

SEASONAL VARIATION IN DIFFERENTIAL NICHE UTILIZATION
BY THE SEXES IN THE GILA WOODPECKER

by

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ABSTRACT

Sexual differences in niche utilization by the Gila Woodpecker, Centurus uropygialis was investigated between December 1968 and April 1971. The degree of niche segregation was related to periods of food scarcity. During January-April the sexes were found to exploit quite different foraging sites. In periods of relative food abundance, May-August and November-December, both sexes utilize the same niches to a larger degree. The remaining months, September and October, were found to be intermediate in both food supply and niche overlap.

INTRODUCTION

Differential niche utilization exists when species or sexes of a species forage to some degree in different areas of the habitat or take different types of food items from a common area. This concept is not new. Closely related species occurring in the same region usually occupy different habitats or if in the same region and habitat, they usually have different feeding habits (Lack, 1944). Studies on the tits (Parus) in England have shown that species very similar in biology and behavior, and often feeding in mixed flocks, are actually exploiting quite different microniches. But the exploitation of niches was not mutually exclusive, and some niche overlap (i.e., utilization of the same food resources) did occur (Gibb, 1954; Hartley, 1953). The amount of overlap in niche utilization in the above studies was apparently a function of food availability. During periods of food abundance more overlap occurred than when food was relatively scarce. Each of the five species studied by Hartley had evolved characteristic methods of feeding, with corresponding structural adaptations, especially of the bill.

Rand. (1952, in Kilham, 1965) questioned whether male and female of a species would avoid competition by

foraging in different microniches. If so, habitats available to them would be used more efficiently. Selander (1966) has suggested the following classification of methods that would reduce competition (Table I).

An example of classification IA of Table I would be the peregrine falcon (Falco peregrinus). Cade (1960) found that the male birds ". . . catch small birds most frequently (passerines and shorebirds in the 30-150 gram categories) but also prey on birds up to the size of teal and ptarmigan (400-600 gram categories). Females are more prone to take larger passerines, shorebirds, and small waterfowl up to 1,500 grams" (p. 243).

An example of class IB would be the now extinct Huia (Neomorpha acutirostris) of New Zealand. The female with her long decurved bill was well adapted to probing deep into crevices whereas the male, with his short icterid-like bill was better adapted to surface foraging. Ligon (1968) found that the male and female Arizona woodpecker (Dendrocopos arizonae) foraged sympatrically, but with different techniques. The males have larger bills, and tend to excavate deeper into the trees; females feed more often on the surface and often scaled off bark with the feet.

Classification IC can be exemplified by the Red-cockaded Woodpecker (Dendrocopos borealis) in Florida

Table I. Methods of reducing intersexual competition for food. (Selander, 1966)

- I. Differential niche utilization within a common home range or territory.
 - A. Sexes employ similar foraging techniques in the same area or strata, but take foods of different average sizes.
 - B. Sexes employ different foraging techniques in the same areas or strata.
 - C. Sexes forage in different areas or strata.
 - II. Allopatry of sexes (except for breeding).
 - A. Macrogeographic allopatry.
 - 1. Sexes exploit similar habitat types or niches.
 - 2. Sexes exploit different habitat types or niches.
 - B. Microgeographic allopatry.
 - 1. Sexes occupy adjacent areas of similar habitat.
 - 2. Sexes occupy different but adjacent habitats.
 - III. Increased territory size.
-

(Ligon, 1968). Ligon's data indicated that the males forage high in the branches of pines, but the females forage mainly on the trunk. Both sexes use the same techniques.

One obvious example of Selander's classification II would be bird species in which the sexes winter in different areas. Ptarmigan (Lagopus) show a strong tendency for spatial and habitat segregation during the non-breeding season (Weeden, 1964). The females leave the breeding grounds above the timberline and winter in shrubby openings in the boreal forest but most males remain on the breeding grounds. The Yellow-bellied Sapsucker (Sphyrapicus varius) is another species in which sexes winter in different areas. The male winters at more northern latitudes than the female (Howell, 1953). This allopatry of the sexes during wintering periods necessarily reduces intersexual competition for food during that period. Also, there would seemingly be different selective pressures on the bird's foraging apparatus for at least some parts of the year. Therefore, adaptations in foraging structure or behavior may be related to differential niche utilization during only part of the year, being neutral or even possibly maladaptive at other times (Selander, 1966). For example, a structural adaptation of the bill resulting from foraging at one time of the year, may cause a change in the behavioral pattern of foraging when the birds are

together if the habitats are very different. The reverse could be true also, but most likely the end result is a compromise, with each affecting the other.

The relationship between sexual dimorphism of foraging structures and differential niche utilization has been well documented by R. K. Selander (1966). In most woodpeckers sexual dimorphism in bill length (exposed culmen) does not exceed 10 percent. Selander has shown that an insular species of woodpecker Centurus striatus is more sexually dimorphic than any of its congeners. In C. striatus, bill measurements of the female were 21.3 percent shorter on the average than those of the male. The male used his longer bill to an advantage and probed more often than the female. Selander's data for the pecking category shows an almost equal use of this technique by both sexes. The female did more gleaning than the male (female 58.1 percent vs. 25.0 percent for the male). In the moderately dimorphic C. aurifrons where the difference in bill length is 9.1 percent, Selander found no significant differences in foraging behavior.

The sexual dimorphism in bill size of the Gila Woodpecker (Centurus uropygialis) ranges from 13.7 percent in C. u. uropygialis in southern Arizona to 16.1 percent in C. u. brewsteri on the southern tip of Baja California (Selander and Giller, 1963). On the basis of this marked

dimorphism (Figure 1) I would expect the sexes of C. u. uropygialis to exploit somewhat different niches. In order to test this hypothesis a preliminary field study was conducted in December, 1968, and March and April, 1969. The results of that study indicated a considerable niche segregation of the sexes while foraging. However, foraging segregation was not complete but contained areas of overlap, which varied with the season. Therefore a full year's study was undertaken to correlate variance in niche segregation and food availability.

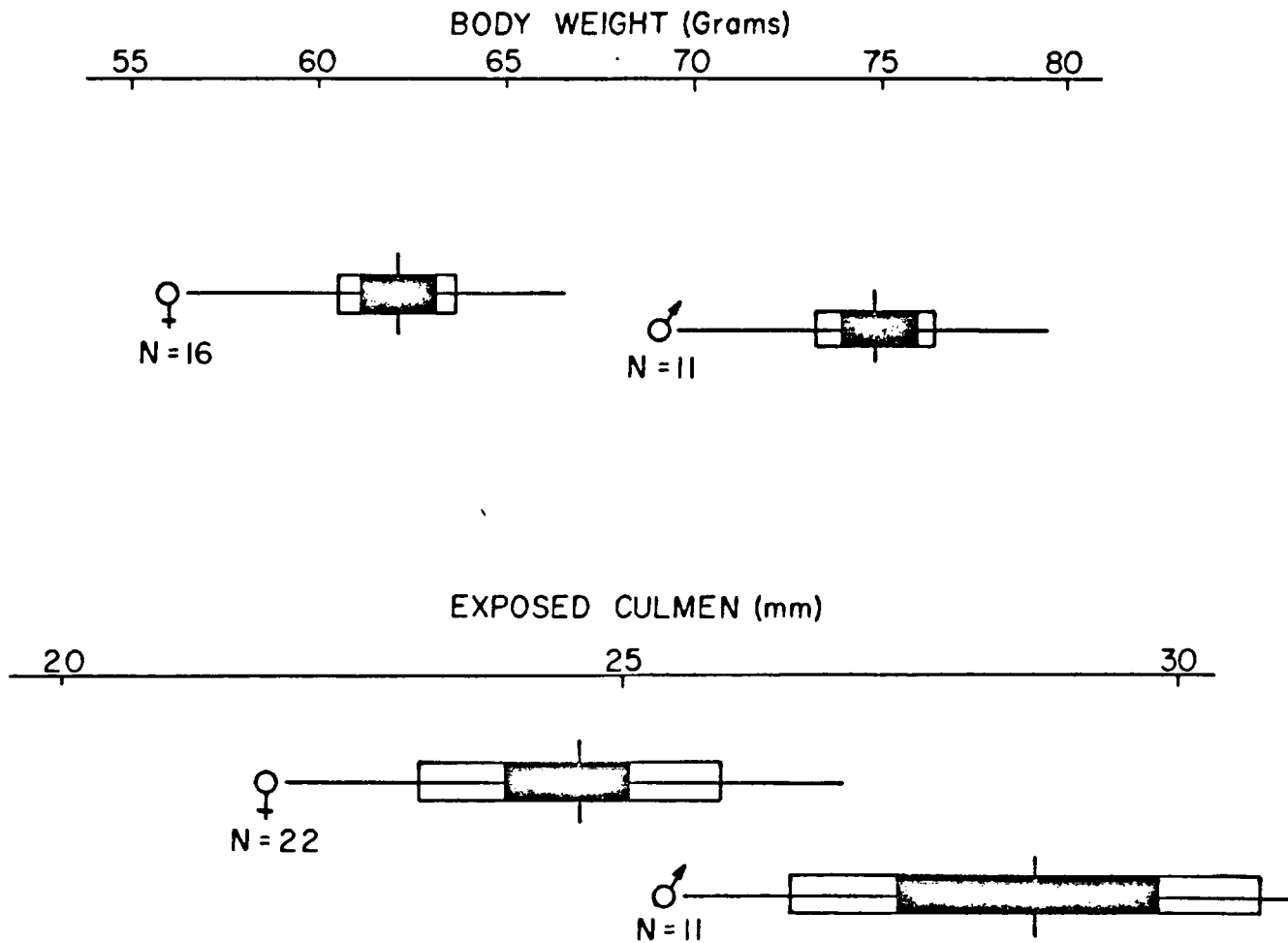


Figure 1. Sexual dimorphism in the Gila Woodpecker (Centurus uropygialis) as indicated by body weight and length of exposed culmen.

METHODS

Study Area

The study was conducted on a 50 acre plot in the Lower Sonoran Life-Zone in the Tucson Mountains west of Tucson, Arizona. The site is located within the boundaries of the Saguaro National Monument on the west edge of Kinney Road about 1/2 mile south of the Signal Hill Picnic area.

The area is on a gentle west facing slope at an elevation of 2400 feet. The vegetation is a typical Cereus-Olneya association (Lowe, 1964). Dominant plants are Saguaro cactus (Cereus giganteus), Ironwood (Olneya tesota) and Foothills Palo Verde (Cercidium microphyllum). Other cacti present include Prickly Pear (Opuntia engelmanni), Chainfruit Cholla (O. fulgida), and Barrel Cactus (Echinocactus sp.). Ground cover is mainly Triangle Bursage (Franseria deltiodea), with lesser amounts of Limberbush (Jatropha cardiophylla) and Creosotebush (Larrea divaricata). There is also an abundance of Desert Mistletoe (Phoradendron californicum) in the Ironwood and Palo Verde trees.

Methods

Observations were made with binoculars and spotting scope without the use of a blind. The birds adjusted readily to my presence and seemed to ignore me except when I moved from one area to another. It proved to be fruitless to follow individual birds due to their rather long flights, usually in excess of 100 yards, and their habit of flying low in the vegetation. Individual birds were timed with a stopwatch as they foraged. The technique they used, their sex, the area of flora utilized, and if possible, the results of the foraging activity, were recorded. Similar observations were made incidentally in various riparian situations in the Tucson area. All daylight hours are represented in the data but most observations were made between sunrise and noon, normally on a twice a week schedule beginning in February, 1970, and continuing through April, 1971. Data from the preliminary study is included.

Definitions

Divisions of foraging areas are: (1) tree trunk, the main stem of any tree or shrub other than the Saguaro cactus; (2) main branches, the large primary branches directly adjoining the trunk; (3) secondary branches, those branches arising from the main branches; Mistletoe was included in this area; (4) twigs, those minor branches

producing leaves, distal to secondary branches; and (5) cactus. The cacti were considered as a whole and all foraging done on any cactus was grouped under this category. I acknowledge that these categories are often subjective and often a decision was called for to decide which category to use in a given situation.

Three major classes of foraging techniques were recognized: (1) Probing. The bird inserts its bill into a crevice, fruit or flower. In most instances I was unable to tell whether the tongue was inserted deeper, but I believe that it usually was. However, in some cases where a flower was probed, the bird would emerge from the flower with an insect of such size that it would seemingly preclude any use of the tongue in its capture. (2) Pecking. Refers to the act of sharply striking an object with the bill. This was at times a sideways motion, presumably to flake off loose material. Pecking was generally a repeated action made in rapid succession but at times the bird would make single blows. (3) Gleaning. Refers to the behavior of a bird moving along a branch or twig superficially gathering small insects or other food items. Picking mistletoe berries was considered gleaning.

Presentation of Data

Results of this study are presented as an index of overlap in niche utilization (Morisita's C_λ , in Horn, 1966)

as observed for each month of the year. Horn suggested that ". . . if we are interested in the overlap in exploitation of alternate food sources from within the same habitat, the diet data could be expressed as the portions of the total diet taken from the various taxonomic categories and the overlap measure of Morisita would be more appropriate" (p. 423). The simplified form for equal sample sizes of X and Y is given as (Horn, 1966):

$$C_{\lambda} = \frac{2 \sum_{i=1}^S x_i y_i}{\sum_{i=1}^S x_i^2 + \sum_{i=1}^S y_i^2}$$

A C_{λ} of 1.0 would indicate total overlap and C_{λ} of 0.0 would be an indication of total separation of foraging activity. Differences between foraging by sexes could not be tested for significance by Chi square due to numerous zero cells in the data.

RESULTS

Foraging substrate data is given in Table II and Figure 2. Overlap was low in January, February, March and April. Overlap peaked in May and June, but declined in the following months until a new peak occurred in November-December.

In periods of low overlap males utilize mainly the trunk and main branches and the females concentrate on the periphery of trees and diseased areas on Saguaro cactus. During May, June and July both sexes concentrate on the flowers and fruit of the Saguaro and other cacti. Foraging during August-October is quite general with males tending to forage more on the larger branches and trunk of trees with a reduction of activity on cacti. Females show a gradual discontinuance of cactus foraging especially on the Saguaro cactus and does not extend into the males' niche as much as the male extends its activity into the females' niche. In November and December both sexes primarily forage on Mistletoe berries.

When feeding nestlings, both sexes brought the same type of food items to the nest, although the female averaged more trips per hour than the male (9.5 trips per hour for the female and 8.2 trips per hour for the male)

Table II. Time (Sec.) and percent of subtotal for male and female Gila Woodpeckers foraging on various substrates, with total time observed and Morisita's Index of Overlap ($C\lambda$).

Mon.	Sex	Trunk		Main Branch		Secondary Branch		Twig		Cactus		Subtotal	Total	$C\lambda$
		Time	%	Time	%	Time	%	Time	%	Time	%			
Jan.	M	552	28.6	794	41.1	585	30.3	-	-	-	-	1931	3096	0.465
	F	-	-	-	-	720	61.8	153	13.1	292	25.1	1165		
Feb.	M	291	17.3	814	48.4	529	31.0	-	-	51	3.3	1685	3217	0.404
	F	-	-	-	-	827	54.0	162	10.6	543	35.4	1532		
Mar.	M	430	18.9	1147	50.3	702	30.8	-	-	-	-	2279	4467	0.409
	F	-	-	-	-	1194	54.6	198	9.0	795	36.4	2187		
Apr.	M	675	30.0	825	37.0	-	-	-	-	740	33.0	2240	3438	0.361
	F	-	-	-	-	164	13.7	400	33.4	634	52.9	1198		
May	M	156	5.0	1080	34.5	-	-	-	-	1896	60.5	3132	4850	0.841
	F	-	-	-	-	274	15.9	-	-	1444	84.1	1718		
June	M	528	19.6	600	22.3	-	-	-	-	1561	58.1	2689	5117	0.848
	F	-	-	-	-	427	17.6	80	3.3	1916	79.1	2423		
July	M	499	50.7	-	-	-	-	-	-	485	49.3	984	4123	0.682
	F	-	-	155	4.9	236	7.5	345	11.0	2904	76.6	3140		
Aug.	M	327	21.2	576	33.1	-	-	-	-	798	45.7	1741	3971	0.708
	F	-	-	-	-	453	20.3	245	11.0	1532	68.7	2230		
Sept.	M	576	24.3	733	35.2	95	4.0	-	-	863	36.5	2367	4751	0.664
	F	-	-	64	2.7	750	31.3	502	21.0	1068	45.0	2384		
Oct.	M	427	20.7	510	24.7	823	39.8	-	-	307	14.8	2067	4391	0.557
	F	-	-	-	-	983	42.3	974	41.9	367	16.3	2324		
Nov.	M	943	25.3	975	26.1	1194	32.0	373	10.0	252	6.6	3735	5523	0.700
	F	-	-	158	8.9	1032	57.6	483	27.0	115	6.5	1788		
Dec.	M	1072	28.5	1147	30.5	1539	41.0	-	-	-	-	3758	5406	0.659
	F	-	-	124	7.6	981	59.5	-	-	543	32.9	1648		

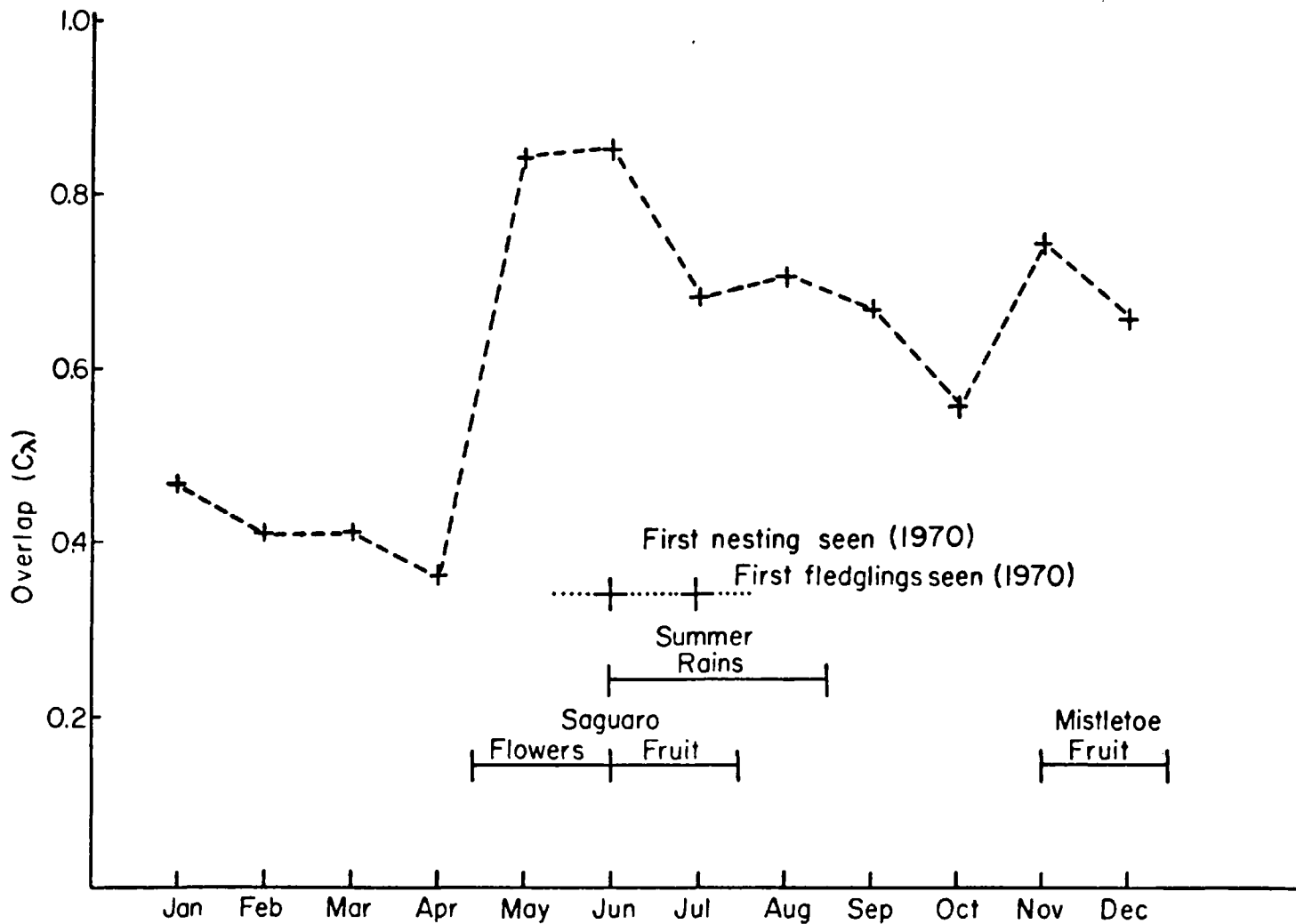


Figure 2. Overlap in foraging sites by male and female Gila Woodpeckers as indexed by Morisita's C_λ . (See Table II for actual values.)

during the early morning and late evening hours, when nestling feeding was most active. Very little feeding of the young birds by either sex occurs during the mid-day hours. Saguaro flowers and fruits are visited most often during the relatively cooler hours when the sun is less direct. During the hotter parts of the day, the birds retreat to the interior portions of the foliage where they either rest or forage in a comparatively cooler environment.

During the reproductive periods, no cases of aggression were observed between the sexes in known pairs. However, the nest area is apparently defended. On five occasions a Gila Woodpecker passing in the vicinity of a nest cactus was chased away by either or both parents. None of these chases extended beyond 20 yards of the nest.

DISCUSSION

It has been suggested that spatial and temporal segregation of foraging allows several species to coexist with reduced or no interspecific competition for food (Stallcup, 1968). Since it is unlikely that male and female of the same species would segregate temporally, then differential niche utilization is the other alternative if a reduction of competition is indicated. Several methods of achieving this are given in Selander (1966: 143). This differential niche utilization by the sexes varies from complete separation (during the non-breeding season) to utilization of different microniches in the same general area. There is also variation to the degree of differential niche utilization during different seasons. In an intensive study of the feeding ecology of the Black-faced Dioch (Quelea quelea) in Nigeria (Ward, 1965) it was found that during the dry season, when seeds are plentiful, there was no obvious sexual difference in food taken. At the beginning of the rainy season in July there was a significant difference in food taken. The early rainy season is a period of relatively low food abundance due to the simultaneous germination of seeds over large areas (Ward, 1965). Also, Hartley (1953) has shown that

in feeding flocks of up to five species of titmice (Parus) in England, during periods of relatively low food supply, each species had a characteristic height distribution of foraging activities. Preferences were also shown for certain parts of trees and for certain trees in a mixed woodland. During times of apparent food abundance this separation of niches disappeared.

January through April is probably the least productive period of the Sonoran desert. There is little to no precipitation and the temperature is quite low (Jan. - mean 47 F, Lowe, 1964). The mistletoe berries are gone, the Saguaro have not yet blossomed, and the cool temperatures suppress any large populations of insects. During this time it would be an apparent advantage to the birds to reduce competition for the limited resources available. Segregation of niches allows for more efficient utilization of a wider range of ecological niches and therefore increases the possible density of the species.

Peak food production is probably reached during the months May through August, with the flowering and fruiting of the Saguaro and other cacti, and the coming of the summer rains in late June or early July.

The dip in the curve (Figure 2) in the month of July could possibly be the result of the onset of nestling feeding. The feeding of nestlings does increase the demand

on the food supply and one would expect a decrease in overlap of foraging sites. In late August after the summer rains have ceased the desert gradually dries up with a corresponding decrease in food availability and the woodpecker population has reached its peak. September and October are periods of low relative food abundance. Food is perhaps not in such short supply as in the early spring period due to the continuing high population of insects. This is evidenced by the overlap index being somewhat intermediate ($C_\lambda = 0.664$ and 0.557) between early spring ($C_\lambda = 0.465$ max. - 0.361 min.) and summer ($C_\lambda = 0.848$ max. - 0.682 min.). In November and December the Mistletoe begins to produce its fruit and there is another, but somewhat smaller than the summer, period of food abundance. This also is a period of gentle rainfall in the desert, but due to the low temperatures, little plant growth of the type utilized by the Gila Woodpecker is seen.

The marked increase in niche segregation during the months of September, October, January, February, March and April correlates well with the apparent food supply at these times. During the months May through August and November and December the birds utilize a relatively abundant food supply with little competition. If the food supply exceeds the demand by the birds then niche segregation would seem to have no advantages.

Other authors have reported differential niche utilization within the Picidae. The mode of achieving niche segregation is not the same in all cases but the adaptiveness would appear to be similar, i.e., survival during the periods of food shortage. The sexes of the Gila Woodpecker utilize different substrates as do the sexes of the White-headed Woodpecker, Dendrocopos albolarvatus (Koch, Courchesne and Collins, 1970), the Downy Woodpecker Dendrocopos pubescens (Jackson, 1970), Red-cockaded Woodpecker D. borealis (Ligon, 1968), and Hairy Woodpecker, D. villosus (Kilham, 1965). The Downy Woodpecker further varies its foraging techniques seasonally as does the Hairy Woodpecker. The technique of D. borealis remained the same all year. This is not surprising in the pine forests of Florida where one would expect little fluctuation in food resources. Another species of Dendrocopos woodpecker, D. arizonae was found to segregate only by technique of foraging for the months of mid-May to mid-July (Ligon, 1968).

Besides the Picidae other avian families show similar patterns in foraging behavior. The Black-faced Dioder (Ploceidae) has previously been mentioned as has the peregrine falcon (Falconidae). Males of four congeneric species of wood warblers (Parulidae) were found to forage higher than females during the breeding season (Morse,

1968). The author suggested that perhaps this partitioning was less an effort to reduce intersexual foraging competition as it was a matter of energy conservation. Females foraged low about the nest area while males tended to forage in higher more conspicuous regions of the foliage. In this way display and foraging could be combined at an energy savings to males, and females could realize a similar savings by combining nest attention and foraging.

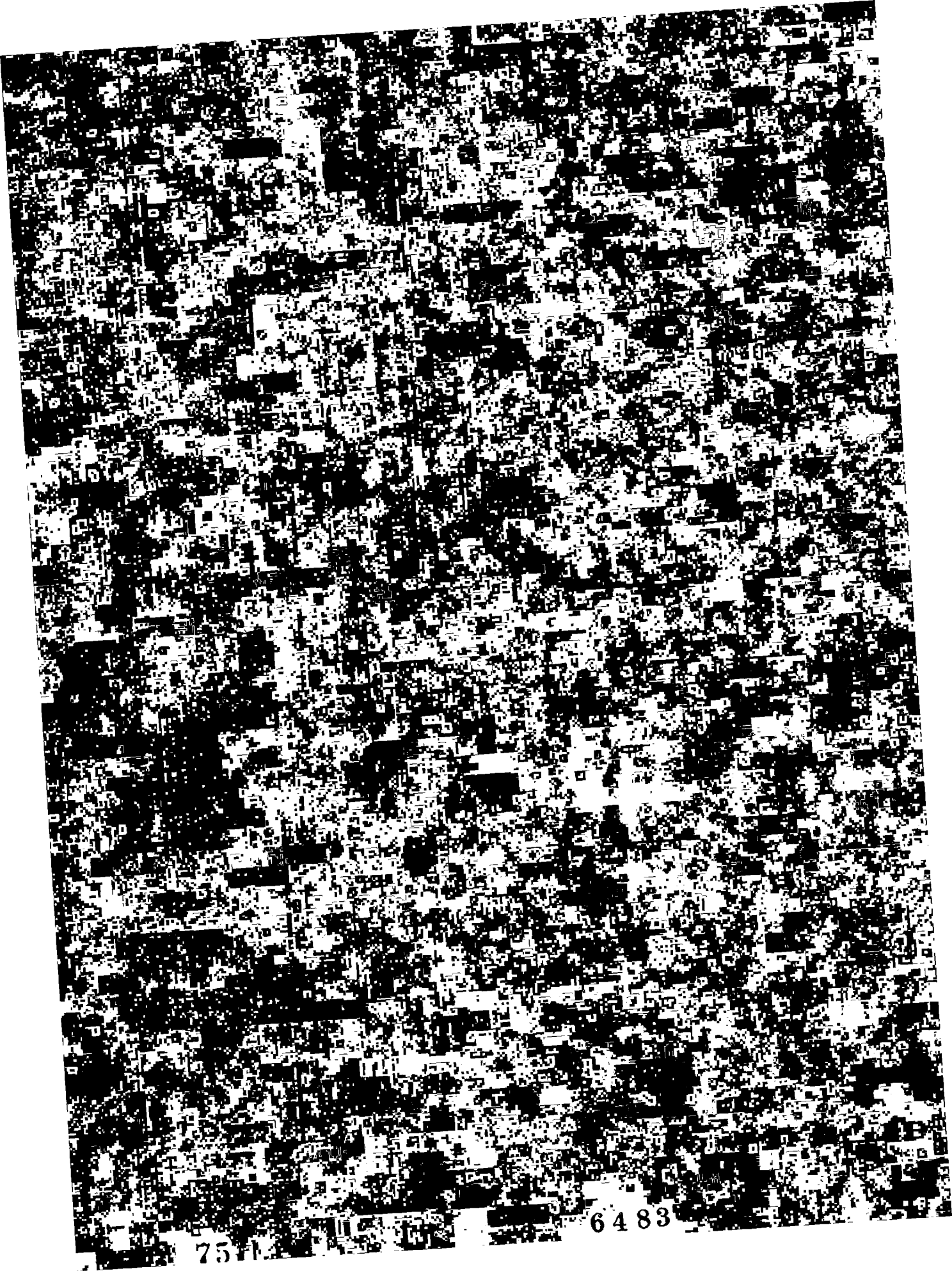
SUMMARY

In the Gila Woodpecker (Centurus uropygialis) the degree of niche segregation appears to follow relative food abundance through the year. During the lean months of January through April the sexes are found to exploit quite different foraging sites ($C_\lambda = 0.465$ max. - 0.361 min.) and in periods of relative food abundance, May through August and November-December, both sexes utilize the same niches to a larger degree ($C_\lambda = 0.848$ max. - 0.659 min.). The remaining months, September and October, are somewhat intermediate in both food supply and niche overlap ($C_\lambda = 0.664$ max. - 0.557 min.).

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