Baxter welcomed us to Wawa and helped us catch juncos there. Judson Mead, Rod Suthers, and Gary Hafner lent us equipment to measure geomagnetism, Zugunruhe, and light intensity, and we thank them. Donald S. Farner kindly read and commented on an earlier version of the manuscript. This work was supported in part by NSF DEB-78-11982 and DEB-81-10457. We dedicate this paper to the memory of Cindy B. Patterson.—ELLEN D. KETTERSON AND VAL NOLAN JR., *Dept. Biology, Indiana Univ., Bloomington, Indiana 47405.* *Accepted 10 Aug. 1983.*

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Mimicry of the human voice by European Starlings: the role of social interaction.—Although vocal mimicry by European Starlings (*Sturnus vulgaris*) has often been noted (e.g., Bent, U.S. Natl. Mus. Bull. No. 197, 1950), the development of it has never been formally studied. The present report describes social constraints on starling mimicry and suggests possible functions. Although the targets of the mimicry here were humans, the major aim of the study was to understand how starlings naturally select sounds for mimicry. In other words, is their mimicry a faithful imitation of their social or physical surrounding or is it, as in most other species, quite biased toward a particular class of sounds? Because humans can detect speech more acutely than avian sounds, speech mimicry was used as an analogue to natural starling mimicry. As the presence of speech could be easily perceived, it would thus be possible to identify the origins of any mimicked sounds, as well as conditions under which starlings mimic their social world.

Methods and materials.—Seven starlings, four females and three males, were captured as five-day-old nestlings (Table 1). They were hand reared in the laboratory by the investigators until approximately 30 days of age. During this period, they were maintained as a group with equivalent and extensive contact with human caretakers. At day 30, a male and a female were assigned to the interactive contact (IC) condition, a male and female to the limited contact (LC) condition, and the remaining three to the auditory contact (AC) condition. IC1 and IC2 each remained in the homes of the respective investigator who had reared them. Each received daily vocal attention and companionship from its human caregiver. In addition, each had a male Brown-headed Cowbird (*Molothrus ater*) housed with it in a 0.7 × 1.3 × 1.3-m hardware-cloth cage. Explicit attempts to "teach" IC1 and IC2 speech were avoided, i.e., food or social contact was not offered as a reward for mimicry although each of these items was clearly sought by the birds. Whistled songs (e.g., "Dixie," "Popeye the Sailorman") were performed daily, usually when the birds were allowed to fly free and interact with their human caregivers. Mimicry by IC1 and IC2 was often imitated by the humans but again only in an unsystematic manner, i.e., the humans did not consciously imitate sounds as a particular strategy. Finally, IC1 and IC2 were exposed to tape-recorded passages of human speech and whistled songs twice daily for one month.

The LC starlings were also housed in homes, but with different caregivers who had not participated in the starlings' care as nestlings. Each bird was also housed with a cowbird companion. Because these birds were less "tame" with their new human caregivers, they were rarely allowed to fly free or to contact humans directly. Each was housed, however, in a room allowing it extensive vocal stimulation from humans. That is, they heard speech in their environment but were not "spoken to" consistently or allowed interaction with humans. The LC birds were not tutored by tape recordings. The AC birds were housed as a group in a cage (4.8 × 4.8 × 3.2 m) on a screened porch belonging to one of the investigators where they could hear all of the interactions inside the home where IC2 was housed. As a result, the auditory environment of the AC birds was yoked to the IC condition. Thus, they were

also exposed to the tape-recorded speech and songs twice daily for a month. Although these birds were originally as tame as the others, they quickly became quite shy with humans in that they both ceased to solicit food from humans and avoided being handled by humans.

All seven birds were fed an identical diet based on the Bronx Zoo diet for omnivorous birds and were given fresh water with vitamins and fresh food daily. Although IC and LC birds also received occasional "snacks" (e.g., fruit or cheese) from their caregivers, the amount of food obtained in this manner was insufficient to be of dietary consequence and was composed of food items already abundantly present in their normal mash. Thus, all the birds had identical exposure to humans until day 30 and then differed subsequently in terms of the social quality of their contact with human caregivers.

All the birds were tape-recorded regularly, producing about 1 h of vocalizations for each bird each week for 4 months. The birds were recorded at different times of the day across this period using a Uher 4200 Report recorder and a Uher 517 microphone.

The tapes resulting from these sessions were then transcribed and the birds' vocalizations were classified into five categories: clear human speech, human-produced sounds (e.g., whistling and indistinct speech), non-conspecific avian vocalizations, mechanical noises, and starling vocalizations. Random passages of tapes from all the birds were coded by a second observer. Observer agreement was high (89%), with the most disagreement involving distinguishing clear speech and speech-like sounds. All transcriptions of clear speech were also analyzed for content to ascertain the human origin of the mimicry.

Results.—Both starlings in the IC condition mimicked human sounds extensively. For IC1, 49% of his mimicry derived from human speech and another 25% from human whistling. Likewise, IC2's percentage of human mimicry was 68%, 28% comprising speech and 40% whistled tunes. For each bird, however, the proportion of mimicked speech that was highly articulate was low, 9% for IC1 and 4% for IC2. This figure derives from use of very strict coding criteria and the high degree of articulation and intelligibility required on the starlings' part to be clearly understood on audiotape. Using the broader criterion of speech-like sounds seems a fairer procedure in that human speech when spoken by humans into tape recorders may not be clearly intelligible but is unmistakably identifiable as human speech. This was the case for the starlings as well.

None of the LC or AC birds ever mimicked human speech although they all mimicked mechanical noises and other birds, most notably the cowbird companions of the LC birds (Table 1). Here their mimicry was frequent and quite accurate, reproducing even some of the higher frequency components of cowbird song (around 9 kHz). This frequency range exceeds that published for the starling voice; previous studies had recorded a maximum of only 8.2 kHz (Brand, Auk 55:263–268, 1938). Finally, no bird ever mimicked the tape-recorded passages although IC1 did mimic the mechanical noise of tape hiss.

Origin of the mimicry.—For both IC1 and IC2 the major part of their human mimicry could be attributed to sounds produced by their human caregivers. This was evident not only by content but by their distinct mimicry of the male caregivers' intonation patterns. It was, in fact, clear to other listeners whom the birds were mimicking. In both cases, the birds rarely mimicked the female spouses of their investigators although the spouses had frequently interacted with the birds after capture. In terms of content, the selectivity of their mimicry was also evident. IC1 mimicked speech patterns such as "Good morning, Rex [IC1's name]" and statements such as "It's time," "Basic research" and "Hi." The latter vocalization he subsequently used in interactions with humans and with other birds. IC2 frequently said her name as well as often repeated statements such as "You're a crazy bird." Both birds were prolific, if off-key, whistlers and produced mimicked whistled songs of several seconds duration that were clearly recognizable. Most often, whistled tunes, easily recognized as distinct to humans, were combined by the starlings, e.g., IC1 would whistle a few

TABLE 1

A SUMMARY OF THE EXPERIMENTAL CONDITIONS AND RESULTS FOR STARLING MIMICRY

	Interactive contact	Limited contact (LC)	Auditory contact (AC)
Subjects	one male and one female, individually housed with a male cowbird	one male and one female, individually housed with a male cowbird	two females and one male, housed together
Experience	daily human companionship and 1 month of tutoring by tape recording	routine care from humans and exposure to human conversation	routine care from humans, 1 month of individual tutoring by tape recording, exposure to human speech of IC2 but limited visual contact
Content of mimicry			
Speech sounds	39%	0%	0%
Whistling	33%	0%	0%
Mechanical noises	5%	1%	0%
Avian sounds	16%	49%	3%
Starling sounds	7%	50%	97%

notes of "Dixie" followed by several notes of "Swanee River." The whistled tunes also appeared to go through many idiosyncratic variations that were solely created and re-created by the starlings. Another interesting feature of their mimicry was their combination of sounds that naturally occurred together, such as an episode consistently mimicked by IC1 comprising the sounds of a door opening and dogs barking, followed by saying "Good morning, Rex," and the production of a whistled tune used by his caregiver as a greeting. This was in fact the daily scenario as the caregivers' dogs were let outside, followed by IC1 being released from his cage and given his customary greeting.

Analysis of the recording sessions also revealed the repetitious quality of the mimicry, especially of the companion cowbird's song or of whistled tunes that would be repeated "verbatim" hundreds of times in rapid succession. For example, LC1 once mimicked the cowbird's song 256 times in succession during one 30-min session.

Sonagrams of mimicry by IC1 appear in Fig. 1. Because the aim of the study was not to determine how accurately starlings could mimic speech, but to learn under what conditions they could produce recognizable speech, no extensive efforts were made to obtain high quality tape recordings for acoustic analysis. Thus, the sonagrams may underestimate the starlings' mimicking accuracy. We judged the quality of mimicry by listening to audio tapes rather than by visual inspection of sonagrams. The actual content of the mimetic sequences was easily determined with this method in the same way that human speech is perceptible and articulate to listeners when heard over the telephone even though much acoustic detail is missing. That such detail is also lacking in starling "speech" is demonstrated by the sonagrams. The question of the absolute accuracy of the starling's mimicry awaits further analysis.

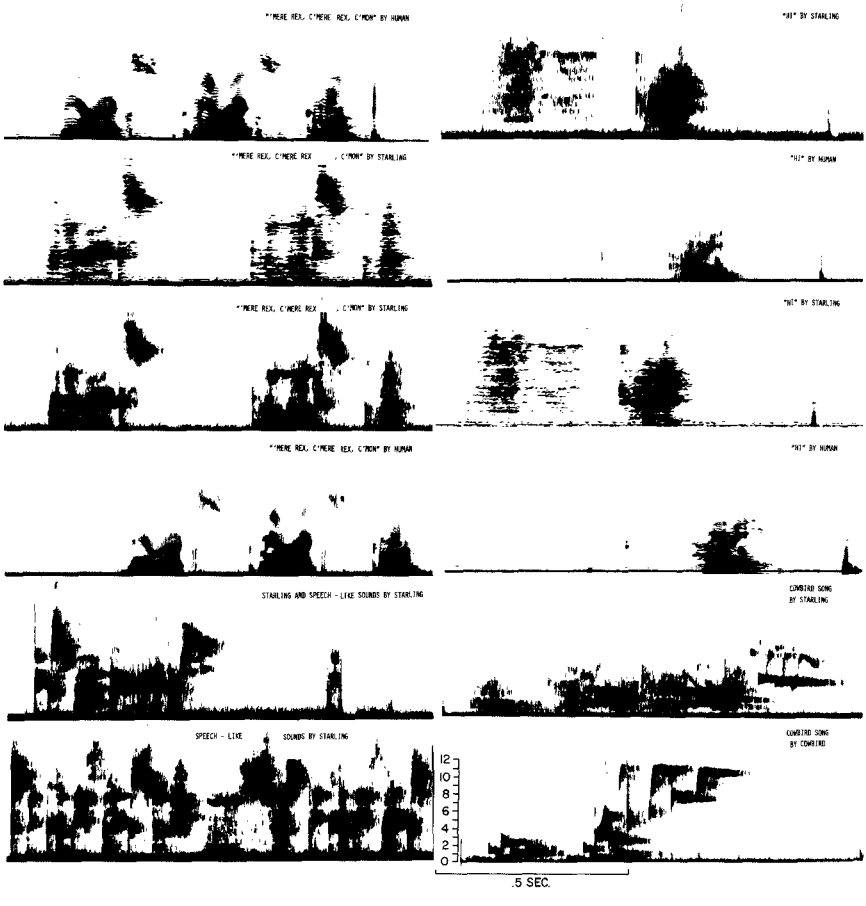

FIG. 1. Transcriptions of the mimicry by IC1: "Mere, Rex, c'mere, Rex, c'mon" by human and starling, respectively, with a narrow band setting; same content with a wide band setting; starling and speech-like sounds by starling; speech-like sounds by starling; "Hi" by starling and human, respectively, with a narrow band setting; same content with wide band setting (the first sound for the starling is his mimicking of a human sniffing followed by "Hi"); starling mimicry of a cowbird song; cowbird song by a cowbird. Sonograms were made on a Kay 6061B SonaGraph.

Several exemplars of the starling's mimicry are shown in Fig. 1. The phrase, "Mere, Rex, c'mere Rex, c'mon," was exceptionally distinct to listeners, particularly its intonational patterns which accurately imitated the cajoling sound of the speaker. This utterance was used frequently by humans to get IC1 back into his cage, a sometimes frustrating task. The word "Hi" is also shown. This word was also used extensively by IC1, especially during contact with humans, which was, of course, the context in which the word was also experienced by IC1.

The category of "speech-like sounds" represented a fascinating array of vocalizations characterized mostly by mimicry of the cadence of human conversation, i.e., the characteristic intonation contours marking statements or questions. To listeners, it sounded like a person talking in a muffled voice. A transcribed version of a sequence such as that shown in Fig. 1 would read as follows: "'because effects,' 'such rules became effects,' whistle, starling sound, 'just because effects'." (It should be noted that neither IC1 or IC2 had ever had extensive experience with conspecific vocalizations as they were hand-reared and removed from contact with other starlings at 30 days of age.) The best human analogue to the starlings' speech-like sounds is the expressive jargon of human infants (Dale, Language Development: Structure and Function, Holt, Rinehart and Winston, New York, New York, 1976). In the early stages of language development, infants produce conversation-like speech with the appropriate intonation although the words are either not clear or are poorly produced. Moreover, as is characteristic of the repertoires of infants (Lenneberg, Biological Foundations of Language, Wiley & Sons, New York, New York, 1967), many of the stock phrases present in the starlings' jargon were often-repeated phrases that typically occurred at the beginning or end of utterances.

A final important quality of the starlings' mimicry of speech was that they also imitated the act of speaking, i.e., the physical sounds of smacking lips and breath inhalation that accompanies speech. Their mimicry thus included the broad vocal context of speaking, not just the linguistic or perceptual event of speech. A related example of this is shown in Fig. 1 where each of IC1's imitations of "Hi" is preceded by a sound unmistakable on tape as a human sniffing. The origin of this combination was most likely the chronic respiratory infection of his caregiver who suffered from allergies to birds.

Discussion.—The data show the selectivity of starling mimicry and its dependence upon the nature of the social interaction between the starling and its mimicked partner. As in duetting or mimicry by other species (Todt, Z. Tierpsychol. 39:178–188, 1975), starling mimicry may function to define particular social relationships. Social relationships formed at an early age may be the most important for determining mimicry. We have subsequently taken IC2 and housed her with a different caregiver who periodically attempted to socialize with her by offering food; she has adopted new, but limited, forms of mimicry. Reinstatement of the type of social interaction present for a young nestling, e.g., dependence upon another for food, and perception of the caregiver as a "surrogate" companion, may facilitate the formation of such social bonds (Hartshorne, Georgia Oriole 26:23–27, 1961).

In any case, we offer these data as empirical evidence of the environmental origins of starling mimicry. Clearly what is important to the starling is the nature of the social relationship with its mimicked partner: only when humans served as actual interactants were they the target of mimicry. Likewise, when cowbirds or starlings filled this role, as in the LC and AC conditions, they constituted the starling's mimicry. Perhaps a function for starling mimicry in large flocks is that their mimicry serves as "passwords." As such, the data are consistent with past work done on other starlings (Bertram, Anim. Behav. Monogr. 3:79–192, 1979) as well as in other social avian species (Payne, Anim. Behav. 29:688–697, 1981; Feekes, Z. Tierpsychol. 58:119–152, 1982).

A final note—in order to distinguish this work from those in which birds, most recently the African Grey Parrot (*Psittacus erithacus*), have also been "taught" to talk (Todt 1975; Pepperberg, Z. Tierpsychol. 66:139–160, 1981). Although our method for transmitting human speech is consistent with the highly social quality of the tutoring methods used by Todt (1975) or Pepperberg (1981), and may in fact rest on similar social principles, our starlings were never consciously trained or taught any particular word or phrase. All speech was used as a method of social interaction modelled after how humans use speech with each other, particularly how adults use speech with children. Our aim was to see if social companionship with auditory exposure and no explicit training would be

enough to produce mimicry. It was. What the outcome of explicit training procedures would be with starlings remains to be explored. We offer these data as an incentive for others to pursue the study of these talented and companionable birds.

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Vocalizations of the Black-throated Gray Warbler.—Vocalizations of birds range from simple notes to complex repertoires that vary in structure and function (e.g., Thorpe, Bird-song, Cambridge Univ. Press, London, England, 1961; Lemon, Condor 77:385–406, 1975; Catchpole, Vocal Communication in Birds, Univ. Park Press, Baltimore, Maryland, 1979). The study of avian vocalization adds to knowledge of pair formation and breeding behavior, territory establishment and defense, and ultimately to aspects of competition and the formation of assemblages of species. In this study we analyze vocalizations of the Black-throated Gray Warbler (*Dendroica nigrescens*), and through playback experiments, describe the information content of these songs. The singing behavior of other *Dendroica* warblers has been described (e.g., Morse, Wilson Bull. 78:444–455, 1966, Wilson Bull. 79:64–74, 1967; Ficken and Ficken, Auk 87:296–304, 1970; Lein, Nature 237:48–49, 1972, Can. J. Zool. 56: 1266–1283, 1978; Kroodsma, Auk 98:743–751, 1981), but controversy surrounds the meanings of different song types (Lein 1972, 1978; Krebs, Anim. Behav. 25:475–478, 1977, Anim. Behav. 26:304–305, 1978; Slater, Anim. Behav. 26:304, 1978). Although songs of the black-throated gray have been compared with closely related congeners (Stein, Living Bird 1:61–71, 1962), we know of no other study that gives details on the singing behavior of this species.

Study area and methods.—Songs of breeding Black-throated Gray Warblers were recorded during April and May of 1981 and 1982 near the west entrance of the Finley National Wildlife Refuge (FINLEY), Benton Co., Oregon, using a Nagra III recorder and Gibson parabolic microphone, model P-200. The study area (about 30 ha) was characterized by a mixture of mature Oregon white oak (*Quercus garryana*) and Douglas-fir (*Pseudotsuga menziesii*). A more complete description of the study area, including a description of the habitat use and foraging behavior of black-throated grays at FINLEY, was given by Morrison (Auk 99:503–513, 1982). About eight male black-throated grays were located in the study area each year. The songs of at least five different individuals were recorded in 1981; we do not know if songs recorded in 1982 were of the same or different individuals as those in 1981. Songs recorded in the wild were analyzed on a Kay Elemetrics Sona-Graph Model 7029A using the 300 Hz wide band filter and the 80–8000 Hz frequency spectrum. The resulting sonagrams were studied to compare song types recorded at FINLEY. All tape recordings made in this study were deposited in the Florida State Museum Bioacoustic Archives as FSM master tape numbers 560, 563, and 577. About 50 h on 20 days for the 2 years of study was spent recording and observing the singing behavior of the black-throated gray. About 70% of the observations were conducted within 3 h of sunrise; 15% were conducted during late morning and 15% during afternoon. About 80% of the fieldwork was conducted in 1981.

Tapes used for playback experiments were made by transferring the original recordings to cassette tapes; experiments were also conducted using the Nagra and the original tapes.