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Two strategies of between-season changes in the song composition of the pied flycatcher

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In Oscine species, changes in songs are age-dependent: some species do not change their singing repertoires after a short sensitive period, whereas others may include new songs throughout their lives. In many cases, changes in singing repertoires are more pronounced between the first and second years of life. I describe changes in song composition from one year to the next in 23 pied-flycatcher males, which differed in breeding plumage coloration. Eight yearling birds showed profound between-season syllable repertoire turnover whereas seven yearlings and eight older males retained their previous song composition. Males with profound changes in their repertoire were significantly paler, arrived later and had smaller first-year repertoires than other males. Although additional studies are needed to clarify the relationship between these factors, it seems plausible that dark- and pale-coloured pied-flycatcher males have different patterns of between-season repertoire turnover: pale males change their syllable repertoire sufficiently between the first and second years of life but not thereafter, whereas dark males develop a rather stabilised repertoire by the first year of life. This agrees with the finding that pale and dark birds exhibit different breeding strategies.

Introduction

A bird song is a powerful means of inter-specific communication, used mostly by males. It provides information on male characteristics that are important in mate choice (Catchpole & Slater 2008). The age of a male is supposed to be a sufficient indicator of its quality: older males are more experienced than younger ones and a long life-span is an honest signal of male genetic quality. Thus, choosing more mature males may be advantageous for females. Females can use males' songs in searching for a good-quality mature mate if males change their songs with age and songs of older males are more attractive to females. Indeed, age-related differences in singing have been described for many Oscine species (*see* Kipper & Kiefer 2010). Laboratory studies provide evidence that such age-dependent changes in songs are often closely related to the phenomenon of song learning: many Oscine species need to hear species-specific songs at an early age to develop a normal singing repertoire. After a short sensitive period in their early life, some species (so-called close-ended learners, such as the zebra finch *Taeniopygia guttata*) lose the ability to learn new songs. Open-ended learners, like canaries *Serinus canarius* and European starlings *Sturnus vulgaris* may learn new types of song syllables and add them in their singing repertoire throughout their life (for references *see* Beecher & Brenowitz 2005a, 2005b).

In a comparative review with both laboratory and field ornithological studies, Kipper and Kiefer (2010) revealed three main patterns of age-dependent changes in bird songs: no changes after developing a final (crystallized) song within the first year of life, pronounced changes between the first and second years of life but not thereafter, continuous changes throughout the life span of the species. These changes may be detected in (1) repertoire size, (2) repertoire turnover (adding or dropping new song types, syllables or elements), (3) spectral and temporal characteristics of songs, and/or (4) the degree of song sharing and other song features (Kipper & Kiefer 2010).

One of the best known patterns of changes in songs is the increase in repertoire size with age. Repertoire size of a bird is calculated as the number of different song elements, syllables or song types performed during a vocal session. In many species, including the willow warbler *Phylloscopus trochilus* (Gil *et al.* 2001), the brown-headed cowbird *Molothrus ater* (O'Loghlen & Rothstein 2002), the collared flycatcher *Ficedula albicollis* (Garamszegi *et al.* 2007) and the pied flycatcher *Ficedula hypoleuca* (Espmark & Lampe 1993) adults have generally larger repertoires than yearlings. In long-term studies of the great reed warbler *Acrocephalus arundinaceous*, where the same individuals were observed over several consecutive years, males increased their repertoire size not only between the first and second years of life, but also thereafter (Hasselquist *et al.* 1996, but *see* Catchpole 1986). These age-dependent changes support the idea that females use songs to find more mature males, as females often prefer males with larger singing repertoires (Catchpole & Slater 2008).

Birds may not only include new song types and/or syllables in their singing repertoires, but also drop old ones. A sufficient repertoire turnover between breeding seasons has been shown for several species (Kipper & Kiefer 2010). In some cases this pattern is related to an increase in song sharing. For example, village indigobirds *Vidua chalybeata* (Payne 1985), thrush nightingales *Luscinia luscinia* (Sorjonen 1987) and great tits *Parus major* (McGregor & Krebs 1989) adjust their song repertoire to repertoires of neighbouring birds and include new song types that are similar to the songs of newly-arrived neighbours. Common nightingales *Luscinia megarhynchos* add "popular" songs (that are often sung by many males) and drop rare variants, adjusting their song repertoire to the population (Kiefer *et al.* 2010). Similarly to an increase in repertoire size, repertoire turnover is often more pronounced between the first and second years of life than between successive years.

The pied flycatcher provides a great opportunity to study age-dependent song changes in individual birds. Pied flycatchers are hole-breeders and they can easily be attracted by nest boxes in a breeding area. Their post-breeding dispersal is low: about 30% of males return to the previous breeding point the following year (Sokolov 1991, Artemyev 2008). During the breeding period, birds can easily be caught, colour-ringed and marked for visual recognition, after which song recordings can be obtained from marked males.

A remarkable trait of this species is polymorphism displayed in breeding plumage colouration in males. Pied-flycatcher males vary from black-and-white variants to pale brown, female-like ones. The type of plumage colour of a male is traditionally described using the Drost scale (Drost 1936), which consists of seven grades (morphs), where black-and-white birds are the first morph, and pale, female-like males — the seventh. Yearling males are in general paler than adult males, but age cannot fully explain the difference in plumage colour (Anorova 1977, Røskaft *et al.* 1986). The type of plumage colour is inherited (Lundberg & Alatalo 1992, Grinkov 2000), and pale and dark-coloured males show differences in ecological, physiological and behavioural traits (Gavrilov *et al.* 1993, Ivankina *et al.* 1995, Kerimov *et al.* 1995, Grinkov 2000, Ilyina & Ivankina 2001).

Males of this species sing actively so-called advertising songs before pairing to attract a female (Eriksson & Wallin 1986). After mating, their singing activity generally decreases (Espmark & Lampe 1993). However, mated birds often start to advertise a new nest-box, trying to attract another female: this species is facultatively polygynous (Lundberg & Alatalo 1992). Mated males also have a short peak of singing activity in the early morning — so-called dawn-singing (Vabishchevich 2011a).

A detailed description of the pied flycatcher song was provided by Espmark and Lampe (1993). These authors described the syllable repertoire of a bird as a set of different syllable types used in 25 consecutive songs. Males were regarded as yearlings if they were registered in the study area for the first time. According to their study, (1) adult birds have, in general, larger syllable repertoires than yearlings, and (2) some individual pied-flycatcher males change their syllable repertoires substantially between years, whereas other males use mostly the same syllable types the following year. The latter finding may reflect the ability to learn new songs in adulthood. The inclusion of new syllables into songs was also shown in a recent study (Eriksen *et al.* 2011): in a field experiment, a conspecific but unfamiliar song was played back to 20 pied-flycatcher males; after a one-week playback treatment three pied-flycatcher males had included foreign song syllables in their songs. Therefore, pied flycatchers are thought to be open-ended learners.

There is a particular interest in searching for a link in between-seasonal changes in song composition and age. In a previous study (Espmark & Lampe 1993) such a relationship was not shown, presumably due to small sample sizes and the method of ageing used. In this paper, I study the link between age and degree of between-seasonal syllable turnover in pied-flycatcher males. To this end, I quantitatively estimated the differences between songs performed in consecutive years for yearling pied flycatchers and older males (adults) of known plumage colour type.

Materials and methods

Data were collected during 2008–2011 in the Ugra National Park (54°02´N, 35°48´E, Russia). Pied flycatchers were attracted by nest boxes, which had earlier been hung in a coniferous forest. During April and May birds were trapped when advertising the nest boxes. I defined the age of a male (yearling or older male) based on the shape of its central tail feathers (Vysotsky 1989) and described the colour type of breeding plumage using the Drost scale (Drost 1936). The accuracy of the method of ageing used here is rather high: in a long-term study of an adjacent pied flycatcher population, birds were correctly aged in 85%–87% of the cases (A. B. Kerimov pers. comm.).

Each male was ringed with coloured and aluminium rings and marked with theatrical grease-paint for easy recognition of individuals. Then advertising songs for each marked male were recorded using a Sennheizer ME66 microphone (frequency response 40 Hz–20 kHz) and Marantz PMD 660 digital recorder (frequency response 20 Hz–20 kHz). I recorded songs of unmated males in the morning (05:30–11:00) during the most active singing period on the first or second day after their arrival at the breeding point. A total of 115 males were ringed over the four years of study. Of these, two males were registered and recorded in all four years, another two in the first, third and fourth years, four males over three consecutive years, and 26 over two consecutive years.

I analysed the songs of 23 males that were recorded in at least two successive breeding seasons. I compared their syllable repertoires performed in the first and second years of registration. For the analysis, I chose consecutive song sequences of 500 syllables (a male usually sang that number of syllables in 50–70 songs). Songs that a male performed when exploring the nest box, or when a female was observed nearby, were excluded from the data because in such cases a male usually switches to another type of vocalization — demonstrative songs (Lundberg & Alatalo 1992).

A typical advertising song of a pied flycatcher is about 2 seconds long (Fig. 1). It consists of syllables that are stable structural units of a song. Syllables are composed of elements, or notes, which are sounds that look like a continuous trace on a sonogram (Catchpole & Slater 2008). A syllable contains one or several elements; in the last case the interval between elements does not exceed 0.02 ms (Espmark & Lampe 1993). Pied flycatchers do not sing distinct song types:

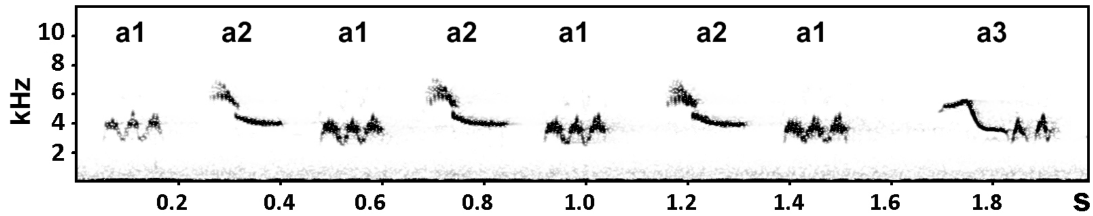

Fig. 1. The structure of a single pied-flycatcher song. The song consists of syllables that belong to different types. This song contains three types of syllables: a1, a2, a3.

they combine syllables in different ways. Syllables often form motifs, which are sequences of 2–4 syllables, occurring together (Lundberg & Alatalo 1992). The syllable repertoire of a male is a set of unique types of syllables used in songs.

For each male a library of all used syllable types was constructed. Different syllable types were defined by eye, as in previous work on this species (Espmark & Lampe 1993, Lampe & Espmark 1994, Eriksen *et al.* 2009, Eriksen *et al.* 2011, Vabishchevich 2011a). Each syllable type was numbered and songs were written as sequences of numbers (Fig. 1). For every syllable type, I calculated its proportion in songs for the first and second years of recording separately.

To estimate the similarity of songs performed in different breeding seasons, I used the index of overlap (OI) suggested by Schoener (1970);

$$\mathrm{OI} = 1 - 0.5\Sigma|p_{i_1} - p_{i_2}|$$

where p_{i_1} is the proportion of syllable type i in songs recorded in the first year of registration of a male, and p_{i_2} is the proportion of the same syllable type in the second year of recording.

For each male, I calculated its repertoire sizes in the first and second year of registration separately. Repertoire size was defined as the number of different syllable types used in a 500-syllable sequence.

A morph value and the date of arrival in the first year of registration of the male were also recorded. To remove differences between years in terms of arrival dates, standardised arrival-order ranks were calculated, using the formula (2 × rank – 1)/(2*n*) (*see* Lampe & Espmark 2003). Arrival-order ranks range from 1 to 0 with early-arriving males achieving values close to zero and late arrivers have values close to one.

Non-parametric statistics were used as the data were not normally distributed. The index of repertoire overlap had a discontinuous bimodal distribution, thus, birds with high and low OI values were divided into different samples. Fisher's exact test was used to compare the age structure of samples of high- and low-OI birds. A Mann-Whitney test was performed to compare OIs, repertoire sizes, morph values and arrival-order ranks in groups of adult and yearling birds (for pairwise comparisons a Bonferroni correction was used). Spearman's rank correlation was applied to check for possible relationships between these variables in yearling birds; Spearman's partial correlations were calculated as well. A Wilcoxon matched pairs test was used to find out if birds increase their singing repertoires from one year to the next. All tests were two-tailed. Statistical analyses were performed using the SAS Statistical Analysis Software ver. 9.1.3.

Results

All 23 males in our study included new types of syllables into their songs the following year. However, the relative abundances of old and new syllable types were quite different. The pied-flycatcher males had a bimodal distribution in their indices of repertoire overlap: eight birds obtained very low values of OI (OI ≤ 0.05) while fifteen males had relatively high OI values (OI ≥ 0.31) (Table 1). The males with low OI values performed many new types of syllables in the second year of recording, whereas most syllable types, common in the first year, were absent (Fig. 2a). The males with high OI values did not show pronounced changes in the structure of their songs: prevalent types of syllables used in the second year of recording matched ones used in the first year (Fig. 2b).

Since OI had a bimodal distribution, I divided the whole sample of birds into two groups: high-OI males and low-OI males to investigate differences between them. The low and high-OI birds were significantly different in terms of age structure (Fisher's exact test: $n = 23$, $p = 0.019$): the group of males with low OI values included only birds that were defined as yearlings in the first year of recording, while the group of males with high OI values contained both yearlings and adults. Moreover, the birds with low OI differed significantly from the high-OI birds in morph (Mann-Whitney test: $Z = 2.40$, $n_1 = 8$, $n_2 = 15$, $p = 0.016$), arrival-order rank ($Z = 3.46$, $n_1 = 8$, $n_2 = 15$, $p = 0.005$) and first-year repertoire size ($Z = -2.03$, $n_1 = 8$, $n_2 = 15$, $p = 0.041$). The low-OI birds arrived in general later, were paler and had smaller repertoires in the first year of study than the high-OI birds (Fig. 3). The size of repertoire in the second year of study did not differ significantly between the high- and low-OI birds ($Z = -0.51$, $n_1 = 8$, $n_2 = 15$, $p = 0.605$). Such a pattern can be observed if low-OI birds increase their singing repertoires the following year. However, no significant increase in repertoire size between years was found in the sample of the low-OI males (Wilcoxon matched pairs test: $Z = 1.61$, df $= 8$, $p = 0.107$).

Arrival order, morph and repertoire size appear to be age-dependent traits in pied flycatchers. In general, adult birds arrive earlier (Potti 1998), are darker (Anorova 1977) and have larger singing repertoires than yearling males (Espmark & Lampe 1993). To determine whether differences between the high-OI and low-OI males in the sample could not be explained by age alone, I divided the sample of yearlings into two groups (high-OI and low-OI yearlings), which I then compared with adult birds, using the Mann-Whitney test with the Bonferroni correction. The low-OI yearlings significantly differed from the high-OI yearling birds in OI, arrival-order rank and morph value (Mann-Whitney test, *see* Table 2). However, the difference in repertoire

Table 1. Between-season changes in the song structure in 23 pied-flycatcher males. Schoener's index of between-season repertoire overlap (OI), age, morph, arrival-order rank and sizes of repertoire in the first and second years of registration (rep. size 1, and rep. size 2, respectively) are presented. Age, morph and arrival-order rank are defined for the first year of registration of a male.

Male	Age	Morph	Arrival-order rank	Rep. size 1	Rep. size 2	OI
A	Yearlings	4	0.97	31	44	0.00
B	Yearlings	6	0.64	35	29	0.00
C	Yearlings	4	0.64	46	43	0.01
D	Yearlings	7	0.65	30	47	0.02
E	Yearlings	6	0.89	30	31	0.02
F	Yearlings	5	0.50	16	20	0.02
G	Yearlings	7	0.65	14	41	0.05
H	Yearlings	5	0.89	25	31	0.05
I	Yearlings	4	0.56	30	54	0.31
J	Adults	4	0.23	34	65	0.39
K	Adults	6	0.04	72	74	0.42
L	Adults	5	0.17	28	43	0.48
M	Yearlings	5	0.76	52	57	0.50
N	Adults	3	0.35	53	71	0.53
O	Yearlings	2	0.17	63	25	0.56
P	Yearlings	4	0.13	34	23	0.56
Q	Adults	3	0.07	41	28	0.60
R	Adults	2	0.04	43	22	0.67
S	Yearlings	3	0.17	66	76	0.68
T	Yearlings	4	0.23	45	30	0.68
U	Yearlings	3	0.23	37	49	0.73
V	Adults	6	0.13	20	18	0.77
W	Adults	5	0.32	26	21	0.87

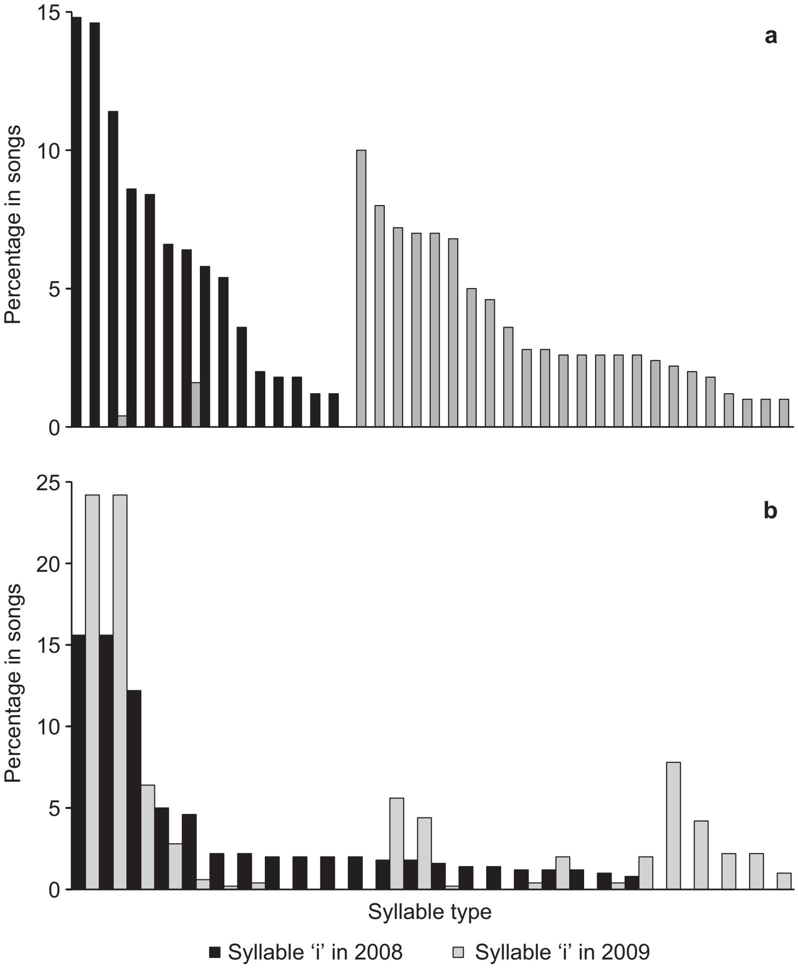

Fig. 2. Changes in song structure between two consecutive years with for (**a**) male D (OI = 0.02) and (**b**) male P (OI = 0.56). For demonstrative purposes, males with median OI values were chosen. Rare syllable types with frequencies < 1% in the first and second years are not shown.

size became non-significant after Bonferroni correction. As compared with the adult birds, the low-OI yearlings had significantly lower values of OI and higher arrival-order ranks. Interestingly, the high-OI yearlings did not differ significantly from adult birds in all studied variables (Table 2). The relationship between the level of between-season repertoire turnover and other characteristics is most pronounced within the group of yearling birds. This means that the different age structures of the high- and low-OI birds presumably cannot explain observed differences in arrival order, morph and first-year repertoire size. These factors may be related to the level of repertoire turnover in pied flycatchers regardless of age.

Spearman's correlation analysis performed for the yearling birds showed only significant negative correlations between OI and arrival-order rank, and between OI and male morph (Table 3, circles in Fig. 3). To check for possible interactions between these variables, partial correlation coefficients were calculated. When controlling for morph or arrival-order rank, no significant correlations were found between OI and other variables (Table 3). It seems that morph may be strongly related to arrival order in the sample.

Discussion

The relationship between age and repertoire turnover in pied flycatchers

Different factors are related to the degree of repertoire turnover in pied flycatchers. Age, morph,

Table 2. Differences between two sets of yearling pied-flycatcher males (low- and high-OI yearlings) and adult males. Morph is the colour type of a male estimated according to the 7-grade Drost scale (Drost 1936), where black-and-white is the 1st morph, and the most pale is the 7th morph. Morph and arrival-order ranks are calculated for the year when a male was first recorded at the breeding site. Rep. size 1 and rep. size 2 are the sizes of the syllable repertoire in the 1st and 2nd years of study, respectively. Bonferroni corrected critical $p = 0.017$.

Variable	Group number			Mann-Whitney test results (compared groups)		
	1 low-OI yearlings (mean ± SD, $n = 8$)	2 high-OI yearlings (mean ± SD, $n = 7$)	3 adult males (mean ± SD, $n = 8$)	1 *vs.* 2	1 *vs.* 3	2 *vs.* 3
OI	0.02 ± 0.02	0.57 ± 0.14	0.59 ± 0.17	$Z = -3.21$, $p = 0.001$	$Z = -3.33$, $p < 0.001$	$Z = 0.06$, $p = 0.954$
Morph	5.5 ± 1.2	3.6 ± 0.1	4.3 ± 1.5	$Z = 2.55$, $p = 0.011$	$Z = 1.55$, $p = 0.121$	$Z = -0.88$, $p = 0.389$
Arrival-order rank	0.73 ± 0.17	0.32 ± 0.24	0.17 ± 0.12	$Z = 2.50$, $p = 0.012$	$Z = 3.32$, $p < 0.001$	$Z = 1.28$, $p = 0.199$
Rep. size 1	28.4 ± 10.3	46.7 ± 14.2	39.6 ± 16.8	$Z = -2.26$, $p = 0.024$	$Z = -1.21$, $p = 0.227$	$Z = 0.93$, $p = 0.354$
Rep. size 2	35.8 ± 9.36	44.9 ± 19.6	42.8 ± 23.9	$Z = -0.87$, $p = 0.385$	$Z = 0.00$, $p = 1.000$	$Z = 0.52$, $p = 0.603$

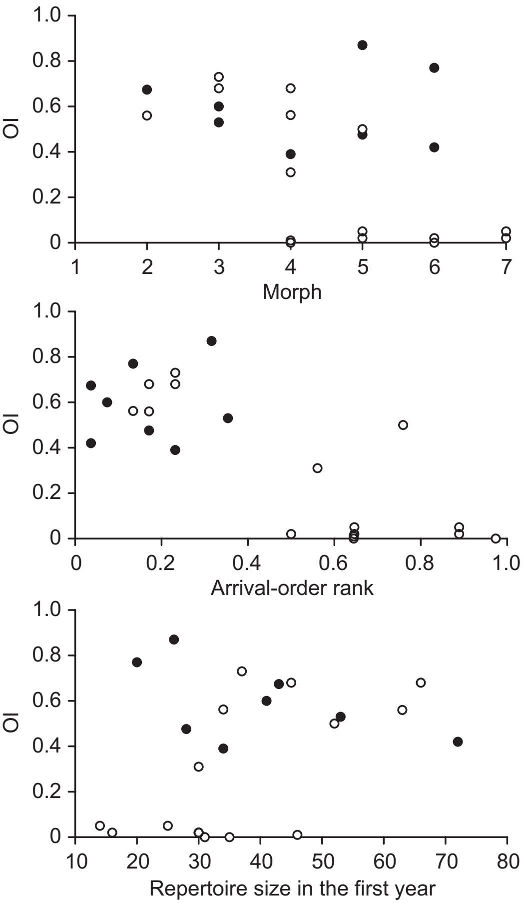

Fig. 3. Relationships between Schoener's index of repertoire overlap (OI) and morph, arrival-order rank, and size of the first-year repertoire for 23 pied-flycatcher males. Yearling and adult males are depicted by circles and dots, respectively. Morph values were defined in the first year of recording a bird using the Drost scale (Drost 1936), where black-and-white males are the first morph, and very pale, female-like males the seventh. Only yearling males obtained low OI values. In the group of yearlings, OI correlates negatively with morph value and arrival-order rank.

date of arrival of a bird and its repertoire size may be regarded as predictors of its index of repertoire overlap over successive years. However, these factors can be interdependent. Yearling males are, in general, paler than adults (Anorova 1977), arrive later (Lundberg & Alatalo 1992, Potti 1998) and have smaller repertoire sizes (Espmark & Lampe 1993). Furthermore, pale males may arrive later than dark ones (Slagsvold & Lifjeld 1988). Below, I discuss possible relationships of these factors with the index of between-season repertoire overlap (OI) in pied flycatchers.

Firstly, age, in combination with other factors, may be the true predictor of the degree of repertoire turnover. In this case two conditions should hold: (1) only yearling males change their songs sufficiently the following year, and (2) colour type, repertoire size and/or arrival date may be related to the level of between-season repertoire turnover in yearling birds. Secondly, the different age structures in birds with high and low indices of repertoire overlap may be a spurious effect if other factors related to age cause repertoire turnover in pied-flycatcher males. For example, reproductive success may serve such a role. It seems plausible that males that failed to attract a female or had a reduced number of hatchings change their song composition sufficiently the following year. Although I did not estimate reproductive success in this study, date of arrival is known to be strongly negatively related to this parameter in pied flycatchers. Males that arrive later produce less offspring than males that arrive early (Potti 1998). Moreover, in many species (Catchpole & Slater 2008), including the pied flycatcher (Lampe & Sætre 1995) males with small repertoires are less attractive to females than males with large repertoires. Thus, late-arriving pied-flycatcher males with small repertoires (that are often yearlings) may suffer from reduced reproductive success and change their songs sufficiently the following year.

The first hypothesis presented above seems more plausible: age, in combination with other factors, influences the level of repertoire turnover in the pied flycatcher. Indeed, age-dependent changes in song composition were described in several bird species; the observation that changes are more pronounced between the first and second years of life (but not thereafter) is well-known (Kipper & Kiefer 2010). During this four-year study, I observed a total of 34 individual males that returned at least once to the breeding point. Their between-season overlap indices were not all calculated and included in the analysis because some birds were not recorded sufficiently, or were only recorded after mating. However, adult birds did not show pronounced repertoire turnover between seasons. Of the eight pied-flycatcher males registered at the breeding point over three or four years, not one changed its songs strikingly between the second and third years of study (Vabishchevich 2011b and unpubl. data). Two birds showed sufficient repertoire turnover between the first and second years of life, but their syllable repertoires of the third year were similar to those of the second year.

As such, it seems that two strategies of age-dependent changes in song composition are present in the pied-flycatcher population. Some males change their song composition markedly between the first and second years of life but not thereafter. Other males develop a "stabilised" variant of a repertoire during the first year of life

Table 3. Correlations between the index of between-season repertoire overlap (OI) and pied-flycatcher male characteristics in a group of yearling males. Spearman correlation coefficients r_S and p values for simple and first-order partial correlations are shown. In partial correlations, one variable (a controlled variable) is kept constant to eliminate its influence on the results.

Variable	Correlation with OI (simple)	Correlation with OI (partial)			
Morph	$r_S = -0.59$ $p = 0.022$	controlled controlled	$r_S = -0.29$ $p = 0.315$	$r_S = -0.44$ $p = 0.112$	$r_S = -0.57$ $p = 0.031$
Arrival-order rank	$r_S = -0.66$ $p = 0.007$	$r_S = -0.47$ $p = 0.089$	controlled controlled	$r_S = -0.58$ $p = 0.029$	$r_S = -0.74$ $p = 0.002$
Rep.size 1	$r_S = 0.43$ $p = 0.110$	$r_S = 0.05$ $p = 0.842$	$r_S = 0.19$ $p = 0.521$	controlled controlled	$r_S = 0.40$ $p = 0.116$
Rep.size 2	$r_S = 0.19$ $p = 0.489$	$r_S = 0.15$ $p = 0.607$	$r_S = 0.47$ $p = 0.085$	$r_S = -0.33$ $p = 0.133$	controlled controlled

and do not change it sufficiently in successive years.

Changes in song structure and the morph of a bird

Although colour type of a pied-flycatcher male is partly age-dependent (Anorova 1977), the yearling and adult birds in this study did not differ significantly in colour type. A significantly negative correlation was found between morph and the index of repertoire overlap in the yearlings. Thus, type of plumage colour may be linked with the level of repertoire turnover between seasons as an independent factor. According to this supposition, pale yearling males are more likely than dark yearling males to change the structure of their songs sufficiently the following year.

Morph differences are observed in different aspects of pied flycatcher biology. Males of the third morph obtain higher values of basal metabolism than do pale birds (Gavrilov *et al.* 1993). In low temperatures, dark-coloured males have higher song rates than pale ones (Ilyina & Ivankina 2001) and they also prefer to sing on open perches, whereas pale birds do not show such preferences (Ivankina *et al.* 1995). Birds of different morphs also have different breeding strategies: reproductive success decreases with age in dark birds (morphs 1–3) but increases in intermediate-coloured and pale males (morphs 4–7) (Grinkov 2000). This may explain why pale and dark yearling birds show differences in their repertoire turnover. Pale males do not achieve maximal reproductive success in their first year of life, and some individuals do not breed at all. These individuals do not need to develop a final singing repertoire, attractive to females, in their first year of life. It seems that pale males produce imperfect, non-attractive songs in their first breeding season but develop a normal repertoire the following year.

On the other hand, dark males are rather sensitive to breeding in the first year of life. It has been shown that breeding success in the first year affects the lifetime breeding success in dark pied-flycatcher males (Grinkov 2000). That means that dark yearlings need to produce high-quality songs that are attractive to females. As such, these dark yearlings develop their final, stabilised repertoire during the first year of life. This hypothesis can be tested by studying how females respond to songs of pale and dark males in their first and second year of life. Presumably songs of pale yearling males will be less attractive than songs of dark yearlings and songs of pale adults. However, there is other evidence in favour of this suggestion. First, birds with low indices of repertoire overlap had relatively small singing repertoires in the first year of life and thus their songs possibly were non-attractive to females, because pied-flycatcher females prefer males with large repertoires (Lampe & Sætre 1995). Second, according to anecdotal observations, these birds sang many odd syllable types that were rare in the population. In the following years syllable repertoires of these birds became more “normal” and usual. The most striking example of a bird with odd songs was a pale pied-flycatcher male who performed very atypical songs, which sounded like willow-warbler songs in the first year of life but switched to typical pied-flycatcher songs the following year.

These results suggest that pale pied flycatchers do not develop a normal typical repertoire during the first year of life as compared with dark pied flycatchers. Pale yearlings produce imperfect songs but replace them with normal ones in the second year of life. Dark males develop a stabilised repertoire during the first year of life and do not change it sufficiently thereafter. That is in agreement with the finding that different morphs have different strategies of breeding (Grinkov 2000). The negative correlation of the repertoire overlap index with date of arrival found here may be explained by the observation that pale birds arrive later than dark birds (Slagsvold & Lifjeld 1988) and sometimes do not perform songs actively early in the season due to cold temperatures (Ilyina & Ivankina 2001).

Reproductive success as a possible explanation for repertoire turnover

Other factors, such as reproductive success, may influence the level of repertoire turnover between years. Results from this study suggest that late arriving birds with small repertoire sizes and possibly low reproductive success are likely to change their songs drastically the following year. Indeed, some late arriving birds with low OI presumably stayed unpaired in the first year of study (male A and one male not included). However, I also observed six males which mated and raised nestlings successfully but changed their singing repertoires sufficiently the following year (males B, C, D, G and two males not included). I also observed an adult male who obviously failed to nest but did not change its songs the following year (male P).

This means that repertoire turnover is unlikely to be directly related to successful mating and nesting. However, if a degree of repertoire turnover really depends on the age and colour type of a pied-flycatcher male, I expect to find a relationship between it and reproductive success, because birds of different morphs exhibited different breeding strategies. Pale yearling males exhibit lower reproductive success than dark yearling males, but their reproductive success increases during successive years, while the reproductive success of dark males decreases (Grinkov 2000).

Timing of changes in song composition

Stabilisation of the singing repertoire in a pied-flycatcher male by the first or second year of life does not necessarily imply that a male does not change its songs at all thereafter. In fact, all males added new syllable types to their songs between years. However, changes in repertoire composition after stabilisation are much less pronounced than the drastic repertoire turnover between the first and second year of life observed in several pied-flycatcher males.

When does the drastic repertoire turnover happen in the pied flycatcher? There are two possible patterns of song changes that provide the same results. First, changes in songs may occur and accumulate gradually during the first breeding season but not thereafter. In that case, pronounced between-season differences in the singing repertoire will occur if songs performed at the beginning of the first breeding season are compared with songs performed in the next breeding season. On the other hand, song composition may remain relatively stable throughout the first breeding season, but change sufficiently in the interval between seasons.

Pied-flycatcher males obviously change their songs to some degree during the breeding season. They may increase and decrease their singing repertoire (Espmark & Lampe 1993, Vabishchevich 2011a, 2011b) and even learn and perform new syllable types that are played back to them (Eriksen *et al*. 2011). Many males included in this study were recorded several times and clearly added new syllable types to their songs during the breeding season (Vabishchevich 2011a, 2011b). However, despite adding new syllable types, changes in song composition were minor (*see* Vabishchevich 2011b, where OIs for 17 males are shown). Nine yearling males and eight adults that were recorded during one season at different times of breeding status (before and after mating), generally produced similar singing repertoires on different days of recordings (Vabishchevich 2011b). Two of these birds (yearlings) had completely different singing repertoires the following year (male A and one male not included). Therefore, I hypothesise that drastic repertoire turnover does not happen during the breeding season, but occurs during the interval between breeding seasons in pied flycatchers.

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