VOCAL RESPONSE TO PREDATORS IN PAIR-BONDED CAROLINA WRENS

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The Carolina Wren (*Thryothorus ludovicianus*) has a social system that is much more characteristic of tropical than temperate zone species. Males and females form permanent pair bonds (Bent 1948, Thomas 1953, and pers. observ. of a color-banded population over 4 years) and pairs defend a territory throughout the year.

Probably due to this social system, Carolina Wrens use all of their vocal signals throughout the year (Morton, in press). Here we present data derived from field observations and laboratory experiments on one of this wren's vocal signals, which we term the *chirt*. Carolina Wren *chirts* are structurally variable and are delivered in temporally variable ways. We hope to explain here how this call varies and how its variation is adaptive within the Carolina Wren's social system. Since *chirt* calls depart from the commonly held view that most bird sounds are rather discrete (Marler 1967, Smith 1968, 1969), a discussion of them may shed new light on sources of selection favoring graded communication systems.

METHODS

LABORATORY STUDY

Eight Carolina Wren pairs were captured from the same woodlot near College Park, Maryland, during October, November, and January (non-breeding season) and tested in the laboratory for their vocal responses to a live Roadside Hawk (*Buteo magnirostris*).

To capture mated pairs a hand-raised female wren was placed in a cage near a tape recorder that played back male song. The captive female responded to the playback with a female "chatter" vocalization. The effect was to duplicate an intruding *pair* of wrens so that both the male and the female wren that we wished to capture would fly to the vicinity of a mist net where they were captured. Six pairs captured in the morning were used the same afternoon; two pairs captured in the afternoon of one day were used the next afternoon. The pairs were color-banded and released on their territories after use.

Each pair was placed in a .6 × .6 × 1 m hardware cloth cage containing two wooden dowel perches; water and food (mealworms) were available on the cage floor. Each caged pair was isolated in a sound-attenuated room for two to four hours acclimation before exposure to the hawk in that room. The room (3.40 × 3.20 × 2.45 m) was completely lined with white blankets to reduce echoes and to create a uniform visual background. It was provided with a one-way observation window.

The hawk was trained to fly across the room to an exposed perch. It flew from a perch concealed from the wrens directly over the caged wrens to a perch in view of the wrens. The hawk was tethered to a monofilament line on a pully which standardized its flight path. When in flight, the hawk passed 1.7 m above the cage to a perch 2.5 m from the center of the wren cage.

Wren sounds elicited were tape-recorded via a microphone in the testing room. Concurrently from an adjacent room, we observed wren and hawk behavior and tape-recorded our observations.

The sounds were analyzed on a Kay Elemetrics Sonograph; amplitude and temporal data were analyzed with a B and K graphic level recorder.

FIELD STUDY

A population varying from 8 to 10 pairs in deciduous forest surrounding one author's residence was color-banded. Nearly daily monitoring of behavioral events within the population was made by Morton from April 1972 to September 1975. Vocalizations were tape-recorded together with observations of contextual events (Morton, in press). Naturally occurring *chirts* were included in this study and are discussed here.

Two field experiments were performed using the same laboratory hawk as a stimulus. In one, the hawk was tethered in a wren territory. In the second, the hawk was tethered and the female member of a wild wren pair was placed in the hardware cloth cage 2.5 m from the hawk while the male was free. We tape-recorded our observations from a blind ca. 15 m away.

RESULTS

LABORATORY STUDY

One or both members of each pair responded to the hawk presentation with short harsh sounds we termed *chirts* (Figs. 1–4). Both males and females emitted *chirts* but two of the females also used a second call termed *dit* interspered with *chirts* (Fig. 1). There was no consistent sexual difference in *chirt* structure, but each pair member had a distinctive quality to its *chirts* such that we could differentiate them by ear, but we do not know if wrens recognize individuals on this basis. The *chirt* response persisted up to three hours before completely habituating, providing a combined total of about 12 h total response from the 8 experiments.

Two aspects of this vocal response appear to be unique in avian communication studies:

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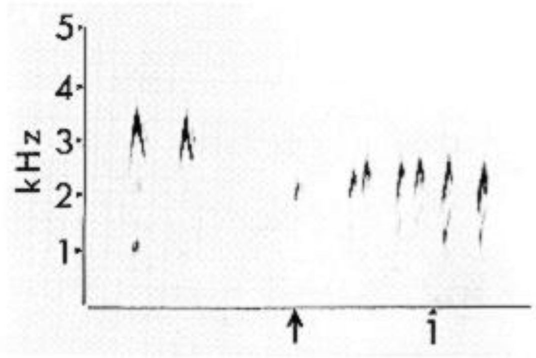

FIGURE 1. Sound spectrogram depicting two *dits* followed by *chirts* elicited by a hawk head movement (at the arrow). In this and subsequent figures the horizontal axis is calibrated in seconds, the vertical axis in kHz. Each figure depicts sounds from a different bird.

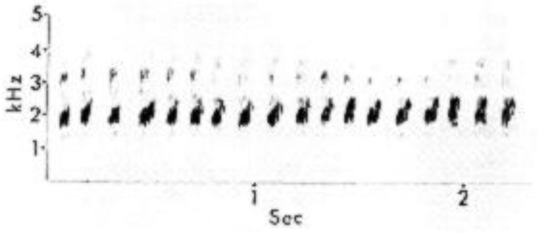

FIGURE 2. Sound spectrogram of the evenly spaced, rapid *chirts* typical of those uttered during the initial reaction to the introduced hawk.

(1) The *chirts* were varied in amplitude, frequency, and inter-*chirt* interval that correlated with the hawk's small movements. They constituted a fine-tuned appraisal of the hawk's movements. (2) Most of the vocalizing was by the female member of each pair; in two pairs *only* the female responded vocally, the male remaining silent.

Each *chirt* consisted of a short (range 32–79 msec for the 16 birds combined) frequency-modulated sound rising in fundamental frequency. They were delivered with the bill closed and were not the sound used by Carolina Wrens when they mob predators.

The start of the vocal reaction to the hawk flight was a sustained bout of evenly spaced *chirts* (Fig. 2) that lasted from 10 seconds to about one minute. During this initial reaction, the average frequency of a *chirt* rose from a beginning at 2.02 kHz to 3.01 kHz. *Chirts* recorded during the first 30 seconds of the response varied from 4.5 to 10.7 *chirts* per second, were evenly spaced in time, and were 1 to 2 db greater in amplitude than later *chirts.*

After this initial reaction, *chirts* were delivered at a slower but variable rate *except when the hawk moved its head,* at which point the *chirts* immediately but momentarily took on the characteristics of those given at the start of the reaction (Figs. 1, 3; Table 1). The *chirt* rate gradually declined from 4.23 to 0.77 per second, until, after two to four hours, only large movements by the hawk (e.g., extending the wings to balance) would elicit *chirts.*

After the initial reaction, *chirts* were delivered in bouts of 1 to 5 (ones, twos, and threes being most common) with short pauses between each bout (Fig. 4; Table 1). A typical sequence would be: *chirt, chirt-chirt-chirt, chirt-chirt, chirt-chirt-chirt, chirt, chirt-chirt-chirt-chirt-chirt,* etc. The second *chirt* in each bout of two or more was .2 to .4 kHz higher in frequency than the first *chirt.* If the bout was elicited by a hawk movement (even a small head turning motion), immediately subsequent *chirts* remained at the higher frequency (Figs. 1–3), otherwise the third and subsequent *chirts* (if present) dropped back to the frequency of the first *chirt* (Fig. 4).

From the observation room we simultaneously recorded the wren vocalizations, one observer's description of the hawk's head movements, and a second observer's description of wren activity. When the hawk moved its head, and particularly when it looked directly at the wrens, the *chirts* would (1) increase in repetition rate, (2) become more evenly distributed in time, and (3) increase in frequency (pitch) and in amplitude (Figs. 1–3; Table 1).

Using the same observation technique, we examined the meaning (message, meaning, and context are here used *sensu* Smith 1965) of these graded signals to the receiving (non-vocalizing) member of the wren pair. Periods when both wrens vocalized were rare, less than 3% of the total time. Two pairs in which the female emitted *dits* showed greater simultaneous calling than was found in the other six pairs. The males would *chirt* while the females called *dit.* (The *dit* is a call specific to the female that is used while mobbing a

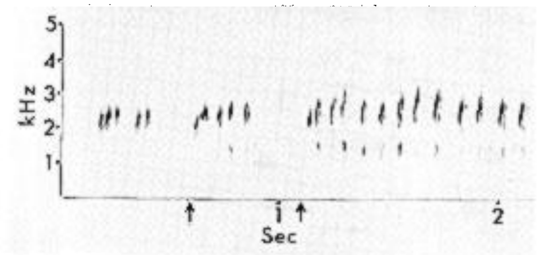

FIGURE 3. Sound spectrogram of *chirts* following two hawk head movements (arrows).

TABLE 1. Characteristics of wren *chirts* emitted when hawk was still or moving its head.[a]

Chirt characteristics (means)	Hawk still	Hawk moving head
	1–5 *chirt* bouts[b]	Continuous *chirts*
No. *chirts* per bout in 60 sec:		
1-*chirt* bouts	5.83 ± 5.06SD	
2-*chirt* bouts	22.64 ± 11.31	
3-*chirt* bouts	15.36 ± 14.19	
4-*chirt* bouts	3.73 ± 5.06	
5-*chirt* bouts	2.09 ± 5.97	
Repetition rate (*chirts*/sec)	1.44 ± 1.26	7.30 ± 3.39
Frequency range (kHz)	1.65 – 2.55	2.02 – 3.01

[a] Data taken from 1 to 30 minutes after hawk introduction.
[b] See text for bout description.

predator or when near an aggressive Carolina Wren.) Only the females vocalized for nearly 85% of the total observation period.

Thus the receiver was usually one member of the pair at any moment and was usually the male. In pair numbers one and six, the male remained silent while the female *chirted*, but began *chirting* when the female stopped. While females used variable numbers of *chirts* in bouts (Fig. 4) without the characteristics of *chirts* that accompanied hawk movements (Figs. 1, 3), males were observed to feed, preen, and explore the cage and seemed to pay little attention to the hawk. When the hawk moved and his female's *chirts* took on characteristics indicated (Figs. 1, 3; Table 1), the male watched the hawk and rapidly bobbed the forepart of his body.

FIELD STUDY

Many *chirt* sequences recorded from free-ranging wrens had forms like those recorded in the laboratory. For example, Morton observed a female wren *chirt* in response to a Red-tailed Hawk (*Buteo jamaicensis*) perched in the forest canopy about 30 m from the wrens. The *chirts* lasted for 35 min and were delivered with the bout structure recorded in the laboratory. They changed to rapid, evenly delivered sounds when the hawk flew. During the female's calling period, the male foraged in the leaf litter. *Chirts* were elicited by many stimuli, such as humans, dogs, cats, hawks, and other Carolina Wrens.

Many *chirts* recorded from free-ranging birds, however, were more structurally varied than the laboratory-induced *chirts* (Figs. 5–8). These *chirts* were delivered during intraspecific encounters, a context not duplicated in the laboratory. Figure 5 shows a harsh *chirt* grading (at ca. 1 sec) into a *chirt* form similar to those elicited by the moving hawk in the laboratory experiments (at 2 sec). This bird had just been attacked by another wren. It had stopped, uttered harsh *chirts*, then changed to clearer *chirts* as it flew away from the approaching winner of the fight. Figure 6 shows another harsh *chirt*, given with bout structure by an adult male after it had chased an intruding immature (unspotted under tail coverts) from its territory. The immature was still visible to the calling adult.

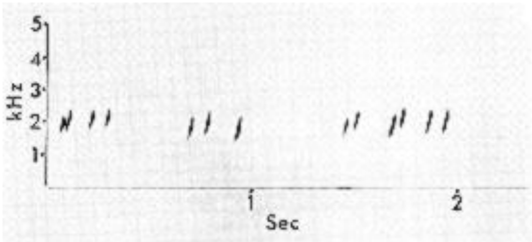

FIGURE 4. Sound spectrogram showing bout structure of *chirts* delivered while the hawk was still.

Figure 7 depicts very rapid *chirts* given by a female as her mate approached. This pair had just encountered a neighboring pair in an area of frequent boundary disputes. Figure 8 shows simultaneous calls from a mated pair. The male gave two *cheer* calls (at 0.2 and 1.0 sec) while his mate gave *dits* (the paired chevron-shaped calls at 4 kHz; see also Fig. 1). The male's calls changed from *cheers* to *chirts* at 1.8 sec as he flew from an approaching male.

The two field experiments with the tethered hawk produced differing results. When both wren pair members were free, they approached to within 10 m of the hawk, one member (sex unknown) uttering *chirts* identical to those elicited in the laboratory tests. In 10 sec after they stopped approaching the hawk, however, the male began cheers, the female began paired *dits* (such as in Fig. 8).

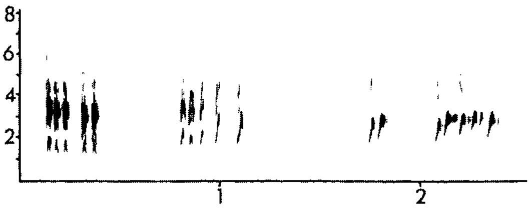

FIGURE 5. Sound spectrogram of harsh *chirts* grading (at ca. 1 sec) into *chirts* similar to those elicited during the laboratory experiments.

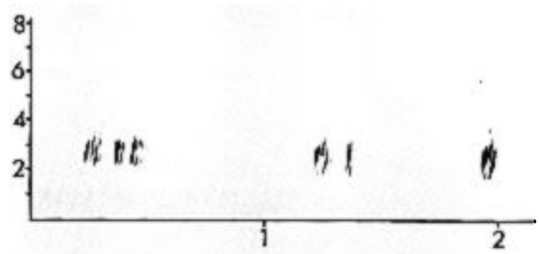

FIGURE 6. Sound spectrogram of harsh *chirts* delivered in bouts by a wren that had successfully repelled a territorial intruder.

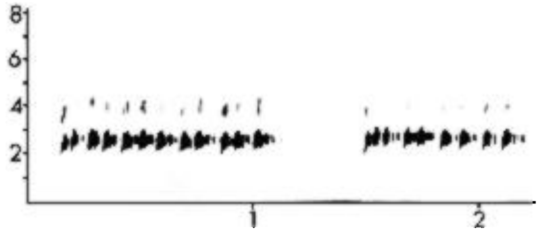

FIGURE 7. Sound spectrogram of rapid, tonal *chirts* delivered by a female wren as her mate approached. This pair had just encountered a second pair in an area of frequent boundary disputes.

This reaction differed from the Red-tailed Hawk observation mentioned above and also from the reaction of a pair to a Sharp-shinned Hawk (*Accipiter striatus*) perched at ca. 1.5 m above ground. In these, the female wren *chirted* continuously and the male was silent.

In the second tethered hawk test (in the territory of a different pair of wrens), this time with the female wren caged 2.5 m from the hawk, the female *chirted* constantly while her free mate gave *cheer* calls. He approached to within 3 m of the hawk, keeping nearer to his caged mate than to the hawk. These vocalizations did not attract other Carolina Wrens to engage in mobbing although birds of other species did mob the hawk.

DISCUSSION

We will discuss first the significance of the Carolina Wren's *chirt* system as it functions in predator avoidance, then its intraspecific use. To understand hypotheses on the evolution of this vocal system, it is important to keep in mind the wren's social and ecological background in which natural selection is operating.

The Carolina Wren is territorial throughout the year, and mated pairs defend areas as a fighting unit. Our observations on the color-banded population (unpubl. data) show that territorial aggression, defined as the number of disputes per day, is highest during the non-breeding season. The size of the territory defended probably is adapted for winter survival rather than breeding purposes. The Carolina Wren suffers large winter mortality when snow covers the leaf litter foraging zone (e.g., Wetmore 1923). The wren is restricted to foraging under windfalls, etc., where the ground is not snow covered, whereas during the breeding season wrens forage in foliage and on tree trunks in addition to the ground (J. Fellers, pers. comm.).

Due to constant aggressive behavior, a wren without a territory is rapidly excluded from habitat good for winter survival. Morton released a male wren captured elsewhere into the field study site and was able to aurally trace the path taken by the introduced bird as it was continually chased from one territory to the next by loudly calling territory holders.

In the Carolina Wren then, most of the vocal communication is adapted to increase the animal's efficiency in territorial defense. The permanent pair bond is part of the normal context in which territories are defended.

Pair bonds are formed in any month and are maintained for the life of each individual. Birds in juvenal plumage in early July of their hatching year (in Maryland they are no more than 2 mo post-fledging and probably just independent of parental care) may form pair bonds. Early and permanent pair bonding is undoubtedly favored because survival (and ultimately, fitness) is so closely related to territory ownership. And, although males establish and are able to maintain territories without mates, females cannot maintain a territory without a male. As discussed below, the sex role difference has probably influenced the usage of the *chirt* system.

CHIRTS AND PREDATOR AVOIDANCE

The laboratory and field results show that the Carolina Wren *chirt* system is a vocal form of

FIGURE 8. Sound spectrogram of simultaneous calls from a mated pair of wrens. The male gave two *cheer* calls (at 0.2 and 1.0 sec) while his mate gave paired *dits* (chevron-shaped calls at 4 kHz). The male's calls changed from *cheers* to harsh *chirts* at 1.8 sec then to "escape" *chirt* as he flew from an approaching male.

predator surveillance. Predator surveillance is chiefly a female role. The message of *chirt* bouts may be that a female is "on alert." This is similar to the message hypothesized for singing behavior in Eastern Wood Pewees (*Contopus virens*) by Smith (1968). The *chirt* system also encodes an escape message that we detected in the laboratory. When the bout structure changed to evenly spaced high frequency *chirts* the hawk was moving. In the wild, wrens giving this *chirt* type were flying away from something. The escape message *chirt* is found even in nestlings that are caused to fledge from the nest prematurely.

Why do females perform the function of predator surveillance? We suggest that selection has favored the female taking this role because, if the predator kills her mate, from an evolutionary viewpoint, it is nearly the same as if the predator had killed her too. The female, by increasing her chances of being taken by a predator (although we do not know by how much since the *chirt* source is difficult to locate and is uttered with a low amplitude) must still increase her chances for future reproduction by providing protection to the male. By protecting the male, she is protecting her territorial integrity (= future reproduction).

Females, even those on a territory for several years, are not able to maintain themselves on a male-less territory. They are rapidly driven away by adjacent pairs expanding their territories. Four out of four females who lost mates were driven out within 6 days, none were subsequently observed, and one was recovered dead 2 km from her former territory. The process of expulsion was observed when we purposely removed a male in June 1975. This female attempted to continue feeding 6-day old nestlings. In her foraging trips she encountered three different pairs in 2 h observation in places that were formerly in her territory. In each case she was chased until the chasing pair encountered a second encroaching pair who then occupied them.

In contrast, males are able to hold territories alone. Young males initially establish their territories alone and older males who lose mates rapidly acquire new ones. One male, whose female of 3 yr was killed 16 December, was associated sequentially with 3 different females until breeding began in April. Females compete with other females for a male-defended territory. Monogamy is maintained through a female's aggression toward other females. This territorial sex role difference is likely related to singing, which is restricted to males. Males have the only long distance sounds (songs, *cheer* call) which function to ward off potential intruders before energy-demanding fights are needed to do so. Males spend a great deal of time and energy singing throughout the year. (One captive male kept outdoors on 11 March 1976 sang 2485 songs of 26 different types during 44 singing bouts from 0615 to 1810 h. He was singing for 3 h 48 min or 32% of his potential foraging time.)

The female's predator surveillance role allows the male to forage even in the presence of a predator. We observed this in the laboratory and in the wild. Carolina Wren foraging behavior (entering cavities and rummaging under leaf litter) reduces their ability to detect predators. Many tropical species with this foraging mode join flocks of mixed species, thereby gaining predator protection (Willis 1972), but the Carolina Wren and most other wrens do not join mixed flocks. Thus the female's predator surveillance increases the male's foraging time, permitting him to allot more energy toward long distance territorial defense (singing) and also decreases his chance of dying during winter snow conditions.

We believe that the combination of the female's decreased viability if her mate were lost and the male's increased viability when permitted to forage in the presence of a predator are the selective factors favoring the female taking the role of predator surveillance. We suggest that this function of the *chirt* calls has favored their use in variable sequences of ones, twos, threes, fours and fives to maintain the male's attention to them so that he will react quickly when the vocalizations change to indicate that the predator is moving.

INTRASPECIFIC USE OF *CHIRTS*

Much of the Carolina Wrens' behavior is under strong selection pressure to increase the efficiency with which they acquire and maintain territory. It is not surprising that a vocalization designed for predator surveillance and containing "on alert" and escape messages would also function in intraspecific social interactions. There is probably little evolutionary difference for the Carolina Wren among being caught by a predator, losing a territory or not being able to acquire one, since they will not reproduce in any case.

However, intraspecifically-used *chirts* are structurally more varied than predator-elicited ones because they encode more motivational information than called for in the predator context. The gradations and variations depicted in Figs. 5–8 are related to "on alert" and escape messages as in the predator surveillance *chirts* in Figs. 1–4, but in addition they carry information about the sender's motivation. This information follows certain structural rules that are described in more detail elsewhere (Morton, in press).

The *chirt* system is particularly prone to encode motivational information because it is used by birds close to one another. Small changes in frequency characteristics will not be masked by differential attenuation rates. Close contact permits greater use of signals that are highly graded in structure rather than stereotyped (Marler 1967).

For example, in Fig. 5, the bird had just been attacked and it used harsh but shrill *chirts* and then "hawk escape" *chirts* as it again escaped from attack. The harsh shrill *chirts* indicate that the sender was ambivalent about attacking or escaping, as expected for a male attempting to establish territory. However in Fig. 6, the harsh quality is not accompanied by higher frequencies (shrillness) since the caller was "on alert" (note bout structure) and highly aggressive (it had just chased an immature). In other words, the quality differences between aggressive sound types (harshness, growls) and appeasing ones (high frequency, whines, pure tones) mentioned by Collias (1960) are present in the sound structures of *chirts*. This motivational information is overlaid on the locomotory message contained in *chirts* to add a new dimension (or complexity) to their communicative use.

The selective background favoring this complexity is probably not uncommon in birds or mammals, but has been largely neglected, particularly in avian work. It may not be by chance that graded signals are found in Carolina Wrens as well as, and widely known in, social primates. The Carolina Wren's communication system may illustrate an evolutionary convergence between avian and primate systems. In the Carolina Wren, the permanent association between a male and a female, and their joint defense of a territory, whose size and quality are directly related to their probability of reproduction (in social primates, the social relations within the troop and the troop's ability to defend a group territory) have produced a selective background favoring the development of graded vocal signals.

SUMMARY

Laboratory experiments and field observations show that pair-bonded Carolina Wrens have a vocal system that functions in predator surveillance. The female takes on the predator surveillance role freeing the male to forage and to allot more energy to territorial defense.

The predator surveillance call is also used during intraspecific encounters wherein it is structurally varied due to the overlay of motivational messages.

Hypotheses are suggested to explain the evolution of this system. The occurrence of graded vocal signals here described may represent evolutionary convergence toward a primate communication system because of similarities in their social background.

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