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# Social Influences on the Whistled Songs of Starlings

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**Summary.** Playback experiments on individuals singing near their nest show that starlings tend to repeat the theme they have just heard even if it is an unfamiliar dialect and not 'programmed' in their own current sequence. The type of response and its temporal characteristics could be related to internal sequential organizational rules. Moreover, starlings discriminate between two dialectal variants of a given theme and respond more often and more quickly to the familiar dialect. A social influence on the choice of theme by the individual can also be observed in foraging flocks and roosts where song is frequently given. Observations of such groups reveal that one theme predominates on each given occasion and that it depends on the number of individuals present and on the type of group (flock or roost). This is probably a function of the tendency to match. Previous observations of flights toward the roost showed that birds originating from different dialectal areas congregate in such groups. A few analyses of songs in flocks and roosts confirm the presence of different dialects simultaneously.

## Introduction

Every act an individual performs is a result of its integration of environmental and particularly social data. The mere presence of conspecifics can influence the behavior of an animal who is thus induced to imitate them. Such social facilitation can lead to collective displays.

Social facilitation can be found in vocal interactions between songbirds either during territorial defense or even more distinctly in collective song chorusing (Armstrong 1963; Gochfeld 1977). It is also found at another level in songbirds with repertoires of more than one song type (or theme), because for them the question of which theme to sing at any given moment constantly recurs.

In starlings, each individual sings between 7 and 12 whistle types. Some of these themes are peculiar to each individual, whereas others can be found in all birds (Hausberger and Guyomarc'h 1981). Moreover, each of these specific themes can be subdivided into different variants that correspond to different dialects. Thus, recordings of birds near their nests in an area of 50 × 40 km have shown that each variant of the rhythmic theme, RT (CR in Hausberger and Guyomarc'h 1981), characterizes a small reproductive colony. Each variant of the other specific themes corresponds to a dialectal area (which includes many of those reproductive colonies). The size of those dialectal areas is different for different themes: 5 to 10 $km^2$ for the theme with inflection, IT (CSDIb); 150 $km^2$ for the theme with 'harmonics', HT (CSDUH); more than 800 $km^2$ for the uniform simple theme, ST (CSDUS), and the composed-call (CC). Thus, a system of five dialects superimposed appears and the number of individuals singing the same dialect varies according to the whistle type considered (Adret-Hausberger, in press). However, at least in roosts, several thousands of birds from several different nesting sites (and thus of different dialects) intermingle (Clergeau 1981) and sing. In those groups, will the birds sing various themes or will they sing preferentially one whistle type? And will they be able to distinguish other dialects from their own?

Furthermore, observations of interactions between neighbors near their nest have shown that birds tend to repeat the theme they have just heard. This implies perceptual capacities to discriminate between different themes. But will the individual be able to recognize the song type even if it hears

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an unfamiliar dialectal variant? Can there be two levels of recognition (the theme and its variants) or do local dialects obscure theme recognition?

## Materials and Methods

Since we were examining vocal interactions during both nesting and foraging, two separate procedures were used and will be described separately.

*Experimental Study of Vocal Interactions Near the Nest.* This study was carried out on the campus of Rennes-Beaulieu (France). A previous study showed that the frequency of emission of the different whistle types varies according to seasonal (in preparation) and diurnal rhythms as well as to nest proximity (Hausberger and Guyomarc'h 1981). To ensure uniformity of data, in this study we made observations only during a limited time span (the nesting phase during the reproductive cycle: about two weeks in May 1980) and only during sunrise and 900 solar hours. Birds were observed only near their nest. Six individuals belonging to two different reproductive groups (three in each) were tested for their responses to tape recordings of various vocal themes. Those six birds shared the same dialectal variants for the themes considered. Individuals were recognized by the following criteria:

1. Nest visitation: it was often possible to observe subjects singing at the same time near their respective nests. This confirmed that only one male occupied one nest.
2. Beak color: it allows the sexes to be easily distinguished.
3. Individual vocal themes as well as minor variations of structure in the specific themes characterize each individual within its colony.

*Playback Experiments.* A loudspeaker was linked to a Uher 4000 tape recorder, which played recordings of various vocal themes. The three themes broadcast were the most frequently used in vocal interactions: IT, HT, ST.

Two dialectal variants of each theme were broadcast. One familiar (F) variant corresponded to the common variant and the other, unfamiliar (NF), was produced by an individual nesting in a site 15 km away (Fig. 1).

The familiar variant was derived from recordings of a nonneighbor individual in order to avoid effects due to individual recognition. Within reproductive colonies, distances between nests vary from one to a few meters. Males do not defend a territory but only the nest hole. Vocal interactions occur between neighboring birds. Therefore, the loudspeaker was placed 1 m above the ground and a short distance from the bird observed (less than 10 m) in a tree where other starlings sometimes sing.

Each whistle was broadcast during the second following an emission by the bird being tested. The order of playbacks was as follows: IT F-NF, HT F-NF, ST F-NF and then again IT, etc. One whistle was played each time. Two identical stimulations were separated by several hours or several days. Nonidentical playbacks were separated by at least several minutes.

Two main problems arose: we needed to know whether the theme given after a test would have been given in any case, that is to say, whether it was expected in the sequence or not. In addition, even under 'natural' conditions, each starling does not seem to answer all the whistles it hears. Thus, only one test with each theme and each bird was not sufficient.

Therefore, each whistle was broadcast ten times to each individual, apart from two birds (B2, B3) (four times each whistle), which began to incubate before the end of the experiments. Thus, a total number of 287 tests were made. A preliminary study of the sequential organization of song was made for each bird and showed that all the individuals tend to repeat themes in a 'normal' sequence (see below). It was necessary to take this fact into account before choosing the theme to be broadcast. Since observations of natural vocal interactions suggest that an individual repeats the theme it has just heard, the broadcast of a given theme was never made immediately after its emission by the bird being tested, but only after that of a song type that does not usually precede it.

We considered that there was a vocal response if the sequence being sung was modified by the broadcast, that is to say, if a transition usually 'nonpreferred' occurred at that moment. The themes given before and after the playbacks were noted, as well as the time interval between the theme broadcast and the one emitted by the bird. The different themes were identified directly by ear, their different structures making recognition easy.

*Analysis of the Sequential Organization.* Birds were observed when they sang alone near their nests, uninfluenced by the songs of other individuals. No temporal limitation was neces-

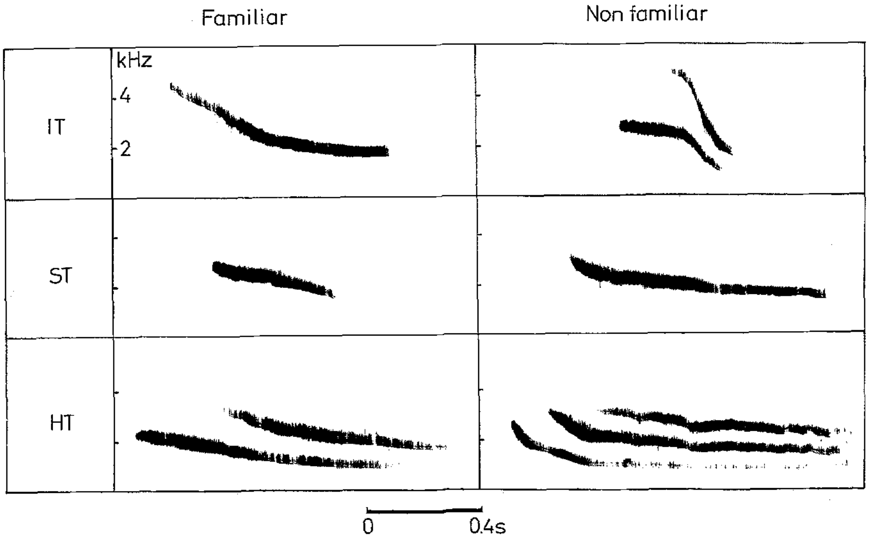

**Fig. 1.** Sonagrams of the variants of the different themes broadcast for the experiments. The six individuals belong to the same dialectal population for the themes considered here

sary to decide if two successive whistles did or did not belong to the same sequence. During this period, whistled sequences were either followed by warbling or by birds flying away. The statistical significance of first-order successions was tested using $\chi^2$ tests (or binomial tests, if expected frequencies were less than five).

*Observations of Foraging Flocks and Roosts.* Most observations of foraging flocks were made during October 1980. Recordings were made while all birds were perched (whistles are not usually given on the ground). Generally, starlings foraged from one to several hours before flying toward high song perches (trees, electric lines) and singing. Most data were obtained between 10 and 14 hours (French legal hours). Varied recording sites were chosen in an area of 50 x 40 km where songs were well known and dialects mapped (Adret-Hausberger, in press). Flocks of 30–500 individuals were observed (the same individual can be found in different flocks in the same day: small flocks congregate to form large flocks at the most attractive sites). Background noise often hindered analysis. Thus, themes were most often identified by ear. Only recordings that permitted easy recognition of themes were retained. Observations of roosts were made at various sites and times. Recordings were made during the interval between the arrival of birds on trees and bushes and the cessation of activities.

## Results

### Natural Song Patterns

Individuals singing alone near their nests show a significant tendency to repeat all themes (Table 1). In addition, the transitions HT→RT and RT→Ind T (individual themes) are preferred. The time interval is always shorter (about 3 s) for preferred transitions (generally repetitions) than for 'nonpreferred' ones (Table 2).

### Responses to Playbacks

*Modifications of Sequence.* About 60% of the time, experimental subjects modified their current sequence upon hearing a stimulus theme from the playback speaker ( the song types given before and after the broadcast correspond to a 'nonpreferred' transition). Three kinds of modification occurred. Most commonly, subjects repeated the theme broadcast (81% of the cases, Table 3a). Secondly, in 10% of the tests, the HT stimulus was followed by RT. Third, a minor number of flights occurred following the stimulus presentation (Table 3d). In general, individual themes were never used to answer the stimulus tape. There was also no significant difference in the rate of response among individuals or groups. When an individual did modify its sequence, the response latency was short, about 3 s, but if no modification occurred, the latency was longer, about 7 s.

**Table 1.** Sequential analysis of the different whistles. Example for one individual (A2). The same results were obtained for the other five individuals. The tests were made on each cell of the matrix. + = 'preferred' transitions which occur more often than expected ($P<0.05$, $\chi^2$-test). − = 'nonpreferred' transitions. *NS* = nonsignificant. Total number of transitions observed for this bird: 1,240

| Whistle type Preceding | Following | | | | | |
|---|---|---|---|---|---|---|
| | IT | HT | CSDIh | ST | RT | Ind. T. |
| IT | + | NS | − | − | NS | − |
| HT | − | + | − | NS | + | NS |
| CSDIh | − | − | + | NS | − | NS |
| ST | − | − | + | + | − | NS |
| RT | − | + | − | − | + | + |
| Ind. T. | NS | NS | − | NS | + | + |

**Table 2.** Average time interval between two whistles according to whether the transition is 'preferred' or 'avoided' (see Table 1). Test of comparison of two means (Schwarz 1963): $^{***}P<0.01$; $^{*}P<0.05$. In brackets: number of such transitions observed

| | Time interval in s | | |
|---|---|---|---|
| | Preferred | | Non preferred |
| A1 | 2.9 (516) | *** | 7.0 (58) |
| A2 | 2.3 (854) | *** | 6.0 (158) |
| A3 | 2.7 (345) | *** | 8.1 (84) |
| B1 | 2.6 (383) | *** | 8.5 (33) |
| B2 | 1.1 (348) | *** | 5.5 (30) |
| B3 | 4.0 (225) | * | 12.1 (60) |

*Recognition of Themes.* Each individual tended to repeat the stimulus theme whether or not it was a familiar one (Table 3a). Thus, each bird recognizes each theme even when it is an unfamiliar dialectal version of that theme. However, the response was the subject's own version of the stimulus theme, not a perfect copy.

*Discrimination of Dialects.* All individuals tended to respond vocally to a familiar dialect stimulus more often (Table 3b) with a shorter latency (Table 3c) than when hearing an unfamiliar dialect. Flights were also more frequent following playback to a familiar one. Flights, when occurring, were in various directions with no tendency of flight toward the speaker.

### Whistles in Flocks and Roosts

Five foraging flocks of 25–50 individuals, seven of 80–100, and ten of more than 150 birds were observed. According to flock size, starlings sing one preferential theme, which constitutes 26%–95% of the whistles emitted. Thus, they prefer to sing HT when they are in groups of 25–50

**Table 3.** Results of the playback experiments. a) % of times the bird tested produces the same whistle type than that broadcast when there is an answer to playbacks of familiar (*F*) or unfamiliar (*NF*) variants. Tests are made on rows by comparison for each variant with responses without matching. b) Comparison of the frequency of answers according to whether the whistle played is a familiar or unfamiliar variant. c) Comparison of the latency of answers according to the dialectal variant broadcast. d) Number of flights observed after a playback according to the dialectal variant broadcast. * $P<0.05$; ** $P<0.01$; *** $P<0.001$; for a, b, d: $\chi^2$-test or Fisher test; for c: test of comparison of means (Schwartz 1963)

| | | Individuals | | | | | | Overall |
|---|---|---|---|---|---|---|---|---|
| | | A1 | A2 | A3 | B1 | B2 | B3 | |
| a) Response with the same theme (%) | F | 64* | 86*** | 85** | 87*** | 100** | 57 | 81*** |
| | NF | 60** | 69*** | 56* | 75*** | 100* | 57 | 61*** |
| b) Frequency of answers (%) | F | 45 | 73** | 78** | 48* | 55 | 55 | 62*** |
| | NF | 23 | 54 | 29 | 17 | 35 | 25 | 30 |
| c) Mean latency (S) | F | 3.9<br>*** | 1.8<br>*** | 2.4<br>* | 2.8 | 3.6<br>* | 5.2<br>*** | 3<br>*** |
| | NF | 13.6 | 8 | 5.3 | 9.2 | 5.8 | 13.5 | 8.5 |
| d) Number of flights | F | 1* | 0** | 1* | 1** | 1 | 1 | 5*** |
| | NF | 6 | 3 | 4 | 5 | 1 | 1 | 23 |

**Table 4.** Relative frequency of emission of the different themes in different foraging flocks. *Underlined:* greatest frequency of emission of one theme. Flocks I: 25–50 individuals, II: 80–100, III: 150–500

| Flocks | Recording duration (min) | Themes (%) | | | | | | Total whistles |
|---|---|---|---|---|---|---|---|---|
| | | IT | ST | HT | RT | CC | Others | |
| I1 | 3 | 5 | 14 | 36 | 23 | 11 | 11 | 44 |
| I2 | 10 | 7 | 20 | 26 | 15 | 25 | 7 | 88 |
| I3 | 18 | 10 | 17 | 43 | 19 | 7 | 4 | 107 |
| I4 | 4 | 13 | 0 | 47 | 13 | 0 | 27 | 15 |
| I5 | 3 | 11 | 4 | 57 | 14 | 14 | 0 | 28 |
| II1 | 12 | 68 | 1 | 11 | 13 | 1 | 4 | 201 |
| II2 | 6 | 49 | 22 | 10 | 7 | 5 | 7 | 59 |
| II3 | 4 | 37 | 22 | 22 | 15 | 5 | 5 | 41 |
| II4 | 11 | 38 | 20 | 29 | 9 | 1 | 3 | 208 |
| II5 | 14 | 78 | 7 | 8 | 3 | 0 | 4 | 92 |
| II6 | 3 | 33 | 15 | 22 | 7 | 7 | 14 | 27 |
| III1 | 19 | 2 | 32 | 11 | 16 | 17 | 2 | 221 |
| III2 | 11 | 9 | 48 | 23 | 21 | 0 | 0 | 149 |
| III3 | 17 | 7 | 47 | 24 | 6 | 8 | 8 | 119 |
| III4 | 14 | 16 | 43 | 22 | 5 | 6 | 8 | 314 |
| III5 | 7 | 22 | 40 | 20 | 12 | 3 | 3 | 78 |
| III6 | 13 | 22 | 40 | 15 | 12 | 3 | 8 | 102 |
| III7 | 29 | 13 | 49 | 13 | 18 | 0 | 7 | 199 |
| III8 | 16 | 12 | 62 | 12 | 2 | 0 | 12 | 103 |
| III9 | 5 | 5 | 95 | 0 | 0 | 0 | 0 | 20 |
| III10 | 15 | 4 | 94 | 0 | 2 | 0 | 0 | 161 |

**Table 5.** Relative frequency in percentage of emission of the different themes from the last preroost to the roost in the same evening and total number of whistles obtained. ** $P<0.001$; $\chi^2$-test

| Roost theme | D2 | | D4 | |
|---|---|---|---|---|
| | Preroost | Roost | Preroost | Roost |
| IT | 12 | 3 | 4 | 2 |
| ST | 14 | 19 | 30 | 26 |
| HT | 58 | 35 | 55** | 14 |
| RT | 25** | 43 | 6** | 54 |
| CC | 0 | 0 | 1 | 1 |
| Others | 0 | 0 | 4 | 2 |
| Total | 157 | 37 | 121 | 43 |

individuals, IT when they are 50–100, and ST when they are more than 150 (Table 4). In all flocks with about the same number of individuals (for example, the five flocks of 25–50 birds), the same theme is preferred (Kendall coefficient of concordance: $P<0.01$). It is interesting to note that in the flocks specific types are sung almost exclusively (only 6% of the whistles are individual types).

In each of the five roosts observed, the rhythmic theme (RT) is greatly predominant, constituting 38%–51% of the total number of whistles heard. No difference appeared between the roosts observed in summer (4) and that observed in winter (1). In two cases, only 1% of the whistles were individual themes. In two cases, the same individuals could be followed from the last preroost to the roost. The frequency of HT was the highest in the preroost, but the same birds sang more RT when they arrived at the roost (Table 5).

Moreover, the number of whistles emitted at the roost was highest when birds chose a perch for the night (Fig. 2).

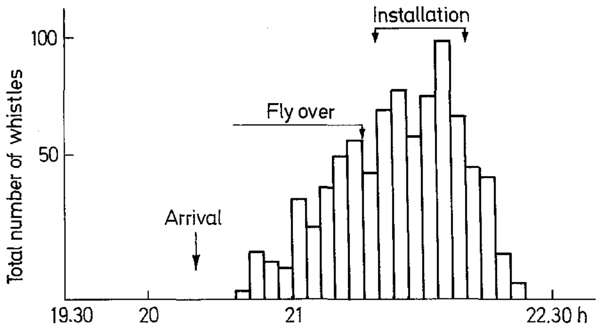

**Fig. 2.** Example of the change in number of whistles produced in a roost observed in May 1980. Fly over: the birds fly over the bushes and sometimes perch, but they are very unstable. Installation: the birds choose a perch for the night. Hours are legal French hours

Only a few analyses were good enough to use to determine the origin of the birds present in the large foraging and roosting congregations by referring to local dialects, a map of which was available for the area (Adret-Hausberger, in press). The analyses confirmed that birds of different dialects mix in feeding sites and in roosts. Thus, in two roosts, analysis of 14 and 35 RT songs reveal, respectively, 13 and 18 different dialectal variants.

Even though the number of good analyses we were able to obtain in foraging flocks (between 4 and 42 in 8 flocks) was very low, different dialectal variants of the predominant theme in the flock were always revealed (apart from ST, probably because of the great size of each of its dialectal areas). The variants observed corresponded to those sung in the dialects nearest to the feeding site considered.

## Discussion

Playback experiments near the nest confirm that starlings tend to repeat the theme they have just heard. Two levels of recognition appear: the bird recognizes the song type even if the whistle broadcast is another dialectal variant of that type; moreover, it can also distinguish its own dialect from another, responding more often and quickly to the familiar ones.

In foraging flocks and roosts, birds also match songs heard but, according to flock size or the context (e.g., preroost/roost), they sing one of the specific themes preferentially. Thus, a given starling can modify its choice of theme according to the social environment. A few sound spectrographic analyses confirm that birds of different dialects mix in roosts and flocks.

There have been several hypotheses proposed to explain song matching in birds.

1. Song matching is a late phase of an escalating conflict and signals imminent attack (Krebs et al. 1981). This hypothesis is not supported by our results. Although we did observe a shorter latency when matching occurs, as did Krebs et al. in the great tit, we did not find any correlation between matching and eventual approach, which could be a probable cue to imminent fighting. During interactions, neighboring birds often stay near their own nests. A relationship between song matching and territorial defense is difficult to study in the starling, which nests in small colonies and seems usually to defend only the nest hole. Moreover, two neighbors can countersing 30–80 times in a 2-h period with 98% of matching without ever physically approaching each other.

2. Song matching may strengthen social relations and thus permit dialectal characteristics to be preserved (Payne 1981). Thus, in Brittany, where starlings are sedentary, each male visits its nest each day in the year and can be observed in the reproductive colony several hours a day mainly in the morning and evening. These visits are accompanied by numerous vocal interactions between neighbors.

Moreover, starlings answer to the broadcast of an unfamiliar dialectal variant by matching, singing their own variant of the theme. This could give two kinds of information to the eventual rival: (1) the 'responder' is of the same species because it also has this theme in its repertoire; (2) it does or does not belong to the same dialectal population. With a nonmatching dialect, the intruder might eventually be led to investigate another site.

As in other species (Lemon 1967; Milligan and Verner 1971; Thielcke 1973; Kreutzer 1974), a stronger response is observed to the familiar dialect. Kreutzer's experiments show that the strength of male wrens' answer is related to the similarity between the unfamiliar dialect and their own. It is possible that an unfamiliar variant is more difficult to recognize by comparison with the 'reference system' of the bird. This could explain the longer latency periods and lower response frequencies observed in response to the unfamiliar dialect. However, the results of Baker et al. (1981) show that the experience of another dialect, but a neighboring one, can be more important than the differences in structure and provoke a greater response from the birds.

3. A variation on the social-relationship hypothesis is that the function of song matching may vary with context. Thus, in the starling, dialectal structures are well defined with relatively precise boundaries when we consider the nest as reference, all the neighbors singing the same dialect. But the observations of flocks and roosts show that at giv-

en times of day, birds move beyond dialectal boundaries. Payne (1981), in his social model of dialects, suggests that either social interactions are absent between birds of different dialects or that if interactions do occur, they are of a different kind. In starlings, such interactions do not seem to occur in nesting colonies, but they do occur in flocks and roosts. Perhaps the ability to discriminate dialects could permit the establishment of different relationships between birds of different dialectal populations. Baker (1975) proposes that dialect differences increase tolerance between foraging birds. Only observations of banded starlings would provide this information. This would imply, however, that the 'level' of tolerance varies according to the number of individuals present and that the different themes have different values according to flock size. No simple relationship could be found between the size of the dialectal populations and that of the flocks where one given theme is sung. However, it is interesting that the theme preferentially sung in roosts is also that (RT) for which each variant characterizes a small reproductive colony.

Wynne-Edwards (1962) suggested that there might be an internal structure in roosts constituted by small groups. All individuals of a given colony are known to go to the same roost and fly off together in the morning, arriving simultaneously at their colony site. One can suppose that the emission of RT, mainly during the choice of place for the night, could permit birds singing the same variant to stay together, constituting small groups, as was proposed by Wynne-Edwards. Such a function of recognition of other individuals or mates was also supposed for the vocalizations in flocks of Corvus brachyrhynchos (Chamberlain and Cornwell 1971) and mynas, other Sturnids (Counsilman 1974).

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