the center of the cactus. We predicted that these quadrants are apt to differ in ecological influences because: (1) significant mean entrance orientations to the northwest reported for woodpecker cavities in saguaros suggest ecological constraints on compass orientation; and (2) the location of the study site at 30°N latitude precludes sunlight from shining directly on the north side of the plant, thus creating a difference in thermal conditions between northern quadrants and southern quadrants. The combination of these ecological and architectural constraints on orientation of cavity entrances should result in different orientation patterns among different quadrants of the cactus.

METHODS

Data collection and organization.—Field work was conducted during spring 1991 in a cardón forest approximately 20 km north of Bahia Kino in Sonora,

Mexico. We randomly selected 35 cardón cacti in sequence and recorded their morphological characteristics. Linear measurements were made with a series of interconnecting poles that were marked with red tape at 1.0-m intervals and white tape at 0.1-m intervals. Height and length of each cactus arm (Fig. 1A) were determined by having one person hold the pole vertically against the arm while a second person noted the measurements from a distance. The length of an arm was determined to be the vertical distance between the point where the arm originated from the main trunk of the cactus (or a second arm) and the apex of the arm. A compass was used to determine the orientation of each arm ($\pm 1°$) with respect to the central axis (Fig. 1B). All angles were measured with respect to magnetic north and corrected to true north using a magnetic declination of 11° east (Defense Mapping Agency 1991). The distance of each arm from the central axis was determined by measuring the horizontal distance from the midline of the trunk to the farthest lateral extension of the arm (Fig. 1A).

Cavities constructed by Gilded Flickers can be distinguished from those made by other piciforms in this region by their larger entrance dimensions (Gilman 1915, Harrison 1979, Korol and Hutto 1984, McAuliffe and Hendricks 1988). Cavity size, shape, and depth were assessed from the ground with binoculars. We recorded only those cavities that both investigators agreed were fully excavated and could serve as functional cavities, based on apparent depth and evenness in the circularity of the entrance hole. Each recorded cavity was designated "flicker" or "woodpecker" based on the size of the hole as judged by both investigators. Cavity placement and orientation were recorded by measuring the height of each cavity entrance and the compass orientation of each hole (Figs.1A, B).

Each cactus arm and cavity was assigned to one of four quadrants (i.e. NW, NE, SE, and SW) delineated by the north-south and east-west axes through the cactus center. A cavity was placed in a specific quadrant by the orientation angle of the arm containing the cavity (Fig. 1B); arms and cavities located in the absolute center were not included in quadrant analyses.

Geometric equations incorporated as algorithms of a Fortran computer program were used to calculate additional geometric relationships from data collected in the field (Fig. 1C). To examine the orientation of a hole with respect to the position of all the other arms on a cactus, the program computed the angle *hb* (Fig. 1C). For every arm (*A*), the program calculated the direct distance in a horizontal plane (line *AB*) to a second arm on the cactus (*B*) and the angle (*AOB*) formed by the two radial distances of each arm from the central axis, *O*. For any arm *A*, these values were calculated for every other arm on the cactus.

Statistical analysis.—Characteristics of cardón cacti were first analyzed by testing the distribution of cac-
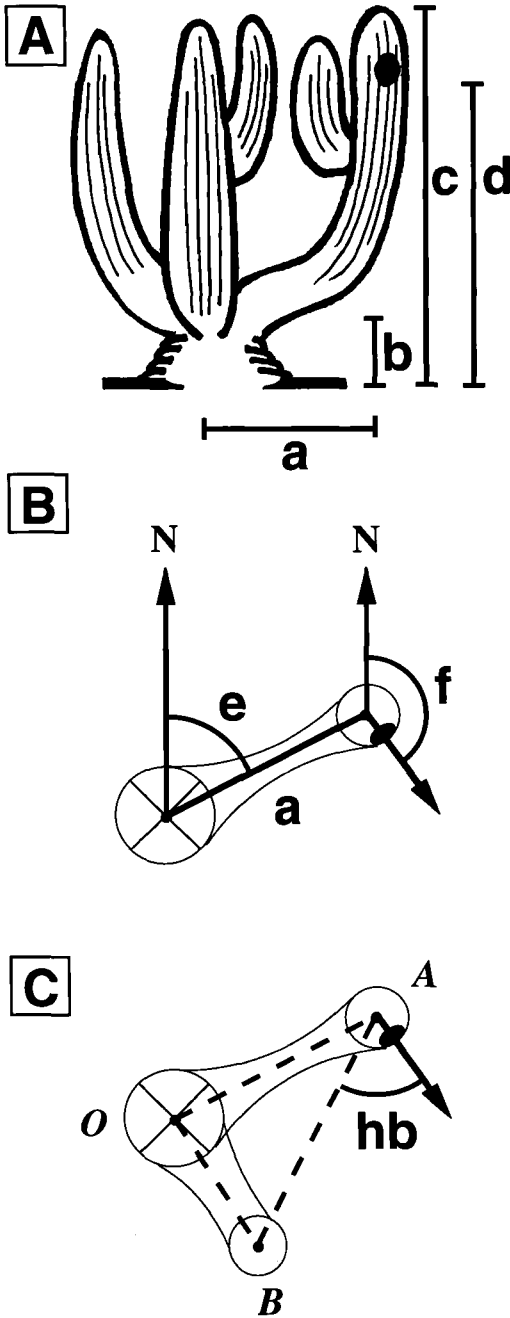
tus arms in the four quadrants using a chi-squared goodness-of-fit test (Zar 1996). Analysis of variance (ANOVA) was used to test for differences in mean arm heights and lengths in the different quadrants using the SAS statistical software package (SAS Institute 1988).

The distribution of cavities throughout the four quadrants was analyzed by testing for differences in the ratio of holes to total number of arms in each quadrant. The overall test uses a chi-squared comparison of multiple proportions; rejection of the null hypothesis of no significant differences is followed by a pairwise analysis among quadrants using the Freeman and Tukey arcsine transformation and the Tukey multiple comparison test for proportions (Zar 1996).

Cavity-hole orientations and the arm positions with respect to the holes (angle *hb*) were tested for nonrandom distribution using Rayleigh's *z*-test; comparisons of mean angles in the four different quadrants were conducted using the Watson-Williams test (Batschelet 1981). For a sample of *n* angles, the Rayleigh test calculates a mean angle and a mean angular deviation and then tests the null hypothesis that the angular data are randomly distributed with respect to the mean angle. It also calculates the index, *r*, of the dispersion around the calculated mean angle. A value of $r = 1.0$ indicates that all angular measures are oriented in the same direction, and $r = 0.0$ indicates maximum dispersion from the mean angle. The *z*-statistic is calculated by the equation:

$$z = (n)r^2 \qquad (1)$$

In a comparison of several statistical tests for circular data, Bergin (1991) determined that this test was subject to Type II errors (failure to reject the null hypothesis of random dispersion) for significant polymodal distributions. For this reason, we examined plots of the raw data for patterns of polymodality ($P > 0.05$) to confirm that the null hypothesis should be accepted.

In addition, the data for angle *hb* also were analyzed using the *V*-test, which examines whether angles are clustered around an expected mean direction (Batschelet 1981). In this case, we tested the hypothesis that the hole is oriented outward, away from the arms of the cactus (angle $hb = 180°$). For a

FIG. 1.   (A) Field measurements of cactus dimensions and cavity-entrance height: *a*, horizontal distance of arm from center of trunk; *b*, vertical distance to point of arm attachment to cactus; *c*, vertical distance to apex of arm; *d*, vertical distance to bottom of the nest hole. (B) Field measurements of orientation angles from true north (N): *e*, angle of arm with respect to trunk center (circle with cross); *f*, orientation angle of entrance hole (arrow). (C) Data computed from field measurements: angle *hb*, angle from entrance orientation to other arms of cactus; angle *AOB*, angle formed at the cactus center (*O*) by arm with cavity, *A*, and secondary arm, *B*; line *AB*, horizontal distance between arm with cavity and secondary arm.

TABLE 1. Location (by quadrant) of Gilded Flicker nest holes relative to cardón cactus arms.

Quadrant	No. of holes	No. of arms[a]	Ratio of holes to arms[b]
Northwest (NW)	28	92	0.304
Northeast (NE)	29	147	0.197
Southwest (SW)	28	156	0.179
Southeast (SE)	24	176	0.136

[a] $X^2 = 27.14$, df = 3, $P < 0.0001$ (NW < [NE = SW] < SE).
[b] $X^2 = 11.22$, df = 3, $P < 0.02$ (NW > [NE = SW] > [SW = SE]).

calculated mean angle ($\hat{u}$) and an expected angle ($\hat{a}$), the V-statistic is calculated by:

$$V = (n)(r) \cos(\hat{a} - \hat{u}) \qquad (2)$$

In this case, angle $\hat{a} = 180°$. Because of the additional information of the expected mean angle, the V-test is considered to be more powerful than the Rayleigh test alone (Batschelet 1981).

RESULTS

Cactus morphology.—We recorded a total of 589 arms on 35 cardón cacti ($\bar{x} = 16.8$, range 3 to 67 arms per cactus). The mean arm height was 4.62 ± SD of 1.62 m, approximately 1.5 m greater than the mean arm length of 3.03 ± 1.68 m. The mean distance of the arms from the center of the cactus was 1.15 ± 0.71 m. The maximum height of each cactus, defined as the height of the highest arm, was 7.1 ± 1.52 m.

Analysis of the distribution of arms around the centers of the cacti indicated that the arms are not evenly distributed around the cactus based on an expected proportion of 0.25 per quadrant (Table 1). There were fewer arms than expected in the northwest quadrant (95% CI for proportion 0.12 to 0.20) and more arms than expected in the southeast quadrant (95% CI 0.26 to 0.36). Arm heights and lengths were not significantly different among quadrants (height: F

$= 1.62$, df = 3 and 585, $P = 0.197$; length: $F = 0.092$, df = 3 and 585, $P = 0.913$).

Cavity distribution.—We recorded 109 cavity holes attributable to Gilded Flickers in 30 cacti. Five cacti (14%) had no cavities of any kind. Gilded Flicker cavity holes had a mean height of 5.6 ± 1.64 m and a mean distance from the top of the arm of 2.2 ± 1.39 m. McAuliffe and Hendricks (1988) reported that Gilded Flicker holes in saguaro cacti were almost exclusively restricted to the upper 3 m of the stems. In cardóns, this effect did not appear to be as strong in that 33 of the Gilded Flicker holes (30%) were more than 3 m below the top of the stem (three holes were more than 5 m below the top). This may indicate differences in internal structure between saguaros and cardóns.

The proportion of holes relative to the number of cactus arms differed significantly among the four quadrants (Table 1). Pairwise comparisons revealed that the northwest quadrant had a greater ratio of holes to arms than the other three quadrants. The northeast quadrant had a higher ratio than the southeast, and the relationship of the southwest quadrant to these two quadrants was unclear (i.e. NW > [NE = SW] > [SW = SE]).

Cavity-entrance orientation.—Cavity-entrance holes exhibited significant nonrandom orientation to the north-northwest (342.5°; Table 2). The influence of quadrant location of a cavity on the orientation of the entrance hole was analyzed by dividing the orientation data into one of the four quadrants, revealing significant nonrandom patterns and strong quadrant effects (Table 2). Patterns of significant nonrandom orientation were evident in all quadrants except the SE quadrant. Gilded Flicker holes were significantly oriented toward the northwest in the NW and SW quadrants (mean angles = 329.5° and 298.5°, respectively), and to-

TABLE 2. Orientation statistics[a] of Gilded Flicker nest-entrance holes in cardón cactus.

	Mean angle	Mean angular deviation	Rayleigh's z	r	P
All holes	342.5	80.6	15.05	0.37	<0.001
Northwest	329.5	52.1	12.26	0.66	<0.001
Northeast	23.5	55.7	11.27	0.62	<0.001
Southwest	298.5	73.8	5.33	0.44	0.004
Southeast	74.4	148.3	0.03	0.04	0.75

[a] From true north; mean angles and angular deviations in degrees.

TABLE 3. Orientation of Gilded Flicker nest-entrance holes[a] in cardón cactus relative to position of cactus arms (angle *hb.*; see Fig. 1C). Data are tested with the Rayleigh test (which tests whether orientation is nonrandom) and the V-test (which tests whether orientation is clustered around an expected angle of 180°).

	Angle *hb*	Mean angular deviation	Rayleigh test			V-test	
			z	*r*	*P*	*V*	*P*
All holes	154.5	85.6	11.58	0.33	<0.001	32.22	<0.001
Northwest	177.5	64.0	8.03	0.54	<0.001	14.97	<0.001
Northeast	171.5	74.1	5.45	0.43	0.004	12.45	<0.001
Southwest	115.5	75.8	4.87	0.42	0.007	5.03	0.090
Southeast	101.5	141.7	0.05	0.05	>0.500	0.24	>0.500

[a] From true north; mean angle *hb* and angular deviations in degrees.

ward the north in the NE quadrant (mean angle = 23.5°). The amount of dispersion was lowest in the NW and NE quadrants (r = 0.66 and 0.62, respectively). High levels of dispersion from the calculated mean angle were indicated for the SE quadrant (r = 0.04). Comparisons of the quadrants with significant mean orientation angles showed equivalent orientations in the NW and SW quadrants (F = 2.84, df = 1 and 54, P = 0.10), with the orientations in the NE quadrant significantly different from both the NW quadrant (F = 13.76, df = 1 and 55, P < 0.001) and the SW quadrant (F = 22.16, df = 1 and 55, P < 0.001).

Hole orientation versus position of arms.—The overall distribution of arms from the directions of hole orientations (angle *hb* in Fig. 1C) was significantly nonrandom. The calculated mean angles and the V-tests (with an expected angle of 180°) both suggested a general preference for facing the opening of the cavities away from the other arms on the cactus (Table 3).

The position of the cactus arms relative to hole orientation was significantly nonrandom for cavities in all quadrants except the SE (Fig. 2). The NW and NE quadrants had mean angles *hb* closest to being directly opposite the hole orientations (NW, 177.5°; NE, 171.5°); this was confirmed by the highly significant P-values for the expected 180° under the V-test. The mean angle *hb* from the SW quadrant, also significant under the Rayleigh test, was positioned to the right of the mean hole orientation (mean angle *hb* = 115.5°). In addition, the V-test for an expected angle of 180° was not significant. The analyses of the calculated mean angle *hb* in the SE quadrant were not significant for either test (Table 3).

DISCUSSION

The orientation of an arm with respect to the center of the cactus appears to be an important factor in cavity placement by Gilded Flickers. The pattern of arm growth implies that climatic or other ecological factors influence growth patterns, with more arms in the southeast and fewer in the northwest. Nevertheless, on the basis of the number of available arms, Gilded Flickers place more holes than expected in the northwest quadrant and fewer holes than expected in the southeast quadrant. This cannot be accounted for by differences in arm dimensions between quadrants, because cactus arms did not differ in mean height or length.

The Gilded Flickers we studied oriented their holes to the north-northwest, which concurs with findings for Gila Woodpeckers in saguaro cactus (Inouye et al. 1981, Korol and Hutto 1984; but see Kerpez and Smith 1990). The r-values (Rayleigh test) we calculated were intermediate between those reported for Gila Woodpeckers by Inouye et al. (1981) and Korol and Hutto (1984). Although our r-values indicated a fair degree of dispersion from the significant mean orientation angle, we believe they indicate a preference for a general direction, i.e. northwest.

Gilded Flickers tended to avoid facing their cavities toward the majority of the cactus arms. Placement of cavities in cardón was such that it created an unobstructed region in front of the entrance. Similarly, when pairs of adjacent branches were present on a saguaro, Gila Woodpeckers tended to place their nest holes in the direction of least obstruction (Korol and Hutto 1984). Orientation of entrances to avoid obstructions would result in increased visibil-
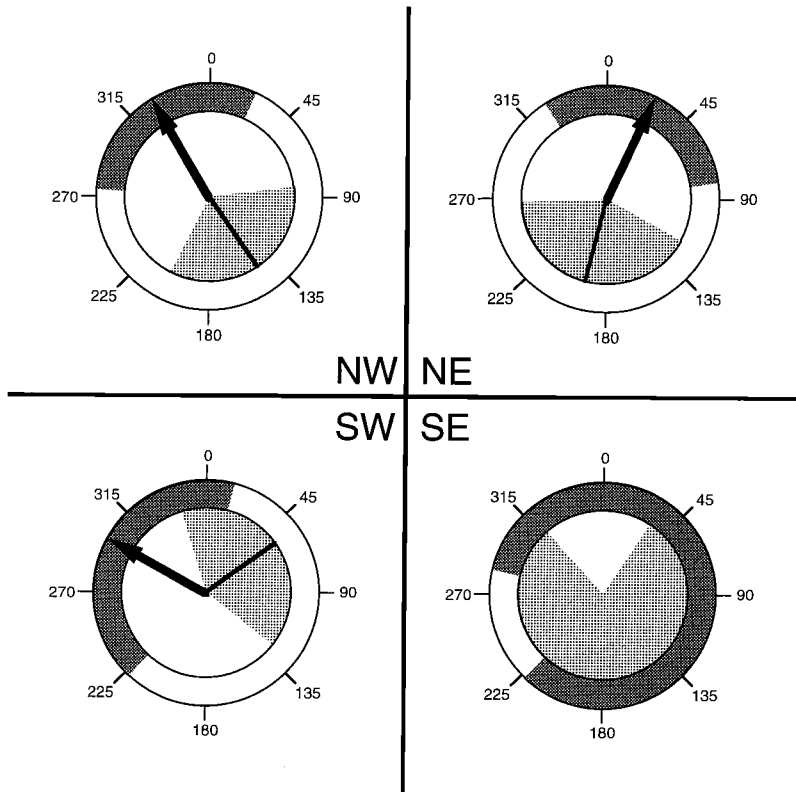
FIG. 2. Gilded Flicker cavity-entrance hole orientations and secondary arm positions analyzed by quadrants. Arrows denote mean hole orientations significant for Rayleigh test of nonrandom distribution. Bars denote mean angles from orientation of holes to secondary cactus arms significant for Rayleigh test or V-test using expected angle of 180°. No arrow or bar indicates that the calculated mean angle was not significant by either Rayleigh or V-test. Shaded areas denote regions between mean angular deviations on either side of means.

ity from and toward the cavity. Visibility has been shown to affect the ability of animals to defend territories and resources (Eason and Stamps 1992), and evidence suggests that territorial boundaries of birds are affected by visibility (Conder 1956, Burger 1974, Reid and Weatherhead 1988). Analyses of Northern Flicker (*Colaptes auratus*) nest-site characteristics have shown that this species prefers open areas versus dense forest (Conner and Adkisson 1977). Visibility at nests also may influence predation risk. For example, Li and Martin (1991) found that depredated nests often were close to large trees and concealed by foliage. In addition, if Gilded Flickers place their nests to take advantage of the cooling effects of prevailing winds, then facing a nest into the bulk of the cardón structure may lessen these effects to an unacceptable degree.

The analysis of data by quadrants supports the hypothesis that compass orientation of cavity entrances and orientation with respect to cactus structure vary with quadrant location. The best location for achieving the goals of facing away from the cactus arms and in a northwesterly direction would be in the northwest quadrant of the cactus, and it is here that we find the strongest statistical support for both a mean orientation angle and a mean angle from the entrance orientation to the cactus arms. The northwest quadrant also contained the highest ratio of holes to cactus arms, with the smallest ratio occurring in the southeast quadrant (although many cavities were located there). In the southeast quadrant, the orientation of holes was random with respect to both compass direction and location of the other arms, reflecting the fact that in this quadrant, the goals of

northwesterly orientation and facing away from nearby arms are in complete conflict.

Hole orientations in the northeast and southwest quadrants suggest that tradeoffs are being made between thermal and architectural constraints (Fig. 2). In the southwest quadrant, facing away from cactus arms would require a southerly exposure; instead, the northwest preference is maintained while sacrificing some of the visibility around the nest entrance by orienting the cavity such that the bulk of the cactus arms are located to the right and slightly behind the cavity opening. This is supported by the nonsignificant results of the V-test for an expected angle to the cactus arms of 180°. In the northeast quadrant, facing away from the bulk of the arms can be achieved without exposure to direct sun, and in this quadrant a northerly orientation achieves this without straying too far from the overall preference for orientation to the north-northwest.

Because Gilded Flickers are relatively large woodpeckers, they may have difficulty losing excess heat. Thus, their thermoregulatory requirements are likely to have a strong influence on cavity orientation. Heat stress in the region where we collected data can be high, and cavities in cacti are subject to greater heat stress than in other substrates because of the larger heat capacity of cactus tissue versus woody tissue (Howe et al. 1987). Avoidance of direct exposure to the sun and possibly taking advantage of prevailing winds may be adaptive if the higher temperatures on the south sides of cacti are detrimental to woodpecker reproductive success.

The cavities built by desert woodpeckers represent an energetic investment, and they constitute a record of behavioral choices made to obtain maximum benefits from the location of a cavity. Undoubtedly, many different factors influence these decision-making behaviors in order that the birds place their cavities in optimal locations. We have identified two factors, directional orientation and orientation with respect to cactus structure, that appear to influence construction of nest cavities by Gilded Flickers in cardón cactus. Moreover, we provide evidence that Gilded Flickers have evolved the ability to make tradeoffs between the complexities of the cardón branching patterns and the environmental factors that influence cavity orientation.

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