

## Response of Eastern Willets (*Catoptrophorus s. semipalmatus*) to Vocalizations of Eastern and Western (*C. s. inornatus*) willets

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The experimental playback of sounds has been used to examine the function and significance of acoustic signals in a wide variety of animals (Falls 1992, McGregor 1992b). In birds, playback has been used to study taxonomy, species and individual recognition, contests between social groups, repertoire size, and song learning (e.g. Nuechterlein 1981, Nelson and Marler 1990, Brindley 1991, Stoddard et al. 1992, Munding 1995; see references in McGregor 1992a). In this study, I used playback experiments to test the biological significance of a divergence in song features in two taxa of Willets (*Catoptrophorus semipalmatus*).

Bird song functions as a species isolating mechanism and as a means of communication between potential mates (Marler 1957, Becker 1982). Reproductive isolation is central to the biological species concept. Hence, the response to species-specific signals, such as song, serves as a critical indicator of specific and subspecific boundaries. For example, Nuechterlein (1981) demonstrated differences in the advertising calls of what were believed to be sympatric "morphs" of the Western Grebe. These differences were used as evidence of reproductive isolation in designating Clark's Grebe (*Aechmophorus clarkii*) and the Western Grebe (*A. occidentalis*) as separate species (AOU 1985).

I used playback experiments to examine the question of species recognition and reproductive isolation in two geographic races of the Willet. The Eastern Willet (*C. s. semipalmatus*) breeds in coastal habitats along the Atlantic seaboard, Gulf of Mexico, and Caribbean Islands, whereas the Western Willet (*C. s. inornatus*) breeds in the interior grasslands of the western United States and western Canada (Sibley and Monroe 1990). I discuss my results within a conceptual framework of signal space as ecological space (Nelson and Marler 1990). This theory holds that a species' acoustical signals define a niche in the sound environment of animal communities. This niche is represented in mathematical terms as a multidimensional signal space. The dimensions are attributes of the signal such as duration, dominant frequency, and numbers of notes and syllables.

*Methods.*—Eastern Willets were studied at sites along the Atlantic seaboard from Nova Scotia to Florida in 1995 and 1996. Playback experiments were used to test the Eastern Willet's ability to recognize

the vocalizations of the Western Willet, in particular the "pill-will-willet" song. Preliminary experiments were conducted in Nova Scotia in June 1995 with taped examples of Western Willet vocalizations. In a general test, examples of Western Willet vocal sequences were broadcast (CFS-1030 Sony cassette player) on terrestrial territories (within 50 m of individuals), and foraging areas (within 50 m of individuals) to determine whether Eastern Willets would respond to vocalizations of Western Willets. Next, playback tests were targeted at specific individuals. The cassette player was placed at the edge of a terrestrial territory and camouflaged. Next to the cassette player I placed either a lifelike mount of a male Willet in alternate plumage or a carved shorebird decoy. Models were alternated between tests, but willets seemed to respond similarly to either model. The carved decoy (a traditional Chincoteague Island "yellowlegs," 33 cm in body length) was not an exact replica of any shorebird species, but it presented a general likeness and was useful in luring Willets to traps. The results of the preliminary tests led to the design of a more formal experiment to test the null hypothesis that Eastern Willets would not differ in their responses to male pill-will-willet songs of Eastern versus Western willets. Because the acoustical signal appeared to be the strongest stimulant in preliminary tests, only the acoustical signal (i.e. without a live mount or decoy) was presented in the hypothesis test.

For field tests, I produced exemplars of male pill-will-willet songs from recordings. Each exemplar included a number of song sequences from a single singing bout. Ten exemplars of songs of male Western Willets were obtained from Utah ( $n = 8$  individuals; Tex Sordahl) and California ( $n = 2$  individuals; Cornell Library of Natural Sounds catalog nos. 49459 [C. Marantz] and 72508 [S. Kaminski]). Eight exemplars of the pill-will-willet song of male Eastern Willets were obtained during the 1995 breeding season using a Marantz PMD 221 cassette recorder, a Sennheiser directional microphone (Model K3-U), and a parabolic recording dish. These recordings were obtained from: Melbourne Lake, Jordan Bay, Gaspereau River, Little Harbour, and Rainbow Beach Provincial Park, Nova Scotia; Wallop's Island and Chincoteague Island, Virginia; and Fort Fisher State Park, North Carolina. The low variability documented in the vocal behavior of Eastern Willets suggested that a modest sample of exemplars would be representative of population variability (Sordahl 1979, Douglas 1996),

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but at least six tests were conducted for each exemplar.

Each exemplar was transferred to a 30-s tape loop using a RACAL recorder and/or the Marantz recorder. Three-min segments of each exemplar were produced using iterations of the tape loops. The sound level (sound pressure level [SPL] reference  $2 \times 10^{-4}$  dynes/cm<sup>2</sup>) of each exemplar was measured (Quest Model 2700 SPL) at a distance of 5 m from speakers placed about 0.8 m above the ground on a grass lawn. Eastern Willet recordings averaged  $70.3 \pm$  SD of 0.84 dB-SPL ( $n = 8$ ), and Western Willet recordings averaged  $71.0 \pm 1.7$  dB-SPL ( $n = 10$ ). Thus, the sound intensity of exemplars presented to subjects was similar. Also, the recordings of Eastern and Western willet songs were of comparable quality.

Recordings were played to Willets at West Chetzetcook ( $n = 1$ ) and Yarmouth Bar ( $n = 1$ ), Nova Scotia; the Barnegat and Brigantine divisions of Edwin B. Forsythe National Wildlife Refuge (NWR), New Jersey ( $n = 57$ ); Slaughter Beach, Delaware ( $n = 8$ ); Merritt Island NWR, Florida ( $n = 5$ ); and the Jekyll Island, Brunswick, St. Simon's, and Sea Island causeways, Georgia ( $n = 52$ ). Willets were approached along roads in a car. Speakers were placed on the edge of embankments at heights of 1.5 to 3 m above the level where Willets were standing. This design maximized broadcast range while keeping the speakers unobtrusive. Elevating a sound source increases broadcast range in a number of environments (Morton 1975, Marten and Marler 1977, Marten et al. 1977, Michelsen 1983, Brenowitz 1986). Eastern and Western willet exemplars were alternately presented on the same dates. Responses did not appear to be as strong to any pill-willet exemplar early in the breeding season, while migration was probably still occurring. Behavior was more predictable once Willets had established territories, so tests were conducted during this time.

A single exemplar of either an Eastern Willet or a Western Willet was broadcast to an individual Eastern Willet during each test. Individuals in this experiment were identified through observation and by the territories they defended. A new exemplar was presented to a different individual for the next test. This was done to avoid the confounding effects of habituation and the problem of pseudoreplication (Hurlbert 1984, Kroodsma 1986, 1989).

Data recorded for the hypothesis test included: (1) distance from speaker to subject, (2) activity level of the subject prior to the test, (3) latency of the response, and (4) intensity of the response. However, a clear test of the hypothesis was achievable based solely upon the dichotomy of "no response" versus "response." In all tests, Willets were observed for several minutes prior to the onset of the test. "No response" meant that the pattern of behavior prior to the onset of the test continued without interruption. At a minimum, a "response" involved an interrup-

tion of behavior and an orientation of the subject toward the playback source. Most responses were stronger than this, including a vocalization, and in many tests, movement toward the speakers. The G-test of independence with Williams' correction was used to analyze the presence or absence of a response to taped playbacks.

I could not determine the sex of all of the subjects tested. However, I tested every Willet that I encountered at the study sites. Considering the large sample size, it seems probable that ample numbers of males and females were tested. Differences in song characteristics probably are a reliable indicator of sex in Eastern Willets (Hansen 1979). Sonagrams indicate that the female's song is lower in frequency and flatter in terms of frequency changes than that of the male (Douglas 1996).

*Results.*—Analyses of sonagrams indicated a high degree of uniformity in song characteristics of Eastern Willets across their geographical range (Douglas 1996). However, temporal and frequency differences existed between the pill-willet songs of Eastern and Western willets. The Eastern Willet's song is higher in frequency and shorter in duration than that of the Western Willet (Fig. 1, Table 1). The pill-willet song was delivered by Willets during aerial flight displays and in other contexts associated with mate attraction and territorial defense (Vogt 1937, Hansen 1979, Sordahl 1979, Howe 1982, Douglas 1996), which provides the basis for formulating my experiment.

In preliminary playback experiments conducted in 1995, Eastern Willets responded to playbacks of all Western Willet vocalizations except the pill-willet (see Sordahl 1979 for explanation of vocalizations). Some Western Willet vocalizations elicited strong responses from Eastern Willets regardless of the context in which they were broadcast. Other types of vocalizations seemed to be context-specific. For example, the "eeee" call (chick distress call) invariably drew a strong response during the brood-rearing period. When broadcast in the *Spartina* marsh, the eeee call of the Western Willet attracted Eastern Willets (as many as 12) to the speakers, with some Willets hovering above or landing nearby the speakers. A similar response occurred at foraging areas, with all of the nearby Willets quickly converging upon the speakers. Playback of the eeee call evoked a lower response prior to nesting. In one such test, a Willet assumed an erect, alert posture and walked steadily toward the speakers. This was the strongest response to eeee observed during the prenesting stage. Some other Western Willet vocalizations, such as "kyah-yah" (a flight enticement call) and "kleep" (a call that increases distance between conspecifics), did not draw as strong a response in foraging areas (mudflats) as when broadcast on terrestrial territories.

Responses to playbacks generally were strongest

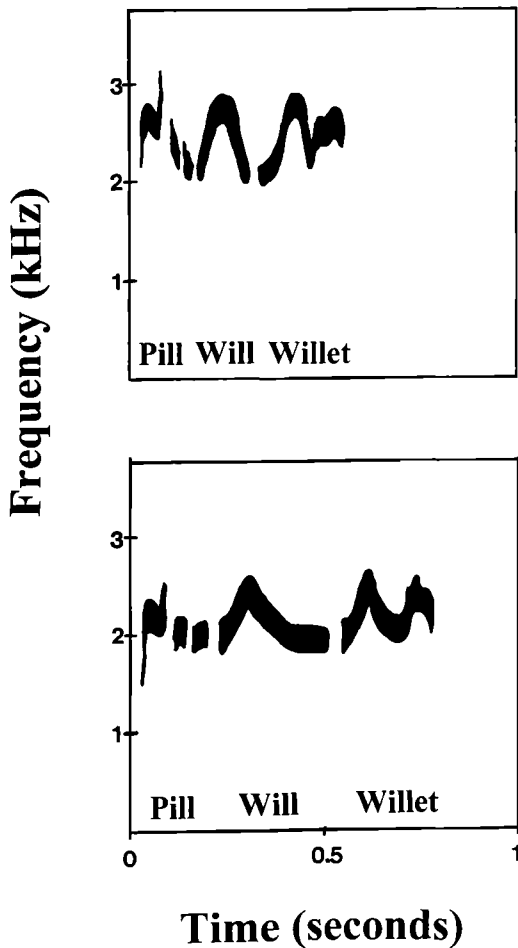


FIG. 1. Sonograms of "pill-will-willet" songs of male Eastern (upper panel) and Western (lower panel) willets.

on nesting and brood-rearing territories. Territorial Eastern Willets responded strongly to the Western Willet copulation notes ("klik" and "dik") and mobbed the mount or model that was presented. The "scream" call (an alarm and mobbing call) also drew

mobbing behavior. The scream attack call drew in neighboring Willets, which mobbed the model and speaker to within one meter. Playbacks of kleep and kyah-yah calls drew vocal responses from Willets, including neighbors that were outside the territory from which the playback was occurring.

Eastern Willets readily recognized and responded to playbacks of all Western Willet vocalizations except the pill-will-willet. Tape loops of the Western Willet's pill-will-willet were played continuously for 25 min in the same location without registering a response from the territory holder or any other Willets in the area. These results suggested that a critical test of song (pill-will-willet) recognition was warranted.

I designed an experimental test with independent replicates to conclusively demonstrate discrimination between songs. In this test, Eastern Willets responded to the pill-will-willet songs of Eastern Willets with a greater frequency than to the songs of Western Willets (83% vs. 22%, respectively;  $n = 118$ ;  $G = 112.7$ ,  $df = 1$ ,  $P < 0.001$ ). It was not necessary to include the variables of activity level, response level, and latency of response in the data analysis. A straightforward interpretation was achievable on the basis of whether a response was recorded. In 28 tests, Willets responding to Eastern Willet song flew toward the speakers and vocalized; the remainder of responses included a variety of less-aggressive behaviors, e.g. walking toward the speakers, vocalizing, ground displays, and orientation to the speakers. In the majority of cases, Eastern Willets did not respond to playback of the Western Willet's song. Of 13 Willets that responded to playback of Western Willet songs, 7 were males, and the sex of 6 could not be determined. The seven males responded with pill-will-willet songs, and three of them flew toward the speakers.

*Discussion.*—Eastern Willets discriminated between the songs of male Eastern and Western willets. Most Eastern Willets readily responded to the male pill-will-willet songs of Eastern Willets but did not readily respond to the pill-will-willet songs of male Western Willets. This suggests that observed differences in the frequency and temporal patterns of the pill-will-willet song (Fig. 1, Table 1; Douglas 1996) are relevant to species recognition. It is possible that

TABLE 1. Parameters of "pill-will-willet" songs of male Eastern and Western willets. Values are  $\bar{x} \pm SD$ , with  $n$  in parentheses.

Song parameter	Western Willet <sup>a</sup>	Eastern Willet	$P^b$
Song durations (s)	$0.78 \pm 0.039$ (68)	$0.59 \pm 0.042$ (127)	$<0.01$
Interval between songs (s)	$0.20 \pm 0.088$ (56)	$0.16 \pm 0.051$ (102)	$<0.01$
No. of "pill" notes	$3.3 \pm 0.46$ (66)	$3.1 \pm 0.46$ (123)	N/A
Maximum frequency (kHz)	$2.5 \pm 0.09$ (69)	$2.7 \pm 0.13$ (125)	$<0.01$
Minimum frequency (kHz)	$1.8 \pm 0.07$ (69)	$2.1 \pm 0.13$ (118)	$<0.01$

<sup>a</sup> Data adapted from Sordahl (1979).

<sup>b</sup> From two-tailed  $t$ -test.

song discrimination between the races results in reproductive isolation. In both races of Willets, the pill-willet song is used for self-advertisement, mate attraction, courtship, and territorial defense (Vogt 1937, Hansen 1979, Sordahl 1979, Howe 1982).

At the same time, Eastern Willets seem to recognize and respond to other vocalizations of Western Willets, and the sonagrams of these vocalizations are similar for the two races (Douglas 1996). Two other Willet vocalizations, "klik" and "dik," are associated with reproductive behavior in that they are given during copulation. Both Eastern and Western willets exhibit these vocalizations (Sordahl 1979, Douglas 1996), which sound similar to humans and appear similar in sonagrams.

Within the limitations of the biological species concept (Zink and McKittrick 1995), it seems reasonable to conclude that Eastern and Western willets have attained an intermediate stage in speciation. Clearly, Eastern Willets discriminate between the songs of their own race, *semipalmatus*, to which 83% responded, and the songs of the western race, *inornatus*, to which only 22% responded. Yet, in another component of reproductive behavior, the copulation notes klik and dik, no discrimination was apparent between the two races. Dobzhansky (1951) and Dobzhansky et al. (1977) argued that only incomplete development of reproductive isolation mechanisms can occur in allopatry, and that reinforcement through secondary contact is essential to complete development. It seems likely that discrimination between the specific signals of the two races of Willet is not yet complete.

Bretagnolle and Robisson (1991) recognized the duration of syllables and silence (i.e. the interval between syllables) and modal frequency as critical encoders of species identity in Wilson's Storm-Petrels (*Oceanites oceanicus*). They also noted that the decoding function in females may be more accurate than that in males. The duration of syllables and silence, and the frequency of the signal, probably are critical encoders for species-specific recognition in Willets. Likewise, the decoding function in female Willets may be more accurate than that in males. Few (if any) female Eastern Willets responded to Western Willet song in this test, and no females responded with song.

Eastern Willets and Western Willets may provide an example of allopatric speciation in progress (Douglas 1996). It is interesting to speculate on how song perception is involved in the speciation process. Nelson and Marler (1990) believed that birds are tuned to natural variation that occurs in conspecific song and reject values that fall outside of a normal distribution. Nelson and Marler tested this principle using synthetic songs in playback experiments with Field Sparrows (*Spizella pusilla*). They advanced the concept of "just-meaningful-difference" as the minimal change in a signal feature that elicits a measur-

able difference in the receiver. A reduction in note duration of 2.5 standard deviations, or an increase in song frequency of 2.5 standard deviations, achieved a "just-meaningful difference," i.e. a weaker response in the receiver.

The greatest differences between Eastern and Western willet song occur in call duration (4.5 standard deviations) and mean minimum frequency (2.3 standard deviations). In mean maximum frequency, Eastern Willet song is 1.5 standard deviations above Western Willet song. Internote intervals differ by only 0.8 standard deviations. The signal space occupied by songs of Eastern and Western willet has shifted in temporal and frequency dimensions (Fig. 1), but the elements of the songs have not been altered significantly. The number of elements, the structure and shape of the elements, and the order of elements essentially are the same (Douglas 1996). The pill syllable is the element that is most similar between Eastern and Western willet songs. The pill is loud, ringing, and staccato-like. In sonagrams, the pill syllables of Eastern and Western willets are similar in frequency and temporal characteristics (Douglas 1996). When an Eastern Willet responds to the song of a Western Willet, the pill syllable may provide the chief stimulus.

Nelson and Marler (1990) discussed the concept of a "perceptual anchor" controlling song recognition. This perceptual anchor in individual male songbirds (i.e. oscines) appears to be related to the characteristics of an individual male's songs. In fact, there are brain nuclei that respond uniquely to a male's own song. Accordingly, Nelson and Marler (1990) suggested that individual differences occur in processes of song recognition. These differences are patterned upon a template comparison of the male's own song structure with that of the incoming stimulus. A response of an Eastern Willet to the song of a Western Willet may be premised upon a similarity between the pill notes. That is, in those cases where recognition occurs, it may be that the frequency and temporal characteristics of the Western Willet's pill notes fall within 2.5 standard deviations of that of the individual Eastern Willet's pill notes. Thus, a gradual divergence appears to be occurring between the song characteristics of Eastern and Western willets, and this divergence has resulted in song discrimination and incomplete reproductive isolation in Eastern Willets.

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