

# GILA WOODPECKER AGONISTIC BEHAVIOR

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**ABSTRACT.**—Agonistic behavior of Gila Woodpeckers, including vocalizations, visual displays, and other related behaviors, is described. Interactions with both con- and heterospecifics were analyzed by stochastic processes, and it is shown that the timing of aggression toward a species coincided with the time during which that species was searching for nest sites or cavities. The behavior shown toward Flickers and Starlings appears to fulfill criteria for interspecific territoriality, and evidence is presented to support the contention that the function of this behavior is protection of nest sites and nest holes from competitors. The effects of intra- and interspecific territoriality on the distribution of the species involved were found to be significantly different. Simultaneous protection of different sized territories is discussed.—*Department of Biology, University of New Mexico, Albuquerque 87131. Present address: Department of Zoology, Michigan State University, East Lansing, 48824. Accepted 21 June 1976.*

GILA Woodpeckers (*Melanerpes uropygialis*), which are commonly associated with the giant cactus (*Carnegiea gigantea*) of Arizona's desert lowland, inhabit cottonwood (*Populus deltoides*) groves along the Gila River in southwest New Mexico. While the behavior of its congeners, the Golden-fronted (*M. aurifrons*) and Red-bellied (*M. carolinus*) Woodpeckers have been studied thoroughly (Kilham 1958, 1961, 1963, Selander and Giller 1959, Stickel 1965), details of Gila Woodpecker behavior in the literature are limited to largely anecdotal accounts. The most striking feature of these reports is that Gila Woodpeckers are consistently described as being highly aggressive toward both conspecifics and a broad range of other species including Bronzed Cowbirds (*Tangavius aeneus*) and thrashers (*Toxostoma* spp.) (Gilman 1915, Bent 1939). My preliminary observations indicated that they are distinctly more aggressive than other species in the region they inhabit.

The main purpose of this study was to determine the ecological functions of Gila Woodpeckers' agonistic behavior. Apparently they are territorial toward conspecifics, Common Flickers (*Colaptes auratus*), and Starlings (*Sturnus vulgaris*). Several lines of evidence suggest that protection of nest sites and nest holes from competitors is the main function of their interspecific aggression. In this paper descriptions of agonistic behaviors are presented first. Then stochastic processes, which have proved useful in demonstrating changes in behavior over time (Stokes 1962), are used to describe changes in levels of agonistic behavior shown toward other pairs of conspecifics and members of other species over the course of the breeding season. Following this quantitative analysis, details of intra- and interspecific territoriality are presented. The functions of Gila Woodpecker territoriality are considered next. The hypothesis that species toward which they are territorial should overlap more in their use of nest sites than other species, is tested and confirmed by comparing nest sites for those species. Direct evidence of competition for nest holes is also presented. Finally the effects of intra- and interspecific territoriality on the distribution of the species involved are compared by examining distances between Gila Woodpecker nest cavities and their nearest conspecific and Flicker nest cavities.

## STUDY AREA AND METHODS

I studied Gila Woodpeckers at Red Rock on the Gila River in Grant County, New Mexico, on 17–18 March and from 17 April to 4 July, 1973, and from 16 to 20 March 1974. The study tract consisted of several cottonwood groves on both banks of the river: each grove contained 1–3 pairs of Gila Woodpeck-

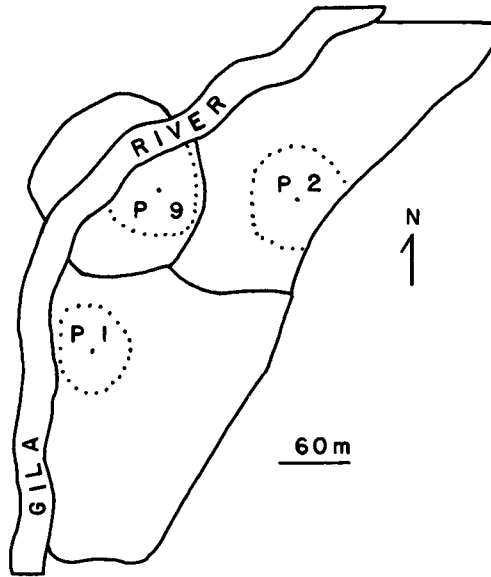


Fig. 1. Territories of Gila Woodpecker pairs 1, 2, and 9. All three territories, as well as those of all other pairs studied, were within the limits of cottonwood groves. Solid lines represent boundaries of intraspecifically defended areas, and dotted lines represent boundaries of interspecifically defended areas.

ers. The canopy was almost exclusively cottonwoods, and the ground was covered with sand and debris, from recent flooding. This riparian zone extended less than 200 m back from the river and adjoined a narrow strip of irrigated farmland. With few exceptions, no trees were found beyond this, and desert formed the remainder of the local habitat (Fig. 1).

Six pairs of Gila Woodpeckers were followed closely through the breeding season, and three additional pairs were watched occasionally. Total observation time was in excess of 400 hours. Although no birds were banded, I could identify three males (designated p3M, p7M, and p8M) and two females (p7F and p8F) by their distinctive calls. Each of these birds remained in a particular territory through the 1973 breeding season. Common Flickers, Ladderbacked Woodpeckers (*Picoides scalaris*), and Starlings were also studied because of their interactions with Gila Woodpeckers.

I recorded vocalizations and drumming on a Uher 4000 Report-L tape recorder at a tape speed of 19 cm per sec with use of a Uher M514 microphone and, sometimes, a 61-cm diameter parabolic reflector. Vocalizations were analyzed by use of a Kay Electric Company Sonagraph model 6061B, with a model 6076 amplitude display and scale magnifier unit. A detailed analysis of Gila Woodpecker vocalizations will be presented elsewhere (Brenowitz 1977).

*Stochastic processes.*—I recorded frequencies of behaviors of other pairs of conspecifics, Flickers, Ladderbacked Woodpeckers, and Starlings (designated preceding events 1–19; see Tables 1, 2, and 3) that sometimes were followed by Gila Woodpecker agonistic behaviors (designated following events A–G). For each repetition of a behavior I recorded whether or not a Gila Woodpecker agonistic behavior followed and, if so, which one (A–G) it was. In situations where birds exchanged several behaviors back and forth, only the initial behaviors were included. No other preceding event was counted until the prior exchange concluded and the pair being watched was again in a position to undertake a following event. Visual displays were excluded from this analysis because they can not be detected reliably in the dense cottonwood foliage. Over 300 hours of observations were made for this analysis.

Probabilities for each preceding event-following event sequence, as well as preceding event-no-following event sequences, were calculated as follows: frequency of a following event (or no-following event)/frequency of a preceding event. The total probability of a preceding event being followed by Gila Woodpecker agonistic behavior also was calculated. The study was divided into three time blocks: the prenestling period (23 April–9 May 1973), the early nestling period (15–29 May 1973), and the late nestling-fledgling period (30 May–4 July 1973). A separate set of probabilities was calculated for each time block (see Tables 1, 2, and 3).

TABLE 1  
RESULTS OF STOCHASTIC PROCESS FOR PRENESTLING PERIOD

Preceding event:	Following event								Sum of A-G
	A Call 1	B Call 2	C Drumming	D Gravel call	E Supplant	F Chase	G Attack	No following event	
Flicker									
1) Intrusion (n = 11)	0.00 (0) <sup>1</sup>	0.09 (1)	0.00 (0)	0.00 (0)	0.46 (5)	0.27 (3)	0.09 (1)	0.09 (1)	0.91 (10)
2) Drumming (n = 34)	0.18 (6)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.82 (28)	0.18 (6)
3) "Kheer" <sup>2</sup> (n = 24)	0.13 (3)	0.13 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.75 <sup>3</sup> (18)	0.25 (6)
4) "Wicka . . ." (n = 5)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (5)	0.00 (0)
5) "Gila-like" (n = 43)	0.35 (15)	0.07 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.58 (25)	0.42 (18)
6) "Eh, eh . . ." (n = 18)	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.94 (17)	0.06 (1)
♂ Gila									
7) Intrusion (n = 3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.33 (1)	0.67 (2)	0.00 (0)	1.00 (3)
8) Drumming (n = 10)	0.20 (2)	0.00 (0)	0.60 (6)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.20 (2)	0.80 (8)
9) "Call 1" (n = 51)	0.18 (9)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.82 (42)	0.18 (9)
10) "Call 2" (n = 8)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (8)	0.00 (0)
♀ Gila									
11) Intrusion (n = 0)	—	—	—	—	—	—	—	—	—
12) Drumming (n = 1)	0.00 (0)	0.00 (0)	1.00 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)
13) "Call 1" (n = 7)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (7)	0.00 (0)
14) "Call 2" (n = 12)	0.17 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.83 (10)	0.17 (2)
Ladderbacked									
15) Intrusion (n = 14)	0.07 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.71 (10)	0.07 (1)	0.00 (0)	0.14 (2)	0.86 (12)
16) Drumming (n = 1)	1.00 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)
17) "Pik . . ." (n = 12)	0.58 (7)	0.08 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.33 (4)	0.67 (8)
Starling									
18) Intrusion (n = 2)	0.00 (0)	1.00 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (2)
19) "Calls" (n = 2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (2)	0.00 (0)

<sup>1</sup> Numbers in parentheses are the "n's" associated with probabilities above them.

<sup>2</sup> All preceding events in quotation marks are vocalizations.

<sup>3</sup> For a preceding event, probabilities should add to 1.00; discrepancies are due to rounding errors.

*Comparison of nest sites.*—Sites of 6 Gila Woodpecker, 5 Flicker, and 3 Ladderbacked Woodpecker nest cavities were scored in the following 2 categories according to diameter: (1) trunks and limbs, (2) branches. Nest sites for these three species were then compared by Fisher exact probability tests.

*Intra- and interspecific distributions of nest cavities.*—Distances from Gila Woodpecker nest cavities to the nearest Gila Woodpecker and Flicker nest cavities were measured and the distributions compared by a Mann-Whitney *U*-test.

#### DESCRIPTIONS OF AGONISTIC BEHAVIORS

Agonistic behavior includes a broad range of activities used in conflict situations. In this study aggression was defined operationally as supplantings, chases, and

TABLE 2  
RESULTS OF STOCHASTIC PROCESS FOR EARLY NESTLING PERIOD

Preceding event:	Following event								Sum of A-G
	A Call 1	B Call 2	C Drum- ming	D Gravel call	E Sup- plant	F Chase	G Attack	No following event	
Flicker									
1) Intrusion (n = 1)	0.00 (0) <sup>1</sup>	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)	0.00 (0)
2) Drumming (n = 6)	0.00 (0)	0.17 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.83 (5)	0.17 (1)
3) "Kheer" <sup>2</sup> (n = 87)	0.01 (1)	0.03 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.95 <sup>3</sup> (83)	0.04 (4)
4) "Wicka . ." (n = 18)	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.94 (17)	0.06 (1)
5) "Gila-like" (n = 0)	— —	— —	— —	— —	— —	— —	— —	— —	— —
6) "Eh, eh . ." (n = 50)	0.08 (4)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.92 (46)	0.08 (4)
♂ Gila									
7) Intrusion (n = 0)	— —	— —	— —	— —	— —	— —	— —	— —	— —
8) Drumming (n = 37)	0.30 (11)	0.03 (1)	0.03 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.65 (24)	0.35 (13)
9) "Call 1" (n = 288)	0.16 (46)	0.02 (6)	0.02 (6)	0.01 (3)	0.00 (0)	0.00 (0)	0.00 (0)	0.79 (227)	0.21 (61)
10) "Call 2" (n = 26)	0.12 (3)	0.12 (3)	0.04 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.73 (19)	0.27 (7)
♀ Gila									
11) Intrusion (n = 0)	— —	— —	— —	— —	— —	— —	— —	— —	— —
12) Drumming (n = 0)	— —	— —	— —	— —	— —	— —	— —	— —	— —
13) "Call 1" (n = 40)	0.03 (1)	0.03 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.95 (38)	0.05 (2)
14) "Call 2" (n = 75)	0.11 (8)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.89 (67)	0.11 (8)
Ladderbacked									
15) Intrusion (n = 1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)	0.00 (0)
16) Drumming (n = 4)	0.50 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.50 (2)	0.50 (2)
17) "Pik . ." (n = 209)	0.04 (8)	0.01 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.95 (199)	0.05 (10)
Starling									
18) Intrusion (n = 31)	0.00 (0)	0.06 (2)	0.00 (0)	0.00 (0)	0.26 (8)	0.10 (3)	0.00 (0)	0.58 (18)	0.42 (13)
19) "Calls" (n = 2)	0.00 (0)	0.50 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.50 (1)	0.50 (1)

<sup>1</sup> Numbers in parentheses are the "n's" associated with probabilities above them.

<sup>2</sup> All preceding events in quotation marks are vocalizations.

<sup>3</sup> For a preceding event, probabilities should add to 1.00; discrepancies are due to rounding errors.

attacks. In Gila Woodpeckers aggression is not the culmination of a series of agonistic behaviors. In virtually all supplantings, chases, and attacks no previous agonistic behavior was observed. I rarely observed aggression in association with other behaviors, although call 2 sometimes accompanied supplantings of Starlings.

*Call 1* is composed of uniform vibrato notes and sounds very much like the "Chaa-ah" territorial call of Red-bellied Woodpeckers (see Kilham 1961). It is used as a contact call by which members of a pair signal their location and is the Gila Woodpecker's primary territorial advertisement display. Males use this call more often than do females.

TABLE 3  
RESULTS OF STOCHASTIC PROCESS FOR LATE NESTLING-FLEDGLING PERIOD

Preceding event:	Following event								Sum of A-G
	A Call 1	B Call 2	C Drumming	D Gravel call	E Sup-plant	F Chase	G Attack	No following event	
Flicker									
1) Intrusion (n = 2)	0.00 (0) <sup>1</sup>	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (2)	0.00 (0)
2) Drumming (n = 16)	0.06 (1)	0.00 (0)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.88 (14)	0.12 (2)
3) "Kheer" <sup>2</sup> (n = 53)	0.04 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.96 (51)	0.04 (2)
4) "Wicka . . ." (n = 17)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.94 (16)	0.06 (1)
5) "Gila-like" (n = 0)	—	—	—	—	—	—	—	—	—
6) "Eh, eh . . ." (n = 95)	0.04 (4)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.96 (91)	0.04 (4)
♂ Gila									
7) Intrusion (n = 1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)	0.00 (0)
8) Drumming (n = 5)	0.20 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.80 (4)	0.20 (1)
9) "Call 1" (n = 119)	0.11 (13)	0.00 (0)	0.02 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.87 (104)	0.13 (15)
10) "Call 2" (n = 14)	0.14 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.86 (12)	0.14 (2)
♀ Gila									
11) Intrusion (n = 4)	0.25 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.75 (3)	0.25 (1)
12) Drumming (n = 0)	—	—	—	—	—	—	—	—	—
13) "Call 1" (n = 31)	0.06 (2)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.94 (29)	0.06 (2)
14) "Call 2" (n = 22)	0.00 (0)	0.05 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.95 (21)	0.05 (1)
Ladderbacked									
15) Intrusion (n = 1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	1.00 (1)	0.00 (0)
16) Drumming (n = 0)	—	—	—	—	—	—	—	—	—
17) "Pik . . ." (n = 2)	0.50 (1)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.50 (1)	0.50 (1)
Starling									
18) Intrusion (n = 24)	0.04 (1)	0.08 (2)	0.00 (0)	0.04 (1)	0.21 (5)	0.13 (3)	0.04 (1)	0.46 (11)	0.54 (13)
19) "Calls" (n = 0)	—	—	—	—	—	—	—	—	—

<sup>1</sup> Numbers in parentheses are the "n's" associated with probabilities above them.

<sup>2</sup> All preceding events in quotation marks are vocalizations.

*Call 2* is a series of sharp "pip, pip" notes. It is most frequently given in response to disturbance by humans, and the presence of intruders of other species. Call 2 is the only vocalization given in conjunction with visual displays (head bobbing and head shaking) and serves as a general alarm call.

*Drumming* is a means of sound production in which the bill rapidly strikes a resonant object such as a dead branch. Drumming is considered a form of territorial proclamation (Lawrence 1967).

*Gravel call* consists of harsh rasping notes spectrographically similar to those of

call 1. It was heard infrequently, in situations where Gila Woodpeckers appeared highly agitated by birds of other species.

*Bill pointing display.*—The bill, head, and neck are extended parallel to the substrate on which an individual is perched, and the pose is held rigidly. The displaying bird orients itself so that its bill points directly at the individual eliciting the display. This display seems similar to the rigid pose of Red-bellied Woodpeckers (Kilham 1961).

*Head bobbing and head shaking displays.*—The head is thrust in a forward and downward arc from a position with the bill parallel to the substrate, to a position with the bill almost perpendicular to the substrate. The return motion of raising the head is less exaggerated. In some instances the arc is increased by bringing the head back so that the bill points above a position parallel to the substrate. The orientation of the displaying bird varies with respect to the individual eliciting the display. Head shaking is similar to head bobbing but with lateral movement accompanying the up-down movement. Displays similar to these have been described for the following genera of woodpeckers: *Picoides* (Lawrence 1967, Kilham 1969, Short 1971), *Sphyrapicus* (Lawrence 1967), and *Colaptes* (Lawrence 1967).

*Supplanting* is replacing an individual at a given place. In supplanting a Gila Woodpecker flies and/or hitches along a branch to the place where another individual is perched or foraging. Commonly the latter leaves when the Gila Woodpecker arrives.

*Chasing* is pursuing a second individual also in motion. Such pursuits were toward the boundaries of a Gila Woodpecker's territory and always away from the nest cavity. Chasing and supplanting often occurred together. On one occasion p9M supplanted a Starling 39 times with chases between successive supplantings.

*Attacking* is movement toward an individual that culminates in forceful contact between individuals.

## RESULTS

### STOCHASTIC PROCESSES

As male Gila Woodpeckers play a more active role in agonistic encounters with both con- and heterospecifics, only results for males are presented here. Tables 1, 2, and 3 show the probabilities of Flicker, Gila Woodpecker, Ladderbacked Woodpecker, and Starling behaviors (preceding events 1–19) being followed by Gila Woodpecker agonistic behaviors (following events A–G) for the prenestling, early nestling, and late nestling-fledgling periods, respectively. Results are presented according to categories of preceding events (intrusion, vocalizations, and drumming).

*Intrusion.*—The activities of intruders in the territory of the pair being watched were grouped together in the "intrusion" category. For members of other species this category was their presence in the space within the circumference of the crown of the nest cavity tree.

One can predict with considerable certainty that during the prenestling period, intrusions of the species studied will be followed by Gila Woodpecker agonistic behavior (see total probabilities, Table 1). Furthermore for all species except Starlings, this behavior will most likely be some form of aggression (supplant, chase, or attack). In no case is it possible to predict with certainty which specific behavior will follow.

In the early nestling period, intrusions by species other than Starlings were rare and were not followed by Gila Woodpecker agonistic behavior. While the number of

Starling intrusions increased, it was not possible to predict that Gila Woodpecker agonistic behavior would follow. When following events do occur, they will likely be some form of aggression.

In the late nestling-fledgling period aggression continued to follow Starling intrusions but, once again, not predictably so. Also, a greater variety of behaviors followed these intrusions so that even when following events are observed, that they will be aggression is less predictable.

It is interesting to note that following intrusions by other species, Gila Woodpeckers were more likely to supplant individuals than chase or attack them. Intraspecifically this trend was reversed. Also, the periods when aggression toward other species occurred coincided with the times that those species were actively seeking nest sites.

*Drumming.*—One can predict that during the prenesting period most male Gila Woodpecker drummings will be followed by agonistic behavior (see Table 1). For Flicker drummings one can predict with some certainty that no events will follow. Ladderbacked Woodpecker and female Gila Woodpecker drumming occurred too infrequently to make reasonable predictions. Predictions regarding Flicker drumming are the same for the remainder of the study, and for other species total probabilities decrease together with the number of instances of drumming.

*Vocalizations.*—Preceding events in quotation marks (see Tables 1, 2, and 3) are vocalizations. For descriptions of Flicker and Ladderbacked Woodpecker vocalizations see Lawrence (1967) and Short (1971), respectively. The most striking observation is that, except for Ladderbacked Woodpecker "Pik..s," one can predict that most vocalizations of all species studied will not be followed by agonistic behavior. This is true for all time blocks.

#### TERRITORIALITY

Most aggressive behavior of Gila Woodpeckers appears to be related to defense of an area, territoriality. By March pairs were regularly spaced along the river (mean distance between cavities: 120 m,  $SE \pm 7$ ,  $n = 6$ ) and most intraspecific encounters were limited to exchanges of vocalizations. Their territories (Fig. 1) were multipurpose (type A, Hinde 1956), and virtually all disputed boundaries coincided with localized food sources; e.g. a newly ripened raspberry bush (*Rubus* sp.) was the location of one encounter.

Gila Woodpeckers persistently defended space up to 40–50 m from their nest cavities from Flickers and Starlings for at least part of the breeding season (see results of stochastic processes). Furthermore all types of agonistic behavior they displayed toward conspecifics they also displayed toward Flickers, and they used all types except visual displays in interactions with Starlings. Thus behavior shown toward these species meets criteria established for interspecific territoriality (cf. Simmons 1951, Lanyon 1956). In contrast, they did not defend space from Ladderbacked Woodpeckers, and the only aggression seen between these species involved one pair of Ladderbacked Woodpeckers and one male Gila Woodpecker on a single day.

Although this study primarily concerns Gila Woodpecker behavior, some mention of other species' responses to their aggression seems appropriate. The commonest response of both Flickers and Starlings to supplantings, chases, and attacks by Gila Woodpeckers was to retreat toward the periphery of the resident's territory. In several instances Starlings held their ground despite Gila Woodpeckers' efforts to supplant them. Once a male (p3M) attacked a Starling perched in its nest cavity tree

only to be attacked itself and driven from that tree by the same bird. This was the only time I witnessed a Starling clearly dominating a Gila Woodpecker. Although Flickers were far less tenacious than Starlings, I recorded one instance in which a pair of Flickers supplanted a male (p1M) from the branch containing its nest cavity. Neither Flickers nor Starlings attempted to exclude Gila Woodpeckers from space around their nest cavities, so apparently neither species reciprocates the territoriality the Gila Woodpeckers show toward them.

*Evidence for the function of interspecific territoriality.*—Nest sites for Flickers, Gila Woodpeckers, and Ladderbacked Woodpeckers were compared by use of Fisher exact probability tests. Gila Woodpeckers used trunks and limbs for nest sites significantly more than did Ladderbacked Woodpeckers ( $P = 0.047$ ), whereas they did not differ from Flickers in this regard ( $P = 0.545$ ). Starlings were excluded from this analysis because a trunk or limb must already contain a cavity to be a potential nest site for them. These results indicate a greater potential for competition for nest sites between Gila Woodpeckers and Flickers than between Gila and Ladderbacked Woodpeckers.

There is also direct evidence of nest hole competition. On 30 April 1973 a pair of Flickers took a cavity from a male Gila Woodpecker (p1M). They subsequently enlarged its entrance and succeeded in rearing young there. Starlings are well known as nest hole competitors of other species of woodpeckers (Kessel 1957, Kilham 1959). They moved into Red Rock in early April, but did not break up into pairs and begin nesting until the early nestling period of Gila Woodpeckers. Three pairs of Gila Woodpeckers (p1, p2, p3) lost cavities to Starlings during the early nestling and late nestling-fledgling periods, and one pair (p2) lost three successive cavities, providing additional evidence that Flickers and Starlings are sometimes dominant over Gila Woodpeckers. No cavities were lost to Ladderbacked Woodpeckers.

*Intra- and interspecific distribution of nest cavities.*—The distance between Gila Woodpecker nest cavities ( $\bar{x} = 120$  m,  $SE \pm 7.4$ ,  $n = 6$ ) was significantly larger than the distance between Gila Woodpecker and Flicker nest cavities ( $\bar{x} = 76$  m,  $SE \pm 16.6$ ,  $n = 9$ ; Mann-Whitney  $U = 30$ ,  $P < 0.05$ ). Once again, Starlings were excluded from this analysis for reasons stated above.

## DISCUSSION

Although most reported cases of interspecific territoriality involve closely related species (Johnson 1963, Cody 1969, Cody and Brown 1970, Murray 1971, Rohwer 1973), Orians and Willson (1964) suggested that it might be profitable for a species to exclude dissimilar potential competitors as well. Gila Woodpeckers appear to be an example of such a species. While protection of nest holes has been largely excluded from considerations of interspecific territoriality (Simmons 1951, Orians and Willson 1964), several lines of evidence strongly implicate it as a function of Gila Woodpecker interspecific aggression. First, the timing of aggression toward a species (as shown by stochastic processes) coincided with the period during which that species was actively seeking nest sites or cavities. Second, it has been shown that Gila Woodpeckers are territorial toward species that overlap with them in use of nest sites and are not territorial toward species that use significantly different nest sites. Direct evidence of competition for nest cavities also was presented.

Orians and Willson (1964) suggest that interspecific territoriality should serve fewer functions than intraspecific territoriality, and the evidence presented here sup-



ports this view. It seemed reasonable to expect that differences in functions of territories might be reflected by differences in the distribution of the species involved. A comparison of the distances between Gila Woodpecker nest cavities and the nearest conspecific and Flicker nest cavities shows that intraspecific distances between nest cavities were significantly larger than interspecific distances.

A territory of given character can relate specifically to intruders of a particular category. Here species that compete with or threaten Gila Woodpeckers in different ways form these categories. Defense against Flickers and Starlings, which compete for nest sites and cavities, and conspecifics differ. Theoretically then, a species can simultaneously maintain more than one territory. In the present case, a space around the nest cavity is defended from con- and heterospecifics, and a larger surrounding space is protected only from conspecifics. Thus, despite a difference in size of spaces defended intra- and interspecifically, both can be considered territories.

Murray (1971) contends that known cases of interspecific territoriality are consistent with the assumption that it is misdirected intraspecific territoriality and, therefore, a nonadaptive characteristic, but he does suggest criteria for recognizing cases of adaptive interspecific territoriality. Observations of competition for cavities and close regulation of aggression both spatially and temporally suggest that Gila Woodpeckers can recognize the behavior of Flickers and Starlings. Response to these species probably is not misdirected intraspecific aggression and appears to be highly adaptive. Also, this behavior fulfills several of Murray's (1971) criteria for adaptive interspecific territoriality.

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