

our understanding of the mechanics involved in niche relationships within mixed flocks. Changes in niche overlap, niche breadth, interspecific aggression, and flock size would be particularly illustrative, although niche relationships can be completely understood only when knowledge of resource abundance and dynamics is secure (Wiens and Rotenberry 1979).

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Sexual dimorphism and parental role switching in Gila Woodpeckers.—Since the seminal work of Selander (Condor 68:113–151, 1966) sexual dimorphism in woodpeckers has generally been considered to be a mechanism for the reduction of competition for food between mates. For a pair of monogamous birds to raise young successfully, they must not only provide food, but must also excavate new nest cavities, clean the nest of fecal material, guard the young, defend the food supply from other birds, and so on. These activities can represent conflicting demands. Using an optimality approach, for instance, Martindale (Behav. Ecol. Sociobiol. 10:85–89, 1982) showed that an individual cannot simultaneously maximize both nest defense and food delivery rate. Size dimorphism may be used to advantage in performing various tasks simultaneously if the pair coordinates their activities, dividing the labor so that each bird specializes in those behaviors for which its size makes it more efficient. In this note, we document the size dimorphism of Gila Woodpeckers (*Melanerpes uropygialis*) and demonstrate that mates coordinate their activities. We consider sexual differences not only in morphology, but also in foraging behaviors, the propensities to attack other birds, and to guard the young as opposed to feeding them. We also present evidence of facultative role switching between mates.

Methods.—Four hundred Gila Woodpeckers were mist-netted in Tucson, Pima Co., Arizona, during the winter months, November–April, from 1971–1979. Lamm banded each bird; its exposed culmen, wing and tail lengths, and weight were measured before it was released. All lengths were measured to the nearest 1.0 mm, and weights to the nearest 0.1 g.

Behaviors were observed by Martindale in Saguaro National Monument (Tucson Mountain Unit), 25 km W of Tucson, during the breeding seasons of 1978–1980. Twelve pairs of birds were observed for at least 20 h. When the woodpeckers foraged on a desert shrub (foothill paloverde [*Cercidium microphyllum*] or desert ironwood [*Olneya tesota*]), the size of the branch the bird was on was noted as small (tertiary branches with leaves, < 2 cm in diameter), medium (secondary branches between the main trunk and the leaf branches, roughly 2–10 cm in diameter), or large (main trunks, > 10 cm in diameter). Records were kept of all aggressive interactions with other birds, distances from the nest of individual birds, and delivery rates of food items to the nestlings (trip/h).

For the morphological measurements, summary statistics (\bar{x} , SD), parametric (*t*) tests for the differences between the sexes, and product-moment correlation coefficients (*r*) among variables were calculated with the BMDP software package on a UNIVAC 1100/82 computer. Two-way contingency tables were used to test for differences between sexes in the categorical data, i.e., parts of shrubs used and species of birds attacked. For ease of interpretation, these tables are summarized here as proportions of observations in each category

TABLE 1
 $\bar{x} \pm SD$ AND DEGREE OF SEXUAL DIMORPHISM IN SELECTED MORPHOLOGICAL CHARACTERS
 IN *MELANERPES UROPYGIALIS*

Character	Males (N = 200)	Females (N = 200)	r^a	Percent dimorphism ^b
Culmen length (mm)	29.8 \pm 1.2	25.5 \pm 1.1	37.8	14.6
Wing length (mm)	132.3 \pm 2.7	127.1 \pm 2.8	19.1	3.9
Tail length (mm)	85.0 \pm 3.8	81.4 \pm 3.5	9.8	4.2
Weight (g)	73.0 \pm 3.6	62.6 \pm 3.8	28.2	14.2

^a All differences in size are significant at $P < 0.001$.

^b Percent dimorphism is the difference between sexes relative to the male size.

for each sex, but the accompanying χ^2 tests of independence (sex \times substrate, sex \times species attacked) are based on the number of observations in all cells of the table.

Size, foraging, and aggression.—Male Gila Woodpeckers were significantly larger than females for each of the four variables measured (Table 1). This species is strongly dimorphic, even for a melanerpine. Selander's (1966:114) graph indicated an average of about 9% (SE = 4.4%) dimorphism in culmen length for 38 species, so our observed value of 14.6% for *M. uropygialis* is well above the average, although not extreme. Selander (1966) indicated that gilans from Baja California (*M. u. brewsteri*) were apparently more dimorphic than mainland birds (*M. u. uropygialis*). This may be the case, but Selander's data indicate *brewsteri* to be about 16% dimorphic in culmen length, which is only slightly greater than our value for *uropygialis*.

Correlations among the morphological characters were rather low (Table 2). Although 7 of the 12 possible correlations were significantly positive, none was greater than 0.47, and most were less than 0.20. Relatively little of the total variance in these characters, then, can be explained by a "size factor" as has often been done in multivariate studies (Sneath and Sokal, Numerical Taxonomy, Freeman and Co., San Francisco, California, 1973). An individual bird may be heavier than others, but weight does not necessarily reflect size of beak or wings. Similarly, mated pairs vary in their degree of dimorphism, depending on the character being considered. On average, however, it is clear that males are about 14% heavier and have 14% longer bills than their mates.

As predicted in the hypothesis that dimorphism reduces resource overlap between mates, we found significant sexual differences in the use of desert shrubs by these woodpeckers (N = 134 observations of males foraging on shrubs and 167 observations of females [$\chi^2 = 39.2$, $df = 2$, $P < 0.001$]). Males used small branches on only 6% of their visits to shrubs, and used large branches and trunks on 60% of their visits. Females, however, divided their effort nearly equally over all parts of these plants, spending 34% of their visits on small branches and 33% on large ones. Martindale (Ecology 64:888–898, 1983) shows that females also spent more time searching for adult insects on plant surfaces rather than pecking for sub-surface larvae. This pattern of males using larger branches and pecking more, while females use smaller branches and glean more has been found in several species of dimorphic woodpeckers (see, e.g., Hogstad, Ibis 120:198–203, 1978, Wallace, Condor 76:238–248, 1974).

Male Gila Woodpeckers were also more aggressive than the females: the males attacked other birds at roughly twice the rate of the females. At the nest most intensively studied,

TABLE 2
CORRELATIONS (*r*) BETWEEN MORPHOLOGICAL CHARACTERS IN *M. UROPYGIALIS*^a

	Culmen ^b	Wing	Tail	Weight
Culmen length (mm)	—	0.11	0.10	0.18**
Wing length (mm)	-0.14*	—	0.31**	0.47**
Tail length (mm)	0.09	0.46**	—	0.24**
Weight (g)	0.10	0.28**	0.19**	—

^a Males (N = 200) are above the main diagonal, females (N = 200) below.

* $P < 0.05$, ** $P < 0.01$.

for example, the male averaged 8.7 attacks/h, while the female averaged 4.6 attacks/h but the hourly rates varied considerably, depending on the time of day, season, and density of other birds.

What is more, the sexes attacked different birds (Table 3). The significant difference arises from the fact that males attacked other Gila Woodpeckers much more frequently than did females (there is no significant sexual difference if Gila Woodpecker attacks are deleted from the table). The difference may again stem from the dimorphism in body size; the males can drive off other males, but the females cannot generally do so. Many of the attacks on other Gila Woodpeckers occurred in the vicinity of the nests, and can be interpreted as defense of the nest, the young, and perhaps of the female. Agonistic behavior directed toward Gilded Flickers (*Colaptes auratus chrysoides*), Ash-throated Flycatchers (*Myiarchus cinerascens*), and Ladder-backed Woodpeckers (*Picoides scalaris*) may reflect competition for nest-sites. Brenowitz (Auk 95:49-58, 1978) argued that virtually all interspecific aggression in Gila Woodpeckers was for nest-sites.

But we witnessed many attacks of another sort, directed toward open nesting species: Cactus Wrens (*Campylorhynchus brunneicapillus*), House Finches (*Carpodacus mexicanus*), Curve-billed Thrashers (*Toxostoma curvirostra*), and White-winged Doves (*Zenaida asiatica*). All these species feed on saguaro (*Cereus giganteus*) flowers and fruit, a primary source of food and water for desert birds in the nesting season (Hensley, Ecol. Monogr. 24: 185-207, 1954). At least 20% of all deliveries to Gila Woodpecker nestlings consisted of saguaro pollen or fruit (Martindale 1983), so some of the observed aggression may be in defense of this resource.

Role switching between mates.—As indicated above, male Gila Woodpeckers are consid-

TABLE 3
BIRDS ATTACKED BY GILA WOODPECKER BY SEX^a

Sex	Species attacked ^b							UI other	No. obs.
	GW	FL	CBT	CW	ATF	HF	WWD		
Males	0.76	0.03	0.02	0.02	0.09	0.03	0.02	0.05	239
Females	0.49	0.04	0.07	0.04	0.15	0.09	0.05	0.06	130

^a Proportions of attacks toward each species are indicated; $\chi^2 = 29.5$, $df = 7$, $P < 0.005$.

^b GW = Gila Woodpecker, FL = Flicker, CBT = Curve-billed Thrasher, CW = Cactus Wren, ATF = Ash-throated Flycatcher, HF = House Finch, WWD = White-winged Dove, U1 = Unidentified.

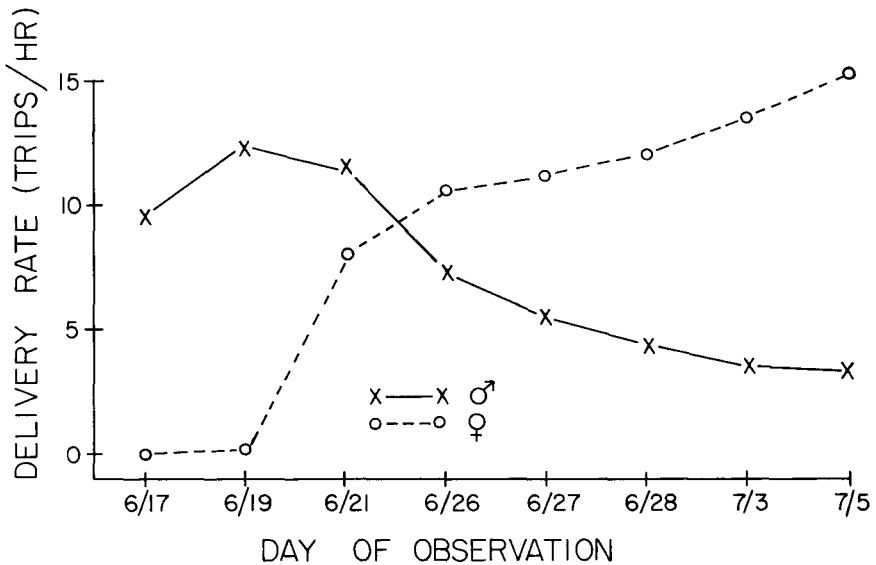


FIG. 1. Rates of food deliveries for a pair of mated Gila Woodpeckers on 8 mornings of observation in 1979.

erably larger than females, and are more aggressive, especially toward conspecifics. Males generally spent more time than females guarding the nest rather than foraging, and males, but not females, exhibited prolonged defensive behavior after experimental attacks (Martindale 1982). If the female stopped feeding the young, however, the male switched to foraging rather than defense. At one nest-site intensively studied in 1979, for instance, the female was exceptionally wary and made no deliveries during the first morning of observation, and only one the second morning. Instead, she stayed close to the nest (mean distance = 51 ± 50.8 m, $N = 156$ plant visits) repeatedly giving the low intensity alarm call. On the third day of observation the female began bringing food, and subsequently increased her rate each day. During this period, she went much farther from the nest than before (mean distance = 148 ± 96.9 m, $N = 350$ visits), as expected for increased foraging efficiency (Martindale 1982). Since the variances in distance from the nest were correlated with the means, we used log-transformed data for significance tests (see Sokal and Rohlf, *Biometry*, 2nd ed., Freeman and Co., San Francisco, California, 1981:419). The change in distance by the female after she resumed delivering was highly significant ($t = 14.7$, $df = 504$, $P < 0.001$).

As shown in Fig. 1, the male compensated for the changes in the female's rate by changing his own rate of feeding the young. When the female initially stopped delivering food, the male maintained a very high foraging rate and went farther from the nest (mean distance on 17 and 19 June: 126 ± 75.9 m, $N = 200$ visits). As the female increased her rate, however, the male decreased his rate, and stayed closer to the nest (mean distance after 26 June: 73 ± 63.9 m, $N = 200$ visits). Again, this change in distance was significant ($t = 219$, $df = 398$, $P < 0.01$). When not actively foraging and delivering, the birds guarded the nest.

The observed temporal pattern appears to represent role reversal by the sexes rather than

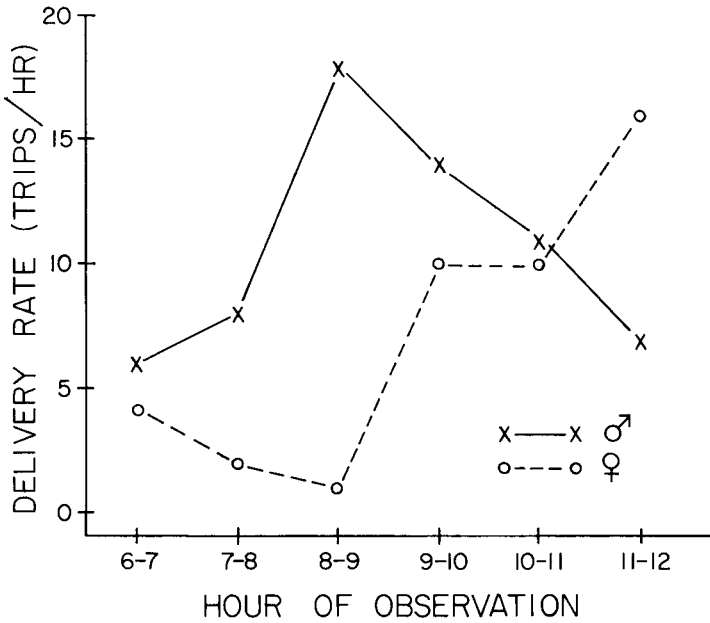


FIG. 2. Hourly rates of food deliveries, for the same pair of birds as in Fig. 1. Data are for 21 June 1979, the day the female resumed delivery.

seasonal differences in parental investment (in the sense of Andersson et al., *Anim. Behav.* 28:536–542, 1980). No similar trends were seen at the other nests where the females were unperturbed. Moreover, role switching often occurred over much shorter time scales than parental investment theory would predict. For example, delivery rate changes by the male at the perturbed site occurred within an hour of changes in the female rate on the day the female resumed bringing food (Fig. 2), but the survival probabilities for parents and offspring clearly do not change appreciably over such short periods. On average, males maintained a rate of about 8 trips/h and females a rate of about 12 trips/h from 07:00 until 12:00, so the pattern does not reflect a diurnal rhythm. We do not know if the male was responding to the female's activities per se or to the vocalizations of the nestlings.

Facultative short-term role switching occurred in a variety of situations. At one site, the pair was able to incubate a second clutch in a different nest while feeding nestlings, by trading back and forth between incubation and food delivery. At 11 of the 12 nests, only the males removed fecal sacs. But at a nest where the male was excavating a second cavity, the female performed this behavior. If a female was guarding a nest or fledgling when a serious attack occurred, she would give alarm calls until the male took over defense, then switch to feeding the young. After experimental attacks (Martindale 1982), the males guarded the nest for an hour or more, but were relieved every 20 min or so by the female. This was short-term role switching: after being relieved, the male would forage for about 5 min, make one delivery to the nest, then resume his guard while the female resumed bringing food to the young.

It is clear from these observations that during the breeding season, the behavior of a Gila Woodpecker depends to a large extent on what its mate is doing. So while the pronounced size dimorphism disposes the sexes generally to perform different parental functions, these roles are not exclusive; they can be traded back and forth between mates.

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Effect of litter on leaf-scratching in emberizines.—Many species of emberizines turn leaves and other litter by a two-footed scratching movement resembling hopping, in which the litter is thrown rearward under the bird (Hailman, *Wilson Bull.* 85:348–350, 1973). These scratches are performed sequentially in bouts, where the probability of adding another scratch to a bout is constant and hence independent of the number of scratches already performed in the bout (Hailman, *Wilson Bull.* 86:296–298, 1974). The quantitative model expressing this relationship predicts that the log frequency of bouts having s or more scratches ($\log f_s$) is a linear function of the number of scratches/bout (s):

$$\log f_s = (s - 1)\log p + \log B, \quad (1)$$

where p is the constant probability of adding another scratch, $\log p$ is the slope and $\log B$ is the intercept of the linear regression. The present study evaluates one ecological variable previously suggested as possibly affecting the value of p : the amount of litter on the ground.

Equation (1) predicts quantitatively the behavior of several species: the White-throated Sparrow (*Zonotrichia albicollis*) and Dark-eyed Junco (*Junco hyemalis*) originally studied (Hailman 1974) and further considered in the present study, the White-crowned (*Z. leucophrys*) and Fox (*Passerella iliaca*) sparrows studied subsequently (Hailman, *Wilson Bull.* 88:354–356, 1976), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) studied independently by E. H. Burt, Jr., and me (Burt and Hailman, *Wilson Bull.* 91:123–126, 1979). Furthermore, Burt showed that p depends in part upon the amount of food available, in that towhees scratch in longer bouts as food becomes scarcer. I had suggested that p depends in part on the amount of litter (Hailman 1974), so it is possible that p is a compound variable, and the present experiments were set up to test the effect of litter.

The study plot consisted of a rectangle outside my study window in Madison, Dane Co., Wisconsin. The plot was divided in half, creating north and south meter-square quadrats. All litter was raked to the dividing line between the two quadrats, one measuring cup of about 235 cm³ of mixed bird seed was scattered homogeneously over each area, and then all litter was raked over one of the two plots, thus creating a "littered" and a "bare" area. Wind, squirrels, and the birds themselves quickly scatter litter so that the bare area does not remain truly bare for long, nor does the littered area remain homogeneously littered; there is, however always a distinct difference in the amount of litter on the two sides.

I observed white-throats and juncos foraging the two areas for about 2 days, then reraked