

Delayed maturation in passerine birds: an examination of plumage effects and some indications of a related effect in song

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In some passerine species, 1st-year males are clearly distinguishable from adults; they have a different, typically dull, plumage. At least 15 explanations of the delayed plumage maturation of 1st-year males have been proposed. In the present study, we investigate if there is a similar widespread phenomenon regarding song, i.e. if males of some species have a distinct song in their first breeding season (delayed song maturation). A comparative analysis of 137 West Palearctic passerines showed that detailed data on how the song changes with age in breeding males is available for only a few species. Moreover, it is difficult to assess whether the song features continue to change considerably year after year or if, as we suggest, the main difference is between 1st-year vs 2-years and older males. We found that species with a suggested delay in song maturation were mostly those with delayed plumage maturation; a preliminary comparison suggests that these species have greater longevity. We also discuss the evolutionary significance of delayed song and plumage maturation and we suggest some possible directions for future research on these phenomena.

KEY WORDS: delayed maturation, song development, oscines, passerine birds, 1st-year plumage.

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INTRODUCTION

In birds, the existence of age-dependent traits appears to be a widespread phenomenon, which can affect the probability of acquiring a mate, the timing of reproduction, egg size, offspring rearing ability, and survival (LACK 1968, PIANKA & PARKER 1975, CURIO 1983, ROBERTSON et al. 1994, MARTIN 1995). Among age-dependent characters, detailed attention has been paid to the marked difference in plumage between 1st-year and adult males of some passerine species (review in WEGGLER 1997). Although the 1st-year males exhibit a different plumage (distinctive dull or female-like in their first breeding season; ROHWER et al. 1980), they are sexually mature and can potentially breed. At least 15 hypotheses have been proposed (summary in Table 1) to explain the occurrence of this delayed plumage maturation (hereafter DPM). However, the occurrence of a similar phenomenon regarding song, i.e. if males of some species have a distinct song in their first breeding season (delayed song maturation, hereafter DSM), has never been reviewed.

Bird song development has probably been studied in more detail than any other aspect of animal behaviour (CATCHPOLE & SLATER 1995). Pioneering works in the sixties pictured young birds at hatching as having a crude template defining the approximate characteristics of the song of their species (KONISHI 1964, MARLER & TAMURA 1964). When these birds hear different songs, during a sensitive phase for memorization, only the songs that match this template are memorized. This classic model still has a fundamental role in our understanding of how learning and maturation refine the innate template of passerine song. However, it is now widely accepted that each species has different phases of memorization (and output) according to the functions of the song (intra- or inter-sexual selection), social and ecological pressures, life-history characteristics, etc. (KROODSMA 1982a). It is generally believed that birds either (1) learn their song after they fledge (learning the

Table 1.

Hypotheses concerning the occurrence of delayed plumage maturation (DPM).

Hypotheses	References
(1) Crypsis	SELANDER 1965, LACK 1968
(2) Winter crypsis	ROHWER & BUTCHER 1988
(3) Female mimicry	ROHWER 1978, ROHWER et al. 1980
(4) Winter female mimicry	BROWN & BROWN 1988
(5) Juvenile mimicry	FOSTER 1978, LAWTON & LAWTON 1986
(6) Status signalling	LYON & MONTGOMERY 1986
(7) Winter status signalling	ROHWER 1975
(8) Moulting constraint	ROHWER 1986
(9) Red plumage production cost	HILL 1996
(10) Reduced investment	PROCTER-GRAY & HOLMES 1981
(11) Breeding threshold	STUDD & ROBERTSON 1985
(12) Territory type	MONTGOMERIE & LYON 1986
(13) Polyterritorial deception	ALATALO et al. 1990
(14) Selection for neoteny	BJÖRKLUND 1991
(15) Facilitate-learning	COLLIS & BORGIA 1993

details from older breeding males) or (2) learn while settling as 1st-year males (learning from older residents) or (3) are able to learn throughout their life (BJÖRKLUND 1989).

A clear-cut difference in song between breeding males of different ages (1st-years and adults) has been demonstrated in only a few species (PAYNE 1982, EENS et al. 1992, ESPMARK & LAMPE, 1993, O'LOGHLEN & ROTHSTEIN 1993, LEMON et al. 1994). This seems surprising since 1st-year and adult males can differ in many life-history traits (SÆTHER 1990, MARTIN 1995).

In this study, we focus on the delay in maturation of two characters, song and plumage, in a data set of 137 West Palearctic passerine birds. On the basis of the widespread occurrence of DPM, we have investigated if there is a similar widespread phenomenon regarding song, i.e. if males of some species have a distinct song in their first breeding season (delayed song maturation, hereafter DSM). Furthermore, we explored the occurrence of DSM and DPM in order to find possible relations between these two delays in maturation. We will discuss some possible functional explanations of the results and we will also examine the relations between DSM and a life-history trait, longevity, that has been already investigated in relation to DPM (STUDD & ROBERTSON 1985, MONTGOMERIE & LYON 1986).

Since we found very few detailed studies on the differences between 1st-year and adult male songs, we urge further attention and research to DSM. This will be important for an understanding of the adaptive/evolutionary significance of this trait. It will also help to design correct procedures in experiments on DSM and DPM, where a correct matching of acoustic (by playback) and visual (with caged or stuffed intruders) signals is essential but has not always been performed (CUCCO & MALACARNE 1999).

METHODS

Our study concerns 137 West Palearctic passerines (Appendix). We first selected the species for which we had field knowledge, particularly of the male plumage observed during ringing operations. A few other species were selected because we were aware of studies on their vocalizations. The data set used for this study is based on (1) a comprehensive search of the literature and of the Internet for information on the songs of adult and 1st-year males (subadults), and (2) the five volumes concerning passerines of "The Birds of the Western Palearctic" handbook (CRAMP 1988, 1992; CRAMP & PERRINS 1993, 1994a, 1994b). In particular, the handbook is a rather rich source of information; the editors have dealt with the song of each species in detail on several pages, while the authors of the species descriptions were specifically asked to pay attention to differences between individuals, sexes and ages (CRAMP 1988: 23). We considered only the full song given by males during the breeding season, thus excluding all subsongs and songs given after hatching by young in late summer, autumn and winter.

We assigned to each species the following codes for the difference in song between breeding adults and subadults: Yes = a difference between the adult and subadult male songs is reported in the literature; No = there is an explicit statement of no difference between the adult and subadult male songs; Unknown = there is no statement about an adult-subadult male song difference.

We scored the difference in plumage between adults and subadults on a three-level scale: No = no evident difference between adult and subadult male plumage; Small = small difference; Yes = marked difference. We based the plumage difference scores on the possibility of assessing age during ringing activity (SVENSSON 1992, JENNI & WINKLER 1994) and on

moult strategies. As reported in Appendix, passerine species whose young have a complete moult in their 1st year of life usually exhibit no strong difference between adult and subadult plumages, while the young of species with partial moult usually show small or marked differences in plumage with respect to adult individuals.

Data on longevity (92 species) were collected from "The Birds of the Western Palearctic" handbook. In agreement with MONTGOMERIE & LYON (1986), longevity was taken as the reported age of the oldest birds, as obtained from ringing data.

Any study of the adaptive significance of life-history variations in birds should consider the effects of phylogeny. Over-representation of a particular taxonomic class is often the source of bias in interspecific comparisons of life-history data (CLUTTON-BROCK & HARVEY 1984). Therefore, we performed two types of analyses on the data, the first being a series of across-taxon analyses conducted at species, genus and subfamily level, the second a within-taxon analysis utilizing phylogenetic classification. In the first series of analyses we investigated relationships between longevity and DSM, or DPM, treating species as independent data points (across-species analyses), then treating genera and subfamilies as independent data points (across-genus and across-subfamily analyses). If qualitatively similar conclusions are reached at different taxonomic levels, this suggests that the level of analysis is relatively unimportant.

In the second analyses, we analyzed the relationship between longevity and DSM, or DPM, using the method of independent contrasts (FELSENSTEIN 1985) to control for phylogenetic relatedness among species (within-taxon analyses). We classified species using the phylogeny of SIBLEY & AHLQUIST (1990), supplemented by the classification of SIBLEY & MONROE (1990) where SIBLEY & AHLQUIST did not resolve groups of species. Despite the potential biases and the criticisms (HOUDE 1987, HARSHAM 1994), it is probably the best avian phylogeny currently available (MOOERS & COTGREAVE 1994). The independent contrasts were calculated using CAIC (PURVIS & RAMBAUT 1995). Because CAIC can be used whenever comparative data including continuous variables are to be analysed, but it is not suitable for investigating correlated evolution among categorical variables, we utilized MacClade's concentrated-changes test (MADDISON & MADDISON 1992) to compare the co-occurrence of the DPM and DSM traits. The concentrated-changes test is designed for testing the association of changes in a binary character with some other binary variable within a clade. The calculation determines the probability that various numbers of gains and losses (of DSM) would occur in certain distinguished areas (i.e. those showing DPM) of the clade, given that a certain number of gains and losses occur in the whole clade. A significant concentration might indicate that changes are not distributed randomly, and they are significantly concentrated either within or outside the distinguished area. In our application of the test, the absence and presence of DSM was coded respectively as 0 and 1. The DPM character was coded as 0 for species showing no plumage difference between adults and subadults, and as 1 in case of large plumage difference; species of the intermediate "small difference" category were prudentially coded as uncertain. We selected probability value given either state 0 or 1 at the ancestral node of clade, thus no assumption was taken on the ancestral state of the characters.

RESULTS

Association between DSM and DPM

Most of the species (108/137) in our database have not been studied sufficiently to be classified with regard to DSM.

For the other 29 species, we found an association between DSM and DPM. In the across-species analysis, most species that did not show DSM also did not have DPM, and most species with DSM also had DPM (Table 2. Fisher exact test, $P < 0.002$; unknown and intermediate "small" categories excluded). Species of the inter-

mediate DPM category (small plumage difference) were similar to species with no plumage difference: those species mostly showed no DSM.

The same association found at the species level was also found at the level of genus (Table 2. Fisher exact test, $P < 0.002$) and subfamily (Fisher exact test, $P < 0.03$).

Controlling for phylogeny did not appear to weaken the relationship between DSM and DPM, as in the within-taxon analysis the DSM trait was found to be significantly concentrated in clades showing DPM (MacClade concentrated-changes test, exact count method: $P < 0.045$).

Relationship between delayed maturation and longevity

In the across-species analysis, species with DSM had a greater longevity than non-DSM ones (Fig. 1. Mann-Whitney U test = 15, $P = 0.039$). The same result was obtained in the comparison conducted at the genus level: genera with DSM had a greater longevity than non-DSM ones (Mann-Whitney U test = 9.5, $P = 0.018$). Comparison at the subfamily level was not performed because of the small number of cases.

Results of the across-species analysis of DPM were similar (Fig. 2), but the values did not reach significance when all three dichromatic categories were considered (Mortality: Kruskal-Wallis test = 0.53, $P = 0.76$; Longevity: Kruskal-Wallis test = 3.9, $P = 0.14$). However, when a comparison between species with large vs absent dichromatism was performed (thus excluding the intermediate category), species with DPM had a higher median longevity than species without DPM (Mann-Whitney U test = 16, $P = 0.037$). The same comparison at the genus level showed

Table 2.
Occurrence of DSM and DPM among 137 passerines.

Song difference	Dichromatism			Total
	No	Small	Yes	
<i>Unknown</i>	29	46	33	108 species
No	11	9	1	21 species
Yes	1	1	6	8 species
No/(No+Yes)%	91.7%	90.0%	14.3%	137 cases
<i>Unknown</i>	22	20	18	60 genera
No	10	6	1	17 genera
Yes	1	1	6	8 genera
No/(No+Yes)%	90.9%	85.7%	14.3%	85 cases
<i>Unknown</i>	13	14	8	35 subfamilies
No	7	6	1	14 subfamilies
Yes	1	1	4	6 subfamilies
No/(No+Yes)%	87.5%	85.7%	20.0%	55 cases

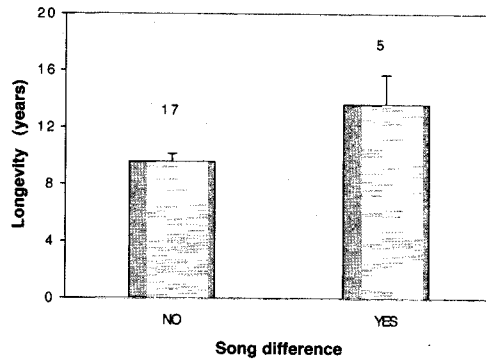


Fig. 1. — Longevity in species with and without delayed song maturation (mean \pm SE).

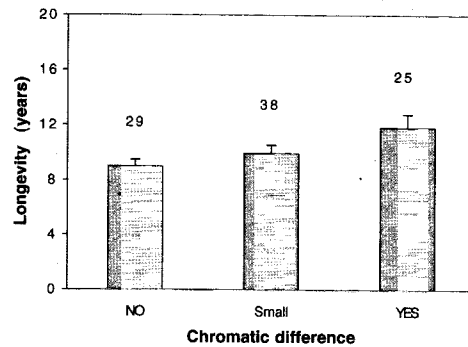


Fig. 2. — Longevity in species with three degrees of delayed plumage maturation (mean \pm SE).

similar results: again, when cases of the intermediate DPM category were excluded (small plumage difference), the genera with DPM had a greater longevity than non-DPM genera (Mann-Whitney U test = 9.5, $P = 0.018$). Comparison at the subfamily level was not performed because of the small number of cases.

Controlling for phylogeny did not appear to weaken the relationship between DPM and the longevity life history trait. The independent contrasts for longevity were significantly different from zero (one sample t-test against an expected value of zero: $t = 2.135$, $P = 0.035$, $n = 91$ contrasts). No phylogeny control was available for the relationship between DSM and longevity because of the small number of independent contrasts available.

DISCUSSION

Two main results of our study should be emphasized. First, despite the prolonged attention to bird song (CATCHPOLE & SLATER 1995) and its development in particular (KROODSMA 1982a), the literature provides little information about differ-

ences in song between 1st-year and older males. There are many possible reasons for this, the main ones being the difficulty in the field of distinguishing age-categories in passerine species with no DPM and, in studies of populations with marked individuals of known age, the need to trace their song features through several years. The second result concerns the existence of a possible relationship between DSM and DPM. We found six cases out of seven where DSM was accompanied by DPM, while most of the 21 species with little or no plumage difference showed no DSM. This suggests that the two traits are somehow linked.

Delayed song maturation?

Among the oscine birds, acoustic learning is the norm (KROODSMA & BAYLIS 1982). Young birds must hear, often during a sensitive early period of life, the song of adult conspecifics in order to develop appropriate songs. Although bioacoustic research on birds has provided much information, it is difficult to manage the proliferation of data due to the heterogeneous findings and the differences among species (WEST & KING 1996). In order to clarify the topic of DSM, we have drawn up a table summarizing the main differences proposed (Table 3). We report five different modalities of song change or, in contrast, song crystallization, in relation to age. The table emphasizes the importance of large vs small year-to-year differences in song features. The first modality "a" represents the classic model of song crystallization, where the species do not change their songs as the birds get older. The second and the last modality ("b" and "e") represent the species that change their song year after year. However, in the "b" modality, changes are small or inconsistent (e.g. both deletion and addition of elements in a repertoire) and cannot be utilized to assess the age of an individual, while in the "e" modality changes are large and can indicate the age of individuals. The "c" and "d" modalities represent the phenomenon of DSM: the song of first-year birds is significantly different from that

Table 3.

A tentative summary of the modalities of crystallization or modification of male song in passerine birds.

Modality	Recognizable song categories			
	A	B	C	...
(a) hatching →	1,2,3,...			
(b) hatching →	1→2→3→...			
(c) hatching →	1	→ 2,3,...		
(d) hatching →	1	→ 2→3→...		
(e) hatching →	1	→ 2	→ 3	→ ...

Year-to-year differences may include deletions, additions, modification of any song feature. The numbers 1, 2, 3, ... represent bird age in years. (Comma: e.g. 1,2) = no evident year-to-year differences, (Short arrow: e.g. 1→2) = small year-to-year differences, only recognizable by tracking song features of the same individual, (Long arrow: e.g. 1 → 2) = large year-to-year differences, recognizable by comparing song features of any two randomly selected individuals of different age.

of older birds, while in the following years birds show no changes ("c") or only small changes ("d") in their song features.

We wish to underline that one should not be surprised by small changes in song features of the same individual; particularly in more complex songs, it could be difficult to replicate all characteristics exactly in the same way year after year. However, small differences will not be sufficient to allow the assessment of age of a randomly selected individual in a population. We suppose that the ageing of a singer would be of great interest to other males and females living in the same area.

Cases of no modification of the full male song with age (the "a" modality, and "b" for small modifications) are widespread among birds. The suboscines, for example, have relatively simple songs, much like the unlearned call notes of songbirds, and variations are minimal (KROODSMA 1996). Among songbirds crystallization is also reported for several species (21 species in Appendix).

Modifications of song features with age seem to be common in songbirds. An increase (or reduction) of the song repertoire with age is a widespread phenomenon (MCGREGOR & KREBS 1989). However, we found that, from the data in the literature, it was not easy to determine whether or not the changes in song features could be assigned to the DSM modalities ("c" or "d"), or if it would be better to consider those species that show differences as cases of the endless-change "e" modality. In several studies, the researchers reported a clear-cut difference between 1-year males and older males (PAYNE 1982, EENS et al. 1992, ESPMARK & LAMPE 1993, O'LOGHLEN & ROTHSTEIN 1993, CUCCO & MALACARNE 1999). However, they cumulated all males 2-years and older and did not discriminate between adult ages. Few studies have found a correlation between a song feature (repertoire) and age that would indicate an "e" modality of song modification (NOTTEBOHM & NOTTEBOHM 1978, CATCHPOLE 1980, YASUKAWA et al. 1980, MCGREGOR et al. 1981, DERRICKSON 1987).

Evolutionary significance

In dimorphic species, conspicuous male traits are supposed to have evolved through sexual selection (DARWIN 1871). Costly traits, in particular, can provide the potential partner with information about the bearer's quality (ZAHAVI & ZAHAVI 1997) or his health (SAINO & MØLLER 1996). In bird studies, acoustic and visual signals have usually been considered separately, and bird sounds have sometimes been considered the acoustic equivalent of visible sexual dimorphism (CATCHPOLE 1982). However, it has been emphasized that the evolution of multiple signals should be considered (MARCHETTI 1998). Traits with varying lability could provide different information about the male's condition or status (HILL et al. 1999). Since plumage development (moult) involves significant physiological costs (PAYNE 1972), the expression of plumage (its morphology and colour) is affected by the animal's condition during moult. Hence plumage expression could reliably indicate a male's genetic quality or long-term survival. Nevertheless, since the moult usually takes place between breeding seasons, plumage expression might not be a valid indicator of the male's condition during mating. Females that base their choice only on male plumage could obtain a misleading impression. If instead their mate choice is based on more dynamic secondary sexual traits (e.g. song and courtship display), in addition to plumage, the females could make a better judgement of male quality. Interestingly, in the majority of species with DSM, there is a matching of the visual and acoustic information in the 1st-year males. This could be explained as an hon-

est signal of status (hyp. 6 in Table 1), conveyed by males both acoustically and visually. However, definitive judgement on the question cannot be made without a more complete analysis of more species (see below, suggestion "d").

Delayed maturation of traits could be related to ecological and social factors (e.g. territoriality, MONTGOMERIE & LYON 1986; high aggressivity of adult males, ROHWER 1978), and/or it could be a feature of long-living species (STUDD & ROBERTSON 1985). Greater longevity should allow individuals to be opportunistic in their first breeding year, i.e. reproducing regularly if there is the chance, or reducing or postponing breeding if circumstances do not allow it. Species with lower lifespan should be less like to evolve DPM and DSM: due to the high mortality rate, individuals in their first breeding season would have a low probability of breeding again the next year and thus should not assume the costs of delayed maturation of secondary sexual characters.

However, many methodological difficulties arise when traits (i.e. DSM, DPM) are compared among a set of species, and one must be cautious about making unjustified statements. The number of hypotheses proposed could lead to uncertainties and it may be difficult to test the theories because sometimes they lead to similar or not contrasting predictions, or they could be at work simultaneously. DPM, and we suppose DSM as well, probably evolved independently in several lines of passerine birds (STUTCHBURY 1991). Thus, these traits could have different explanations in different species.

Suggestions for future research

The difficulties stressed above and the insufficiency of available data highlight the need for future research on the DSM phenomenon. The following are five potentially fruitful areas of investigation:

(a) As KROODSMA (1996) pointed out, song development in birds exhibits a diversity of patterns and a variety of consequences. An understanding of why species differ so enormously in their styles of vocal development and their adult vocalizations requires a comparative, ecological framework. When more data become available, a carefully implemented comparative approach using rigorous hypothesis testing (HARVEY & PAGEL 1991) could tell us much about the ecology and evolution of delayed vocal development in birds.

(b) To examine appropriately 1st-year and adult song, we must evaluate all features of sound that could differ between individuals. For example, vocalization characteristics that are known to be important in birds include repertoire size or complexity (CATCHPOLE 1980, YASUKAWA et al. 1980, MCGREGOR et al. 1981), singing activity (WASSERMAN 1977, MØLLER 1983), song rate (GREIG-SMITH 1982), strophe length and drift (LAMBRECHTS & DHONDT 1987, BIJNENS 1988), voice (WEARY & KREBS 1992, LAMBRECHTS & DHONDT 1995; but see BEECHER et al. 1994), and note or syllable durations, frequencies, sequence and rhythm (BAPTISTA 1996, CUCCO & MALACARNE 1999). For all vocalization features, the findings will have to be assessed in light of the "comparability problem" outlined by KROODSMA (1982b) for repertoire (with across-species comparison, the song repertoire of one species cannot be directly compared to that of another. It might be meaningless to compare the repertoire sizes of species which sing in very different ways).

(c) There is the need to conduct detailed individual analyses of song maturation in order not to be confounded by differential mortality, which could influence

the results in less detailed studies. For example, in an accurate study of the Blue Tit *Parus caeruleus*, BIJNENS (1988) showed that the difference in strophe length between the 1st-year and the older male categories was not due to a change (i.e. increase) of song duration with age. Each individual retained his song from one year to the next, but there was a difference in mortality. Birds that did not survive beyond one year sang shorter strophes than those living longer. As a consequence, a larger proportion of males with longer strophe survived the second winter than males with shorter strophe length.

(d) Predictions generated by some hypotheses concerning DPM could be evaluated in the light of the findings for DSM. In particular, all hypotheses concerning crypsis, mimicry and status signalling (hyp. 1-7, Table 1) would be contradicted when there is no matching of visual and acoustic signals. If, as our results suggest, DSM is present more often in DPM species than in non-DPM ones, the acoustic and visual information about age is in agreement. When the selection of sexual characters was so strong that a species evolved DPM, the working hypothesis is that the same force should have led to a delay in maturation of other sexual characters as a reinforcement of the same information. Other hypotheses in Table 1 do not require that DSM and DPM be positively or negatively correlated. In these cases, visual and acoustic signals could convey different, unrelated information (or no information at all) about male quality.

(e) Non-passerine birds were outside the scope of this study. However, future research could focus on the relationship between age and song features in non-passerine birds. Indeed, several species delay reproduction and maturation of adult plumage (BAKER 1993), have a higher annual survival rate than non-passerines (SÆTHER 1989) and use song extensively (MALACARNE et al. 1991). Moreover, a delay in voice maturation has been described in at least one species (WANKER 1999).

(f) Experiments on DPM or DSM should carefully consider the matching of visual and acoustic signals. A typical experimental design concerning the importance of plumage characteristics could include the use of stuffed or caged individuals. Sometimes it is operationally advantageous to attract the free-living birds toward the dummy by playback of male song, if sound is perceived at a longer distance than visual stimuli. In this case, it will be important that both the song played back and the plumage of the dummy pertain to the same age-category. We found good examples of studies where the experimental design accounted for both song and chromatic differences (HUHTA & ALATALO 1993, MUEHTER et al. 1997), while in others there was no matching of them (LANDMANN & KOLLINSKY 1995a, 1995b) and interpretation of the results is still being debated (CUCCO & MALACARNE 1999). In another experimental study, on the Black-headed Grosbeak *Pheucticus melanocephalus*, there was no song and plumage matching because the adults and subadults appeared to have similar songs (HILL 1989); however, the findings of the present study suggest that a more detailed analysis of song features in 1st-year and older grosbeaks is necessary. In general, the importance of an accurate acoustic-visual matching merits further investigation, since recent findings have shown that, at least during the process of song learning, paired stimuli can increase song acquisition (HULTSCH et al. 1999).

CONCLUSIONS

Males of several passerine species exhibit a delay in plumage maturation and there have been many studies of the significance of DPM (we found 15 hypotheses in

the literature). However, it is unclear whether or not there is also widespread delay in song maturation, since we found no detailed information about song variation after the first breeding season for 80% of the examined species. We urge further research for an understanding of the adaptive and evolutionary significance of DSM trait. Consideration of the possible existence of DSM will help in the design of correct procedures in experiments on visual or multichannel communication in birds.

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APPENDIX

Species	Longevity (years)	Moult	Dichromatism	Song difference	Ref.
<i>Melanocorypha calandra</i>		Compl: SC	No	?	
<i>Calandrella brachydactyla</i>		Compl: SC	No	?	
<i>Galerida cristata</i>		Compl: SC	No	?	
<i>Lullula arborea</i>		Compl: SC	No	No	1
<i>Alauda arvensis</i>	8.4	Compl: SC	No	No	2
<i>Riparia riparia</i>	9.0	Compl: sp,WC	No	?	
<i>Ptyonoprogne rupestris</i>		Part: sp,wp	Small	?	
<i>Hirundo rustica</i>	15.9	Compl: WC	No	?	
<i>Hirundo daurica</i>	7.8	Compl: WC	No	?	
<i>Delichon urbica</i>	14.5	Compl: WC	No	?	
<i>Anthus novaeseelandiae</i>		Part: sp,wp	Small	?	
<i>Anthus campestris</i>		Part: sp,wp	Small	?	
<i>Anthus trivialis</i>	7.7	Part: sp,wp	Small	?	
<i>Anthus pratensis</i>	7.7	Part: sp,wp	Small	?	
<i>Anthus cervinus</i>		Part: sp,wp	Small	?	
<i>Anthus spinoletta</i>	8.8	Part: sp,wp	Small	?	
<i>Motacilla flava</i>	8.4	Part: sp,wp	Small	?	
<i>Motacilla cinerea</i>		Part: sp,wp	Small	?	
<i>Motacilla alba</i>	9.9	Part: sp,wp	Yes	?	
<i>Bombycilla garrulus</i>	12.6	Part: sp	Yes	?	
<i>Cinclus cinclus</i>	7.8	Part: sp	Small	?	
<i>Troglodytes troglodytes</i>	6.6	Part: sp,wp	Small	?	
<i>Prunella modularis</i>	9.0	Part: sp	No	No	3
<i>Prunella collaris</i>		Part: sp	Small	?	
<i>Erithacus rubecula</i>		Part: sp	Small	?	
<i>Luscinia megarhynchos</i>	7.9	Part: sp	Small	?	
<i>Luscinia svecica</i>		Part: sp,wp	Yes	Yes	1
<i>Phoenicurus ochruros</i>	8.4	Part: sp	Yes	Yes	4
<i>Phoenicurus phoenicurus</i>	9.5	Part: sp	Small	?	
<i>Saxicola rubetra</i>		Part: sp,wp	Yes	?	
<i>Saxicola torquata</i>	6.0	Part: sp,wp	Yes	?	
<i>Oenanthe oenanthe</i>	7.0	Part: sp,wp	Yes	?	
<i>Oenanthe hispanica</i>		Part: sp,wp	Yes	?	
<i>Monticola saxatilis</i>		Part: sp,wp	Yes	?	
<i>Monticola solitarius</i>		Part: sp,(wp)	Yes	?	
<i>Zoothera dauma</i>		Part: sp	Yes	?	
<i>Turdus torquatus</i>	8.2	Part: sp	Yes	?	
<i>Turdus merula</i>	20.3	Part: sp,(wp)	Yes	?	
<i>Turdus obscurus</i>		Part: sp	Yes	?	
<i>Turdus naumanni</i>		Part: sp	Yes	?	
<i>Turdus ruficollis</i>		Part: sp	Yes	?	
<i>Turdus pilaris</i>	18.0	Part: sp	Small	?	
<i>Turdus philomelos</i>	13.8	Part: sp	Small	?	
<i>Turdus iliacus</i>	18.8	Part: sp	Small	?	
<i>Turdus viscivorus</i>	9.5	Part: sp	Small	?	
<i>Cettia cetti</i>	7.3	Part: sp,(wp)	No	No	5
<i>Cisticola juncidis</i>		Compl: SC,wp,(sp)	Small	?	
<i>Locustella naevia</i>	4.1	Compl: sp,WC	No	?	

(continued)

Appendix (continued)

Species	Longevity (years)	Moult	Dichromatism	Song difference	Ref.
<i>Locustella luscinioides</i>		Compl: sp,WC	Yes	Yes	6
<i>Acrocephalus melanopogon</i>		Compl: SC,wp	Small	?	
<i>Acrocephalus paludicola</i>		Compl: (sp?),WC	No	?	
<i>Acrocephalus schoenobaenus</i>	6.3	Compl: sp,WC	No	?	
<i>Acrocephalus palustris</i>	7.9	Compl: sp,WC	No	No	7,8
<i>Acrocephalus scirpaceus</i>	12.0	Compl: sp,WC	Small	?	
<i>Acrocephalus arundinaceus</i>	9.8	Compl: sp,W1C,(w2p)	No	Yes	9
<i>Hippolais icterina</i>	10.0	Compl: WC	No	?	
<i>Hippolais polyglotta</i>		Compl: W1C,(w2p)	No	?	
<i>Sylvia undata</i>	4.0	Part: sp,wp	Small	?	
<i>Sylvia cantillans</i>		Part: sp,wp	Yes	?	
<i>Sylvia melanocephala</i>		Part: sp,wp	Small	?	
<i>Sylvia hortensis</i>		Part: sp,wp	Yes	?	
<i>Sylvia nisoria</i>	12.0	Compl: sp,WC	Yes	?	
<i>Sylvia curruca</i>	7.0	Part: sp,wp	Small	?	
<i>Sylvia communis</i>	8.0	Part: sp,wp	Small	No	10
<i>Sylvia borin</i>	7.8	Compl: sp,WC	No	No	11
<i>Sylvia atricapilla</i>	8.0	Part: sp,(wp)	Small	?	
<i>Phylloscopus inornatus</i>		Part: sp,wp	No	No	12
<i>Phylloscopus bonelli</i>		Compl: sp,WC	No	?	
<i>Phylloscopus sibilatrix</i>	6.1	Compl: sp,WC	No	?	
<i>Phylloscopus collybita</i>	7.8	Part: sp,wp	Small	No	5
<i>Phylloscopus trochilus</i>	7.8	Compl: sp,WC	No	No	5
<i>Regulus regulus</i>	7.0	Part: sp	No	?	
<i>Regulus ignicapillus</i>		Part: sp	Small	?	
<i>Muscicapa striata</i>	9.3	Compl: sp,WC	No	?	
<i>Ficedula parva</i>		Part: sp,wp	Small	No	13
<i>Ficedula albicollis</i>	7.9	Part: sp,wp	Yes	?	
<i>Ficedula hypoleuca</i>	15.0	Part: sp,wp	Yes	Yes	14
<i>Panurus biarmicus</i>	6.0	Compl: SC	No	?	
<i>Aegithalos caudatus</i>	8.1	Compl: SC	No	No	13
<i>Parus palustris</i>	11.5	Part: sp	Small	No	13
<i>Parus montanus</i>	8.9	Part: sp	Small	No	15
<i>Parus cristatus</i>	7.6	Part: sp	No	?	
<i>Parus ater</i>	9.5	Part: sp	No	?	
<i>Parus caeruleus</i>	12.3	Part: sp	Small	No	16
<i>Parus major</i>	15.0	Part: sp	Small	No	17,18
<i>Sitta europaea</i>	9.0	Part: sp	No	?	
<i>Tichodroma muraria</i>		Part: sp,wp	No	?	
<i>Certhia familiaris</i>	7.7	Part: sp	No	?	
<i>Certhia brachydactyla</i>		Part: sp	No	No	13
<i>Remiz pendulinus</i>	5.8	Part: sp,(SC?)	No	?	
<i>Oriolus oriolus</i>	14.8	Compl: sp,WC	Yes	Yes	13
<i>Lanius collurio</i>	7.4	Compl: sp,WC	Small	?	
<i>Lanius minor</i>		Compl: sp,WC	Small	?	
<i>Lanius excubitor</i>	5.8	Part: sp,wp	Small	?	
<i>Lanius senator</i>		Compl: sp,WC	Yes	?	
<i>Garrulus glandarius</i>	17.9	Part: sp	Yes	?	
<i>Pica pica</i>	15.1	Part: sp	Small	?	

(continued)

Appendix (continued)

Species	Longevity (years)	Moult	Dichromatism	Song difference	Ref.
<i>Nucifraga caryocatactes</i>	8.0	Part: sp	Yes	?	
<i>Pyrhcorax graculus</i>	11.0	Part: sp	Small	?	
<i>Pyrhcorax pyrrhcorax</i>		Part: sp	Small	?	
<i>Corvus monedula</i>	14.3	Part: sp,(wp)	Small	?	
<i>Corvus frugilegus</i>	19.9	Part: sp	Yes	?	
<i>Corvus corone</i>	19.0	Part: sp	Small	?	
<i>Corvus corax</i>	16.0	Part: sp	Yes	?	
<i>Sturnus vulgaris</i>	20.1	Compl: SC	Yes	Yes	19,20
<i>Sturnus roseus</i>	11.0	Compl: WC	Yes	?	
<i>Passer domesticus</i>	12.9	Compl: SC	No	?	
<i>Passer italiae</i>	11.3	Compl: SC	No	?	
<i>Passer montanus</i>	12.8	Compl: SC	No	?	
<i>Petronia petronia</i>		Compl: SC	No	?	
<i>Montifringilla nivalis</i>		Compl: SC,(wp)	No	?	
<i>Fringilla coelebs</i>	14.0	Part: sp,wp	Small	No	21
<i>Fringilla montifringilla</i>	14.8	Part: sp	Yes	?	
<i>Serinus serinus</i>	8.6	Part: sp,(SC)	Yes	?	
<i>Serinus citrinella</i>	5.7	Part: sp	Yes	?	
<i>Carduelis chloris</i>	12.6	Part: sp,(SC)	Yes	?	
<i>Carduelis carduelis</i>	8.4	Part: sp,(SC)	Small	?	
<i>Carduelis spinus</i>	10.9	Part: sp,(SC)	Small	?	
<i>Carduelis cannabina</i>	8.9	Part: sp,(SC)	Small	?	
<i>Carduelis flavirostris</i>	6.1	Part: sp	Small	?	
<i>Carduelis flammea</i>	8.0	Part: sp	Small	?	
<i>Loxia leucoptera</i>		Part: wp	Yes	?	
<i>Loxia curvirostra</i>	7.1	Part: sp,(SC)	Yes	?	
<i>Carpodacus erythrinus</i>	9.0	Part: wp,(WC)	Yes	No	22
<i>Pyrhula pyrrhula</i>	17.5	Part: sp	Yes	?	
<i>Coccothraustes coccothraustes</i>	11.7	Part: sp	No	?	
<i>Calcarius lapponicus</i>	6.0	Part: sp,wp	Yes	?	
<i>Plectrophenax nivalis</i>	4.1	Part: sp,(wp)	Small	?	
<i>Emberiza leucocephalos</i>		Part: sp,wp	Small	Yes	23
<i>Emberiza citrinella</i>	9.5	Part: sp,(wp)	Small	No	24
<i>Emberiza cirulus</i>	6.1	Part: sp,wp	Small	?	
<i>Emberiza cia</i>		Part: sp	Small	?	
<i>Emberiza hortulana</i>		Part: sp,wp	Small	?	
<i>Emberiza pusilla</i>		Part: sp,wp	Small	?	
<i>Emberiza schoeniclus</i>	10.7	Part: sp,wp	Small	?	
<i>Emberiza melanocephala</i>		Compl: sp,WC	Yes	?	
<i>Miliaria calandra</i>	10.5	Compl: SC	No	No	25

References: 1: CRAMP 1988; 2: CRAMP 1988; 3: SNOW & SNOW 1985; 4: CUCCO & MALACARNE 1999; 5: CRAMP 1992; 6: SCHIERMANN 1924; 7: DOWSETT-LEMAIRE 1979; 8: DOWSETT-LEMAIRE 1981; 9: CATCHPOLE et al. 1985; 10: SAUER 1954; 11: SAUER 1956; 12: MARCHETTI 1998; 13: CRAMP & PERRINS 1993; 14: ESPMARK & LAMPE 1993; 15: HAFTORN 1993; 16: BIJNENS 1988; 17: MCGREGOR & KREBS 1989; 18: LAMBRECHTS & DHONDT 1987; 19: EEENS et al. 1991; 20: EEENS et al. 1992; 21: GOODFELLOW & SLATER 1990; 22: BJORKLUND 1989; 23: CRAMP & PERRINS 1994b; 24: CRAMP & PERRINS 1994b; 25: MCGREGOR & THOMPSON 1988; 26: BALSBY & DABELSTEEN 1999.

Moult code: Part, p: partial; Compl, C: complete; s, S: summer; w, W: winter. Dichromatism and song difference codes are reported in the methods section.