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ORIGINAL PAPER

Are there age-related differences in the song repertoire size of Eurasian blackbirds?

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Abstract Most oscine bird species possess a repertoire of different song patterns, and repertoire size is thought to signal aspects of male quality. As age is assumed to be related to male quality in terms of experience and/or viability, repertoire size may be expected to reflect male age. Here, we investigated the relationship between repertoire size and age (yearlings or older) in Eurasian blackbirds, *Turdus merula*, a species with a large repertoire delivered in a highly variable manner. We found that older males tended to have larger repertoires than yearlings though the two age groups overlapped considerably. Thus, compared to other species with large repertoires, age-related differences in repertoire size seem rather small in male Eurasian blackbirds. We also compared repertoires of three individuals in two successive years (as yearlings and in the year following) and found a large element turnover. Our investigation revealed that this turnover was almost complete in the quiet terminating twitter part of the song. Such turnover may allow a young bird to adjust his repertoire to his neighbours' repertoires, which could be useful for song matching interactions.

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Introduction

In several oscine bird species, males have elaborated repertoires of different song patterns. Females of some species prefer larger repertoires, and a few studies have shown that repertoire sizes also have an effect in intra-sexual contexts (Collins 2004; Catchpole and Slater 2008). Repertoire size has been linked to different aspects of male quality such as body size, body condition, immunocompetence, social status and learning ability (Spencer et al. 2004; Boogert et al. 2008, overview in Catchpole and Slater 2008) corroborating the hypothesis that repertoire size serves as an honest signal of male quality. Another possible correlate of male quality is age. Older males may be more experienced and therefore have better territories, offer better parental care or other direct benefits to females. Older males have also proven their superior quality by the mere fact of surviving, offering indirect benefits (Brooks and Kemp 2001). In some bird species, it has been shown that older individuals have better survival expectations or reproductive success (Martin 1995). For instance, in American redstarts *Setophaga ruticilla*, older males bred more successfully (Lemon et al. 1992), and in red-winged blackbirds *Agelaius phoeniceus*, older and longer-lived males sired more young by extra-pair fertilisations (Weatherhead and Boag 1995). In Eurasian blackbirds (from now on referred to as 'blackbirds'), older males had more offspring, which were in better condition, than yearling males (Préault et al. 2005; we use the term 'yearling' for individuals in their second calendar year, i.e. that are approximately 1 year old and 'adult' for individuals that are at least in their third calendar year, i.e. at least approximately 2 years old).

Song repertoire sizes increase with age in several species (Garamszegi et al. 2007), especially in species with large repertoires, e.g. common nightingales (Kiefer et al. 2006, 2009) and whitethroats (Balsby 2000; Balsby and Hansen 2009), but typically not in species with small repertories, e.g. zebra finches (Immelmann 1969; Nordby et al. 2002) and blue tits *Cyanistes caeruleus* (Poesel et al. 2006). In general, most differences in repertoire sizes have been found between yearlings and 2-year-old males, while in older birds, often no or only smaller changes were found (reviewed in Kipper and Kiefer 2010, but see Mountjoy and Lemon 1995 and Forstmeier et al. 2006).

Two different non-mutually exclusive mechanisms could lead to these age-related changes in repertoire sizes. One is an actual repertoire size increase with age, either by means of addition of new song or element types acquired later in life (Hultsch and Todt 2004), or by means of adding previously 'silent' song (or element) types, which are memorised in an early sensitive phase, but only reproduced later (Geberzahn and Hultsch 2003). The other mechanism could be that males with different repertoire sizes (reflecting differences in male quality) could suffer different mortality rates, leading to larger average repertoires in older males (Hiebert et al. 1989; Gil et al. 2001; Forstmeier 2002). In both cases, differences in repertoire size potentially contain information about the quality of the signaller. While a cross-sectional approach is suitable for revealing age-related differences in repertoire size and reflects the situation faced by a conspecific listener, only longitudinal studies including mortality data can reveal which of the two principally different mechanisms is active. However, longitudinal studies may underestimate the actual differences between age groups if they only include surviving males of high quality. This may explain why a cross-sectional study in the common nightingale found that older males had 53 % larger repertoires than yearlings (Kiefer et al. 2006), while a longitudinal study in the same population showed an increase of only 24 % between yearlings and 2-year-old males (Kiefer et al. 2009). The possibility that this difference was due to a further repertoire increase in males older than 2 years can be excluded since in older birds (from the same population), repertoire sizes did not change between years (Kipper et al. 2004). Hence, a combination of the cross-sectional and longitudinal approaches may be most appropriate in investigating the development of repertoire size.

In this study, we applied these approaches to test for a relationship between repertoire size and age in blackbirds. We cross-sectionally compared repertoire sizes of yearling males with those of adult males. In addition, we compared repertoire sizes of three individuals in multiple years (i.e. as yearlings and 2-year-old males, respectively).

Blackbird song

Male blackbirds produce a complex song with a large repertoire in a discontinuous singing style where discrete songs are separated by silent breaks (Todt 1981; Dabelsteen 1984). Each song typically starts with the low-frequency, long-ranging whistle part and ends with the twitter part, which has a much broader frequency range, lower sound pressure level and thus considerably shorter transmission range (Dabelsteen 1984; Dabelsteen et al. 1993) than the whistle. The blackbird combines song elements in shorter, more or less fixed sequences ('motifs', Dabelsteen 1984; Rasmussen and Dabelsteen 2002), and different motifs are combined within songs in a flexible way. Thus, the blackbird has no fixed song types. Even though it is one of the most common species in Europe and has a very conspicuous song, almost nothing is known about the role of repertoire size for this species. However, as blackbirds are reported to be open-ended learners (Messmer and Messmer 1956; Thielcke-Poltz and Thielcke 1960), they may be able to increase their repertoire sizes with age by adding new element types.

Methods

Study population

We conducted this study on the island of Helgoland, Germany, hosting a blackbird population consisting of about 80 breeding pairs at the time of the study. The population has been studied since 2003 (Sacher et al. 2006). Birds were marked with a unique combination of three colour rings and one aluminium ring (ringing permission given by the Institute of Avian Research 'Vogelwarte Helgoland'). For ring marking, birds were either caught in the nest as nestlings or with spring loaded net traps. Yearlings are distinguishable from adult males by a moult border in the greater coverts, which is clearly visible in males (Glutz von Blotzheim and Bauer 1985; Svensson 1992). In addition, of the 11 males that we used in this study, the exact age of six was known since they had been ring marked as nestlings. Two males were ringed in the year of hatching when the plumage is still distinct from that of adults (Glutz von Blotzheim and Bauer 1985), one as a yearling and two as adults.

Song recording and analysis

We recorded dawn song of 11 territorial males in the breeding seasons of 2006–2008, between 6th of April and 18th of June, starting approximately 1 h before sunrise (between 0355 and 0630 hours Central European Summer Time). In our study population, the whole breeding (and singing) season lasts at least 4 months. We recorded each bird on a single morning except for two individuals, who did not produce enough songs on one morning. For those, recordings from 2 days were used: for one bird, the recordings were made on two successive days, while for the other, the second recording session took place 6 days later. Songs were recorded with a Marantz PMD670 solid state recorder with a sample rate of 22,050 Hz (2006) or 44,100 Hz (2007 and 2008) and a directional microphone (Sennheiser K6/ME67). Avisoft-SASLab Pro 4.4–4.52 was used for all sound analyses. Recordings made in 44,100 Hz were down sampled to 22,050 Hz, and all recordings were filtered (Butterworth; high pass, 1.5 kHz; low pass, 10 kHz). We defined songs as bouts of singing that were separated from each other by a silent break of ≥0.5 s, or, if only twitter elements (see below) followed, by a silent break of ≥1 s. We printed spectrograms of songs (settings: FFT length, 512; window Hamming; bandwidth, 56 Hz; resolution, 43 Hz; frame size, 100 %; overlap, 75 %; resolution, 5.8 ms; graphical scale on prints, 1 s=36 mm and 1 kHz=6 mm) and visually compared elements for repertoire analyses. We classified all elements in a recording into different element types depending on their overall appearance on the spectrogram (frequency and temporal domain, Fig. 1). We measured repertoire size as the number of different element types per male and classified element types as either a whistle (low frequency, almost pure toned and high sound pressure level) or a twitter (broader frequency range, more energy on overtones and lower sound pressure level) element (Fig. 1; more details about element classifications in Hesler 2010 and Hesler et al. 2011).

In blackbird song, even after 300 or more songs, new element types can occasionally occur, although the largest portion of the repertoire is presented within approximately the first 100 songs (Fig. 2). However, for this study, we were more interested in inter-individual differences in repertoire sizes than in the birds' absolute repertoire sizes (and the same may be true for a female choosing a mate). Inter-individual differences can become apparent, long before the asymptote of new element types is reached (Gil and Slater 2000). In another study, we found that the repertoire size found in approximately 40/100 (adults/yearlings) songs already correlated strongly with the repertoire size found in about 140/170 songs in 6/6 birds (exact Spearman rank correlations, rho>0.9, $P<0.05$, Hesler 2010). Therefore, we felt confident that repertoire sizes calculated from 240 songs per male formed a reasonable estimate of actual repertoire size, even though we could not assess their complete repertoires. Due to the extreme expenditure of time for repertoire analyses in the blackbird's complex song, we had to restrict the analysis to a relatively small sample of birds.

As the number of elements per song can vary to a large extent (results from a different sample of adult males in the same population: number of elements per song on average=11.2, minimum=2, maximum=58, N=31 males, 5,464 songs in total, Hesler 2010), we used four different measures of repertoire size: the 'song-standardised combined repertoire' as the number of different element types in the first 240 analysed songs; the 'element-standardised combined repertoire' as the number of different element types in first 2,345 analysed elements; the 'whistle repertoire' as the number of whistle element types found in the first 1,400 analysed whistle elements; and the 'twitter repertoire' as the number of twitter element types in the first 870 analysed twitter elements (analysed numbers of songs and elements were the respective numbers of songs or elements available in the shortest recording).

All repertoire analyses were carried out by the same person (NH), but an independent person, B. Klump, analysed 102 songs of one bird after being instructed on how to do so. She obtained a combined repertoire size of 253 element types compared to NH's result of 257 element types, i.e. a difference of 0.02 %.

Cross-sectional comparison

We compared repertoire sizes of the two age groups (yearlings and adults, N=5 for each age group) using exact Mann–Whitney U tests. Since we did this four times for our four different repertoire size measurements of which at least some are likely to correlate (namely the two combined

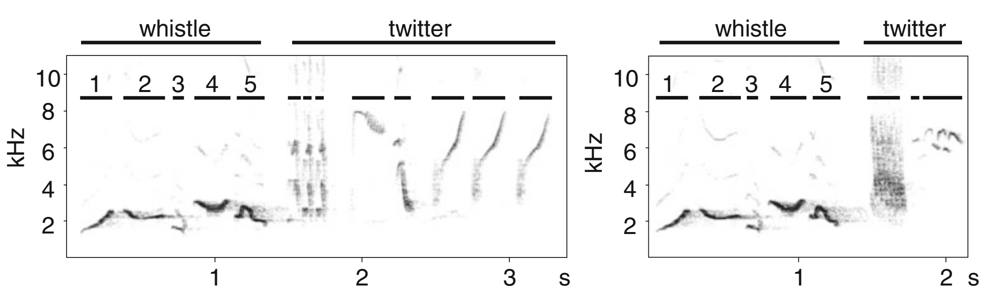


Fig. 1 Spectrograms of two blackbird songs with indication of whistle/twitter parts and single elements (*black bars*). *Numbers* indicate element types, which occur in both songs. In this example, the whole whistle parts are identical in both songs, while the twitter parts are different. Songs are usually separated by silent intervals of about 1.5–7.5 s (Dabelsteen 1984)

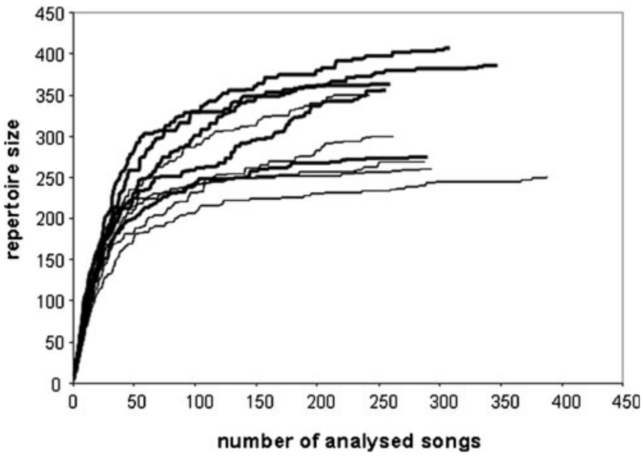


Fig. 2 Cumulative element repertoire, song-standardised. The numbers of different element types (repertoire size) are plotted against the number of analysed songs. *Thin lines* Yearlings (N=5), *bold lines* adult males (N=5)

repertoire sizes as well as the whistle with the combined and the twitter with the combined repertoires), we corrected for multiple testing using Fisher's omnibus test with a P value determined based on a permutation procedure (Adams and Anthony 1996; Manly 1997). In principle, Fisher's omnibus test combines a number of P values into a single chi-square distributed variable with degrees of freedom equalling twice the number of P values (Haccou and Meelis 1994). However, this procedure requires independent P values, which cannot be assumed in the case of our four different repertoire measurements from the same individual. Hence, the theoretical chi-square distribution is not valid (Potter and Griffiths 2006). In order to achieve a valid test nevertheless, we permuted the age group across subjects, calculated the four Mann–Whitney U tests again, and finally combined the P values derived into a chi-square value like in Fisher's omnibus test. We ran 252 permutations (enumerating all possible permutations of the data), and determined the P value assigned to the chi-square of the original data as the proportion of permutations revealing a chi-square at least as large as that of the original data. R (version 2.9.1; R Development Core Team 2008) was used for statistical analyses.

Longitudinal comparison

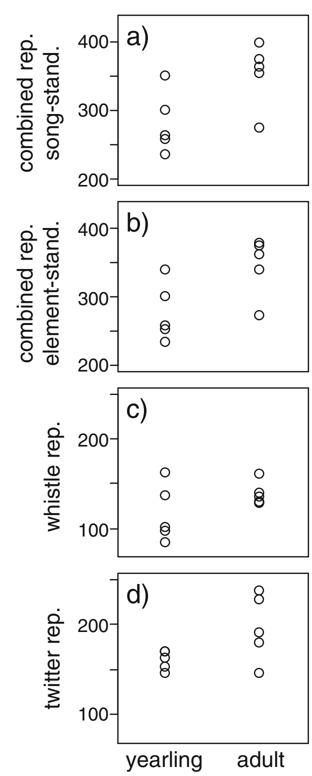
For three yearlings, we analysed recordings from the subsequent year, i.e. when they were approximately 2 years old, in order to get an impression of how the repertoire develops between years. The yearling data from two of these males were already used in the cross-sectional investigation, while the data from one male was not. Since we did not have 240 songs for the latter male, he could not be included in the cross-sectional study. In the second year, we had only shorter recordings of the same individuals containing 103, 104 and 175 songs, respectively. For each bird, we compared the same number of songs or elements from both years. We compared repertoire sizes and measured the degree of sharing between the 2 years. For each of the three birds, we applied a binomial test to see whether the number of non-shared elements differed significantly between years using the function 'binomdist' of Microsoft® Office Excel 2003 SP3.

Results

Cross-sectional comparison

Overall, adult males tended to have larger repertoires than yearlings (Fisher's omnibus test combined with permutation procedure: χ^2=18.96, P=0.063). In particular, adult birds tended to have larger combined repertoires, both in terms of song-standardised (adult males, 352±47.2; yearlings, 280±45.3 element types; mean±SD; Mann–Whitney U test, U=2, N=10, P=0.032) and element-standardised repertoires (adult males, 345.6±43.5; yearlings, 276.6±42.9 element types; U=3, N=10, P=0.056; Figs. 2 and 3a, b). A separate check for whistle and twitter repertoires revealed differences between the age groups in the same direction, though none of these were significant (whistle repertoire: adult males, 138.4±13.4; yearlings, 116.2±32.3 element types; U=8, N=10, P=0.142; twitter repertoire, adult males, 196±37.2; yearlings, 160.2±10.4 element types; U=4.5, N=10,

Fig. 3 Repertoire sizes of the two age groups. Repertoires are standardised to 240 songs (**a**), 2,345 elements (**b**), 1,400 whistle elements (**c**) and 870 twitter elements (**d**). N=5 yearlings, 5 adult males



P=0.103; Fig. 3c, d). On average, repertoire sizes of older birds were approximately 20 % (song-standardised combined repertoire), 19 % (element-standardised combined repertoire), 12 % (whistle repertoire), or 19 % (twitter repertoire) larger than those of yearlings.

Longitudinal comparison

Our longitudinal analysis of three males as yearlings and in the following year showed a slight increase in repertoire size between years (Fig. 4). This was the case for the combined repertoire of all three individuals, both in terms of song-standardised (average increase by 11.3 %, Fig. 4a) and element-standardised repertoire (average increase by 9.2 %, Fig. 4b). All three birds also increased their twitter repertoire sizes between the years (average increase of the twitter repertoire by 14.2 %, Fig. 4d). However, there was almost no difference between the years in terms of the whistle element repertoire—one individual's repertoire size even decreased (average increase in the whistle repertoire by 3.5 %, Fig. 4c).

We also examined the proportions of elements that were shared between the 2 years vs. the elements, which we found only in 1 year (Fig. 5). With an average of 11 %, the amount of shared elements was rather small. The proportion of elements only found in the second year (46.3, 49.1, and 46.0 %, respectively) was consistently, but not much, larger than the proportion of elements, which we found only in the first year (40.2, 43.5 and 41.6 %; Fig. 5a). Dividing the repertoire into whistle and twitter elements revealed that the turnover between years was largest in the twitter repertoires. While, on average, 23 % of the whistle elements occurred in both years, only 3 % of the twitter element repertoire was found in both years (Fig. 5b, c).

In none of these cases did the numbers of element types occurring solely in the first and solely in the second season differ significantly from one another (three subjects times three repertoires=nine binomial tests: N=58–311, mean of 170 elements per test, smallest P=0.07, average p=0.34, no error level correction applied). Thus, the increases in repertoire size between years that we found in all three birds were not significant.

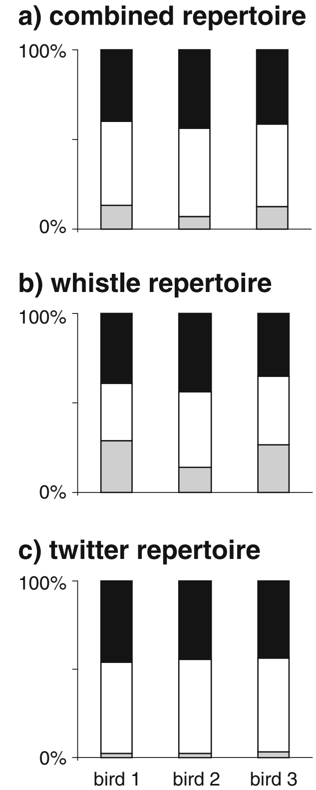


Fig. 5 Element sharing between years. The graph shows percentages of combined, whistle and twitter element types which the three birds sang only in one of the years (*black* as yearling, *white* as 2-year-old bird) or which were shared between the years (*grey* both years)

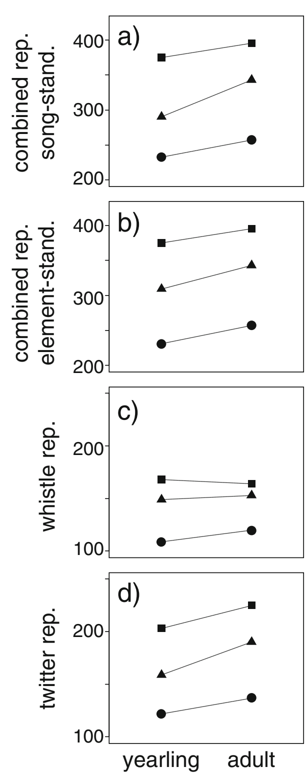


Fig. 4 Repertoire sizes of three males in two successive years: as yearlings and 2-year-old males. Shown are a) the song-standardised combined repertoire, b) the element-standardised combined repertoire, c) the whistle repertoire and d) the twitter repertoire. For each male, repertoires are standardised to the same number of songs or elements in both years. The *three symbols* are used to depict the three males in all plots

Discussion

Adult blackbird males tended to have larger repertoires than yearlings, but there was a considerable overlap between the age groups. The fact that this tendency did not reach statistical significance may be due to the small sample size, but the overlap between the age groups' repertoires suggests that age-related differences in repertoire sizes are indeed rather small. Separating the whistle and twitter repertoire did not reveal significant differences, but showed that the whistle repertoire overlapped completely between the age groups, while in the twitter repertoire, only one adult bird's repertoire size fell in the range of the yearlings (Fig. 3). Results of the longitudinal approach were comparable in that repertoire sizes increased consistently but not significantly from the first to the second breeding season.

Thus, the blackbird seems to be intermediate between species in which repertoire size does not obviously increase from the first to the second breeding season [e.g. zebra finch, Immelmann (1969) (longitudinal); song sparrow, Hiebert et al. (1989) (cross-sectional: older males had larger repertoires than yearlings, but due to higher mortalities of individuals with small repertoires), Nordby et al. (2002) (longitudinal); blue tit, Poesel et al. (2006) (cross-sectional); great tit *Parus major*, Rivera-Gutierrez et al. (2010) (cross-sectional); reviewed in Kipper and Kiefer (2010)] and others that show a clear increase in repertoire size between the first and the second breeding season [e.g. starling, Eens et al. (1991) (cross-sectional), Mountjoy and Lemon (1995) (cross-sectional, longitudinal comparison with over 2 years old males); whitethroat, Balsby (2000) (cross-sectional), Balsby and Hansen (2009) (longitudinal); willow warbler *Phylloscopus trochilus*, Gil et al. (2001) (cross-sectional and longitudinal); common nightingale, Kiefer et al. (2006) (cross-sectional), Kiefer et al. (2006) (longitudinal); collared flycatcher, *Ficedula albicollis*, Garamszegi et al. (2007) (cross-sectional); sedge warbler, Nicholson et al. (2007) (longitudinal); reviewed in Kipper and Kiefer (2010)]. Compared to these latter species in which repertoires differed between the first and second breeding season by, for instance, 53 % [common nightingale, Kiefer et al. (2006), cross-sectional comparison], or 60–330 % [whitethroat, Balsby (2000), longitudinal comparison], the differences in repertoire size we found in the blackbird were rather small (on average 20 % for the combined element-standardised repertoire). Given this relatively slight increase in repertoire size and the considerable overlap between the age groups' repertoire sizes, song element repertoire size seems to be an unreliable indicator of a blackbird's age. These results seem surprising, since the overall picture from the literature suggests that repertoire sizes tend to increase between the first and second breeding season, especially in species with large repertoires (common nightingale and whitethroat) or medium repertoires and a complex song organisation (willow warbler, collared flycatcher and sedge warbler), but not in species with small repertoires (zebra finch, song sparrow, blue tit and great tit). The blackbird with its large element repertoire and complex song structure thus does not seem to fit in this pattern. Nevertheless, a song development between years could also play out in the use of the repertoire, e.g., a changing frequency distribution of the different element types, flexibility of their sequential order or the accuracy in their repetition.

Despite the small differences in repertoire size between age groups, the longitudinal analysis revealed a dramatic turnover of repertoires between the first and second breeding season: Birds dropped a large part of their repertoires and added many new elements, so that they used only a small proportion of their repertoire in both years (on average 11 % of the combined repertoire, 23 % of the whistle and only 3 % of the twitter repertoire). A large repertoire turnover between years was also observed in other species: 43 % overlap in the common nightingale (Kiefer et al. 2009) and 16 % in the whitethroat (Balsby and Hansen 2009), both between yearlings and 2-year-old individuals; 33–44 % overlap in sedge warblers [also older than 2-year-old individuals; Nicholson et al. (2007)]. Thus, such repertoire turnovers may be a common phenomenon.

One possible function of these large repertoire turnovers may be to increase the proportion of the repertoire, which is shared with neighbouring males by dropping non-shared element or song types and adding shared ones (Kiefer et al. 2010). Shared element or song types are used in vocal interactions in several songbird species during which one male matches the other's song, that is, singing the same song or element type as a conspecific (Collins 2004; Beecher and Brenowitz 2005). This allows addressing specific individuals or announcing the belonging to a local neighbourhood and has been shown to be an aggressive signal (e.g. McGregor et al. 1992; Collins 2004, overview in Beecher and Brenowitz 2005). Blackbirds share parts of their repertoires with neighbours, whistle parts (Rasmussen and Dabelsteen 2002) as well as twitter parts (Klump et al. 2012), and match whistle element types ('Startklassen') during 'countersinging' interactions (Todt 1968, 1970, own observations). Hence, a high amount of repertoire sharing may be advantageous for male blackbirds. Whether and how repertoire size and the degree of repertoire sharing are related and also the question of whether repertoire sharing with neighbours increases with age and correlates with male quality are all topics that need further research. Interestingly, the incomplete turnover of the whistle part may also allow the preservation of individual elements to announce individual identity. Since blackbird males often use the same territory over several years (Snow 1958; own observations), the preserved individuality may facilitate recognition of previous 'dear enemies' (Fisher 1954; Ydenberg et al. 1988; Temeles 1994) among the neighbours already at the start of the breeding season and hence reduce some of the territorial aggression, which can be very intense and risky at this time of the year.

Concerning the question of how the differences between age groups arise, i.e. due to different mortality rates or a real increase by addition of new element types, the whistle gives a different picture than the twitter repertoire (Figs. 3 and 4), although none of the results regarding only whistle or twitter repertoires were significant. In the whistle part, in the cross-sectional comparison, adult repertoires were on average 12 % larger than yearling repertoires, but repertoire sizes overlapped completely between age groups with a higher variation among yearlings than adults (Fig. 3c). The longitudinal comparison revealed a small increase, in one case even a decrease, from 1 year to the other (Fig. 4c). This pattern could be explained by different mortality rates of low- and high-repertoire individuals resulting in slightly larger average adult repertoires and a lower variation among adult males. In the cross-sectional comparison of twitter repertoire, adults also had larger repertoires than yearlings, though not significantly larger. However, in this comparison, age groups overlapped considerably less and only in one bird (Fig. 3d). This combined with the fact that all three individuals from the longitudinal comparison indeed increased their twitter repertoires (Fig. 4d) suggests that a real increase in repertoire size may explain the larger repertoires of adults. Different mortality rates of low- and high-repertoire individuals alone could not explain non-overlapping differences between age groups, since the surviving individuals would have the same repertoire size already as yearlings.

Whether the 2-year-old blackbirds increased their repertoires by ‘silent’ element types that have been acquired in the hatching season, but not reproduced before the second breeding season (Geberzahn and Hultsch 2003), or by adding new element types acquired during the first breeding season, cannot be distinguished in this study. As blackbirds are reported to be open-ended learners (Messmer and Messmer 1956; Thielcke-Poltz and Thielcke 1960), the addition of new element types might be possible, but the two mechanisms are not exclusive. To distinguish between these mechanisms, longitudinal laboratory experiments that control everything an individual hears and sings in progressive years would be necessary.

In conclusion, we found that older males tended to have larger element repertoires than yearling males. Even though in a larger sample, this trend may become significant, we found a considerable overlap between age groups making it difficult to pinpoint the age group of a male blackbird solely by his song element repertoire size. However, previous findings of correlations between male body size and element repertoire size in blackbirds (Hesler 2010) combined with the assumption that both body size and age correlate with aspects of male quality make it plausible that repertoire size may serve as a signal of ‘overall’ male quality in blackbirds. Thus, repertoire size may play a role in both inter- and intrasexual selection. In a territory intrusion experiment, male blackbirds did not respond differently towards playback of conspecific song with different repertoire sizes (Hesler et al. 2011). We can, however, not exclude that this indifferent but generally strong response was due to a ceiling effect in our experiment and can therefore not rule out that repertoire size does play a role in other intra-sexual contexts despite our negative results (Hesler et al. 2011). We are currently analysing paternity data to investigate a role of repertoire size in mate choice.

Our longitudinal approach showed a large turnover in the repertoire composition between the first and second breeding season, especially in the twitter repertoire. Once it is possible to apply automated element type classifications, we will be able to investigate whether this turnover leads to a larger degree of repertoire sharing with neighbouring males and if and how this degree of sharing relates to male quality.

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