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This thesis, directed and approved by the candidate's committee, has been accepted by the Graduate Committee of The University of New Mexico in partial fulfillment of the requirements for the degree of Master of Science

AGONISTIC BEHAVIOUR IN

GILA WOODPECKERS

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AGONISTIC BEHAVIOUR IN GILA WOODPECKERS

By

Gene L. Brenowitz

B.A., S.U.N.Y. College at Old Westbury, 1972

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science in Biology
in the Graduate School of
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Albuquerque, New Mexico
August, 1974

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ABSTRACT OF THESIS

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ABSTRACT

Agonistic behaviour of Gila Woodpeckers (Centurus uropygialis), including vocalizations, visual displays and other related behaviours, is described. Aggressive interactions with both con- and hetero-specifics were analyzed by stochastic processes. Results indicate that Gila Woodpeckers are far less aggressive than qualitative descriptions suggest and reasons for this discrepancy are presented.

The ecological correlates of Gila Woodpecker aggression were investigated and it appears that most aggression is related to defense of areas both intraspecifically and interspecifically. The effects of the two types of territoriality on the distribution of the species involved were compared and found to be significantly different. A model is presented to explain how an individual can defend more than one territory which overlap in time and space.

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INTRODUCTION

The behaviour of Gila Woodpeckers (Centurus uropygialis), which inhabit cottonwood groves along the Gila River in southwestern New Mexico, is not well known. Anecdotal accounts describe them as being highly aggressive toward both conspecifics and members of other species (Bent, 1939; Gilman, 1915). My preliminary investigation agreed with these earlier reports.

To date, most behavioural studies of interactions of free ranging birds have been largely descriptive in nature and the result is a rapidly growing body of information on many species. However, sequential behaviour related to maintenance activities (Andrew, 1956a; Delius, 1969), communication within a social group (Altman, 1965) and agonistic behaviour (Dingle, 1969; Hazlett and Bossert, 1965, 1966; Hazlett and Estabrook, 1974; Stokes, 1962) have been studied quantitatively by stochastic processes. Because of the potential these techniques have, it seems appropriate to assess the relative merit of applying them to study interactions of free ranging individuals.

In this study I used stochastic processes to analyze aggression shown by Gila Woodpeckers toward Flickers (Colaptes auratus), Ladderbacked Woodpeckers (Dendrocopos

scalaris) and Starlings (Sturnus vulgaris), as well as conspecifics. Because the behaviour of Gila Woodpeckers has not been presented in detail, a description of their agonistic behaviour, including calls, visual displays and other related behaviours, precedes the results of the stochastic analysis. Furthermore, qualitative information and results of quantitative analysis are compared and contrasted and, then, are used in conjunction with each other in an attempt to determine the ecological correlates of Gila Woodpecker aggression.

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- 4 July, 1973 and from 16-20 March, 1974. The study area consisted of several cottonwood (Populus deltoides) groves on both banks of the river. The canopy was almost exclusively cottonwoods, while the ground cover, usually grasses, was covered with sand and debris, as a result of recent flooding. This riparian zone extends less than 100 m back from the river and adjoins a narrow strip of irrigated farmland. With few exceptions, no trees are found beyond this, and desert forms the remainder of the local habitat.

Six pairs of Gila Woodpeckers were followed closely through the breeding season, and three additional pairs were observed occasionally. Although no birds were color banded, I could identify three males (designated p3M, p7M and p8M) and two females (p7F and p8F) by their vocalizations. Sonagrams of calls of these birds made early and late in the study indicate that they all remained in a particular area through the 1973 breeding season.

I recorded vocalizations and drumming on a Uher 4000 Report-L tape recorder at a tape speed of 19 cm per second with use of a Uher M514 microphone and a

61 cm diameter parabolic reflector. Analyses of vocalizations were carried out on a Kay Electric Company Sonagraph model 6061B with a model 6076C amplitude display and scale magnifier unit.

On an "observation day", I restricted my activities to recording behaviour for stochastic analysis. Generally, I observed one pair of Gila Woodpeckers for an entire day (pairs 7 and 8 were observed together), often staying in their territory from dawn until dusk. In all, there were 36 such days and 367 hours of observations were logged (an average "observation day" = 10.2 hours of observations). Other days were devoted to the collection of other types of data.

Stochastic Analysis

I recorded two act sequences of behaviour, a preceding event and a following event. Preceding events were behaviours of Flickers, Gila Woodpeckers, Ladderbacked Woodpeckers and Starlings that sometimes elicited aggression. In all cases, following events were aggressive behaviours of Gila Woodpeckers. I also recorded the absence of any aggressive behaviour following a preceding event. Aggressive encounters often started with Gila Woodpecker vocalizations, but because these calls were used for aggressive and non-aggressive purposes, I only recorded sequences initiated by the

behaviour of individuals other than the pair I was observing, i.e., aggressive "responses". While encounters were often composed of several events, I considered only the initial preceding and following events. Furthermore, aggressive behaviour had to follow a preceding event immediately to be counted. Delius (1969) warns that inclusion of behaviours that are hard to detect can lead to unreliable results. Threat displays, which were hard to detect in the dense foliage of cottonwood groves during spring and summer and were therefore excluded.

The transitional probabilities of a preceding event leading to aggressive behaviours of Gila Woodpeckers were calculated. These probabilities are equal to:
$$\frac{\text{number of times a preceding event leads to a particular following event}}{\text{total number of times a preceding event leads to aggressive behaviour}}$$
 Although the symbol "p" is used to express these probabilities, they are not the result of a statistical test. A total probability of responding was also calculated. The study was divided into three time blocks: the prenestling period (4/23-5/9/74), the early nestling period (5/15-5/29/74) and the late nestling-fledgling period (5/30-7/4/74). A separate set of probabilities was calculated for each time block. Because of linear dependence between

outcome measures (probabilities for a given preceding event) and several problems intrinsic to the study of an unrestricted field situation, the most serious of which was the lack of continuous presentation of a preceding event to a pair in all time blocks, these results were not amenable to statistical analysis.

RESULTS AND DISCUSSION

Description of Behaviours

All species with which Gila Woodpeckers interact aggressively in a regular, meaningful way are able to best them in encounters, at least part of the time. Thus, it is likely that a Gila Woodpecker's behaviour is motivated by both a tendency to attack and a tendency to escape, i.e., the behaviour is the result of the conflict of tendencies to approach and to withdraw (Schnierla, 1959). Here aggressive behaviour is considered as that portion of the agonistic behaviour spectrum related to self-assertion and intimidation of others, and includes calls, visual displays and active aggression. Diversionary behaviour, irrelevant acts and behaviour resulting from the intermingling of components of tendencies to approach and withdraw are agonistic behaviours characterized by the masking of the approach or attack component.

Vocalizations

Although some woodpeckers have as many as 13 different vocalizations (Ligon, 1970), Gila Woodpeckers regularly use only two. A third, less common vocalization will be described. Kilham (1966) emphasizes the importance of variation of tone and

pattern, along with accompanying behaviours, as means by which Hairy Woodpeckers (Dendrocopos villosus) increase the information content of their vocalizations. Such factors may be extremely important for Gila Woodpeckers, for despite their limited repertoire, vocalizations appear to be their most important aggressive displays.

Call 1. This call is composed of uniform vibrato notes (Fig. 1a) and although simple in temporal structure is harmonically rich. The sound varies with changes in frequency and relative amplitude of the harmonics, and by variation in overall intensity. It has been likened to a call given by Flickers (Gilman, 1915) and spectrographically resembles the "pulsed 'location' call" of Golden-fronted Woodpeckers (Centurus aurifrons) described by Selander and Giller (1959). Call 1 serves in pair location and is the Gila Woodpecker's primary territorial advertisement display. Results of the stochastic analysis show that males use this call more often than do females (Fig. 3).

Call 2. A series of sharp, complaining notes (Fig. 1b). Variations in sound are achieved by slight changes in length of notes, and by the means described for Call 1. Call 2 is most frequently given in response to disturbance by humans, and the presence of intruders

of other species. It often is given in conjunction with threat displays and serves as a general alarm call.

Gravel Call. A call that spectrographically resembles Call 1 (Fig. 1c). The harsh rasping sound of this call is partially caused by emphasis of different harmonics than Call 1 and by differences in the length of the notes. Heard infrequently, this call is given in conflict situations.

Drumming. 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), but is infrequently used by Gila Woodpeckers.

Visual Display

Bill Pointing Display. In this uncommon display the bill, head and neck are extended parallel to the substrate on which an individual is perched, and the pose is rigidly held. I observed bill pointing twice; once it was directed at a drumming male Flicker, the second time at me. In each instance the displaying bird oriented itself so that the bill was pointing directly at the individual eliciting the display.

Head Bobbing and Head Shaking Displays. These displays have been described in some form for the following genera of woodpeckers: Dendrocopos (Kilham, 1969;

Lawrence, 1967; Short, 1971), Sphyrapicus (Lawrence, 1967) and Colaptes (Lawrence, 1967). Head bobbing and head shaking are the most common threat displays of Gila Woodpeckers and are given by both sexes. However, they seem to be less important in communication than are vocalizations. This may be related to the dense foliage, and concomitant decreased visibility in cottonwood groves during spring and summer.

In the head bobbing display, 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 bill 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. Short (1971) feels that this orientation reflects the relative contributions of attack and escape tendencies in the display.

Head shaking is similar to head bobbing. In addition to the up-down component of the head movement, there is lateral movement. The two displays are often given together and are frequently accompanied by intense Call 2's, given as the head is thrust downward. In all

instances, head bobs greatly outnumber head shakes. The combination of head movements and calls creates a striking display in which the actions of the displaying individual are intense and exaggerated. These displays are given in response to a variety of intruders including Flickers, Cooper's Hawks (Accipiter cooperii) and humans.

Active Aggression

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 departs with the arrival of the Gila Woodpecker. This movement toward an individual does not signal the beginning of an attack; there is a qualitative difference. Occasionally a Gila Woodpecker flew to where a Starling was perched yet the Starling would only sidle over a few steps for a short time before one of them left.

Chasing is flying in pursuit of 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. An intruder would be supplanted, then chased, supplanted from another location and pursued further. On one occasion p9M supplanted a Starling 39 times with chases between successive supplantings.

Attacking is rapid, intense movement toward an individual that culminates in forceful contact initiated by the attacker. I never heard vocalizations given in conjunction with an attack.

In Gila Woodpeckers, active aggression is not the culmination of a series of aggressive behaviours. In virtually all supplantings, chases, and attacks, no previous agonistic behaviour was observed. I rarely observed active aggression in association with other behaviours, although Call 2's sometimes accompanied supplantings of Starlings. The proximate motivation for active aggression appears to be different than for vocalizations and visual displays.

Table 1 provides a summary of the behaviours used by Gila Woodpeckers in interactions with those species that elicited more than a vocal response. Aggression toward Flickers, Ladderbacked Woodpeckers and Starlings, as well as other Gila Woodpeckers, comprises most of a Gila Woodpecker's aggressive output. Aggression toward these species was analyzed by stochastic processes, as described above.

Diversiory Behaviour

Male Gila Woodpeckers at Red Rock used inactive cavities in an apparent effort to divert the attention of other species from their nest cavities (see Table 2).

Typically, a male flew to a cavity other than its nest cavity and behaved in a conspicuous manner by means of Call 1's, Call 2's, repeated intention movements of climbing into the cavity, and excavation activity. My movements in the vicinity of a pair's nest cavity, as well as the presence of Starlings in a pair's nest cavity tree, elicited this behaviour. Hebard (1950) saw a Red-cockaded Woodpecker (Dendrocopos borealis) fly to an inactive cavity as he approached its nest cavity and considered this to be diversionary behaviour. Ligon (1970) reported similar behaviour in this species.

P5M used the same three cavities (which were in varying states of completion) on six occasions. Often, he flew to a cavity half-way across his territory, then to a cavity midway between there and his nest cavity and finally to another cavity in the same tree. The sequence of cavities visited was at times reversed, but the same three cavities were used. At each cavity p5M stopped and exhibited some conspicuous behaviour. His active nest cavity was harder to find than that of any other pair.

Other birds were more flexible in their behaviour. At 08:40 on 7 May, 1973 p3M excavated at an inactive cavity and at 09:22 he was supplanted from his nest cavity tree by a Starling. After giving Call 2's and

attempting unsuccessfully to supplant the Starling, he flew to a partially excavated cavity, bobbed his head in and out and gave more Call 2's. By 16:48 that afternoon, p3M had visited five different inactive cavities, making himself conspicuous at each by vocalizing, making intention movements of entering and excavating.

Because diversionary behaviour occurred well before young were hatched (see Table 2), I suggest that it is used to distract other hole-nesting species from cavities possessed by Gila Woodpeckers. Pair 2 lost their nest cavity to a pair of Starlings, but subsequently reared young in a cavity which p2M had partly excavated while engaged in diversionary behaviour. Possessing even partially excavated cavities enables a pair to re-nest faster should they lose their primary cavity to a competitor and thus provides additional adaptive value for excavation done as diversionary behaviour.

Ambivalent Behaviour and Irrelevant Acts

"Displacement pecking" (Lawrence, 1967), preening and head scratching often occur in conflict situations and appear irrelevant in the context in which they occur. While the cause of such behaviour has been debated (Andrew, 1956b; Armstrong, 1965; Moynihan, 1955; Tinbergen, 1952), these behaviours in a particular context are generally taken to be signs of conflicting

tendencies.

Another result of intense conflict is the intermingling of the components of the different tendencies. The "combination call" (Fig. 1d) is composed of notes of both Call 1 and Call 2 and was heard twice as I harassed p3M. This may be an example of "ambivalent behaviour" (Hinde, 1970), a single behaviour containing components of the conflicting tendencies.

Stochastic Analysis

As male Gila Woodpeckers were almost always more aggressive than females, only results for males are presented here. Figs. 2, 3 and 4 show the transitional probabilities of Flicker, Gila Woodpecker, Ladderbacked Woodpecker and Starling behaviours being followed by the various Gila Woodpecker aggressive responses. Results are presented according to category of preceding event.

Presence

The activities of intruders in the territory of the pair being observed (which rarely included vocalizations) are grouped together in the Presence category. For intruders of other species this category is the Presence in the area described by the circumference of the crown of the nest cavity tree.

During the prenestling period, most intrusions of the species considered brought a response ($p \geq 0.86$).

While Starlings elicited only Call 2's, active aggression followed most intrusions by other species (for supplant + chase + attack, $p \geq 0.9$). In the early nestling period, intrusions by species other than Starlings were rare and evoked no response. While the number of Starling intrusions increased, proportionately fewer were followed by Gila Woodpecker aggression ($p=0.4$), however, active aggression accounted for most of this response (for supplant + chase, $p=0.85$). In the late nestling-fledgling period, active aggression toward Starlings continued, but a greater variety of responses were employed. Starlings were the only species to elicit the Gravel Call, and did so only in this time block.

Drumming

In the prenestling period, most male and female Gila Woodpecker and Ladderbacked Woodpecker drumming brought a response ($p \geq 0.8$). Drumming was the usual response to either sex of Gila Woodpecker ($p \geq 0.75$). Both Flickers and Ladderbacked Woodpeckers elicited Call 1's exclusively. In the early nestling period, Call 1's followed most male Gila Woodpecker drumming ($p=0.85$). While the probability of responding to Flickers remained about the same ($p=0.18$), Call 1 was the only response given. In the late nestling-fledgling period, male Gila Woodpeckers and Flickers were heard

drumming. Male Gila Woodpeckers elicited Call 1's exclusively, and Flickers elicited Call 1's and drumming equally.

Vocalizations

All preceding events in parentheses (see Figs. 2, 3 and 4) are vocalizations. For descriptions of Flicker and Ladderbacked Woodpecker vocalizations, see Lawrence (1967) and Short (1971), respectively. With the exception of Ladderbacked Woodpecker "pik..'s", no vocalizations were responded to more than half of the time. While the total probability of responding to most Flicker and Gila Woodpecker vocalizations stayed about the same or decreased through the study, response to Ladderbacked Woodpeckers and Starlings was more erratic.

In the prenestling period, Flicker "wicka's" were not responded to and Flicker "eh,eh's" were followed by Call 2's exclusively. According to my observations, neither has self-advertisement as a primary function. The remaining Flicker vocalizations, as well as male Gila Woodpecker Call 1's, and Ladderbacked Woodpecker "pik..'s" all serve aggressive purposes at least part of the time and were responded to most frequently with Call 1's (for Flicker "kheer's", Call 1 and Call 2 followed equally; for all others, $p \geq 0.83$). Female Gila Woodpecker Call 1's were not responded to and their

Call 2's elicited Call 1's, exclusively. Male Gila Woodpecker Call 2's never evoked a response.

In the early nestling period, seven of nine different vocalizations recorded were followed by proportionately more Call 2's than in the previous time block, and in several cases this shift was marked. The exceptions were female Gila Woodpecker Call 1's and Flicker "eh,eh's", both of which elicited Call 1's exclusively. Male Gila Woodpecker Call 1's and Ladderbacked Woodpecker "pik..'s" still were followed most often by Call 1's ($p \geq 0.78$). In the late nestling-fledgling period, female Gila Woodpecker Call 2's were the only vocalization followed by Call 2's ($p=1.0$). For those calls that elicited more Call 2's in the early nestling period, response shifted back toward Call 1's; in five of these cases, only Call 1's were given.

As the probability of a particular two act sequence of behaviour occurring increases, the strength of the probabilistic relationship between those behaviours increases concomitantly (sample size must be kept in mind). Even when a relationship is found to be significant statistically, it can be difficult to interpret biologically. However, when these results are considered in conjunction with qualitative descriptions of behaviour, these relationships often appear to be

functional. For instance, in all three time blocks, male Gila Woodpecker Call 1's were followed by Call 1's far more than by any other behaviour. These results agree with the qualitative observation that Call 1 is the Gila Woodpecker's primary self-advertisement display.

Male Gila Woodpeckers apparently can differentiate between male and female Gila Woodpecker vocalizations, as there are marked differences in the distributions of responses. Moreover, they may be able to discriminate between aggressive and non-aggressive vocalizations of other species, as evidenced by their responses to different Flicker vocalizations. Aggression toward Ladderbacked Woodpeckers was more intense than would be predicted on the basis of ecological data presented later. In light of this fact, it must be asked if all strongly probabilistic relationships, and aggression in general, serve adaptive functions. Murray (1971) has raised a similar question.

Active aggression toward a given species coincided with the time that species was searching for and establishing nest cavities, and interspecific aggression appeared to be as intense as intraspecific aggression. Starlings, which moved as flocks into the Red Rock area in early April, did not break up into pairs and begin nesting until the early nestling period of Gila

Woodpeckers. In interspecific interactions Gila Woodpeckers supplanted opponents more than they chased and attacked them. Intraspecifically, the opposite was true.

Following the hatching of their young, Gila Woodpeckers became subdued and furtive in the vicinity of their nest cavities. In this early nestling period, there was a distinct shift to use of Call 2. The use of this alarm call may be related to this apparent change in psychological state. By the late nestling-fledgling period, the response pattern shifts back to use of Call 1. As no qualitative changes in behaviour were noticed I can not explain these observations.

Aggression in Gila Woodpeckers is dynamic. Both total probability of responding and the nature of that response differ with respect to time in the breeding season, species involved, and the preceding events that occur. Such changes can cause problems in a stochastic analysis if it is assumed that there is no appreciable change over time (Delius, 1969). In this study, these changes, considered in conjunction with descriptions of behaviour, yield important information regarding the ecological correlates of that behaviour. This will become more apparent later.

Frequency and Temporal Distribution of Responses

From the actual frequencies of preceding events and the total probabilities of responding (see Figs. 3, 4 and 5), I calculated the total number of aggressive responses to each category of preceding event. I then calculated the average number of intrusions (Presence), drummings and vocalizations responded to on an average observation day for each of the three time blocks. Results are presented in Table 3.

The intervals between aggressive responses were calculated for five randomly chosen observation days in each time block. Then, an average Coefficient of Dispersion (variance/mean ratio) was calculated for each time block. For the prenestling, early nestling and late nestling-fledgling periods, the Coefficients of Dispersion were: 46, 42 and 32 respectively, indicating that the distributions of aggressive responses were highly clumped in all time blocks. Essentially, aggression occurs in bouts.

Even though only aggressive responses and two act sequences of behaviour were considered, this analysis does not corroborate the characterization of Gila Woodpeckers as highly aggressive (cf. Gilman, 1915; Bent, 1939). Frequency of aggressive responses is extremely low (Table 3). Because aggression occurs in

bouts, it is likely that a casual observer is inordinately impressed by what aggression he does see and hear.

Furthermore, Gila Woodpeckers are "noisy" birds and disturbance by humans often leads to intense calling.

While it is virtually impossible to determine that a particular series of call notes is serving an aggressive function without considering it in context with the behaviour of other individuals, this "noisiness" contributes to the impression that Gila Woodpeckers are highly aggressive. This contrast in the impressions gained through qualitative and quantitative approaches points out the need for quantitative analyses of behaviour in the field, despite several unavoidable problems that make rigorous analysis of such data difficult.

Ecological Correlates of Aggressive Behaviour

Most aggressive behaviour of Gila Woodpeckers appears to be related to defense of an area, i.e., territoriality, as defined by Noble (1939). Although Carpenter (1958) and Emlen (1957) state that territoriality is a behavioural phenomenon, it seems to be a behavioural expression of ecological phenomena. Aggressive behaviour is generally related to maximization of individual survival and reproduction (Brown, 1964). Brown argues that natural selection should favor aggression if the resources necessary to reach these ultimate goals are defensible.

Intraspecific territoriality supposedly is far more common than interspecific territoriality (for general reviews see Brown, 1969; Hinde, 1956; Nice, 1943). In March, when I began making observations, Gila Woodpeckers were regularly spaced along the river and intraspecific aggression usually was limited to vocalizations. They showed Type A (Hinde, 1956) usage of an area. Margins of territories along which more than one pair often were active were sites of most conflicts. In virtually all cases, the common territorial border coincided with a localized food source, e.g., a newly ripened raspberry bush (Rubus sp.) was the location of one encounter.

Interspecific Territoriality

The aggressive behaviour displayed by Gila Woodpeckers toward Flickers and Starlings appears to be interspecific territoriality. An area up to 40-50 m from the nest cavity was persistently defended from these species, for at least part of the breeding season. Furthermore, every category of aggressive behaviour displayed toward other Gila Woodpeckers also was displayed toward Flickers, and all categories except displays were used in interactions with Starlings. Thus, aggression shown toward these species meets the behavioural criteria established for interspecific territoriality (Lanyon, 1956; Simmons, 1951). In contrast, Gila Woodpeckers did not defend an area from Ladderbacked Woodpeckers and all active aggression recorded occurred on one day between one pair of Ladderbacked Woodpeckers and one male Gila Woodpecker.

Because interspecific territoriality cannot be maintained without a sufficient combination of sign stimuli which elicit interspecific aggression (Cody, 1969; Cody and Brown, 1970; Johnson, 1963; Murray, 1971; Rohwer, 1973), it is not surprising that most reported cases of interspecific territoriality involve closely related species. However, even in light of divergences in releasers (such as plumage) it might be profitable

for a species to exclude potential competitors of other species (Orians and Willson, 1964).

Similarities of Flickers and Gila Woodpeckers include the barred backs and Call 1. Starlings, of course, bear little resemblance to Gila Woodpeckers, yet aggression toward them is strong and would appear to be highly adaptive. What then evokes aggression toward Starlings? Their vocalizations do not elicit the self-assertive Call 1 from male Gila Woodpeckers and in the prenestling period, prior to cavity exploration, Starlings do not elicit active aggression when intruding. I suggest that, initially, Gila Woodpeckers respond aggressively to the non-specific image of a bird at a cavity. Observations of Gila Woodpeckers supplanting other species, such as Weid's Crested Flycatchers, only as they investigated cavities lend support to this suggestion. Then, as Starlings continue to investigate cavities, Gila Woodpeckers begin to respond specifically to them, even when they are not at a cavity.

Functions of Territoriality

The most commonly cited function of interspecific territoriality is protection of a food supply. Considering the species involved and based on my limited foraging data, this does not seem to be true in these cases. Active aggression toward a species occurs when that

species is actively searching for and establishing nest cavities. Therefore, protection of nest cavities seems a likely function for the aggression observed. Because aggression shown toward Flickers and Starlings is different than that shown toward Ladderbacked Woodpeckers, one might expect less potential or actual competition between Gila Woodpeckers and Ladderbacked Woodpeckers than between Gila Woodpeckers and Flickers or Starlings.

To test this hypothesis, I scored locations of Flicker, Gila Woodpecker and Ladderbacked Woodpecker nest sites in the following categories, according to diameter: trunks (largest), limbs, 1° branches and 2° branches (smallest). Starlings were excluded because of their inability to excavate cavities. I then pooled trunks and limbs, and 1° and 2° branches into two categories and compared nest sites for these three species by using Fisher exact probability tests. Gila Woodpeckers and Ladderbacked Woodpeckers differed significantly ($p=0.047$) in the proportion of large and small branches they used for nest sites, whereas Gila Woodpeckers and Flickers did not differ significantly ($p=0.545$) in this regard. Thus, the prediction that there should be less potential or actual competition between Gila Woodpeckers and Ladderbacked Woodpeckers for nest sites is upheld.

There also is direct evidence for competition for cavities. I saw a pair of Flickers supplant a male Gila Woodpecker from a cavity. The Flickers enlarged the entrance to the cavity, making it unsuitable for Gila Woodpeckers, and successfully reared young there. Three pairs of Gila Woodpeckers (half of the pairs studied regularly) lost cavities to Starlings; one pair lost three successive cavities. No cavities were lost to Ladderbacked Woodpeckers.

Simmons (1951) arbitrarily excluded protection of nest sites by hole-nesters from his consideration of interspecific territoriality. Orians and Willson (1964) suggest that centering aggression on the nest site should be the easiest way to protect it. However, Gila Woodpeckers did not restrict defense to the environs of the nest cavity; they defended an area comparable in size to the largest Red-winged Blackbird (Agelaius phoeniceus) territories measured by Orians (1961). There is little basis for rejecting protection of nest sites as interspecific territoriality, on the grounds of function alone. This is especially true in light of the difficulty in demonstrating direct evidence for any given function of territoriality (Brown, 1964).

Orians and Willson (1964) suggest that interspecific territoriality should serve fewer functions than

intraspecific territoriality. If true, one might expect intraspecific and interspecific territoriality to have different effects on the distributions of the species involved. Factors such as protection of a food supply and isolation of breeding pairs, commonly cited as functions of intraspecific territoriality, should lead to a more uniform distribution than protection of a nest cavity, which would require a smaller area.

To test this hypothesis, I measured the distances from Gila Woodpecker nest cavities to the nearest neighboring Gila Woodpecker and Flicker nest cavities. Starlings were excluded for reasons stated earlier. I then compared the intraspecific and interspecific distributions by use of a Mann-Whitney U-test (Table 5). The results show that the intraspecific distribution is more uniform than the interspecific distribution (compare Coefficients of Variation), and that this difference is significant ($U=30$, $p<0.05$). Thus, intraspecific and interspecific territoriality do have different effects on the distributions of the species involved.

If there is a basic difference in size of areas defended intraspecifically and interspecifically, should both be considered territories? A territory is defined in terms of the species it is defended against and is specific for one category of intruders. Therefore, this

territory will be independent of other territories defined in terms of different categories of intruders. In this study, species which overlap in ecology with Gila Woodpeckers in different ways form these categories. One territory is defended from Flickers and Starlings which compete for cavities, and a second, independent territory is defended from conspecifics. Theoretically, then, a species can maintain more than one territory. By superimposing these hypothetical territories upon each other (see Fig. 5), and considering that they overlap in time and space, one can explain the field observations. Specifically, an area around the nest cavity is defended from con- and hetero-specifics and a larger surrounding area is protected only from conspecifics, giving the impression that the latter is not defended as much.

Murray (1971) contends that known cases of interspecific territoriality are consistent with the assumption that it is misdirected intraspecific territoriality and, therefore, a non-adaptive characteristic. He does, however, allow for the possibility that adaptive interspecific territoriality might evolve when two species compete for some material resource when they occur in the same habitat. Murray argues that in such a case it can be adaptive for only one species in a pair, since interspecific territoriality is a form of competition, and

that, on the average, the subordinate species will be pushed out of its habitat. Following these assumptions, he predicts that territorial behaviour should evolve in only one species. He rejects the possibility that interspecific territoriality is an adaptation permitting the coexistence of two species in the same habitat (cf. Cody, 1969; Cody and Brown, 1970).

The stochastic analysis shows that active aggression toward Starlings occurs at a time when active aggression toward conspecifics and Flickers has ceased. Active aggression toward a given species coincided with the time that that species was searching for and establishing nest cavities. Furthermore, different sized areas were defended intraspecifically and interspecifically. These findings imply that Gila Woodpeckers are able to recognize the behaviour of Flickers and Starlings and that aggression toward them probably is not misdirected intraspecific aggression. In light of direct evidence for competition for cavities and close regulation of aggression both spatially and temporally, this aggression appears to be highly adaptive.

Because he could not find a case in which a non-territorial species had been pushed out of its habitat, Murray felt that a case of adaptive interspecific territoriality had yet to be demonstrated. In the model

presented above (see Fig. 5), only the hatched area is defended interspecifically. The remaining space is open for occupancy by Flickers and Starlings. Thus, it is possible for Gila Woodpeckers to exclude these species from interspecifically defended areas without totally excluding them from their own habitat. Based on this model, and on empirical data, the intraspecific territoriality described here allows Flickers and Starlings to coexist with Gila Woodpeckers, in the same habitat.

SUMMARY

Vocalizations, although few in number, appear to be Gila Woodpeckers' primary means of communication and aggressive display. Active aggression by Gila Woodpeckers toward another species coincided with the time that species was prospecting for and establishing nest cavities. Results suggest that Gila Woodpeckers can distinguish between vocalizations of male and female conspecifics and can recognize cavity seeking behaviour of other species as well.

Gila Woodpeckers defend large, multipurpose intra-specific territories and aggression toward Flickers and Starlings appears to be interspecific territoriality. Several lines of evidence indicate that protection of cavities from competitors is the primary function of this interspecific aggression. Intraspecific and interspecific territoriality lead to significantly different distributions of the species involved.

Analysis of behaviour by stochastic processes indicates that Gila Woodpeckers are far less aggressive than qualitative descriptions suggest. This study emphasizes the need for quantitative field studies of behaviour. These studies should supplement qualitative description, for, used in conjunction with each other, they yield information that neither provides alone.

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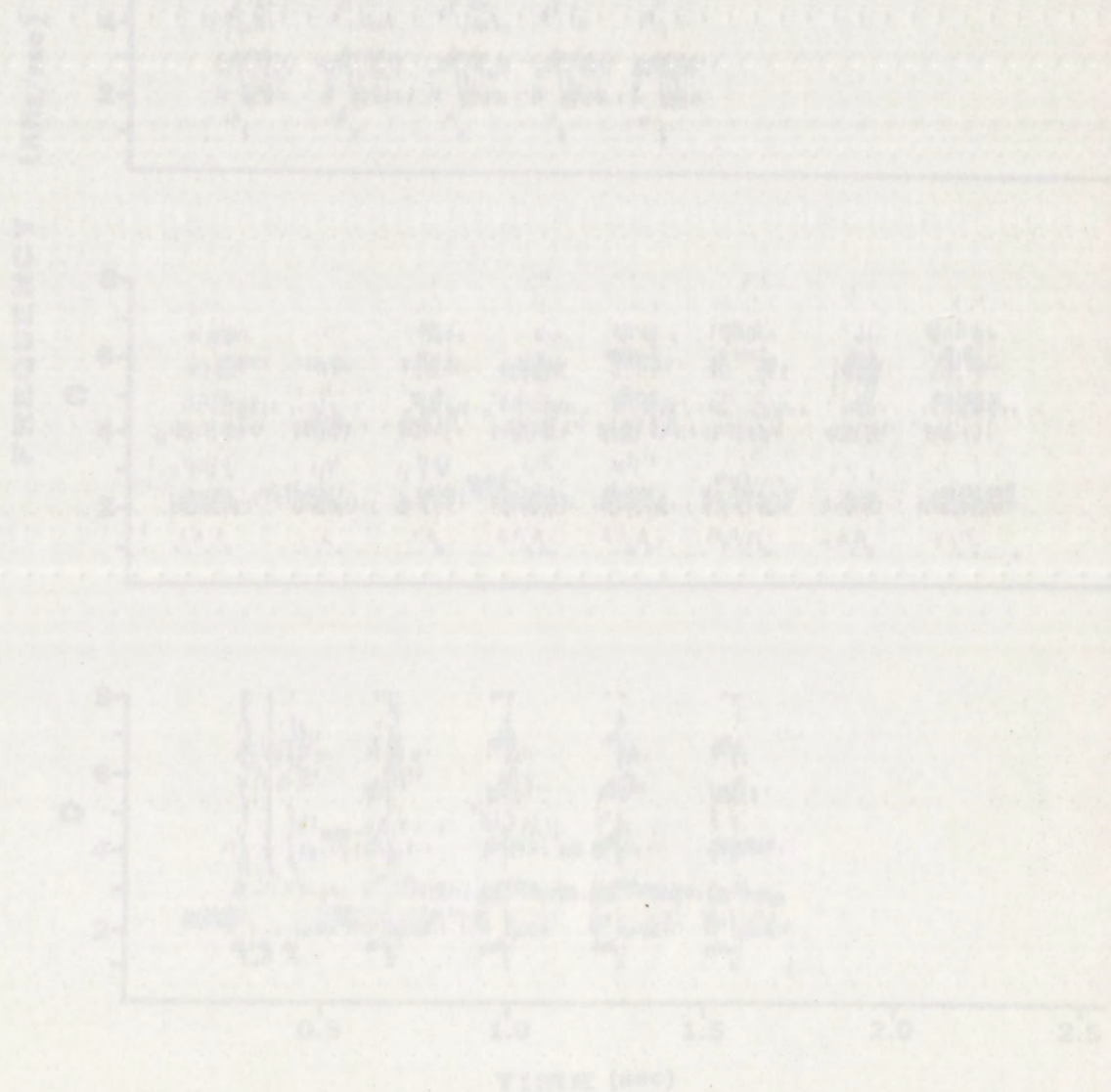
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Fig. 1

Sonagrams of Gila Woodpecker vocalizations. (a) Call 1 of p3M. (b) Call 2 of p3M. (c) Gravel Call of p3F. (d) Combination Call of p3M. The first note is like the notes that compose Call 1 and the following four notes are like the notes that compose Call 2. The wide filter, emphasizing time characteristics, was used for all of the above.



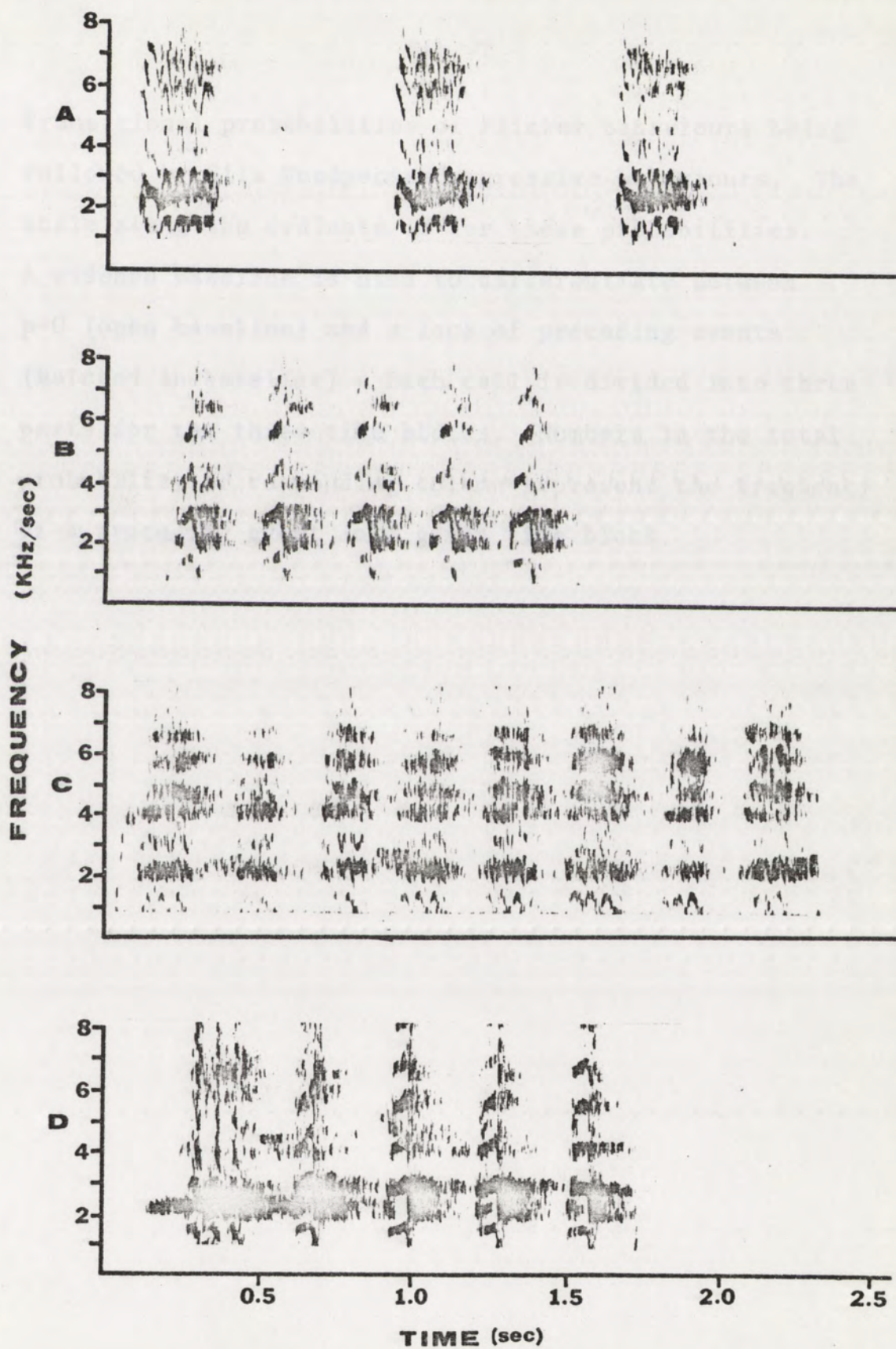


Fig. 2

Transitional probabilities of Flicker behaviours being followed by Gila Woodpecker aggressive behaviours. The scale along the ordinate is for these probabilities. A widened baseline is used to differentiate between $p=0$ (open baseline) and a lack of preceding events (hatched in baseline). Each cell is divided into three parts for the three time blocks. Numbers in the total probability of responding column represent the frequency of a preceding event in a given time block.

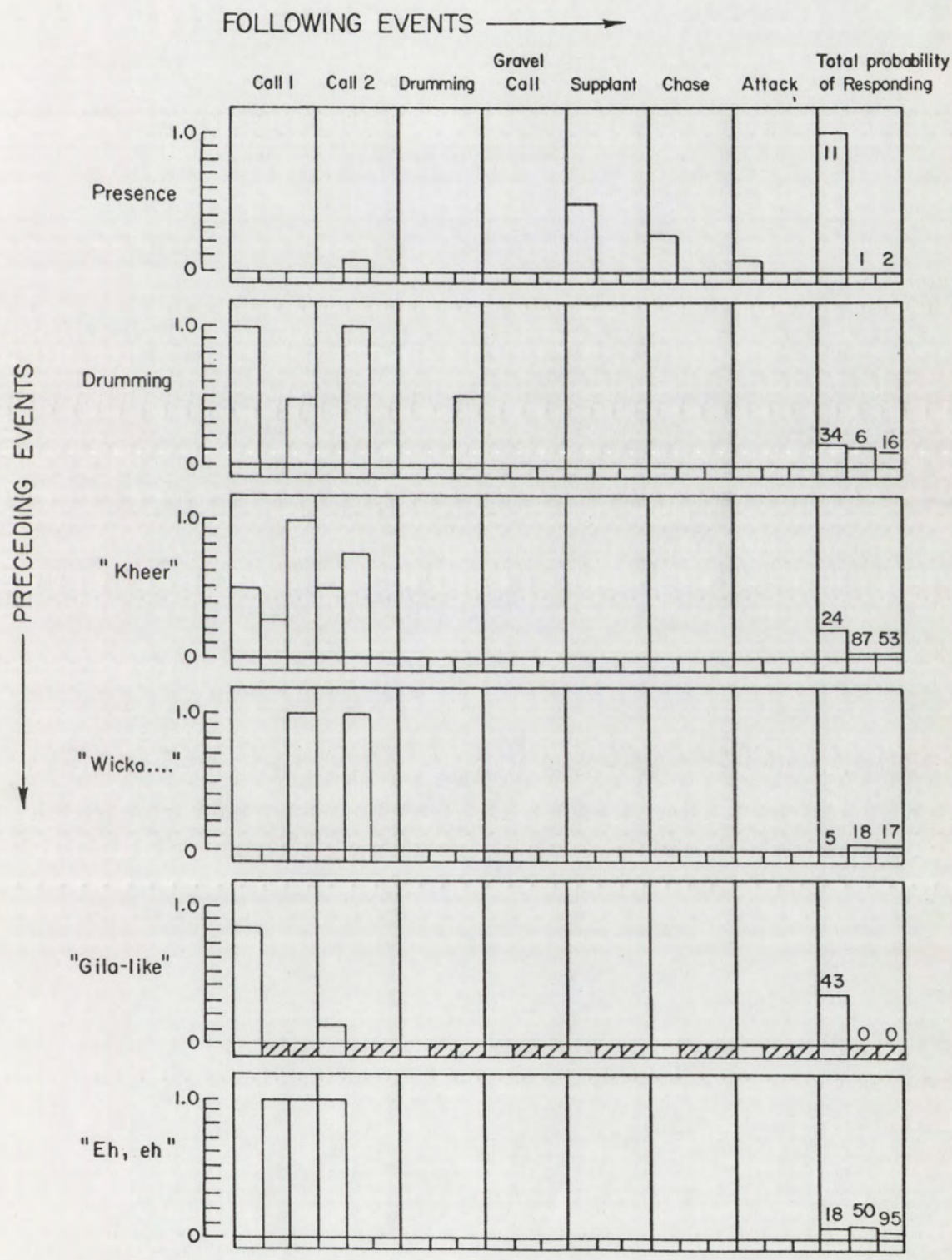


Fig. 3

Transitional probabilities of male and female Gila Woodpecker behaviours being followed by Gila Woodpecker aggressive behaviours. See Fig. 2 for details of presentation.

FOLLOWING EVENTS

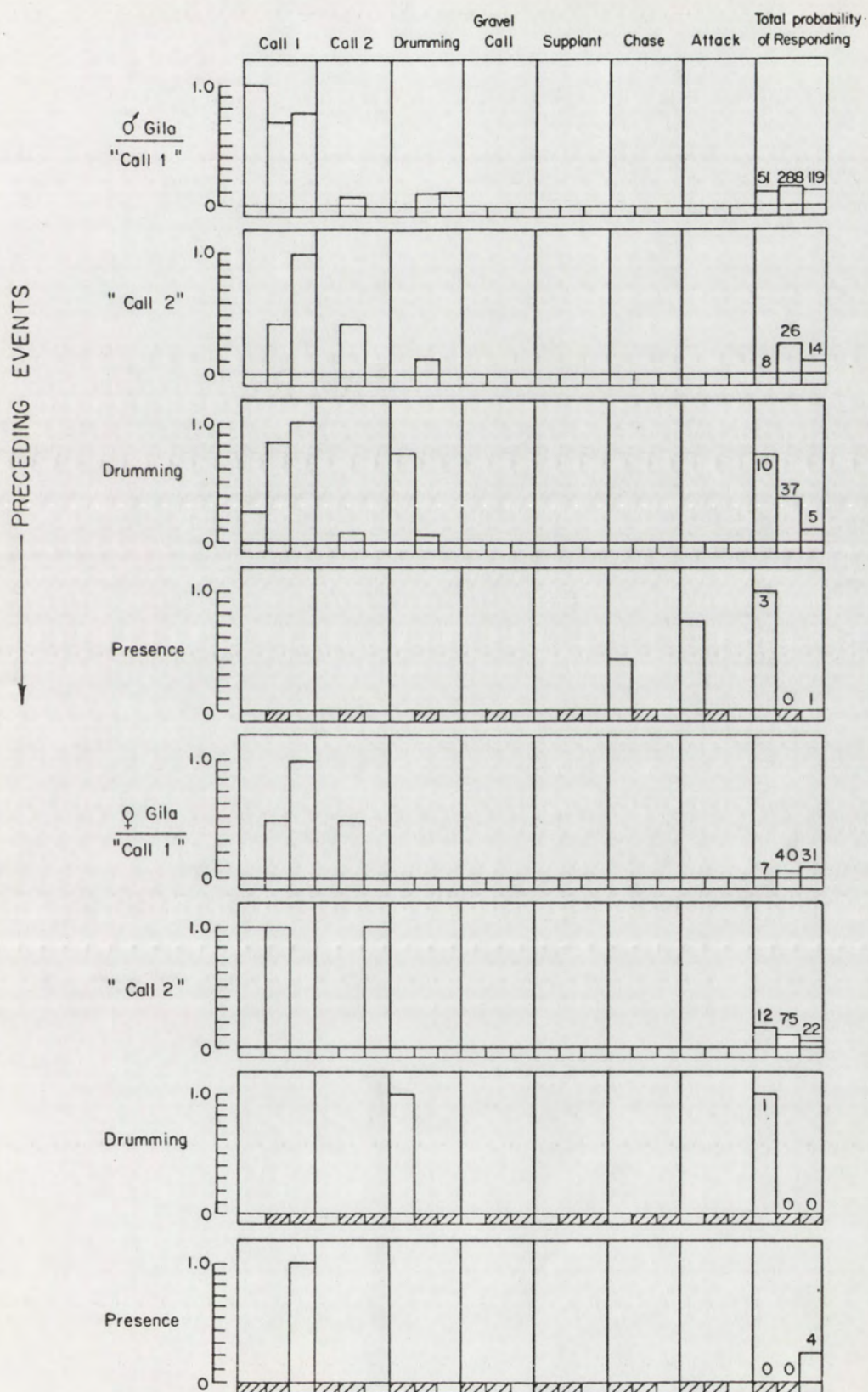


Fig. 4

Transitional probabilities of Ladderbacked Woodpecker and Starling behaviours being followed by Gila Woodpecker aggressive behaviours. See Fig. 2 for details of presentation.

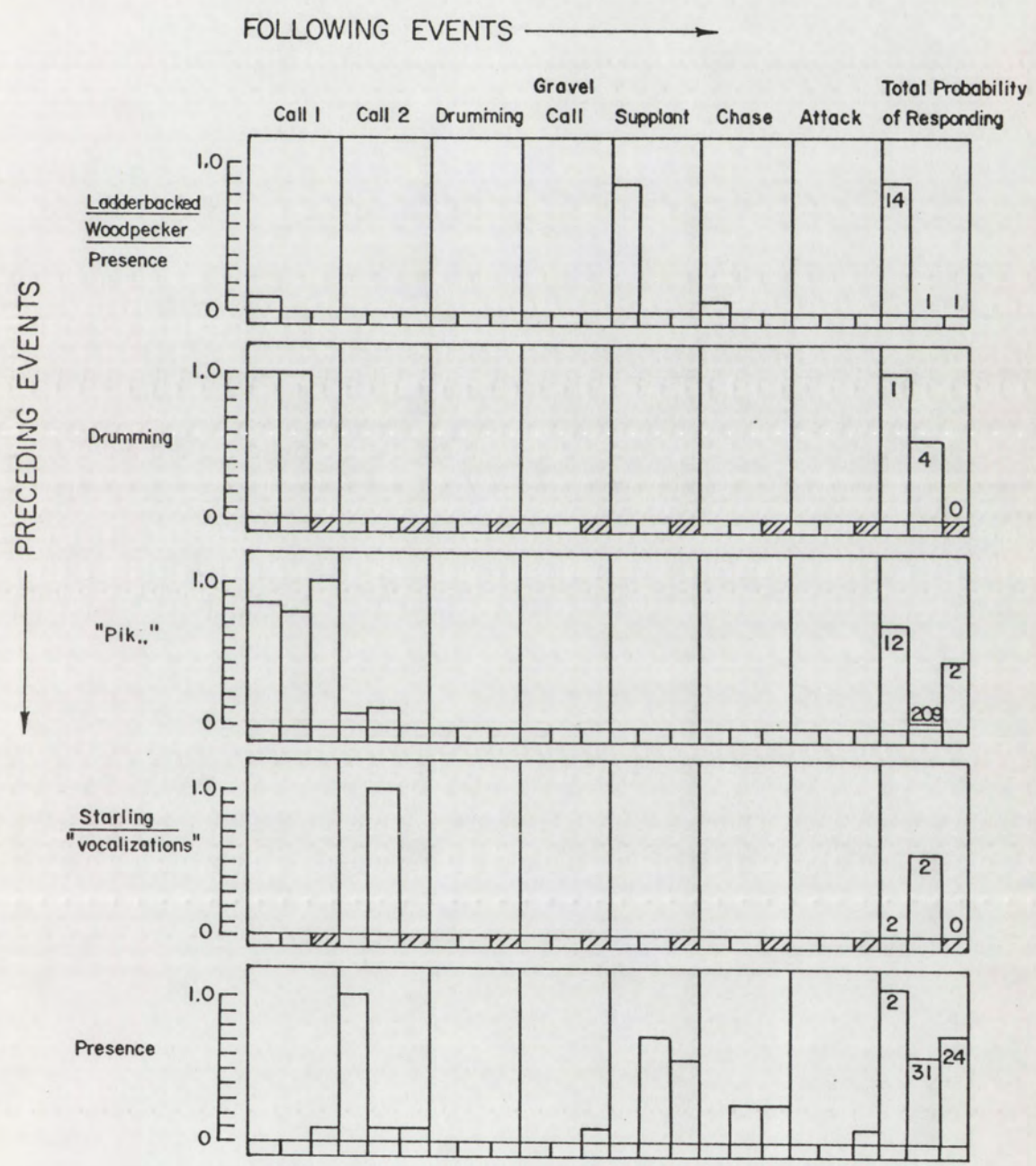


Fig. 5

A model of intraspecific and interspecific territoriality. By superimposing hypothetical intraspecific and interspecific territories upon each other (left side) and considering that they overlap in time and space, one can explain the field observation that an area around the nest cavity is defended more than a larger surrounding area (right side).

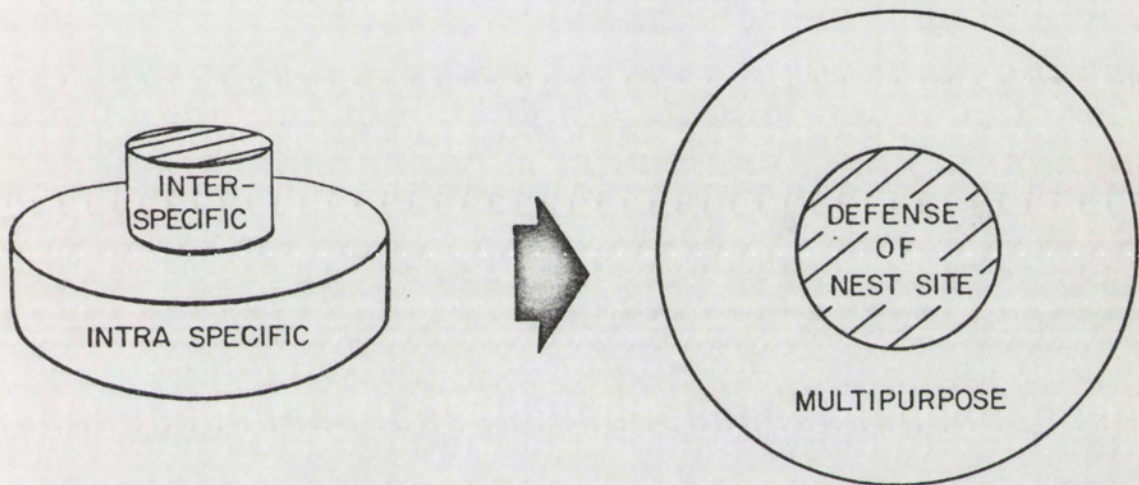


Table 1. Aggression by Gila Woodpeckers

Species	Attack	Chase	Display	Supplant	Vocalization	Frequency
Cooper's Hawk (<u>Accipiter cooperii</u>)			X		X	rare
Mourning Dove (<u>Zenaidura macroura</u>)				X		rare
Common Flicker (<u>Colaptes auratus</u>)	X	X	X	X	X	common
Gila Woodpecker (<u>Centurus uropygialis</u>)	X	X	X		X	common
Hairy Woodpecker (<u>Dendrocopos villosus</u>)		X		X	X	common*
Ladder-backed Woodpecker (<u>Dendrocopos scalaris</u>)		X	X	X	X	common
Wied's Crested Flycatcher (<u>Myiarchus tyrannulus</u>)				X	X	occasional
Vermilion Flycatcher (<u>Pyrocephalus rubinus</u>)	X					rare
Starling (<u>Sturnus vulgaris</u>)	X	X		X	X	common

*Hairy Woodpeckers were not seen in the study area after April, 1973.

Table 2. The use of inactive cavities in diversionary behaviour

Individual	Date	Frequency	# inactive cavities used
p2M*	5/8/73	4	4
	5/29/73	1	1
p3M*	5/7/73	12	5
	5/9/73	2	2
	5/22/73	1	1
p5M	5/4/73	6	3
p7M	5/2/73	1	1
		<hr/> Total = 27	

*birds that had to renest before rearing young

Table 3. Frequency of aggressive response to presence,

drumming and vocalizations*

Preceding event	Prenestling	Early Nestling	Late nestling-Fledgling
Presence	2.3	1.0	1.0
Drumming	1.4	1.2	0.33
Vocalizations	3.6	9.8	2.8
Total	7.3	12.0	4.1

*all numbers = frequency/average observation day of 10.2 hrs.

Table 4. Locations of nest cavities

Part of tree used	Flicker	Gila Woodpecker	Ladderbacked Woodpecker
Trunk	3	1	0
Limb	2	4	0
1° Branch	0	0	0
2° Branch	0	1	3
Total:	5	6	3

(category of part used was determined by diameter)

Table 5. Distances from Gila Cavities
to nearest Gila and Flicker Cavities

	N	Mean± S.E.	Coefficient of Variation	U
Gila- Flicker	6	75.7±16.6m	53.6%	30 (p<0.05)
Gila- Gila	6	120.3±7.4m	15.2%	