SOCIAL RECOGNITION AND RESPONSE TO SONG IN COOPERATIVE RED-WINGED FAIRY-WRENS

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ABSTRACT.—We presented cooperatively breeding Red-winged Fairy-wrens (*Malurus elegans*) in Western Australia with recorded songs of nonbreeding helpers in their own social group and of unfamiliar helpers from other groups. Breeding females responded more often and more intensely to song of unfamiliar birds than to song of familiar birds. They responded more strongly when they had only one or two helpers than when they had more helpers in their group. They responded to song of their own helpers regardless of matrilineal kinship. We conclude that recognition is based on location and familiarity, and responsiveness is conditional upon the size and composition of the breeding group. The stronger response to song of strangers than to familiar individuals, matched for sex, age, and status, suggests that strangers are perceived by breeding females as threats in competition for helpers or other resources. *Received 7 September 1990, accepted 7 March 1991.*

SOCIAL RECOGNITION involves a differential response of individuals to members of their own species. For example, some songbirds can distinguish the calls and songs of their mates, parents, offspring, and neighbors with whom they have social relationships from the calls and songs of unfamiliar individuals (Wiley and Wiley 1977; Falls 1982; Colgan 1983; Beecher 1988, 1989; Marzluff 1988; Ydenberg et al. 1988). Social recognition may be especially important in cooperatively breeding birds, where individuals live in a social group and give or receive alloparental care with others in the group (Emlen and Vehrencamp 1983; Brown 1987; Curry 1988a, b; Emlen and Wrege 1988; Stacey and Koenig 1990). The members of a cooperative social group often are closely related to one or more of the breeders, but they are not always kin (Brown 1987, Stacey and Koenig 1990). We expect cooperatively breeding birds to recognize their social companions and to behave differently toward members of other social groups. Cooperative birds may direct their social behavior to group members because they are familiar and live in the same site (Sherman and Holmes 1985, Beecher 1988, Emlen and Wrege 1988, Waldman 1988).

The behavioral response that we use to assess a bird's ability to recognize others may depend not only on its familiarity or kinship with other individuals, but also on social conditions, which include the number of breeders and helpers in a group. In several species of the cooperatively breeding Australian fairy-wrens (*Malurus* spp., Maluridae), females have higher breeding success when helpers in their group aid them in rearing their young (Rowley 1965, 1981; Russell and Rowley 1988; Rowley et al. 1988). Within a species, the social groups vary in composition; and within a group, more than one female sometimes breeds at the same time. When two females breed they may compete with each other for helpers to care for their young (Payne et al. 1985, 1988b; Russell and Rowley 1988; Rowley et al. 1989). This variation in group membership and plural breeding allowed us to test breeding fairy-wrens both for their recognition of members and for their responsiveness to song under different levels of social competition.

We tested the responses of breeding females to song in the Red-winged Fairy-wren (*Malurus elegans*). To test whether they were more aggressive toward the unfamiliar birds, we compared the responses of breeding females to songs of familiar birds in their own group and to unfamiliar songs of birds in other groups. To test the importance of kinship, we compared female response to helpers in her own group when the helpers were her kin and when they were not. And finally, to test the variation in response to the social composition of a breeding group, we compared groups in which a breeding female had one or two helpers to groups where she had three or more helpers.

METHODS

The study population.—We observed Red-winged Fairy-wrens in the forest at Smith's Brook Nature Reserve, near Manjimup, Western Australia (34°22′S, 116°08′E). The forest is a 98-ha tract dominated by the karri (*Eucalyptus diversicolor*). The fairy-wrens live in the understory of bracken (*Pteridium esculentum*) and shrubs and in swordgrass (*Lepidosperma longitudinale*) along the streams (Meney and Brown 1985). The same population was studied by Webster (1948), who noted more than two adults attending a nest. Fairy-wrens have been banded and observed in the population from the late 1970s (Brown and Brown 1987, Rowley et al. 1988).

The population in 1985 and 1986 included approximately 110 color-banded adults in 28 social groups in an area of 34 ha. Group territory size averaged 1.2 ha. The number of breeders and helpers ranged from 2 to 9; group size averaged 4. Brood size is 2 or 3 and usually one brood is raised in a season (Rowley et al. 1988). Nonbreeding helpers are usually the resident offspring from an earlier year. Most adult helpers and many breeders were banded as nestlings. A few were banded as adults. Matrilineal kinship of the female and her helpers and birds in other social groups was known from observations of behavior at the nest in earlier years. Both sexes often remain and breed on their natal area. Males are more likely to survive between years, and females are more likely to disperse and breed in another group (Rowley et al. 1988).

Field and song playback techniques.—We recorded songs and tested the response of fairy-wrens to song during the breeding seasons of 1983, 1985, and 1986. We determined the breeding or helping status of each bird by observing the group while it had an active nest. We compared the response of a breeding female to the song of a helper in her own group with her response to song of a helper in a different group. The test songs were recorded from birds matched for sex and age. The helper that gave the song recorded in the other group was at least two territories distant from the subject's group. Except for one case with eggs, all female subjects had young in the nest. All subjects had helpers; breeding females in single pairs were not tested. The subjects were never seen together with the "other" helpers, although they might have heard their songs.

Each breeding female was tested with two playback songs. On one day she was tested with three repetitions of a song of her helper, and on the other day she was tested with three repetitions of a helper from another group. Each group of three songs was called a *trial* and two trials made a *test*. The two trials were alternated with the female's own helper first in every other test and on consecutive days (5 tests) or with a day between trials (17 tests). Songs used in the two trials for each female were recorded at close range

(<10 m), undistorted by obvious habitat degradation and other fairy-wren sounds, and similar in length and complexity (Fig. 1). We recorded the songs while the bird approached the nest or foraged nearby, its color bands were visible, and it appeared aggressive or alerted to other fairy-wrens or to us.

We completed tests of 22 breeding females. We initiated additional tests but the females lost their nests to predators or to weather before we could complete the tests. Twenty-two different helpers' songs were the test songs from the subjects' own groups. Eighteen different helpers' songs were the test songs from the "other" groups (four were used twice). We presented each female with different (and in four cases reciprocal) experimental and control songs for independence of tests (Kroodsma 1989).

Songs were recorded with a Sony TCM-5000 cassette recorder and a Sennheiser ME-40 microphone. The field recordings were copied to a playback tape at equal peak amplitudes as indicated by the meter on the tape recorder. Each song was recorded three times on the playback tape. Songs were broadcast from a remote Aiwa A5 amplifier-speaker positioned 0.3–1.7 m aboveground facing the nest and 4 m from it, which allowed us to see the nest, the speaker, and the bird. Playback songs were broadcast with sound-pressure levels averaging 75.8 dB, measured with a Precision sound-level meter (AN5 S 1.4-1971, type S1A, A-weighted) and General Radio sound-level calibrator 1567 located 1 m above the ground on a tripod and 1 m from the speaker on its axis, as determined between tests.

Before a playback trial, we observed the nest area for 1 h to determine if there were activities that would affect the behavior of the breeding female. Although we could not observe most birds continuously, they called infrequently and we detected no chasing or intense singing or other intense activity at this time. The birds did not appear to be disturbed by us, and they continued to feed their nestlings. The females remained farther than 3 m from the speaker, and none approached it except during broadcast song.

We began a trial after this observation period when we saw the female within 5 m of the nest and the speaker. We observed her for 15 min after playback or until she disappeared, and we set 8 min after playback as the end of the trial. One observer directed a trial and recorded running comments and bird calls on another tape recorder, and the other watched the breeding female. We tested each bird at the same time of day within 2 h for its two trials. We avoided testing in wind and rain.

Criteria and predictions of response.—In preliminary tests in 1983, we observed that Red-winged Fairy-wrens respond to a playback of song near their nests. Both males and females respond to an unfamiliar conspecific song by singing and approaching the speaker. We reasoned that birds were responding as if they
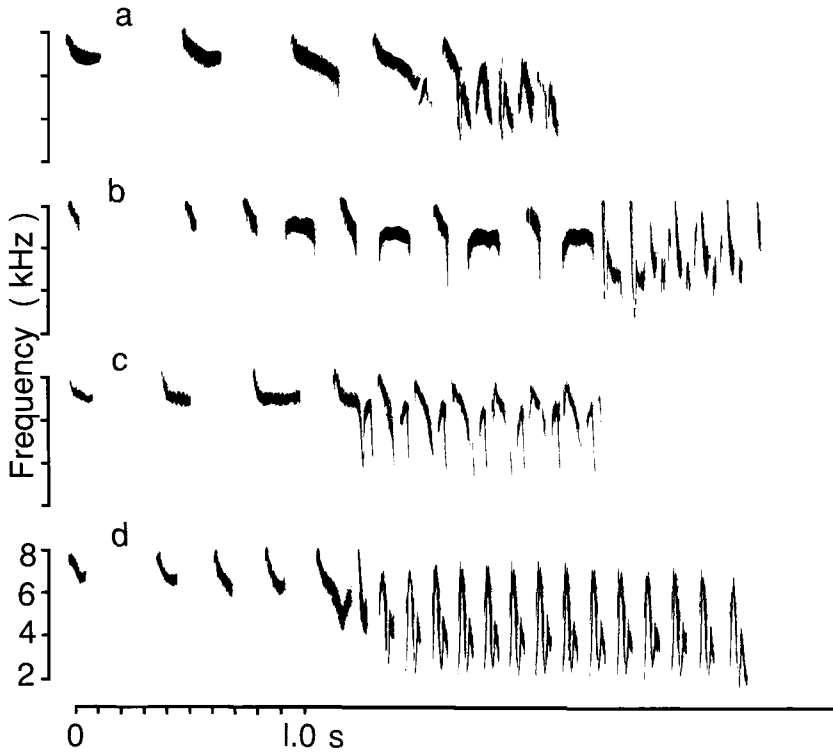
Fig. 1. Songs of four *Malurus elegans* helper females used in testing the responses of breeding females. In these tests, *a* and *b* songs were reciprocally matched in pairs (*a* was the "other" helper in the test where *b* was the female's own helper, and vice versa), and *c* and *d* were matched; the songs in other tests were not matched in pairs.

perceived the song and singer as a threat, and that the incidence and intensity of response would vary with the urgency of a threat. During observations we saw the resident fairy-wren chasing an intruder, singing as it drove off an intruder of the same sex; we saw these chases in both males and females. The behavior and predictions for the direction of a difference in response to songs of helpers from the female's group and helpers from another group were similar to those with Splendid Fairy-wrens (*Malurus splendens*; Payne et al. 1988b). Our techniques differed slightly from those used for that species because of the denser vegetation and lower visibility of Red-winged Fairy-wrens.

We regarded the following behaviors as responses and used them as criteria of response to a song. (1) The bird looked in the direction of the speaker during the song playback by turning its head toward the speaker. (2) The bird hopped higher on its perch while the song was broadcast. (3) The bird approached at least 1 m closer to the speaker during the playback test. (4) The bird moved halfway from its perch site at the beginning of playback to the speaker during the playback. For each test we predicted a higher

incidence of response (i.e. more females would respond in each of these criteria) to the song of a helper from another group than to the song of a helper in her own group.

Several behaviors varied in frequency, intensity, or time, and we used these to grade the degree of responsiveness to different songs. (1) Time (s) to respond (latency to the first-observed of the four criteria of response listed above). Time varied among trials, some birds flew to the speaker while the first song was still being played, and others waited until the end of the trial. (2) Time to approach at least 1 m closer to the speaker, or the end of the trial if the bird did not approach. (3) Distance (m) of closest approach to the speaker; a few birds flew within 1 m. (4) Time that the bird was within 2 m of the speaker. (5) Number of changes of perch while song was broadcast. (6) Number of flights over the speaker or passing within 4 m of it while song was broadcast. (7) Time between the end of playback and the first song of the fairy-wren, or the end of the trial—some birds countersang during playback, although more birds sang after playback ended. (8) Number of songs given during the first 2 min after the last playback song.

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TABLE 1. Incidence of response of 22 breeding female Red-winged Fairy-wrens to song of helpers in their own group and in another group. Levels of significance: $* = P < 0.05$, $** = P < 0.01$, one-tailed, binomial test.

| | Test song | | | | |
| | Same group | | Other group | | |
Response	Yes	No	Yes	No	P
1. Looks toward speaker?	12	10	22	0	**
2. Perches higher?	11	11	21	1	**
3. Approaches >1 m?	13	9	21	1	**
4. Approaches halfway?	9	13	15	7	*

We predicted the direction of difference in response of female Red-winged Fairy-wrens to their helpers and to unfamiliar helpers on the basis of (1) our field observations when female Red-winged Fairy-wrens responded to intrusions of birds from other groups, and (2) our expectation of greater activity to songs of unfamiliar individuals. We predicted that females would respond more rapidly and persistently, approach more closely, change perches more frequently, increase the number of flights during playback, and sing at higher rates to the songs they perceived as more of a challenge to their own interests, and that these songs would be the songs of unfamiliar birds from another group. We predicted the greater perceived challenge to give lower scores of graded variables 1, 2, 3, and 7, and higher scores of variables 4, 5, 6, and 8.

We compared the responses of a subject in its two trials with Wilcoxon matched-pairs signed-ranks tests and the incidence variables with binomial tests. We used other analyses (median test, sign test, Mann-Whitney U-test, Spearman rank correlation, Fisher exact test, Fisher's combined probabilities test) for tests of unbalanced design, such as comparing helper sex and number of helpers, where different sample sizes were involved within a test.

RESULTS

Social organization and context of singing.—In most groups only one female nested in a season. The oldest female was observed to incubate and to brood the nestlings, and when the group was caught in a mist net near the nest, the oldest female was the only bird with a brood patch. All members of each group fed the nestlings. In three groups in 1985 and 1986, we observed two individual females nesting; and in the two with nests active at the same time, we saw no interference between the females.

Song in Red-winged Fairy-wrens is a series of downslurred whistles followed by a tinkling trill (Fig. 1). All adults—both breeders and helpers—sang in their group territory during aggressive contexts (when birds from neighboring territories appeared along a common boundary) and during feeding (when they called back and forth).

Social group membership.—If females recognize the songs of helpers in their own groups, then we expect them to respond more strongly to songs of unfamiliar helpers from another group than to songs of their familiar helpers. Females usually responded to songs of unfamiliar helpers, but they responded in only half of the trials to songs of their own helper. As predicted, they were significantly more likely to look at the speaker, perch high, approach 1 m closer to the speaker, and approach halfway to the speaker in response to a song from another group than to the song of their own helper (Table 1).

Breeding females responded more intensely to the song of a helper from another group than to the song of their own helper. The response was significant in 7 of the 8 graded variables. In all 8 variables, the response was stronger to the song of a helper from another group than to the song of their own helper (Table 2). The sequence listed in Table 2 is similar to the sequence of behavior observed during a trial, and the later behaviors were associated less directly with the stimulus song and more likely influenced by preceding events. Nevertheless, these later responses also differed significantly in the predicted direction.

Test sequence.—If response is facilitated or habituated by an earlier playback, then the incidence or intensity of response should differ between first and second trials. The proportion of females that responded did not differ between first and second trials (binomial tests on all four response categories, $P > 0.05$, NS). The intensity of response did not differ between first and second trials in any of the 8 graded criteria of responsiveness (Wilcoxon tests, $P > 0.05$, NS). Together with our test design in which we alternated the sequence of song trials between subjects, the result indicates that trends in response between familiar and unfamiliar helper were not due to the sequence of songs.

Kinship.—If kin recognition is based on social context and location in the natal area (Sherman and Holmes 1985), then cooperative behavior should be directed to kin whether or not the individuals actively recognize each other as kin.

TABLE 2. Intensity of response of 22 breeding female Red-winged Fairy-wrens to song of helpers in their own group and in other social groups. Levels of significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant; one-tailed, Wilcoxon matched-pairs signed-ranks test.

Response (unit)	Own group ($\bar{x} \pm$ SE)	Other group ($\bar{x} \pm$ SE)	P
1. Time to respond (s)	458 ± 96.4	129 ± 67.0	***
2. Time to approach (s)	302 ± 89.1	107 ± 55.0	NS[a]
3. Nearest approach (m)	4.00 ± 0.40	2.68 ± 0.40	*
4. Time within 2 m (s)	6.32 ± 2.64	40.4 ± 11.3	**
5. N changes of perch	1.59 ± 0.25	2.91 ± 0.29	***
6. N flights over speaker	0.45 ± 0.13	1.09 ± 0.21	*
7. Time to first song (s)	471 ± 93.8	259 ± 85.7	*
8. Songs in 2 min (n)	0.59 ± 0.25	1.86 ± 0.52	*

[a] $P = 0.10$.

In contrast, if individuals more directly assess kinship, then the response of a female to her helpers should differ according to their degree of relatedness.

To test whether the behaviors of the breeding female toward helpers that were related to her were different from those toward her helpers that were not her kin, we compared responses to songs of related and unrelated helpers in her group. We compared responses in 17 groups for which we knew the nesting history and matrilineal relationships of the breeding female and her helpers. The helper was not closely related to the breeding female (coefficient of relatedness $r \leq 0.25$) in five tests (in four, she had recently immigrated; in the other, the helper had immigrated). In 12 tests her helper was a close relative ($r = 0.5$), either her offspring or, in one case, her sibling.

The breeding female responded to song of her helper no differently when it was related to her than when it was not, either in the four incidence variables (Fisher exact tests, $P > 0.05$, NS) or in the eight graded variables (median tests, $P > 0.05$, NS). Considered together, her response differed in the direction predicted (higher response toward unrelated helpers) for only 4 of the 12 scores. The sample of females with unrelated helpers is small, but the results indicate no difference in behavior toward a relative and an unrelated bird in her group.

Sex and breeding status.—If a breeding female is more aggressive toward an unfamiliar female than an unfamiliar male (as expected if females compete for helpers), then she should respond to songs of female helpers more intensely than to those of male helpers. We did not design the study to test response differences to helpers of same and other sex as few male songs were used.

Playbacks involved 4 tests of male-helper song and 18 of female-helper song. Responses of breeding females were compared separately for song of male and female helpers. The incidence was not associated with the sex of the helper in any of the four criteria of response, either to familiar song of a female's own helper or to unfamiliar song of another group (Fisher exact tests, $P > 0.2$, NS). We also found no different response in the variables of Table 2, either to song of helpers in a female's own group or to song of helpers in another group ($n = 16$ median tests, $P > 0.1$, NS).

If female behavior varies with the potential for competition for helpers, or if her behavior varies with the nutritional demands of her growing young, then we would expect the intensity of response to vary with the stage of nesting. Under the competition model, a female should be more responsive early in the nesting cycle (because competition is more likely with overlapping periods of parental care); and under the model of nutritional demand, she should be more responsive later in the nesting cycle (because older nestlings require more food). We tested the effect of breeding status by comparing response with the nest day (day 1 = first day of incubation, day 14 = 1-day nestlings, day 23 = 10-day nestlings, and so on). Nest day was not associated with response (8 Mann-Whitney U-tests, two-tailed $P > 0.05$). Only one comparison of graded scores was significant (number of flights after trial of other helper, Spearman rank $R_s = 0.45$, $P < 0.05$), a proportion expected in 16 analyses by chance as a type I error where $\alpha = 0.05$.

Group size and number of helpers.—In Red-winged Fairy-wrens, groups with helpers have higher breeding success than do single pairs,

TABLE 3. Variation in the incidence of response of breeding female Red-winged Fairy-wrens to song of helpers, with number of helpers in female's group (1-2, $n = 10$; ≥ 3, $n = 12$).

Response	Number of helpers				
	1-2		≥ 3		
	Yes	No	Yes	No	P^a
A. Response to song of helper in own group					
1. Looks toward speaker?	6	4	6	6	0.49
2. Perches higher?	7	3	4	8	0.10
3. Approaches >1 m?	7	3	6	6	0.31
4. Approaches halfway?	6	4	3	9	0.11
B. Response to song of helper in other group					
1. Looks toward speaker?	10	0	12	0	
2. Perches higher?	10	0	11	1	0.55
3. Approaches >1 m?	10	0	11	1	0.55
4. Approaches halfway?	8	2	7	5	0.27

ᵃ Fisher exact test.

and groups with three or more helpers produce more fledglings than groups with one or two helpers, mainly because females renest in the larger groups (Rowley et al. 1988). If they compete for helpers, then females should respond differently to song tests in groups with ≥ 3 helpers than in groups with only 1-2 helpers, and the response should be greater in the smaller groups. The prediction assumes that a breeding female in a large group will retain some helpers even if another female breeds and attracts the aid of 1-2 helpers for her own brood.

In the groups tested, 10 females had 1-2 helpers, and 12 had 3-5 helpers. Considered separately for each variable, the incidence of response was not significantly different in small and large groups (Table 3; Fisher exact tests, $P > 0.05$, NS). For the graded variables, a female was significantly more responsive in nearest approach to the speaker, in time she was within 2 m of speaker, and in number of flights (Table 4; Mann-Whitney U-tests, one-tailed $P < 0.05$) when she had only one or two helpers (for both the song of her own helper and song of unfamiliar helper). The difference was in the direction opposite from prediction only in behaviors 7 and 8, and these were observed at the end of a trial, when the female might have been affected by intervening events.

Considered together, the responses differed in the direction predicted for 10 of the 12 scores to the song of a female's own helper (Tables 3 and 4; sign test, one-tailed $P = 0.055$), and in

the direction predicted for 9 of the 12 scores to song of an unfamiliar helper (sign test, one-tailed $P = 0.07$). Combining these scores and excluding the one tied score, females in groups with 1-2 helpers were significantly more responsive than females in larger groups (sign test, one-tailed $P = 0.005$). Fisher's combined probabilities test, which sums the natural logarithms of probabilities of each test to approximate a chi-squared value ($\chi^2 = -2 \Sigma \ln P$; Sokal and Rohlf 1981: 779-781), also indicated that females in small groups were significantly more responsive in the playback tests than were females in larger groups ($\chi^2 = 94.6$, $P < 0.001$).

DISCUSSION

Breeding female Red-winged Fairy-wrens discriminated between song of their own helpers and song of unfamiliar helpers. The differences in response were in the direction predicted if outsiders were perceived as more of a threat than the members of her group. Females with 1-2 helpers responded more strongly than females with ≥ 3 helpers. Females did not respond differently to song of their own helpers when they were related and when they were not close kin. We suggest that individual familiarity with their helpers and the social composition of their group are more important than kinship between fairy-wrens in directing their social behavior.

The ecological significance of kin recognition involves avoidance of inbreeding and directing cooperative behavior toward kin (Sherman and Holmes 1985, Waldman 1988). The significance of distinguishing familiar individuals from strangers in group-living birds applies in the benign interactions among group members and the uncertain and potentially harmful behavior of strangers. Within a social group the fairy-wrens perch together, preen each other, help rear the young of the breeding pair, and defend a group territory against competing groups (Rowley 1981, Rowley et al. 1988). In contrast, outsiders may compete with a group member—regardless of kinship—for a mate, for breeding status and helpers to care for their young, and for resources such as food.

Our field observations of the behavior of breeding fairy-wrens are consistent with our conclusion that social recognition, and not kin recognition, explains the results of the playback tests and the mechanism of recognition by song.

TABLE 4.   Variation in intensity of response of breeding females to song of helpers, with number of helpers in female's group (1–2, $n = 10$; ≥3, $n = 12$). Levels of significance: * = $P < 0.05$, ** = $P < 0.01$, Mann-Whitney U-test.

Response (unit)	1–2 helpers ($\bar{x} \pm$ SE)	≥3 helpers ($\bar{x} \pm$ SE)	P
A. Response to song of helper in own group			
1. Time to respond (s)	372 ± 143	529 ± 132	0.49
2. Time to approach (s)	290 ± 133	312 ± 125	0.40
3. Nearest approach (m)	2.90 ± 0.50	2.63 ± 0.47	0.005**
4. Time within 2 m (s)	11.9 ± 5.06	1.67 ± 11.3	0.02*
5. No. of perch changes	1.90 ± 0.28	1.33 ± 0.40	0.16
6. No. of flights over speaker	0.70 ± 0.14	0.25 ± 0.13	0.04*
7. Time to first song (s)	569 ± 136	389 ± 130	0.07
8. Songs in 2 min (n)	0.20 ± 0.20	0.92 ± 0.41	0.07
B. Response to song of helper in other group			
1. Time to respond (s)	97.2 ± 89.2	155 ± 31.8	0.42
2. Time to approach (s)	106 ± 88.3	108 ± 72.6	0.10
3. Nearest approach (m)	1.80 ± 0.42	3.42 ± 0.57	0.02*
4. Time within 2 m (s)	64.4 ± 17.9	20.4 ± 12.3	0.02*
5. No. of perch changes	3.10 ± 0.43	2.75 ± 0.41	0.25
6. No. of flights over speaker	1.60 ± 0.31	0.67 ± 0.22	0.01**
7. Time to first song (s)	281 ± 135	241 ± 115	0.34
8. Songs in 2 min (n)	1.10 ± 0.43	2.50 ± 0.86	0.19

In Splendid Fairy-wrens the helpers remain in their natal group, but their natal residence is not sufficient to establish the kinship of helpers with both of the breeders. Matrilineal kinship as observed from their behavior is consistent with maternal kinship as determined in genetic studies. In contrast, paternity is uncertain due to a high frequency of extrapair fertilization by males from neighboring groups (Brooker et al. 1990). Based on observation of their behavior, Red-winged Fairy-wrens sometimes breed with a close relative. In 1985 and 1986 we observed daughter and father matings (where kinship is uncertain because of possible extrapair fertilizations in this species), and mother and son matings and sister and brother matings (where assessments of kinship are likely to be accurate). No molecular evidence of parentage is available in this species. Red-winged Fairy-wrens sometimes rear a parasitic cuckoo, at the expense of their own young (Rowley et al. 1988), and this misdirected parental care suggests that the fairy-wrens do not recognize their kin in a genetic sense (Sherman and Holmes 1985, Crozier 1987).

Although the breeders receive aid of the helpers in caring for their young, the breeders also might suffer a cost from others in their group. When two females breed in a group, one may lose a helper to the other. The level of competition in a group with several helpers might be less intense because the first female retains her other helpers. The difference in the response of a breeding female to song in the small and large social groups that we observed was predicted from a hypothesis of competition for helpers (Payne et al. 1985, 1988b; Rowley et al. 1989). The second female to nest in a plurally breeding group may attract no helpers, or she may attract some of them, depending on the success and stage of the first nest. We observed both outcomes at nests of plurally breeding Splendid Fairy-wrens (Payne et al. 1985, 1988a; Rowley et al. 1989). Because a larger group has more helpers, a breeding female with many helpers may incur no cost in breeding success if a second female breeds and attracts one or two helpers. The stronger response by a female with only one or two helpers indicates that behavior depends on the social composition of her group as well as on recognition between familiar and unfamiliar individuals. Competition among breeding females for helpers has also been suggested in other cooperatively breeding species (Zack and Rabenold 1989, Davies 1990, Dow and Whitmore 1990, Rabenold 1990, Rabenold et al. 1990, Stacey and Koenig 1990).

Alternative explanations of the ecological significance of discrimination by breeding females of familiar and unfamiliar fairy-wrens include competition for food and other re-

sources in the group's territory. Hypotheses of (1) social competition between actual and potential breeders for helpers and (2) competition for other resources in groups of different sizes could be distinguished by additional playback experiments (e.g. by comparing the response of a breeding bird [of either sex] to the song of another bird of the same sex and a bird of the other sex). Our field observations of Red-winged Fairy-wrens did not suggest competition for other resources. If competition for resources other than helpers is important, then competition might be directly related to group size. In 1985 and 1986, the number of fairy-wrens in a group was not obviously related to territory size. Also, territory size was consistent across years even when the number of adults in a group was not (Rowley et al. 1988). Competition for resources should be more severe in larger groups, but the response to song was stronger in smaller groups. Another explanation of the difference in response with group size is that a breeding female responds less strongly in large groups because she is supported by other group members. In our observations during the playback tests, we saw no interference or support by other birds, the playback trials were short, only the subject female was nearby, and no other group members approached the speaker.

The greater responsiveness of female Red-winged Fairy-wrens to unfamiliar song of helpers from other groups is similar to that in Splendid Fairy-wrens (Payne et al. 1988b). Both species are cooperative breeders, although Red-winged Fairy-wrens live in forests and have smaller territories, larger groups, and delayed female dispersal from the natal group (Rowley et al. 1988). In both species the responses to song of familiar and unfamiliar birds differ significantly, but responses to songs of kin and unrelated birds do not. The familiarity gained in living together may maintain the cooperative behavior between breeders and helpers in fairy-wrens.

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