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ABSTRACT

The song repertoires of a local group of blackbird *Turdus merula* males were determined and quantified with respect to individuality and sharing between neighbours. We focused on the long-ranging, introductory whistle part of the song and its motifs of fixed sequences of sounds. These motifs, whether they are used to start the song or placed centrally in the song, constitute the largest units of song that are repeated in the same way every time they are sung. Blackbird motifs therefore are equivalents of song types in other species. The result shows that one needs to analyse more than 200 songs to estimate a male's repertoire, which averaged 44 different motifs. Relative to other species, this is a medium to large song repertoire. The size of the repertoire of start motifs (on average 32) varied only a little between the individuals, whereas that of central motifs (on average 12) varied rather much between the same individuals, suggesting that they form a potential cue for assessment of male quality. The males within the neighbourhood showed a high degree of start motif sharing, which, together with the relatively large repertoires, could be constraining neighbour recognition. However, in most males the possession of a few individually distinctive and frequently repeated motifs could counter such an effect.

Key words: blackbird, song repertoire, repertoire sharing, individuality, neighbour recognition.

INTRODUCTION

Passerine males often have a repertoire of structurally different, but functionally synonymous, songs that they shift between. A part of this repertoire may be shared with other males, especially neighbours. Repertoire sizes, degree of song sharing, and pattern of singing shared and non-shared songs vary considerably between species. Some of this variation may be explained by differences in the way song types and

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repertoires are defined, but most of it seems to be the result of between-species differences in evolution where song repertoires have evolved to support different aspects of the two main functions of bird song: female attraction/stimulation and male deterrence (see e.g. Catchpole and Slater 1995). In some species, song repertoires may enhance singing males' possibility of addressing particular rivals by singing songs resembling those of the rivals (e.g. Krebs et al. 1981, McGregor et al. 1992), and such song matching will be even more precise if performed with songs that are shared with a rival (e.g. Falls et al. 1982). Song repertoires may also allow female assessment of males (or their territory) in species where repertoire size is correlated with aspects of male or territory quality (e.g. Searcy 1984, Catchpole 1986, Hiebert et al. 1989, Lampe & Espmark 1994, Hasselquist et al. 1996). And, because songs suffer different degradation after transmission through the habitat (e.g. Dabelsteen et al. 1993, Holland et al. 1998), in some species, song repertoires may help ensure that some of a singing male's song types always arrive relatively intact at a particular receiver.

Whatever function song repertoires and song sharing subserve, they seem to push the evolution in the direction of larger repertoires and higher degrees of song sharing. However, in some species the size of the song repertoire and the extent of song-sharing is very low or non-existent, suggesting that the evolution of these aspects has been constrained by other considerations, for example the possibilities for neighbour recognition by song (see e.g. Kroodsma 1976, Krebs and Kroodsma 1980, Falls 1982, Schroeder and Wiley 1983). Experimental investigations of the constraining effect of repertoire size suggest that repertoires of less than about 25 song types should not interfere with neighbour recognition, whereas repertoires larger than 100 may pose a problem (e.g. Stoddard 1996, Molles and Vehrencamp 2001). Species with repertoire sizes between these two extremes are therefore especially interesting because they could also be intermediate with respect to the possibilities for neighbour recognition. Alternatively, they could have crossed a threshold where neighbour recognition was no longer possible, or they could have preserved the full possibility of neighbour recognition due to some special song repertoire design that overcomes one or more of the proposed main constraints of large repertoires (see e.g. Krebs and Kroodsma 1980, Falls 1982). Unfortunately, species with such medium sized repertoires are the least studied in this respect.

The present study concerns the Eurasian Blackbird *Turdus merula*, which seems to have a medium sized repertoire (e.g. Ince and Slater 1985). It is also known to show song sharing (see e.g. Figure 3 in Thielcke-Polz and Thielcke 1960, and Figures 5-6 in Dabelsteen 1988) and perform song matching (e.g. Todt 1968, 1970). We investigate the possibilities for song based neighbour recognition in the

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blackbird by quantifying three aspects of song repertoires in the blackbird: size, individuality and sharing between neighbours.

The blackbird song

The song of the blackbird has been studied intensively over the last three or four decades, but a detailed and concomitant study of these three aspects of song repertoires has not previously been made. Two factors, both of which complicate investigations of song repertoires, may be responsible for this: the apparent capability of open-ended song learning (e.g. Thielcke-Polz and Thielcke 1960, Hall-Craggs 1962), and the variability of the song which makes such investigations very time consuming and also render the definition of a proper level of analysis difficult.

A full song (also referred to as a phrase or strophe) of the male blackbird starts with a loud and low frequency whistle part (sometimes called the motif part), and ends with a quiet and high frequency twitter part (Figure 1a) (e.g. Dabelsteen 1984). Both parts consist of sound figures each of which consists of only one discrete sound element (the most common type of sound figure) or groups of such elements with inter-element pauses not exceeding 50 ms. The sound figures vary considerably with respect to their frequency-time patterns, although within certain species-specific limits. Individuals possess a limited number of easily distinguishable whistle part sound figures that vary only slightly, if at all, between their repetitions by the same individual. Most of these sound figures are sung in fixed sequences of two to five sound figures. We call these fixed sequences *motifs*. The whistle part of the song often consists of only one such motif. Sometimes it is more complex including one or two extra motifs. Sometimes a motif lacks the last sound figure or is followed by a sound figure that is 'non-tied' in the sense that it does not form part of any particular motif. The twitter part shows a much higher variability and also seems to contain motifs although this has yet to be investigated in detail.

The repertoire size of an individual blackbird would be very large if it was defined simply by the number of different sound elements or sound figures sung, and it would be even larger if it was defined by all possible combinations of motifs, motifs lacking a sound figure, and single sound figures from both the whistle and the twitter part. We have chosen to focus on the long ranging whistle part and quantify its motifs which constitute the highest level of repeated unit in the blackbird song and hence are the most obvious equivalents of the units used to classify song repertoires in other species (e.g. Kroodsma 1982). We distinguished between two types of motifs that differ only with respect to their location in the song: *start motifs* that

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start songs, and *central motifs* that, if present, constitute the second or the third motif of a song. The repertoires of both types of motifs were determined, but an inter-individual comparison was only made for the start motifs, which seem to be the most important (e.g. for song matching (Wolffgramm and Todt 1982) and perhaps also as supplier of cues for species recognition (Dabelsteen and Pedersen 1992, 1993)).

METHODS

Songs of six males constituting a local neighbourhood were recorded. Their territories were clustered in a mixed deciduous forest adjacent to a meadow at Strødam Biological Field Station, Denmark (54.9^0 N, 12.1^0 E). The distance (mean ± S.E. (range)) between territory centres, as determined from minimum convex song post polygons, was 103 ± 12 m (40-175 m). Most of the males were present from late March and settled on territories during April. Male 2 showed up after mid June and established a territory on the fringes of the forest at the meadow. All of the males, of which two were colour ringed (male 4 and 5), were followed during their respective breeding seasons. Their songs were recorded in the morning and sometimes in the evening, during their first period with high song activity, i.e. from about the time when their mates laid their first eggs until hatching of the eggs (Snow 1958). Male 1: 16-17 May; male 2: 27-28 June; males 3 and 4: 15-24 May; male 5: 25-29 April; male 6: 23 April-3 May. For males 1, 4 and 5 we recorded some extra songs one or two months later on a day during the period with revived high song activity, i.e. on 29, 27 and 29 June respectively.

A total of 1124 full songs were recorded with a Sennheiser MKH 816T directional microphone (frequency response 100-20,000 Hz ± 2 dB) connected to a Sony TCD-D10 Pro DAT-recorder (frequency response 40-15,000 Hz ± 3 dB) and subsequently filtered (Krohn-Hite model 3750; HP: 1 kHz; LP: 10 kHz; 24 dB/octave). Sonagrams of the filtered songs were produced with a Kay Elemetrics Corp. DSP 5500 sonagraph (frequency range: 0-8,000 Hz; input shaping: flat; filter bandwidth: 234 Hz; analysis window: Hamming).

The whistle (start + central) motif repertoires of the six males were determined by visual inspection of the sonagrams. For motifs, which were repeated, this was straightforward. Sequences of sound figures that were only observed once (in 6.9% of the songs) were defined as consisting of one motif only although some of them might have included more. This made the determination of the motif repertoire sizes conservative.

To determine the number of shared start motifs we focused on the sound figures' frequency-time patterns. Two sound figures were defined identical and shared when frequency patterns were judged

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identical and were sung by two different males. This procedure resulted in almost total agreement when applied independently by the two authors.

A start motif was defined shared by two males if one of four levels of motif similarity occurred: (1) all of the sound figures of the males' respective renditions of the shared start motif were identical, (2) all but one sound figure of their renditions were identical, (3) only the first sound figure of their renditions were identical, and (4) as (1) or (2) but the shared motif occurred as a central motif in one of the males. Examples of the four levels of similarity are shown in Figure 1. Other levels of motif similarity could undoubtedly be identified. Our determination of the extent of start motif sharing was therefore also conservative.

Statistical tests were made according to Siegel (1956).

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RESULTS

Repertoire size

The size of both start + central motifs repertoire of the six blackbirds averaged 44 ± 4 (34-63) (mean ± S.E. (range)), and the males had almost three times as many different start motifs (32 ± 1 (29-35)) as central motifs (12 ± 3 (3-28)). Cumulative plots of new start motifs found, as a function of the number of songs analysed, approached asymptotes (four males) or ended at values comparable to those of the asymptotes (birds 3 and 6) (Figure 2). This suggests that an increase in the number of songs analysed at the point of the asymptote would increase the present average repertoire size slightly and that it is necessary to analyse more than 200 songs to get an estimate of the start motif repertoire size. Most of the songs were recorded within a relatively short time span during the males' first breeding cycle, but males 1, 4 and 5 had some additional songs recorded more than a month later. Exclusion of these late-recorded songs from the analysis would reduce each of the three males' repertoires by one start motif only.

If parts of the repertoires were acquired or activated during the pauses between the different recordings one would expect the above-mentioned cumulative plots to have "sub-plateaus" inserted between the recordings. This was actually the case since the plots for all of the males except male 2 curved off in a "sub-plateau" (consisting of ≥20 start motifs analysed without finding a new type) at least once before they started to increase again on their way up towards the final asymptote. Male 4 had the longest such "sub-plateau" inserted (40 start motifs analysed without finding a new type), but the recording resulting in this long "sub-plateau" and the successive recording giving

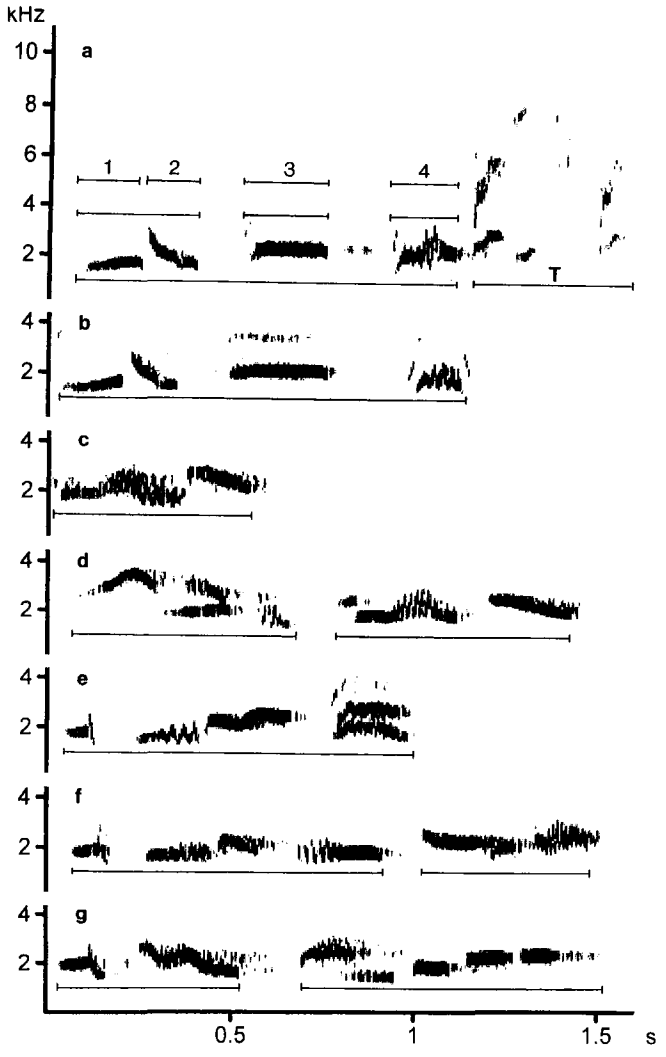
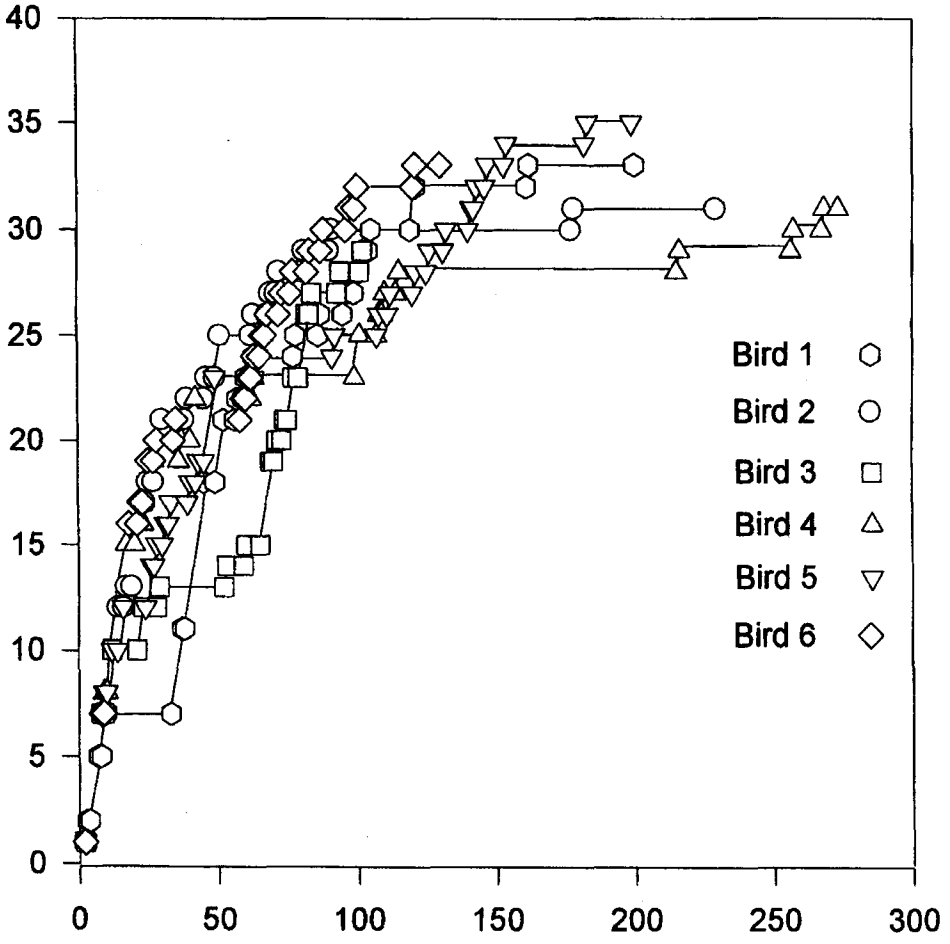


Figure 1. Examples of start motif sharing in the blackbird. **a**: A typical blackbird full song with the introductory whistle part and the ending twitter part (T) underlined. The whistle part only consists of one motif, which is therefore a start motif. The lines immediately above the start motif indicate three sound figures; those in the upper row indicate four sound elements (1-4). **b** – **g**: Six whistle parts with underlined motifs. **b**, **c** and **e** with one start motif; **d**, **f** and **g** with a start motif as well as a central motif. Whistle parts **a** and **g** originate from male 3, **d** and **f** from male 4, **b**, **c** and **e** from males 6, 5 and 1, respectively. Whistle parts **a** plus **b** is an example of start motif sharing between two males where all of the sound figures of the males' respective renditions are identical; **e** plus **f** all but the fourth and the last half of the third sound figures are identical; **g** plus **e** or **g** plus **f** only the first sound figures of the start motifs are identical; **c** plus **d** the shared start motifs occur as a central motif in one of the males.

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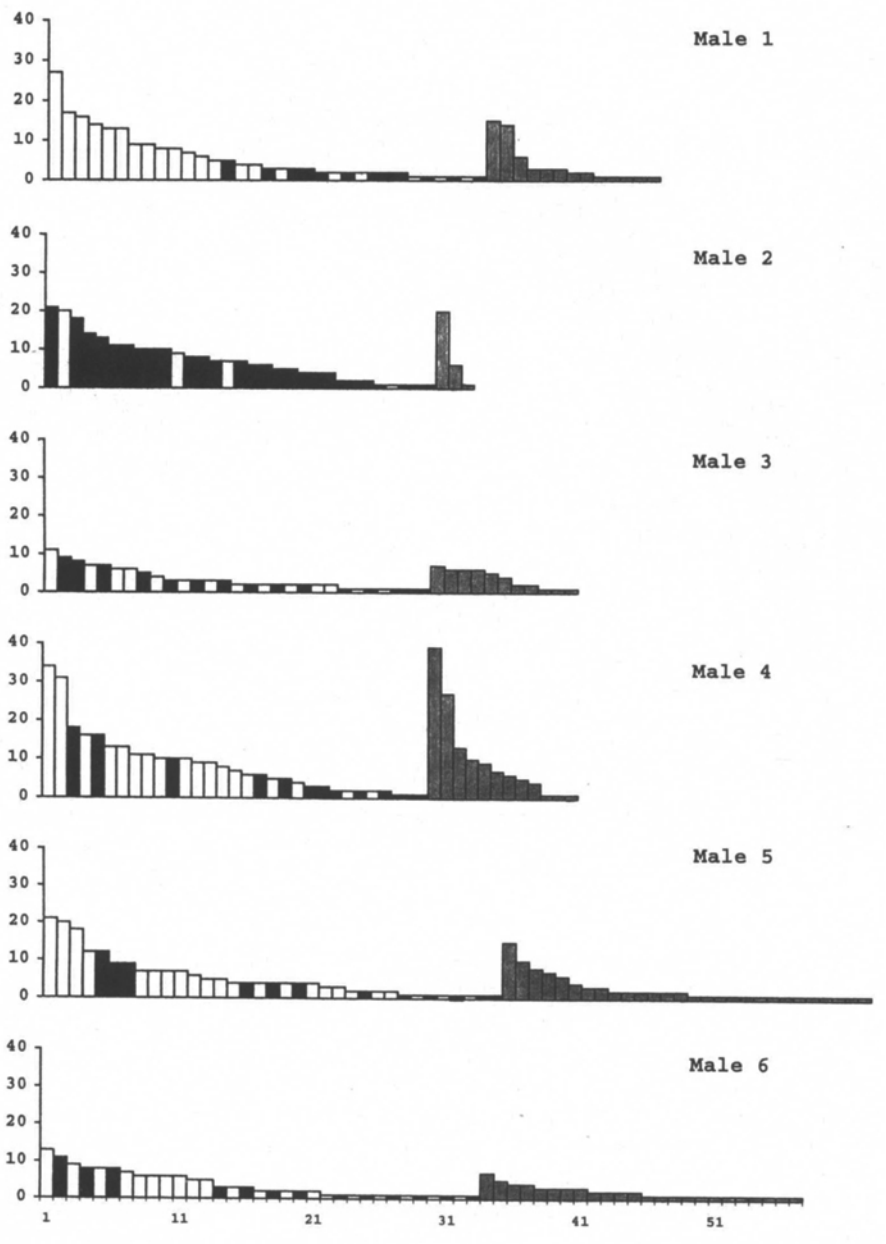


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Figure 2. Cumulative plots showing the number of new start motifs found as a function of the number of songs analysed for the six different blackbird males.

rise to the resumed increase were made on the same day. In males 1, 3, 5 and 6 corresponding recordings were separated by 2, 9, 4 and 9 days, respectively.

All of the individuals sang some motifs very frequently and others very rarely (Figure 3). The 20% of the repertoire that was used most frequently (6-7 start and 2-3 central motifs), accounted for more than 50% of the respective motifs sung. Interestingly, the most frequently used central motifs were not only tied to the most frequently used start motifs, but in almost 3/4 of the cases to those belonging to the category of shared start motifs.



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Figure 3. Frequency with which the motif repertoire of the six different blackbird males were sung. White columns indicate shared start motifs, black columns indicate individual start motifs that were not shared with any of the other five males, and grey columns indicate central motifs.

Individuality and sharing of start motifs

About half (mean ± S.E.: 48 ± 8%) of each male's repertoire of start motifs was individual in the sense of not being sung by any of the other five individuals (Figure 3). The large variation was mainly due to male 2, which had an exceptional number of non-shared start motifs in its repertoire (90%). Without male 2 the percentage of the repertoire that was individual fell to 41 ± 3%. The individual start motifs made up an even lower percentage of the total number of start motifs that were actually sung by the males (39 ± 10% with male 2 included, 30 ± 6% without male 2). The difference, which was significant at $p = 0.032$ (two-tailed sign test, $N = 6$, $x = 0$), indicates a non-random use and hence some kind of active choice of start motifs for at least some of the males. The ratio of individual start motifs to shared start motifs was lower for the most frequently used half of the start motif repertoire (left half on Figure 3) than for the least used half (two-tailed Wilcoxon matched-pairs signed-ranks test, $N = 6$, $T = 0$, $p = 0.05$). However, most of the males (5/6) had some of their individual start motifs among their most frequently used start motifs (Figure 3).

It follows from the above that, on average, more than half of the repertoire of each male consisted of shared start motifs and that the shared start motifs were sung more frequently than expected from their percentage of the repertoire. Among the four identified types of start motif sharing, level 1 and 2 (shared motif identical or almost identical in the two males; see Methods) constituted, respectively, 28% and 57% of all cases of sharing, whereas level 3 (shared motifs of the two males identical only with respect to the first sound figure) and level 4 (shared motifs occurred as a central motif in one of the males) only constituted 6 and 9% of the cases, respectively. This suggests that motif sharing usually is an 'either or' feature.

Although more than half of the start motif repertoires of males 1, 3, 4, 5 and 6 on average consisted of shared motifs, each of these motif sharing males only shared about one quarter (mean ± S.E.: 25 ± 2%) of its repertoire with each of the other males. Male 2 is an exception also in this respect. Relative to the other males of the neighbourhood, it is considered a non-sharing male since it only shared 7% of its start motifs with each of the other males. On the other hand, the few shared start motifs of male 2 were shared with most of its five neighbours, its most frequently used shared start motif was shared with all of them, the second most used with four of them. If the degree of sharing between two males was reflecting the amount of song the two males had received from each other, one would predict the degree of sharing to be negatively correlated with factors such as the distance between the males' song/listening posts and positively correlated with factors such as the time they have been able to receive each others'

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songs. We do not have good data on the number of breeding seasons or the part of the present season when the study males had been neighbours or within receiving distance of each other. However, the distances between the centres of the present year's song post polygons could be determined and we did find a negative correlation between this distance and the number of start motifs shared by the five motif-sharing males (Spearman rank correlation test, one-tailed, $r_s = -0.49$, df = 8, Kendall's t = 2.03, p = 0.05).

DISCUSSION

The present study determined the blackbird song repertoire to include at least 44 different whistle part motifs. This number is probably underestimated, especially for the central motifs, which were analysed less thoroughly than the start motifs. However, it is clearly larger than the repertoire sizes of 26 and 32 motifs determined by Hall-Craggs (1962) and Ince and Slater (1985), respectively. Hall-Craggs (1962) and Ince and Slater (1985) are, as far as we know, the only other studies that have directly counted the whistle part motifs, but they only looked at one individual each. Their very small repertoires may therefore have resulted by mere chance, because they analysed too few songs (Ince and Slater 1985), or because the terminology was slightly different (Hall-Craggs 1962). Ince and Slater (1985) only analysed 73 songs whereas the present study suggests that more than three times as many are necessary. Hall-Craggs (1962) distinguished between 26 basic phrases and 24 variants. At least some of these variants seem to consist of a start motif followed by a central motif.

The repertoire of central motifs varied considerably between the males (Figure 3). Males four and five, both of which were colour-ringed and more than three years old, had rather large such repertoires, whereas that of male two was very small. Male two was also special by having an extremely low degree of song-sharing and a late arrival, suggesting that it was a young floater coming in from another location. We cannot conclude from this single male that an individual's number of different central motifs increases with age. However, the great inter-individual differences in the number of different central motifs suggest that these motifs make up a potential cue for intra- or inter-sexual assessment of male quality. Unlike this, the size of the start motif repertoire varied rather little, both between individuals (Figure 3) and over the breeding season, as shown by the three mid-summer recordings which only added one extra start motif to the repertoires of the respective males.

The cumulative plots of different start motifs found versus number of songs analysed were based on analyses of a number of recordings from each male. Most of these plots approached asymptotes,

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but they also had some interesting sub-plateaus preceding the analysis of a new recording (Figure 2). Theoretically, the resumed increases of the plots following these sub-plateaus could indicate that learning of new start motifs had taken place between the two recordings. However, the fact that very few, or no (male 4), days passed between recordings with sub-plateaus inserted, makes learning an unlikely explanation of the resumed plot-increases. We believe they represent some dynamic aspect of singing, for instance active choice of start motifs to, for instance, increase matching to the songs of different singing neighbours.

The blackbird is known to perform song matching and respond to such matching (e.g. Todt 1968, 1981). Therefore, song sharing in the blackbird cannot simply be considered a functionless epiphenomenon of song learning. The present study indicates that it is possible for a territory owner to match about one quarter of the start motifs of each of its neighbours (Figure 3). Because of the apparent capability of open-ended song learning (e.g. Thielcke-Polz and Thielcke 1960, Hall-Craggs 1962) even a newcomer (like male two of the present study) will probably soon be able to match some of the start motifs of its neighbours. This is indicated by the fact that the most frequently used shared start motifs of male two were shared with almost all of its five neighbours.

The present study shows that blackbirds have relatively large or medium sized song repertoires and show high degrees of song sharing. According to the repertoire constraint hypothesis (Krebs and Kroodsma 1980, Falls 1982), relatively large repertoires should constrain individual recognition by song in this species for at least three reasons: (1) the perceptual memory could somehow become overworked; (2) the single song could be sung and therefore heard relatively infrequently by neighbours, reducing the possibility for learning the songs; (3) a large repertoire could increase song similarity and therefore diminish the differences between individuals, because the frequency-time patterns giving rise to the different songs can only vary within certain species-specific limits (Krebs and Kroodsma 1980, Falls 1982). The high degree of song sharing should contribute to the reduction in the differences between individuals and might therefore also interfere with individual recognition (e.g. McGregor and Avery 1986, Stoddard et al. 1991, Stoddard 1996). However, the present study also shows that each blackbird has a number of start motifs that are individual, and a few of these are among the most frequently sung motifs in most individuals. By concentrating on these few very frequent individual start motifs of their neighbours, blackbirds would certainly not be constrained by the capacity of their perceptual memory anymore than would low repertoire species, and their learning effort would be minimal as would the risk of inter-individual similarity of the start motifs forming the basis for individual recognition.

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A previous study suggested that all of the most frequently sung motifs, the so-called preferred motifs (Dabelsteen 1984), formed the basis for individual recognition because the human observer could identify individual blackbirds by these motifs. This is different from the findings of the present study that only a few of the preferred motifs are actually individual. If males from outside the present local neighbourhood were included in the analysis, it is even possible that this number could be reduced, although only slightly because the degree of song sharing decreased with distance. However, blackbirds repeat their repertoires of motifs according to certain syntactical rules (e.g. Todt 1972, Todt and Wolffgramm 1975). Repeated individually distinctive orders of motifs could therefore represent other cues for individual identification, both to blackbirds and to humans, and it is possible that such cues may somehow have tied individual and non-individual motifs in the recognition process and led to the wrong conclusion that all of the preferred motifs were individual (Dabelsteen 1984).

The extents to which orders of motifs will add to the individuality of blackbird singing has to be investigated further. For the present, it seems that the blackbird would not normally need to include order cues or other extra cues in the process of individual recognition. The exception would perhaps be if individuals (like male 1 in this study) do not sing any of the individual motifs very frequently. The high degree of song-sharing and the relatively large to medium sized song repertoires of blackbirds probably will not hinder song-based song recognition of most individuals in this species, as otherwise would be predicted by e.g. the repertoire constraint hypothesis (Krebs and Kroodsma 1980, Falls 1982). To counter the constraints of large repertoire and high degree of song sharing, the blackbird seems to have evolved a special system in which most males repeat a few individually distinctive motifs very frequently. By focusing on these motifs, receivers can identify the singer.

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