

ORGANIZATION OF SONG IN THE EUROPEAN STARLING : SPECIES-SPECIFICITY AND INDIVIDUAL DIFFERENCES

by

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SUMMARY

In this paper we give a detailed description of the song and the song organization of the European starling (*Sturnus vulgaris* LINNAEUS) during the breeding season. We recorded songs of 25 males in Belgium and of 2 males in New Zealand. We show that there are clear species-specific characteristics in the complex song of the starling, but also reveal many individual differences.

During the breeding season, male starlings sing the majority of their song (90 % or more) in long and complex song bouts. These song bouts consist of a rapid succession of a great variety of different song types resulting in a song with much contrast. Although there are large differences in average song bout length among males (range : 15-35 seconds), the song bouts of all males we studied, both in Belgium and New Zealand, were composed of four categories of song types following each other in a fixed order.

Detailed analysis of the sequencing of song types within song bouts of two males showed that song types are not presented randomly : a given song type can be preceded and followed by only a limited number of other song types.

The majority of song types in the repertoires of starlings is individually characteristic. We found large differences in repertoire size among males, extending from 21 to 67 song types.

There appeared to be little difference between Belgian and New Zealand starlings in song organization.

Key-words : European starling, *Sturnus vulgaris*, song, organization of song, song repertoire size, repertoire composition, New Zealand

INTRODUCTION

Nearly all bird species can be identified by their vocalizations (KROODSMA, 1975). Indeed, one of the most consistent and striking characteristics of bird vocalizations is species-specificity. This is related to the fact that most sounds are directed toward conspecifics whose reactions should be appropriate to the content

of the message. Hence, the coding of species-specificity is typically the basis for effective acoustical communication (BECKER, 1982).

Many characteristics of singing contribute to specific distinctiveness among songbirds, but two of the most notable differences among species are the number of different song types per individual (i.e. song repertoire size) and the manner of presentation of those song types during a singing performance (KROODSMA, 1975, 1982).

As clearly stated by KROODSMA (1982), detailed description of the song and the song organization of a species must precede the functional study of song and is a prerequisite to any experimental work. The aim of this paper is to give a detailed description of the song and the song organization of the European starling, *Sturnus vulgaris*. First, we describe in detail the song, the organization of song, the song repertoire size and the composition of the repertoire of 25 male starlings recorded in Belgium. Then, we present data from two males recorded in New Zealand, where European starlings were introduced in 1862 (LONG, 1981; BULL *et al.*, 1985).

The complex song of the European starling has only recently received attention (ADRET-HAUSBERGER and JENKINS, 1988; EENS *et al.*, 1989). EENS *et al.* (1989) revealed that starling males sing very long and complex song bouts during the breeding season, some of which can extend over one minute in duration. These song bouts consist of a rapid succession of a great variety of different song types. We also showed that starling song bouts have a characteristic sequential organization. However, the previous analysis was based upon a detailed study of only three males (EENS *et al.*, 1989).

STUDY AREAS AND METHODS

Study areas in Belgium

In the first part of this study we provide detailed information on the song organization of 25 male starlings recorded in Belgium. The song of 12 males was recorded in a nest box colony in Zoersel (51°13'N, 4°40'E), near Antwerp, in the breeding season of 1987. Detailed information on the study area, the study population and the general methods can be found elsewhere (PINXTEN *et al.*, 1989a,b, 1990, 1991; PINXTEN and EENS, 1990; EENS *et al.*, 1991). The song of 13 other males was recorded in large outdoor aviaries located on the campus of the University of Antwerp (51°10'N, 4°25'E) in Wilrijk during the breeding seasons of 1988 and 1989. More details on the outdoor aviaries can be found in EENS *et al.* (1990, 1991). The data from these two groups of males were pooled. This is justified since we have shown that captivity has little or no effect on the singing behaviour of starling males (EENS *et al.*, 1990, 1991). In the Zoersel colony, all males were unmated at the time they were recorded. The captive males were recorded with a female starling in the aviary, as it has been shown that males sing vigorously in the presence of a female (EENS *et al.*, 1990). At the time of recording, males were not yet paired.

All males in the outdoor aviaries and nearly all males in the field were individually marked with wing tags and with colour rings.

Study area in New Zealand

The first European starlings were introduced to New Zealand in 1862 by the 'Nelson Acclimatisation Society'. They are now widespread and abundant in both the North and the South Islands and have reached many of the offshore and outlying islands (LONG, 1981; see also BULL *et al.*, 1985).

We recorded the song of several starlings at a semi-isolated colony at Belmont (41°10'S, 174°54'E), near Wellington, New Zealand. The study area is a 1500 ha sheep farm, 250-400 m above sea level, with practically no trees or natural nest sites for starlings within 3 km. The colony was established in 1970 by John and Meg Flux: nest boxes were built into ventilation shafts of abandoned ordnance storage bunkers (see FLUX and FLUX, 1981, 1982 for more details). Between 15 and 17 November 1990 (the breeding season lasts from October to December in this colony), we recorded the song of several males. From one male (male 1) we obtained a large number of high quality recordings enabling us to determine his repertoire size. This male was unpaired at the time of recording. Additional recordings were made from three neighbouring males, one of which was unpaired (male 2), the other two paired at the time of recording. From the latter two males only a few whistles were recorded since they only sang rarely. Each of the four males had a nest box very close to each other in the same bunker (bunker 3). None of the males was individually marked.

Song Recording

Male starlings defend only their nest hole and its immediate surrounding, and this is also where they do most of their singing. All song recordings, both in Belgium and in New Zealand, were made with small electret microphones (Sony ECM-16T or ECM-50 PS) implanted close to or in the nest boxes (see EENS *et al.*, 1989, 1991). These microphones were connected to a Uher 4400 Report Stereo IC tape recorder or a Uher CR 1601 cassette recorder via a long cable. Recordings were made from transportable hides (in the Zoersel colony), from behind one-way glass from permanent observation hides placed close to the outdoor aviaries, or from a car (in New Zealand).

Song Analysis

Song was analysed using a UNIGON 4600 Spectrum analyser (UNISCAN). Hard copy output of all recordings was obtained with an Epson FX-850 printer.

In a previous paper, we showed that male starlings sing very long and complex song bouts during the breeding season (EENS *et al.*, 1989). We define a song bout here as a period of at least five seconds of song containing no pauses longer than 1.5 seconds (modified after HINDMARSH, 1984; see EENS *et al.*, 1991). We obtained

on average 26.8 song bouts (SD = 10.7; range 12-51) from each of 25 males recorded in Belgium.

Statistical tests follow SIEGEL (1956) and SOKAL and ROHLF (1981). Throughout the paper values given are means \pm SD unless stated otherwise. All tests are two-tailed.

RESULTS

General organization of song

Detailed analysis of the song of 25 male starlings recorded in Belgium showed that males sing three categories of song during the breeding season :

1. very long and complex song bouts including heterospecific imitations (see Figs 1 and 2);

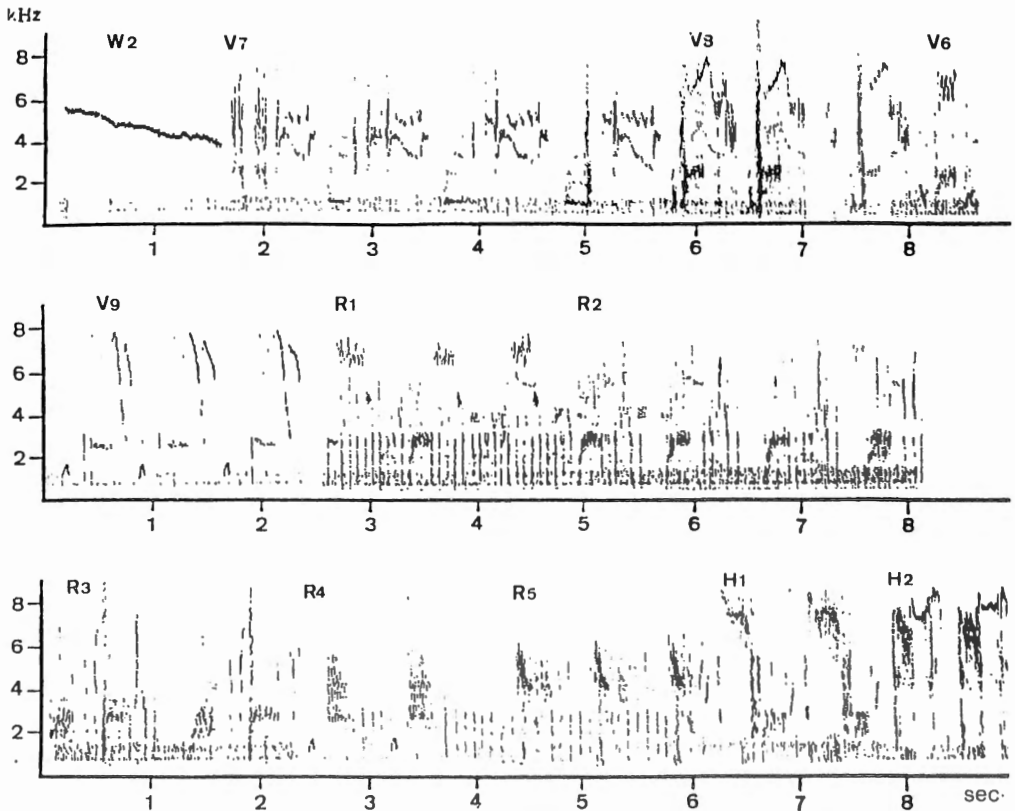


Fig. 1. — Illustration of a complete song bout of male 14F-87 recorded in the colony in Zoersel, Belgium. This song bout lasted 25 seconds and contained 12 different song types: W2 was sung only once, V7 was sung four times, V8 three times etc. (W = whistle, V = variable song type, R = rattle song type, H = high-frequency song type). For more details, see text.

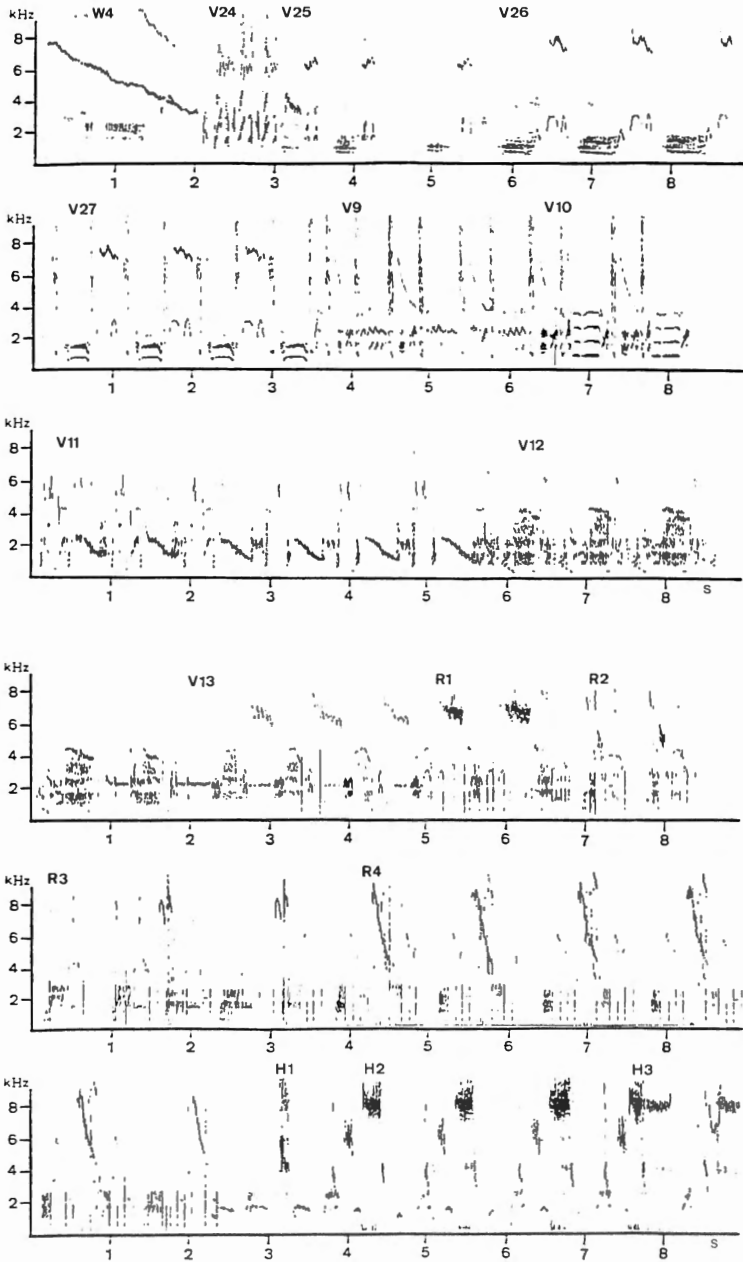


Fig. 2. — Illustration of a complete song bout of male OR-BLA89 recorded in the outdoor aviaries. This song bout lasted 50 seconds and contained 17 different song types (W = whistle, V = variable song type, R = rattle song type, H = high-frequency song type). For more details, see text.

2. simple whistles, occurring between song bouts ;
3. imitations of other birds or of non-avian sounds, also occurring between song bouts and never sung as part of a song bout (see Fig. 3A).

Table 1 shows the time devoted to each category of song in the total duration of song analysed for five males (three males of the Zoersel colony and two aviary males were chosen at random). All five males sang the majority of their song (95 % or more) in song bouts. The whistles and the heterospecific imitations that are not sung as part of a song bout account only for a very small percentage (5 % or less) of the total amount of song produced in the breeding season. Note that there is little variation among the five males in this respect (Table 1).

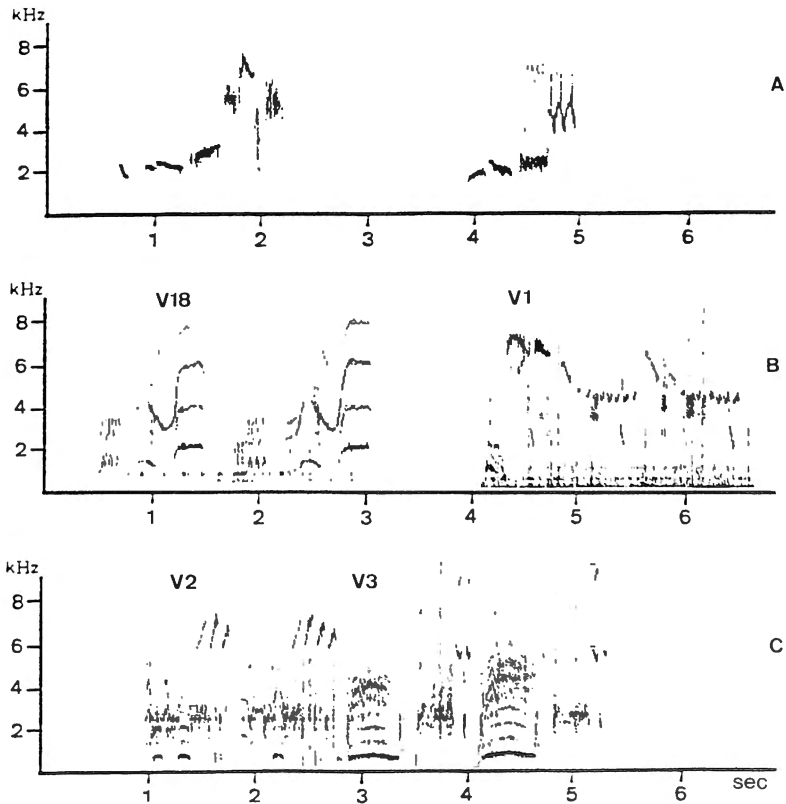


Fig. 3. — Illustration of heterospecific imitations sung by male Starlings. A = two Blackbird imitations by two different males that were sung apart from a song bout. B = two variable song types that are entirely or almost entirely made up of heterospecific imitations: V18 is a lapwing imitation, V1 consists largely of a blue tit imitation. Note also the small differences in successive repetitions of the same imitation. C = two heterospecific imitations that are integrated with other notes in a variable song type: V2 contains a cuckoo imitation, V3 contains a collared turtle dove imitation.

TABLE 1

Time devoted to each category of song in the total duration of song analysed for five males recorded in Belgium. The first three males were recorded in Zoersel in 1987; male four and five were recorded in large outdoor aviaries in Wilrijk.

<i>Male</i>	<i>Total duration of song analysed</i>	<i>Song sung in song bouts</i>	<i>Whistles</i>	<i>Imitations</i>
1	1015.3 s	967.4 s (95.3 %)	15.7 s (1.5 %)	32.2 s (3.2 %)
2	867.2 s	839.0 s (96.7 %)	12.7 s (1.5 %)	15.5 s (1.8 %)
3	431.5 s	409.5 s (95.0 %)	11.1 s (2.6 %)	10.5 s (2.4 %)
4	1029.1 s	995.4 s (96.7 %)	13.7 s (1.3 %)	20.0 s (2.0 %)
5	253.7 s	241.1 s (95.0 %)	12.6 s (5.0 %)	0.0 s (0.0 %)

Organization of song bouts

Average song bout length

Average song bout lengths vary considerably among males, ranging from 14.7 to 35.0 seconds. The overall average for 25 males is 24.8 ± 5.4 seconds (see also EENS *et al.*, 1991).

Organization of song bouts

Starling song bouts consist of a succession of song types (or motifs in the terminology of ADRET-HAUSBERGER and JENKINS, 1988), which are fixed combinations of varied acoustic elements (although different repetitions of the same song type can vary slightly : see below and Figs 1 and 2). The majority of song types are repeated immediately once or twice before the next one is sung (see below).

Starling song bouts are composed of four categories of song types, as can be seen in Figs 1 and 2 (see also EENS *et al.*, 1989).

The majority of song bouts begin with one or several 'whistles' (i.e. relatively pure tonelike sounds) : the overall average was 55.1 % (SD = 20.3 ; N = 25 males). The proportion of song bouts that starts with one or several whistles differs highly significantly between males ($G_{\text{williams}} = 100.7$, $df = 24$, $P < 0.001$) and ranges from 23 % (6 out of 26 song bouts of male OR-BL89 start with a whistle) to 93 % (14 out of 15 in male OR-BL88). Each male has a repertoire of 2 to 11 different whistles, with an average of 6.1 (SD = 2.3 ; N = 25 males). Fig. 4 shows the total repertoire of whistles of male ORX-BL89 : this male sang a total of 11 different whistles. Some whistles can be found in the repertoires of most males (for instance

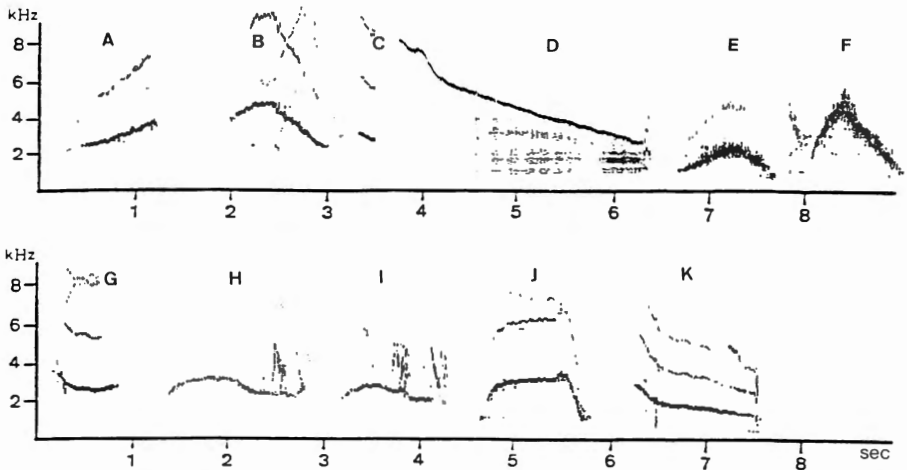


Fig. 4. — Illustration of the total repertoire of whistles of male ORX-BL89. This male sang all together 11 different whistles.

a long descending whistle with an initial frequency of about 8 kHz : compare for instance the introductory whistle in Fig. 2 with the fourth whistle in Fig. 4 (D) and with the whistles shown in Fig. 5), whereas others are unique to the individual. Whistles sung as part of a song bout are mostly not repeated (see Table 2) and are sung rather loudly. As shown in Fig. 5, there can be substantial differences in the exact form of the same introductory whistle. This Figure shows seven variations of

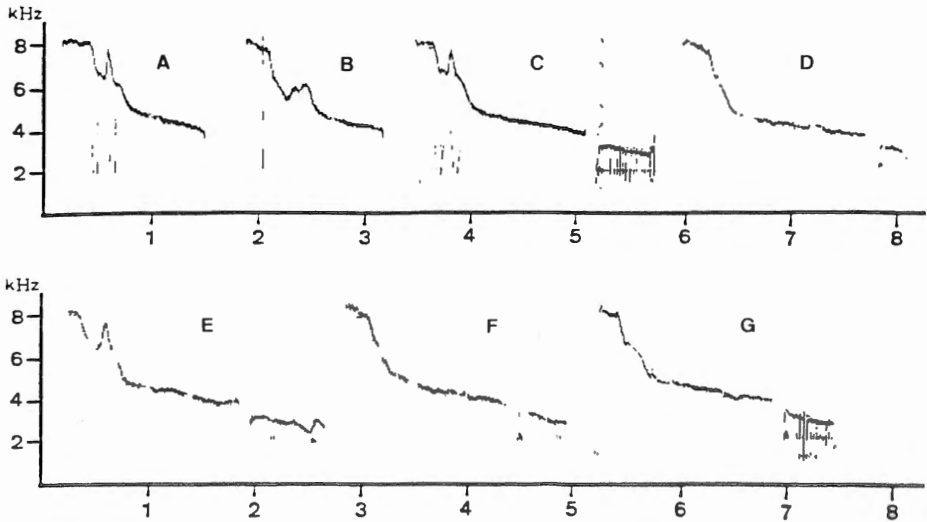


Fig. 5. — Seven song variations on one song type (long descending whistle) of male 1-87 recorded in Zoersel 1987.

the same whistle of a male. It can be seen that there are large differences in the shape of the whistle (compare for instance A with B). Furthermore, in some cases the long whistle is followed by a second smaller one (compare A and B with the rest). There are also large differences in the shape (compare for instance D with E) and the position (sometimes the second whistle is in direct line with the first (F), in other cases not) of the smaller whistle. Finally, in some cases the second whistle is accompanied with a creaking sound produced simultaneously with the whistle (especially C and G : double voicing).

In a song bout, the introductory whistle(s) is (are) always followed by a large number of 'variable song types'. In addition, about 40 % ($39.6\% \pm 20.1$ SD ; range : 7-77 % ; 25 males) of the song bouts start with a variable song type (i.e. the introductory whistle(s) is (are) omitted). Unlike whistles, variable song types have a very complex structure : they usually contain many different notes, many of them covering a wide frequency range in a short time (see Figs 1 and 2). It can be seen that there are large differences in structure between the variable song types of a given individual (see Figs 1 and 2), resulting in a song with much contrast and making it difficult to characterize this category of song type. Variable song types very often contain overlapping notes as a result of double voicing (see for instance most variable song types in Fig. 2 and V2 and V3 in Fig. 3C). Typical for these song types is that they contain most of the heterospecific imitations that are sung in a song bout (see EENS *et al.*, 1989). Some variable song types are entirely made up of heterospecific imitations : V18 in Fig. 3B for instance is entirely made up of an imitation of a lapwing *Vanellus vanellus* (LINNAEUS), whereas V1 (Fig. 3B) consists largely of a blue tit *Parus caeruleus* (LINNAEUS) imitation. In other variable song types, the heterospecific imitations are mixed with other notes : the two notes with a frequency of about 600 Hz in V2 (Fig. 3C) are a cuckoo *Cuculus canorus* (LINNAEUS) imitation (when this song type is sung a second time only one cuckoo note is sung : see Fig. 3C), whereas the note with harmonics in V3 (Fig. 3C) is an imitation of a collared turtle dove *Streptopelia decaocto* (FRIVALDSZKY).

Each male has a repertoire of 10 to 35 different variable song types, with an average of 23.8 (SD = 7.8 ; N = 25 males). Each male has a (nearly) unique reper-

TABLE 2

Average number of times that each of the four categories of song types in a song bout are repeated. To investigate this, we analysed one complete song bout (i.e. in this case a bout containing all four categories of song types; one male who had no high-frequency song types, was excluded from this analysis) of each male (N = 24) and determined the average number of times that a whistle, a variable, a rattle and a high-frequency song type was sung per male.

The table shows the overall average (X \pm SD) for the 24 males.

Category	Whistle	Variable song type	Rattle song type	High-frequency song type
x \pm SD	1.1 \pm 0.3	2.3 \pm 0.4	2.3 \pm 0.4	2.6 \pm 0.9

toire of variable song types : compare for instance the variable song types of male 14F-87 (Fig. 1) with those of male OR-BLA89 (Fig. 2). Even neighbouring males nesting only a few meters apart in the same colony, have no variable song types in common. On average, a variable song type is sung 2.3 ± 0.4 times before another is introduced (see Table 2). Variable song types are sung rather quietly.

In a song bout, variable song types pass into what we call 'rattle song types' (see Figs 1 and 2). In addition, four per cent of the song bouts ($4.1 \% \pm 8.5$ SD ; range : 0-36 % ; $N = 25$ males) start with a rattle song type (i.e. without whistles and/or variable song types being sung). Rattle song types are all made up of a rattling sound consisting of a rapid succession of clicks (a click is a short burst of wide frequency noise) with maximum energy below 4 kHz and sung at a rate of about 15 per second ; at the same time several other notes are sung (see Figs 1 and 2). Each male has a repertoire of 2 to 14 different rattle song types, with an average of 8.2 (SD = 3.1 ; $N = 25$ males). On average, a rattle song type is sung 2.3 ± 0.4 times before another is introduced (see Table 2). Most rattle song types are sung at relatively low amplitude, although rattle song types preceding the final high-frequency song types often are sung louder. Some rattle song types can be found in the repertoires of many males (for instance R5 of male 14F-87 in Fig. 1), whereas others are characteristic of one individual (compare for instance the rattle song types of the two males shown in Figs 1 and 2).

A starling song bout typically ends with a series of high-pitched song types which we call 'high-frequency song types' (see Figs 1, 2 and 6). Frequencies of these song types range mainly from 6 to 10 kHz. High-frequency song types are sung the loudest of a starling song bout. One male out of the 25 did not sing any high-frequency song types despite the fact that we recorded 32 song bouts of this male. Each male sings between 0 and 6 high-frequency song types, with an average of 3.5 (SD = 1.5). One per cent ($1.2 \% \pm 3.2$ SD ; range : 0 - 12.5 % ; $N = 25$ males) of starling song bouts starts with high-frequency song types : in this case the song bouts are mostly made up of high-frequency song types only. On average, a high-frequency song type is sung 2.6 ± 0.9 times before another is introduced (see Table 2). When comparing the high-frequency song types shown in Figs 1, 2 and 6, it can be seen that there are only a limited number of different high-frequency song types or, in other words, most males have one or several high-frequency song types in common. For instance H1 in Fig. 1, H2 in Fig. 6A, H1 in Fig. 6B and H2 in Fig. 6D all are very alike. Four males (three recorded in the field and one recorded in the outdoor aviaries) out of the 25 deviated from the described sequential pattern in that they sometimes returned to rattle song types after the high-frequency song types and eventually again sang high-frequency song types.

Only 30.7 % (SD = 18.4 ; $N = 25$ males) of the song bouts end with the high-frequency song types due to the fact that the song can be interrupted at any stage during a bout. The percentage of song bouts that ends with high-frequency song types (i.e. complete song bouts) differs highly significantly among males ($G_{\text{williams}} = 122.2$, $df = 24$, $P < 0.001$), extending from 0 % (0 out of 32 song bouts of male OR-WHI89 ended with high-frequency song types) to 82 % (23 out of 28 in male 8-87).

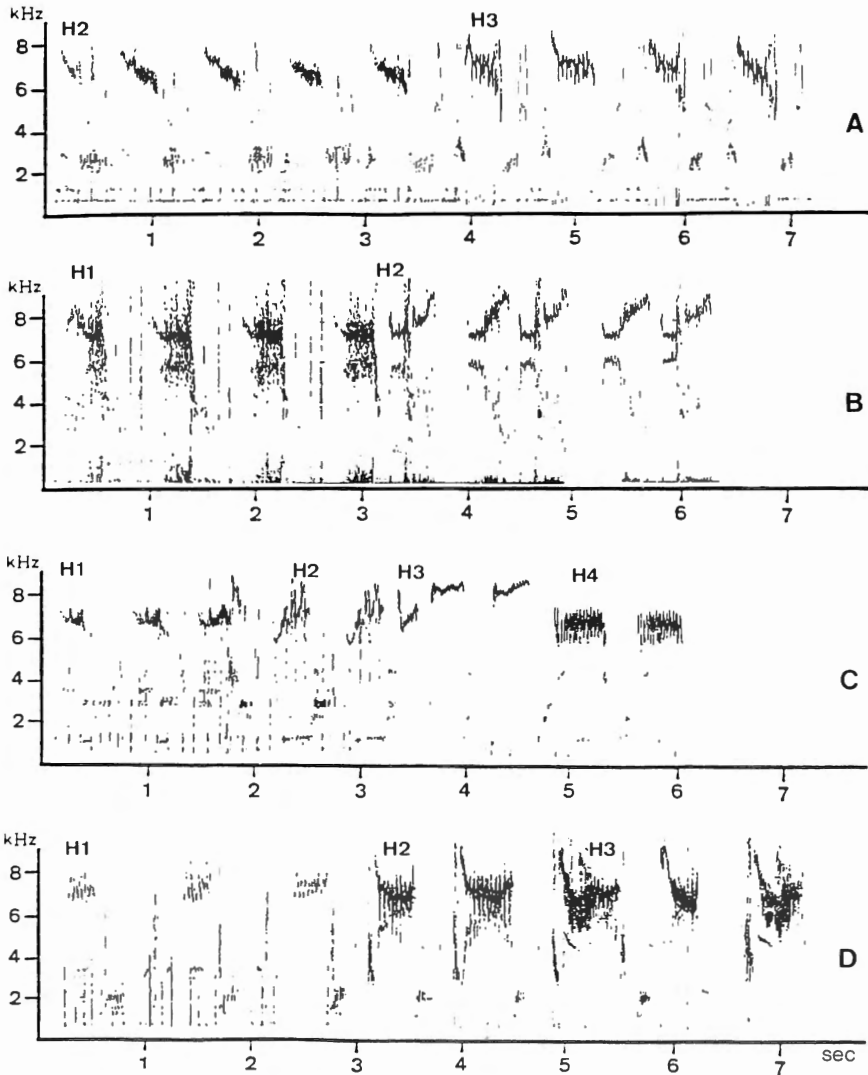


Fig. 6. — Illustration of high-frequency song types found in four different males.

Repetition of song types

To test whether there are differences among males in repetition rate of song types, we analysed one complete song bout of each male ($N = 24$ since we excluded the male that had no high-frequency song types in this analysis) and determined the average number of times a song type is sung before another is introduced, for each male. We found significant differences among males in the number of times a song type is sung before another is introduced, with averages ranging from 1.8 to 2.8

(Kruskal-Wallis analysis of variance $H = 37.2$, $P = 0.03$). The overall average is 2.2 ± 0.3 ($N = 24$).

Detailed sequential organization of song bouts

In Table 3, we provide detailed information on the sequential organization of the song types within the song bouts of two males. These data show that the song types of a given bird are not presented randomly in a song bout. It can be seen that a given song type can be preceded and followed by only a limited number of other song types. If for instance, in the case of male RE-GRE88, a song bout starts with whistles 1 and 2, indicated by W1 and W2, then the variable song types V1, V2, V3, V4 etc. always follow. If, on the contrary, a song bout starts with whistle 3 (W3), then another series of variable song types always follows (see Table 3). So in fact the introductory whistle or whistles (or the introductory variable song type(s)) allow us to predict which succession of song types comes next. It can also be seen that the endings of a song bout are highly stereotyped, irrespective of how the song bouts start. In the case of male RE-GRE88, all complete song bouts end with the rattle song types R5, R6, R7, R8 and high-frequency song types H1, H2, H3. Similarly, the endings of the song bouts of male 11-87 are also highly stereotyped. Stereotyped endings of a song bout are typical for all the starling males we studied.

Although the sequencing of different song types in a song bout is rather stereotyped, a certain amount of variability nevertheless exists. First, a particular song type is sometimes skipped in a sequence of song types: for instance if the typical sequence of song types is V1 V2 V3 V4 V5 V6, then sometimes V1 V2 V4 V5 V6 is sung (the repetitions of a given song type are ignored here). Second, the number of repetitions of a given song type is not always exactly the same from one song sequence to another. Third, when a male switches from one song type to another sometimes intermediate forms occur: for instance if the typical sequence is V1 V1 V1 V2 V2 V2 V3 V3, sometimes V1 V1 (V1V2) V2 V2 V2 V3 V3 occurs whereby V1V2 is composed of a part of song type V1 and a part of song type V2. Fourth, small differences can be found in successive repetitions of a given song type due to the omission or addition of one or a few notes: compare for instance the first and second utterance of variable song type V7 in Fig. 1 and of variable song type V2 in Fig. 3C.

It can be concluded that although starling song bouts have a clear sequential organization, there still is a certain degree of variability. Consequently, a particular male will rarely if ever sing two totally identical song bouts even if the sequence of song types is the same.

Heterospecific imitations not sung as part of a song bout

There are marked differences among males in the number of heterospecific imitations sung apart from a song bout: the number of such imitations ranges from 0 to 11, with an overall average of 1.4 ± 2.3 . Fig. 3A shows heterospecific imitations of a blackbird *Turdus merula* by two different males. A detailed description

TABLE 3

Sequential organization of song types within song bouts of two male starlings. Each combination of a letter and a figure stands for a particular song type (W = whistle, V = variable song type, R = rattle song type, H = high-frequency song type). The repetitions of a given song type are ignored here. The figure in front of each sequence of song types denotes how many times a given song bout pattern was observed. This presentation is further simplified in two ways. First, as clearly stated in the text, not all song bouts end with the high-frequency song types. Due to lack of space and in order to give a surveyable view of the sequential organization of song bouts, it is not possible to show the organization of each individual song bout of a male nor to indicate at which stage each song bout ended. Second, sometimes a particular song type is skipped in a song bout. (four song types of male 11-87 (1 whistle, 3 heterospecific imitations) were never sung as part of a song bout).*

Male RE-GRE88 : TOTAL REPERTOIRE SIZE : 31 song types

6 WHISTLES (W)

14 VARIABLE SONG TYPES (V)

8 RATTLE SONG TYPES (R)

3 HIGH-FREQUENCY SONG TYPES (T)

9	W1 (W2)	V1 V2 V3 V4 V5	R1 R2 R5 R6 R7 R8	H1 H2 H3
3		V1 V2 V3 V4 V5	R1 R2 R5 R6 R7 R8	H1 H2 H3
2	W6	V1 V2 V3 V4 V5	R1 R2 R5 R6 R7 R8	H1 H2 H3
6	W5 W4	V6 V7 V8 V9 V10 V11	R3 R4 R5 R6 R7 R8	H1 H2 H3
3	W3	V12 V6 V7 V8 V9 V10 V11	R3 R4 R5 R6 R7 R8	H1 H2 H3
5		V13 V14 V3 V4 V5	R1 R2 R5 R6 R7 R8	H1 H2 H3

Male 11-87 : TOTAL REPERTOIRE SIZE : 46* song types

4 WHISTLES (W)

26 VARIABLE SONG TYPES (V)

8 RATTLE SONG TYPES (R)

5 HIGH-FREQUENCY SONG TYPES (H)

7	(W1) W3	V1 V2 V3 V4 V16 V6 V7 V8	R1 R2 R3 R4 R5 R6 R7	H1 H2 H3 H4 H5
2	W3	V1 V9 V10 V11 V12 V13 V14 V15 V8	R1 R2 R3 R4 R5 R6 R7	H1 H2 H3 H4 H5
1		V24 V25 V26 V10 V11 V12 V13 V14 V15 V8	R1 R2 R3 R4 R5 R6 R7	H1 H2 H3 H4 H5
2	W2	V17 V18 V19 V20 V21 V22 V16 V6 V7 V8	R1 R2 R3 R4 R5 R6 R7	H1 H2 H3 H4 H5
2		V17 V18 V19 V20 V21 V22 V16 V6 V7 V8	R1 R2 R8 R5 R6 R7	H1 H2 H3 H4 H5
7		V23 V5 V6 V7 V8	R1 R2 R8 R5 R6 R7	H1 H2 H3 H4 H5

of the heterospecific imitations sung both in and apart from song bouts awaits further study.

Repertoire size

There were large differences between males in repertoire size, extending from 21 to 67 different song types. The average for 25 males was 42.9 ± 12.4 song types. Fig. 7 shows cumulative plots of new song types against the total number of song types analysed, for four males. It can be clearly seen that the graphs become asymptotic for all four males, doing so more rapidly for the two low repertoire males than for the two high repertoire males. Note that three out of four males still sang new song types after they had already sung 300 song types. One male even sang one new song type after having already sung 800. We analysed 632.5 ± 200 song types ($N = 25$ males; range : 325-960 song types) from each male. Consequently, we think we have nearly always obtained the total repertoire size.

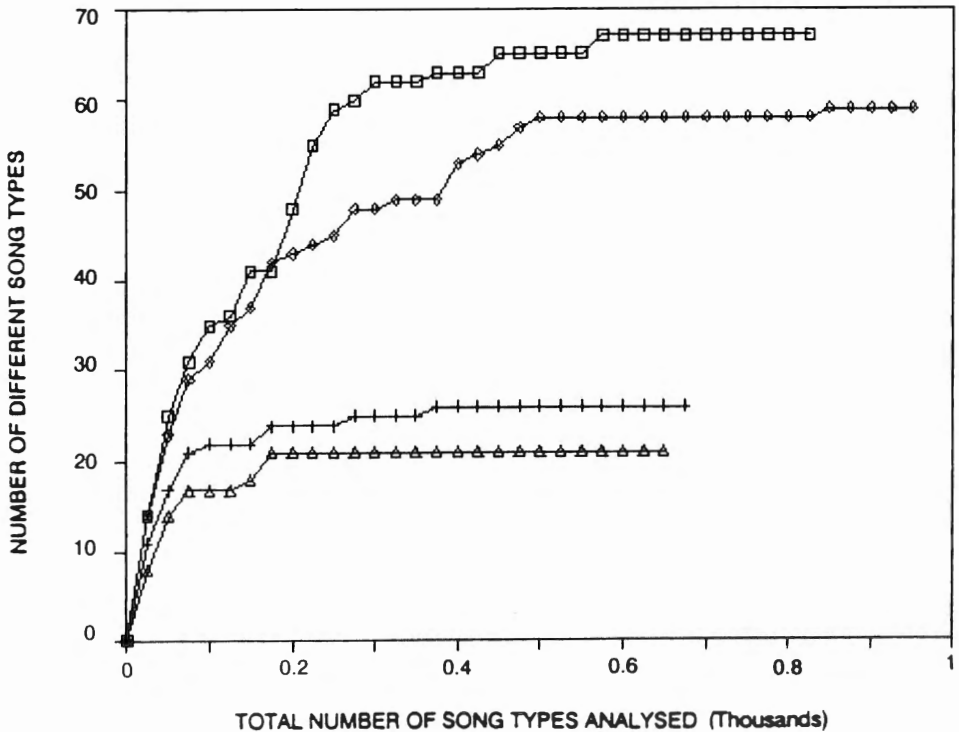


Fig. 7. — Cumulative plots of new song types against the total number of song types analysed for four males. For more details, see text.

We found a highly significant positive correlation between repertoire size and average song bout length (Spearman rank correlation coefficient : $r_s + 0.812$, $N = 25$, $P < 0.00001$; see Fig. 8).

There was no difference in the proportion of song bouts that end with high-frequency song types (*i.e.* in the proportion of complete song bouts sung) between low and high repertoire males (low and high refers to the median repertoire size ; Mann-Whitney U-test : $U = 51$, $N_1 = 12$, $N_2 = 12$, $P = 0.23$). There also was no difference in repetition rate of song types between low and high repertoire males (Mann-Whitney U-test : $U = 61.5$, $N_1 = 12$, $N_2 = 12$, $P = 0.54$) nor between males with short and long average song bouts (Mann-Whitney U-test : $U = 53.5$, $N_1 = 12$, $N_2 = 12$, $P = 0.28$).

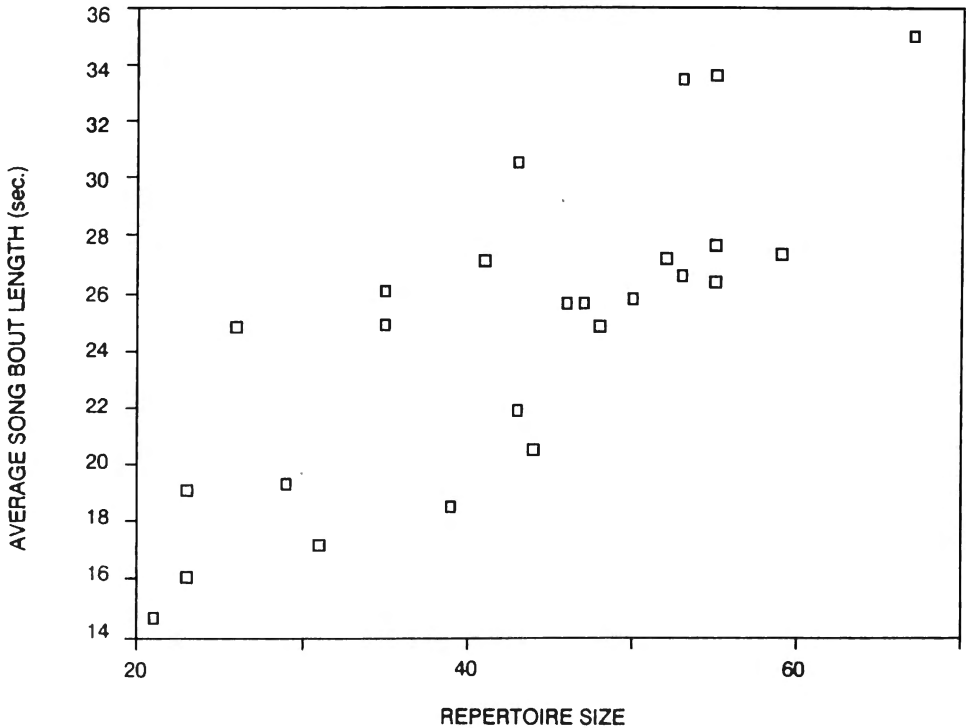


Fig. 8. — Relationship between repertoire size and average song bout length (sec.) for 25 Starling males recorded in Belgium.

Song of New Zealand males

As with the Belgian males, both males recorded in New Zealand sang the majority of their song ($> 90\%$) in song bouts (Table 4).

Altogether, we recorded ten song bouts of male 1 and eight of male 2. As in the Belgian males, the song bouts of the two New Zealand males were composed of four categories of song types (see Fig. 9). In both males, the majority of song bouts started with a whistle : all song bouts (10 out of 10) of male 1 began with a whistle, while five out of eight (62.5 %) song bouts of male 2 started with a

TABLE 4

Time devoted to each category of song in the total duration of song analysed for two males recorded in New Zealand.

<i>Male</i>	<i>Total duration of song analysed</i>	<i>Song sung in song bouts</i>	<i>Whistles</i>	<i>Imitations</i>
1	278.0 s	259.5 s (93.3 %)	18.5 s (6.7 %)	0.0 s (0.0 %)
2	201.8 s	190.7 s (94.5 %)	9.3 s (4.6 %)	1.8 s (0.9 %)

whistle. None of the introductory whistles was repeated in a song bout. In the two New Zealand males we studied, as can be seen in Fig. 9, the introductory whistle was also followed by a long series of variable song types, which in their turn passed into rattle song types. A starling song bout also typically ended with several high-frequency song types. Analysis of one complete song bout of male 1 showed that this male sang a given song type on average 2.2 (SD = 0.6) times before switching to another.

We were able to determine the repertoire size of male 1, from which we analysed in total 342 song types. This male had a repertoire size of 42 different song types and an average song bout length of 25.95 seconds (SD = 12.7; N = 10 song bouts). Male 1 had 10 whistles, 18 variable song types, 9 rattle song types and 5 high-frequency song types in his repertoire. Two variable song types of male 1 contained an imitation of an Australian magpie (*Gymnorhina tibicen* CAMPBELL). Male 2 had an average song bout length of 23.9 seconds (SD = 14.2, N = 8 song bouts). We were unable to determine his repertoire size due to the low quality of the recordings as a result of the windy conditions at the time of recording. At least two variable song types of male 2 contained a heterospecific imitation: one contained a call of a common chaffinch (*Fringilla coelebs* LINNAEUS), the other a call of a house sparrow (*Passer domesticus* LINNAEUS). Male 2 also sang a blackbird imitation though not in a song bout. All four species mentioned have been introduced into New Zealand.

As starlings have large repertoire sizes and as there are large differences in the exact structure of song types between male starlings even from the same colony and nesting only few meters apart (see above), it is difficult to compare song structures from males of different populations in a quantitative manner. However, using a more qualitative approach, some interesting points can be raised. First, both male 1 and 2 of New Zealand often started a song bout with a long descending whistle with a beginning frequency of about 8 kHz (see Fig. 9): four out of ten song bouts of male 1, and two out of five song bouts of male 2 started with such a whistle. This type of whistle is also the most frequently used introductory whistle in Belgian starlings (compare whistle W6 of male 1 in Fig. 9 with Figs 2, 4D and 5). Second, eight of the nine other whistles of male 1 were of a type also found in Belgian star-

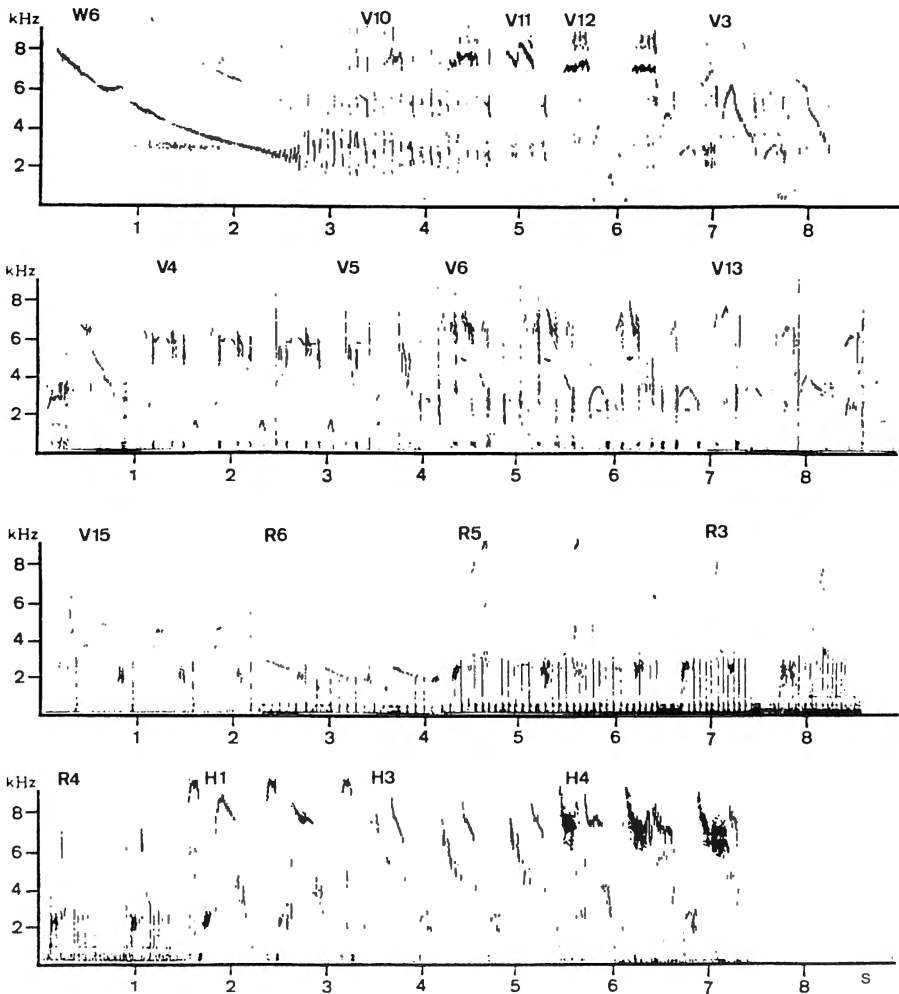


Fig. 9. — Illustration of a complete song bout of male 1 recorded in New Zealand. This song bout lasted 34 seconds and contained 17 different song types. (W = whistle, V = variable song type, R = rattle song type, H = high-frequency song type). For more details, see text.

lings. Only one whistle of male 1 was of a type never found in Belgium : interestingly, all four males of bunker 3 sang this whistle (see Fig. 10). Third, the variable and rattle song types of male 1 were very similar to those found in Belgian starlings except, of course, for the heterospecific imitations of the Australian magpie (compare Figs 1 and 2 with Fig. 9). Fourth, most of the high-frequency song types recorded in New Zealand were very similar to those found in Belgium : for instance H1 in Fig. 9 is similar to the first H2 in Fig. 6A, while H4 in Fig. 9 is very similar to H3 in Fig. 6D.

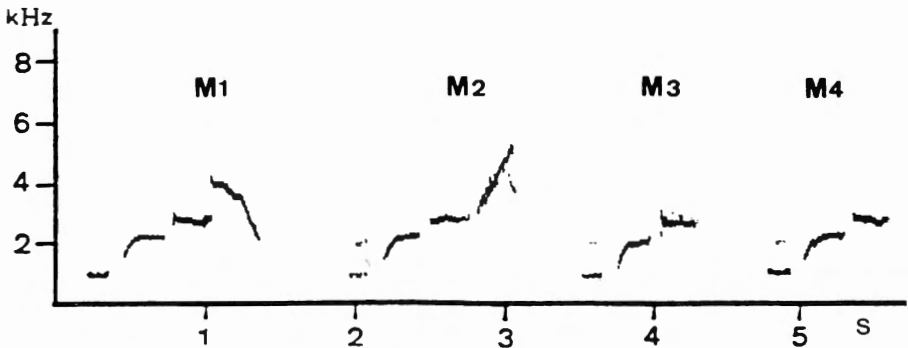


Fig. 10. — Illustration of a whistle type not found in Belgium, that was sung by all four males of bunker 3 in New Zealand. Male 1 and 2 (M1 and M2) sometimes omitted the fourth note when singing this whistle.

DISCUSSION

The European starling has an extremely complex and varied song. We showed that the majority of song, both in Belgium and New Zealand, is sung in song bouts during the breeding season. These song bouts, which in some males can extend over one minute in duration and which have an average duration of about 25 seconds ($N = 25$ males recorded in Belgium), consist of a rapid succession of a great variety of different song types resulting in a song with much contrast. Our study showed some clear species-specific characteristics in the starling song, but also revealed many individual differences (see also EENS *et al.*, 1989).

Although there are large differences in average song bout length and in song repertoire size between males, the song bouts of all males we studied, both in Belgium and New Zealand, are composed of four categories of song type. The starling song is an uninterrupted sequence of structurally complex song types, progressing from relatively simple pure-tone whistles to the more complex variable and rattle song types and ending with high-pitched trills. We found that, both in Belgium and New Zealand, the introductory whistles are mostly not repeated. Song types of the other three categories are mostly repeated. The number of repetitions of song types differed between Belgian males, with averages ranging from 1.8 to 2.8. The one New Zealand male we analysed sang a given song type on average 2.2 times before switching to another, suggesting that the tendency to repeat a given song type before singing another is typical for all starlings (see also ADRET-HAUSBERGER and JENKINS, 1988).

When comparing the song of Belgian and New Zealand starlings, there appeared to be little difference in the organization of song, the general characteristics of the four categories of song type or in the structure of many song types (compare Figs 1 and 2 with Fig. 9). We found for instance that both in the Belgian and New Zealand males we studied, a long descending whistle was often used as an introductory whistle. It is also interesting to note that some variable song types

of the New Zealand males contained heterospecific imitations, which is in agreement with our results from Belgium (EENS *et al.*, 1989; this study). One whistle (exclusively sung apart from song bouts) which was found in all four males recorded (Fig. 10) was of a type never found in Belgium. However, since we are not familiar with the song of all New Zealand birds, it is not unlikely that it was a heterospecific imitation.

Detailed analysis of the sequencing of song types within the song bouts of two males showed that starling song bouts are determinate to a great extent (cf. EENS *et al.*, 1989), although we also showed that a certain degree of variability always occurs.

Although four categories of song type can be found in the song bouts of all males, most song types in the repertoires of starling males are individually characteristic. This raises the question how song repertoires develop in the starling. All songbirds studied to date have been found to learn details of their songs from other individuals (SLATER, 1989). The observation that a large part of the repertoire of each starling from the same colony, even if nesting only a few meters apart, is unique suggests that starlings probably do not learn songs from their neighbours or learn them very inaccurately. Since starlings spend most time of the year in flocks (FEARE, 1984), especially in a non-resident population, such as the one of Zoersel, it is not unlikely that juvenile starlings learn their song from many different models. Another, not mutually exclusive, possibility might be that the individuality of song is to some extent the result of improvisation (MARLER and PETERS, 1982; see EENS *et al.*, 1989). As yet, little is known about the timing of vocal learning in the starling. BÖHNER *et al.* (1990) recently found that starlings are able to learn new songs at an age of 11 to 12 months.

Our results on the organization of song in the starling differ in several respects with those found by ADRET-HAUSBERGER and JENKINS (1988) who recorded starling songs in France and New Zealand. First, although they gave no exact figures, ADRET-HAUSBERGER and JENKINS (1988) found that starling song bouts always start with an 'individual motif', and never with a whistle (or several whistles). Second, although they also found 'high pitched trills' at the end of song bouts, their results suggest that each male has only one or two of these song types. We found an average of 3.5 high-frequency song types per male with individual values ranging from 0 to 6. Male 1 recorded in New Zealand sang a total of 5 high-frequency song types. Third, whereas we found an overall repertoire size of about 43 song types with individual repertoire sizes ranging from 21 to 67 song types, ADRET-HAUSBERGER and JENKINS (1988) found repertoires ranging from 11 to 36 song types with an overall average of 23.6 song types ($SD = 7.5$; $N = 14$ males). ADRET-HAUSBERGER and JENKINS' more limited recording time per male may have resulted in an underestimation of repertoire size and this may account for the latter two differences (see EENS *et al.*, 1991). The first difference, however, might suggest that there may be differences among populations in the organization of song. Another possibility might be that the differences between both studies are due to differences in the timing of recording. We recorded the songs of males at the time they were still unmated. Since ADRET-HAUSBERGER and JENKINS (1988) did not individually

mark their males, they probably had no information on the mating status of their males at the time of recording. In the mockingbird (*Mimus polyglottos*) it has been found that the social situation in which the singing behaviour occurred can alter significantly the estimate of repertoire size : DERRICKSON (1987, 1988) found that estimated repertoire sizes are larger for male mockingbirds when associated with females than in agonistic situations. Since the song of the starling seems to function largely in male-female interactions (CUTHILL and HINDMARSH, 1985 ; EENS *et al.*, 1990 ; EENS and PINXTEN, 1990), it is not unreasonable to assume that the recording of the song of already-mated males might lead to an underestimation of the song repertoire size.

Worth mentioning is the observation that starlings can sing over a large frequency range. The cuckoo and collared turtle dove imitations shown in Fig. 3C for instance have a minimum frequency of about 600 Hz while some of the high-frequency song types can have a frequency of 10 kHz or even more. We know of no other European songbird species that is able to sing frequencies as low as the starling. The marsh warbler *Acrocephalus palustris* for instance which has a capacity for heterospecific mimicry unequalled by any other species studied so far (LEMAIRE, 1974 ; Dowsett-Lemaire, 1979), is unable to imitate the sounds emitted by the *Colombidae* and the cuckoos, since their low-pitched voices fall outside its frequency range (1500-8000 Hz) (LEMAIRE, 1974 ; DOWSETT-LEMAIRE, 1979). As demonstrated above, this is not the case in the starling.

We showed that there is considerable inter-individual variation in average song bout length and in repertoire size between males. Average song bouts ranged from about 15 to 35 seconds, while repertoire sizes ranged from about 20 to almost 70 song types. Since we recorded a large amount of song from all males, we have probably nearly always obtained the total repertoire size. However, it should be noted that in the repertoire of a given male, some song types are relatively common, while others are sung very rarely : in the case of male 11-87 (see Table 3) for instance, variable song type V8 occurred in every song bout, whereas variable song types V24, V25 and V26 were found only once. Therefore, the possibility that some rare song types were not found by us cannot completely be excluded.

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REFERENCES

- ADRET-HAUSBERGER, M. and P. F. JENKINS (1988) — Complex organization of the warbling song of starlings. *Behaviour*, **107** : 138-156.
- BECKER, P. H. (1982) — The coding of species-specific characteristics in bird sounds. In : D. E. KROODSMA and E. H. MILLER (eds.). *Acoustic Communication in Birds*, Vol. 1. Academic Press, New York : 213-252.
- BÖHNER, J., M. CHAIKEN and P. MARLER (1990) — Song acquisition in photosensitive and photorefractory male European starlings. *Horm. Behav.*, **24** : 582-594.
- BULL, P. C., P. D. GAZE and C. J. R. ROBERTSON (1985) — *The atlas of bird distribution in New Zealand*. The ornithological society of New Zealand Inc., Wellington, New Zealand.
- CUTHILL, I. and HINDMARSH, A. M. (1985) — Increase in starling song activity with removal of mate. *Anim. Behav.*, **33** : 326-328.
- DERRICKSON, K. C. (1987) — Yearly and situational changes in the estimate of repertoire size in northern mockingbirds (*Mimus polyglottos*). *Auk*, **104** : 198-207.
- DERRICKSON, K. C. (1988) — Variation in repertoire presentation in northern mockingbirds. *Condor*, **90** : 592-606.
- DOWSETT-LEMAIRE, F. (1979) — The imitative range of the song of the Marsh Warbler *Acrocephalus palustris*, with special reference to imitations of African birds. *Ibis*, **121** : 453-468.
- EENS, M. and R. PINXTEN (1990). — Extra-pair courtship in the starling *Sturnus vulgaris*. *Ibis*, **132** : 618-619.
- EENS, M., R. PINXTEN and R. F. VERHEYEN (1989) — Temporal and sequential organisation of song bouts in the European starling. *Ardea*, **77** : 75-86.
- EENS, M., R. PINXTEN and R. F. VERHEYEN (1990) — On the function of singing and wing-waving in the European Starling *Sturnus vulgaris*. *Bird Study*, **37** : 48-52.
- EENS, M., R. PINXTEN and R. F. VERHEYEN (1991) — Male song as a cue for mate choice in the European Starling. *Behaviour*, **116** : 210-238.
- FEARE, C. J. (1984) — *The Starling*. Oxford University Press, Oxford.
- FLUX, J. E. C. and M. M. FLUX (1981) - Population dynamics and age structure of starlings (*Sturnus vulgaris*) in New Zealand. *New Zealand J. Ecol.*, **4** : 65-72.
- FLUX, J. E. C. and M. M. FLUX (1982) — Artificial selection and gene flow in wild starlings, *Sturnus vulgaris*. *Naturwiss.*, **69** : 96-97.
- HINDMARSH, A. M. (1984) — Vocal mimicry in Starlings. *Behaviour*, **90** : 302-324.
- KROODSMA, D. E. (1975) — Song patterning in the Rock Wren. *Condor*, **77** : 294-303.
- KROODSMA, D. E. (1982) — Song repertoires : problems in their definition and use. In : D. E. KROODSMA and E. H. MILLER (eds). *Acoustic communication in birds. Vol. 2*. Academic Press, New York : 125-156.
- LEMAIRE, F. (1974) — Le chant de la Rousserolle verderolle (*Acrocephalus palustris*) : étendue du répertoire imitatif, construction rythmique et musicalité. *Le Gerfaut*, **64** : 3-28.
- LONG, J. L. (1981) — *Introduced birds of the world*. David & Charles, London.

- MARLER, P. and S. PETERS (1982) — Subsong and plastic song : their role in the vocal learning process. In : D. E. KROODSMA and E. H. MILLER (eds). *Acoustic communication in birds*. Vol. 2. Academic Press, New York : 25-50.
- PINXTEN, R. and M. EENS (1990) — Polygyny in the European Starling : effect on female reproductive success. *Anim. Behav.*, **40** : 1035-1047.
- PINXTEN, R., M. EENS, L. VAN ELSACKER and R. F. VERHEYEN (1989a) — An extreme case of polygyny in the European Starling. *Bird Study*, **36** : 45-48.
- PINXTEN, R., M. EENS and R. F. VERHEYEN (1989b) — Polygyny in the European Starling. *Behaviour*, **111** : 234-256.
- PINXTEN, R., M. EENS and R. F. VERHEYEN (1990) — Intermediate clutches in the Starling (*Sturnus vulgaris*) : replacement clutches, additional clutches of polygynous males or late first clutches? *J. Ornithol.*, **131** : 141-150.
- PINXTEN, R., M. EENS and R. F. VERHEYEN (1991) — Conspecific nest parasitism in the European starling. *Ardea*, **79** : 15-30.
- SIEGEL, S. (1956) — *Nonparametric statistics for the behavioural sciences*. McGraw-Hill, New York.
- SLATER, P. J. B. (1989) — Bird song learning : causes and consequences. *Ethol. Ecol. Evol.*, **1** : 19-46.
- SOKAL, R. R. and F. J. ROHLF (1981) *Biometry*. Freeman, San Francisco.