

Song variation in long-lived male pied flycatchers, *Ficedula hypoleuca*

Ellen Andersen Lønaas



CEES

Centre for Ecological and
Evolutionary Synthesis

Master of Science Thesis

UNIVERSITY OF OSLO

2016

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2016

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Ellen Andersen Lønaas

<http://www.duo.uio.no/>

Print: Reprosentralen, Universitetet i Oslo

Acknowledgements

I would like to thank my supervisor Helene M. Lampe for her guidance and support throughout this thesis and for giving me the opportunity to work with this thesis. Thanks to my co-supervisor Tore Slagsvold for guidance and advice. I would also like to thank Luis Cadahia-Lorenzo for helping me with the statistics for my thesis. Lastly I want to thank my fellow study room students for advice and for a great working environment.

Abstract

Bird song is used for both intra-sexual and inter-sexual interactions, in male-male competition and for attracting females. In species that use song for attraction, the females often prefer males with larger repertoires and more complex songs. This would be beneficial for the females if the song is an honest signal of the males' quality. If so a female that chooses a male with a complex song may gain benefits such as good territory quality, good parental care or good genes. The song repertoire of several passerine birds have been found to correlate with age, and some have found correlations between the song repertoire and male qualities like body mass, wing and tarsus length, plumage colour and arrival date. These have also been found to correlate with the song repertoire and song versatility in the pied flycatcher *Ficedula hypoleuca* in a population, and correlation between song and age has been found in individual pied flycatchers. Delayed maturation in song and other traits such as colour, length, and body mass would also suggest a correlation between these variables and song. There are also external factors that may affect the song of the pied flycatcher. The temperature and precipitation have been seen to affect the males singing rate, and the number of males that are close by might suggest how many possible song tutors there are available and how much song a male is able to hear and learn. I studied the song repertoire and song versatility of 10 long-lived male pied flycatchers, to see if there was a correlation between the song and male qualities and to see if the song was affected by external variables. By using mixed effects models I found that most of the variables tested were not significant in explaining the variation in the song repertoire or the song versatility. The population size_{t-1} with the added effect of arrival date was, however, significant in explaining the variation in the song repertoire, and was with the added effect of NDVI data significant in explaining the variation in the song versatility. If the population size was big the previous year the males tended to have larger song repertoires and higher song versatility. Although not significant, some of the variables showed the same trends as have been found previously. The interaction between age and arrival date was also found to be significant in explaining the song repertoire, but this was, however, most likely caused by two individuals who had plastic song as juveniles, and the significance disappeared when these two individuals were removed. The wing length and plumage colour were shown to have delayed maturation, but the song repertoire did not.

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1 Introduction

Birds use sounds to communicate with each other, and these sounds can be divided into calls and songs (Catchpole and Slater, 1995). While calls usually are short and simple sounds that are used by both sexes throughout the year, songs are usually longer, more complex, and they are mostly produced by the males during the breeding seasons (Catchpole and Slater, 1995). During spring when all the migratory birds return and both they and the non-migratory birds start their breeding season, the males of many species can be observed singing as they occupy and defend their territories (Catchpole and Slater, 1995). This song can be used by the males either in keeping and defending their territories from other males, intra-sexual interactions, the song can also be used for attracting a suitable female to mate with, inter-sexual selection, or a combination of the two (Catchpole and Slater, 1995). In oscine passerines a connection has been suggested between the repertoire size, length and complexity of the birds' song and the function of the song, where the longer and more complex songs serve inter-sexual functions and the shorter less complex songs serve intra-sexual functions (Catchpole and Slater, 1995). These complex songs are likely to have evolved through sexual selection, and the females of several of the species that use song for attraction have been found to prefer males with larger song repertoire or more complex songs over males with shorter song repertoire or less complex songs (Baker et al., 1986, Catchpole, 1987, Eens et al., 1991, Lampe and Sætre, 1995). A reason for why a female should choose males with larger and more complex songs could be if the males' song reflects their quality (Balsby, 2000). If the song reflects the quality of the males, a female who chooses a male with larger song repertoire or more complex song might obtain benefits such as high quality territories, better parental care, or the female might gain genetic benefits for her offspring (Trivers, 1972, Alatalo et al., 1986, Kirkpatrick and Ryan, 1991).

Several studies on passerines have looked at the relationship between song complexity and male qualities. The song repertoires of several passerine birds have been shown to be larger in older males than in younger males, often with the largest increase taking place between 1 year of age and 2 years of age, e.g. whitethroat *Sylvia communis* (Balsby and Hansen, 2010), willow warbler *Phylloscopus trochilus* (Gil et al., 2001), common nightingales *Luscinia megarhynchos* (Kiefer et al., 2009). There are different reasons for why the song repertoire may increase with age, for example the male may be unable to learn a large song repertoire in one season and needs to build on the repertoire from previous years (Balsby and Hansen,

2010). Another possibility is that the male has learned all the syllables during a sensitive period early in its life, but did not express all of them during the first breeding season (Geberzahn et al., 2002). In addition to age the song repertoire or song variability have been found to correlate with other measures of male qualities, e.g. male eurasian blackbird *Turdus merula* with long tarsi had larger repertoires than those with shorter tarsi (Hesler et al., 2012), male whitethroats were found to have positively correlated song variability and wing length (Balsby, 2000), common nightingale males' repertoire was found to be positively correlated with wing length and body mass (Kipper et al., 2006), and early arriving male oriental great reed warblers *Arcocephalus orientalis* were found to have larger repertoires than later arriving males (Park et al., 2009).

The pied flycatcher *Ficedula hypoleuca* mainly use their song for attracting females, which can be seen by the fact that they stop or drastically decrease their song activity after acquiring a partner (Espmark and Lampe, 1993) and song is rarely heard when two males interact or fight (Gottlander, 1987). The female pied flycatcher, as other female passerines, have been shown in a field study to have an active mate choice (Dale et al., 1990), and they have also been shown, in an experiment, to prefer males with larger song repertoires over males with smaller song repertoires (Lampe and Sætre, 1995). In a previous study of individuals in a population of pied flycatchers, with one song recording per male, the song repertoire and song versatility were found to correlate with arrival date, breeding experience, plumage colour, body mass, and body condition (body mass divided by wing length) (Lampe and Espmark, 1994). In another study the total number of figures/syllables, strophe and song versatility were found to increase in individual males from one year to another (Espmark and Lampe, 1993). Eriksen et al. (2011) found evidence in a field experiment that the male pied flycatcher may be an open-ended learner. Open-ended learners are able to learn and memorize new syllables through their whole life, while closed-ended learners only have certain period of time they are able to learn and memorize new syllables (Thorpe, 1958, Mundinger, 1970, Nottebohm and Nottebohm, 1978). As an open-ended learner the pied flycatcher would be able to learn new syllables through its life that it can use to build on and increase its song repertoire. Since the males learn song from close singing conspecific males (Lundberg and Alatalo, 1992) the number of males in an area may affect how much an individual is able to hear and learn, and how much the male can build on its repertoire for the next breeding season.

In many birds the plumage colour have been found to fully mature in males a year after they have reached sexual maturity, with the males having female-like plumage colour their first breeding season (Rohwer et al., 1980). Reasons for this delayed colour maturation have been suggested to be to mimic the females to deceive older males, to prioritize survival by avoiding aggressiveness, and to have less detectable colours (Rohwer et al., 1980). In a study by Dale et al. (2002), they found that that the plumage colour became darker, wing length, tarsus length, and body mass increased in the pied flycatcher after they were sexually mature. This delayed maturation might be an effect of trade-off, by spending less resources on growth and plumage colour they may use these resources for survival instead (Dale et al., 2002). The development of song with age and delayed maturation in male qualities also gives support to the correlation found between the males' song and their other qualities.

There are different external factors that may affect the song of the pied flycatcher like temperature, precipitation and food availability. Precipitation in the breeding area may affect the singing activity of the males and Gottlander (1987) found that the singing activity increased with higher temperature, which she suggested probably was caused by increased insect mobility with higher temperature. Along the migration route of the pied flycatcher there are stopover sites that may vary in food abundance from year to year. The availability of food in these stopover sites may affect the condition of the males and their singing ability. Normalized Difference Vegetation Index (NDVI) can be used as an estimate of insect abundance, because the insects depend on plant productivity (Møller and Szep, 2005). Since pied flycatchers mostly eat insects (Lundberg and Alatalo, 1992), the NDVI can be used as an estimate of food abundance in stopover sites (Møller and Szep, 2005).

I wanted to investigate if the different male qualities and variables that have been found to correlate with song repertoire and versatility in individuals in a population of pied flycatchers also correlate in long-lived individuals. In addition to these variables, I also wanted to investigate if the song repertoire and song versatility were affected by the population size_{t-1}, weather conditions (temperature and precipitation) in the breeding area, and a proxy for food availability in a stopover site along the migration route, that affects arrival date (Cadahia et al., in review). To investigate this I used song recordings and measurements that had been taken close to arrival of ten individual males together with data of the population size, weather data from the breeding area and NDVI data from a stopover site from the migration route.

Each male had been recorded and/or measured over several breeding seasons, from they were one or two years old and to their last breeding season when they were at least four years old.

My hypotheses are that the song repertoire and song versatility of individual male pied flycatchers will correlate with other measures of male qualities, that the number of males in a previous year will affect how many syllables a male have learned to use, and that weather conditions and food availability may affect the song. I also hypothesize that some of the male qualities will show delayed maturation.

My predictions are that the song repertoire and the song versatility will:

- Increase with higher body mass, better body condition, longer wings and tarsus, darker/blacker plumage colour, age, and breeding experience.
- Decrease with increasing arrival date.
- Increase with a higher mean temperature in the breeding area and increasing NDVI for stopover site, and decrease with higher precipitation in the breeding area.
- Increase with larger population size the previous year.

I also predict that plumage colour, tarsus length, body condition, wing length and song repertoire will show delayed maturation.

2 Materials and methods

2.1 Study species

The pied flycatcher is a small (12-13g) passerine bird belonging to the family Muscicapidae and the genus *Ficedula* (Lundberg and Alatalo, 1992). The colour of the males varies from white and black to beige and brown, while the females usually are beige and brown (Svensson, 1992). It is a migratory bird that spends its breeding season in forested areas in the Palaearctic regions and then, in late summer, starts migrating towards the wintering areas in West Africa (Lundberg and Alatalo, 1992). In spring the males usually arrive first in the breeding areas where they find nesting sites/territories (Lundberg and Alatalo, 1992). The pied flycatcher uses cavities in trees for nesting, but, if provided, they prefer good quality nest boxes (Lundberg and Alatalo, 1992). After the males have acquired a territory/nesting site they start to sing to attract a female. After pairing the female will start nest building and after that, start laying eggs which are incubated only by the female, for about two weeks (Lundberg and Alatalo, 1992). Some males are polyterritorial and will find another nesting area to try to acquire a second female during this period (Lundberg and Alatalo, 1992). When the eggs hatch the male will help the primary female to feed the nestlings, the secondary female receives little or no help. The adults and nestlings mainly feeds on insects, with a preference for caterpillars (Lundberg and Alatalo, 1992).

2.2 Study area

The study area was Sinober in Sørkedalen (59°58'N 10°37'E), Oslo. This is an area with mixed coniferous and deciduous forest. Sinober has been used as a study area for pied flycatchers for many years. Already in 1981 a few nest boxes were put up, but it started on a larger scale in 1985 and during the study period around 300 nest boxes have been put up approximately 50 meters apart in the area (Eriksen et al., 2011, Cadahia et al., in review). The pied flycatcher use these nest boxes as nest sites during the breeding season, but they are also used by great tits *Parus major*, blue tits *Cyanistes caeruleus*, coal tits *Periparus ater*, and 1-2 nuthatches *Sitta europaea* every year.

2.3 Data collection

The data collection of the males in my study started in 2003, and the recordings of the males were done in the period from 2006 – 2015 (Table 1). During the breeding season the area was monitored daily and arrival date for all the males was noted. The males' song were recorded between 7:00 and 12:00 with TC-D5 ProII Sony cassette recorders (in 2006), and Sound Devices 702 (2007-2015) and a Marantz PDM 661 digital recorder (2013-2015), all recorders were equipped with Telinga parabolic microphones. The song recordings were done when the males were presumed unmated. For each male a recording of at least 25 spontaneous strophes were made.

Table 1: The breeding seasons where the male pied flycatchers were observed in the study area and varying amount of morphological data were recorded (light blue) and breeding seasons were both morphological data and the song were recorded.

Male (id nr.)	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
3H43075	Adult												
3H43110	Juv.												
3H43302			Adult										
3H43320				Juv.									
3H43330				Juv.									
2H59480				Juv.									
3H43334				Juv.									
6H39088					Juv.								
2H59886							Pullus	Juv.					
9H48234											Adult		

All the males that were recorded were captured afterwards by using playback of male pied flycatcher song and a nest box trap. The unmarked males were ringed with colour rings and a metal ring with an ID number for later identification, while the ID and colour codes were noted for the returning males. The body mass of all males was measured to the nearest 0,1g using a Pesola spring balance. The length of tarsus and the maximum length of the wing were measured to the nearest 0,5mm (see fig. 1). Using the Drost scale (Drost, 1936) the plumage colour of the males was decided. The Drost scale is a scale from 1 to 7, where 1 is a black male and 7 is a brown male, and the ones in between is a mixture of brown and black in varying degree (Drost, 1936).

To determine the age of the males, either to be 1 year olds (juvenile) or older (adult), the condition of the tail feathers and the colour of the outer greater wing coverts were used. One year olds usually have greater covers with white tips that form a step or wedge (Svensson, 1992). They also have slightly pointed tail feathers that usually are a little worn, while older males, tail feathers are rounder and not worn (Svensson, 1992). The age of three of the males were uncertain for their first year, but using their colour data and wing and primary length, one was placed as juvenile and the two others were placed as adults. Younger males have shorter wing length but longer first primaries than older males (Alatalo et al., 1984), and because of delayed maturation in plumage colour yearling males tend to be browner than older males (Dale et al., 2002). All the data were collected by Helene M. Lampe and others.



Figure 1: Measurements of a male pied flycatcher being taken.

The NDVI and the weather data were obtained through Luis Cadahia-Lorenzo. The data obtained were the climatic data that correlated the best with arrival date; i.e. NDVI for the Iberian peninsula and temperature and precipitation for Oslo in spring. The NDVI data for 2006 were obtained from the NOAA AVHRR-based data from GIMMS (Global Inventory Modelling and Mapping Studies) data set, made available by the University of Maryland Global Land Cover Facility (Cadahia et al., in review). For the period 2007-2015 the MODIS data, provided by the USGS Land Processes Distributed Active Archive Centre, were used (Cadahia et al., in review). The NDVI data were from the Iberian Peninsula from April. The weather data consists of temperature and precipitation data. This dataset was obtained through the e-Klima service of the Norwegian Meteorological Institute (<http://eklima.met.no>), using

the Blindern station, which is located about 9km from the study area (Cadahia et al., in review). For the temperature data the period from 9 April – 26 May and for precipitation the period from 9 May – 4 June was used, based on analysis of arrival time by Cadahia-Lorenzo.

2.4 Song analysis

A total of 10 males were recorded over two or more seasons, with a total of 34 song samples. All the males included in the study were long lived, becoming 4 years or older. Sonograms of all the song samples were made using the program RavenPro 1.4 (The Cornell Lab of Ornithology, <http://www.birds.cornell.edu/raven>). The song of the pied flycatcher consists of different syllables. A syllable or figure is defined as a short continuous sound that is interrupted by a silent period of maximum 0,02 seconds (Espmark and Lampe, 1993). The syllables make up strophes, which are separated by intervals that are 1 second or longer (Fig. 2) (Espmark and Lampe, 1993). The total number of different syllables the male use in 25 song strophes is the male's song repertoire. The pied flycatcher does not have specific songs, but rather have a certain number of different syllables that they combine in different ways (Lundberg and Alatalo, 1992). In the analyses, 25 song strophes were used for each song sample. All the different syllables were visually identified and the song repertoire (the total number of different syllables) and song versatility (number of different syllables divided by the total number of syllables in a song sample) was determined. Two of the males had rather large repertoires as juveniles with several similar syllables that were hard to identify.

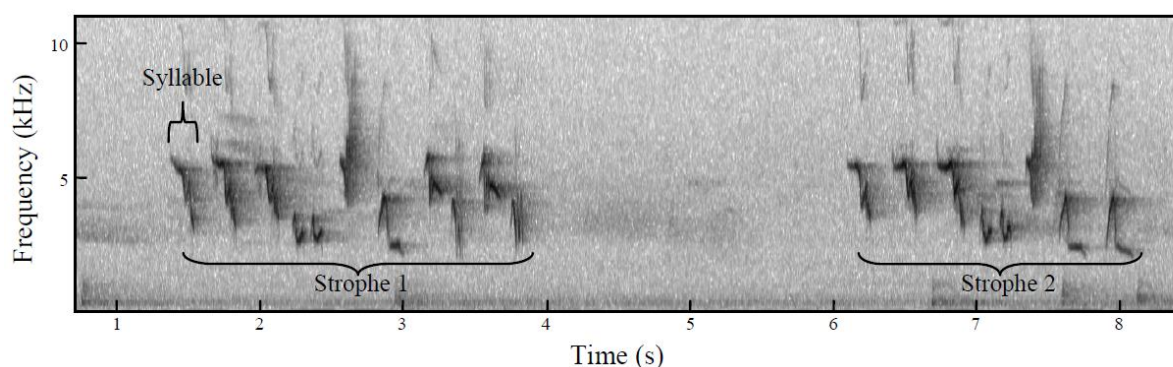


Figure 2: Sonogram of two strophes from male pied flycatcher song showing six different syllables and a total of 19 syllables.

2.5 Statistical analysis

All the statistical analyses were done using the software environment for statistical programming R version 3.2.3 (R Core Team, 2015, <https://www.r-project.org>). To see if there was any correlations between the dependent variables, song repertoire and song versatility, and the independent variables I used mixed model effects. This method was chosen since it takes into account random effects. All the males have been recorded several times, which may give clustered data and pseudoreplication, and therefore the individual is used as a random effect. The year of recording was also used as random effect since there might be unmeasured variables from year to year that might affect the song. The variables that were used as independent variables or fixed effects were: age (juvenile/adult), age in years, experience, arrival date, relative arrival date, plumage colour, tarsus length, wing length, body mass, relative body mass, body condition, relative body condition, population size_{t-1}, NDVI, temperature, precipitation, and year. The body condition was calculated by dividing body mass on tarsus length, relative body mass is the body mass relative to the population's mean body mass that year and the relative body condition is calculated by dividing the relative body mass on tarsus length. The males were either put as experienced if they had been registered in the study area in a previous breeding season or unexperienced if they had not. The arrival date is calculated as Julian dates, and relative arrival date is calculated as the number of days since the first male arrived. To determine the age in years the three males that were adult at their first time of breeding in the study area were put as two years old, since most males breed for the first time in their first year or second year of age (Lundberg and Alatalo, 1992, and references therein).

I used Shapiro-Wilk test and found that the two dependent variables, song repertoire and song versatility, were normally distributed. To run mixed effects models in R I used the R package lme4 (Bates et al., 2015). The first mixed effects models were run with song repertoire as dependent variable against all the different independent variables, one at a time, and with individual as random effects. The same models were run again with both individual and year as random effect. The next models were run with song versatility as dependent variable against all the different independent variables, one at a time, and with individual as random effects. The mixed models with song versatility as dependent variable were repeated with both individual and year as random effects. Then I ran mixed models with song repertoire as dependent variable and different combinations of two or three independent variables, first

with individual as random effect and then with both individual and year as random effects. The same models were run with song versatility as dependent variable. I also ran mixed effects models with song repertoire as dependent variable with both individual and year as random effects and the interaction between age and arrival date, once with age in years and once with age juvenile/adult, as independent variable. To obtain p-values from the mixed effect models, anova was run using R package car (Fox and Weisberg, 2011) for all of the different mixed effect models.

To see if there was delayed maturation in plumage colour, tarsus length, wing length, body condition, and song repertoire, mixed effects models were run using data from the three first years of life of the males. The five different male qualities and also arrival date were put as dependent variables and run once each with age in years as independent variable and individual as random effects.

3 Results

The average song repertoire was 29 (range: 12 – 51) and the average song versatility was 0.14 (range: 0.072 – 0.278). Two of the males had rather large repertoire when they were juveniles, with syllable repertoires of 51 and 41, with many unstable syllables (syllables that were very similar to each other and hard to identify).

In the mixed effects models with only one independent variable, no independent variables were significant (see appendix table A and B), but the population size_{t-1} tended to be significant for song versatility ($\chi^2=2.76$ df=1 p=0.096) both with individual as random effects and with individual and year as random effects. The results of the mixed effects models with more than one independent variable that were significant or tended to be significant can be seen in table 2 (see appendix table C and D for more details). Population size_{t-1} were significant for song repertoire when added with arrival date, and when added with age (years) and arrival date (table 2), the song repertoire was larger if the population size the previous year was large than if it was small. For the song versatility, the population size_{t-1} was significant when added with NDVI, and when added with age (juvenile/adult) and NDVI (table 2), the song versatility were higher if the population size the previous year was large than if it was small.

Table 2: Results of the mixed effects models for the ten male pied flycatchers, with more than one independent variable, that were significant or tended to be significant. Df = 1 for all tests.

Dependent variable	Independent variable	Individual as random effects		Individual and year as random effects	
		χ^2	p	χ^2	p
Song repertoire	Arrival date	2.76	0.097	2.54	0.11
	Pop. size _{t-1}	4.047	0.044	3.71	0.054
Song repertoire	Arrival order	3.28	0.07	3.028	0.082
	Pop. size t-1	3.64	0.057	3.41	0.065
Song repertoire	Age (years)	0.84	0.36	0.76	0.38
	Arrival date	3.2	0.074	3.01	0.083
	Pop. size _{t-1}	4.4	0.036	4.025	0.045
Song repertoire	Arrival order	3.0	0.083	2.89	0.089
	Rel. body cond.	0.082	0.77	0.047	0.83
	Pop. size t-1	3.39	0.066	3.27	0.07
Song repertoire	Age (juv/ad)	0.19	0.66	0.037	0.85
	Arrival date	2.82	0.093	0.31	0.58
	Pop. size _{t-1}	4.09	0.043	2.86	0.091
Song versatility	Arrival date	0.29	0.59	0.29	0.59
	Pop. size t-1	2.94	0.087	2.94	0.087
Song versatility	NDVI	0.047	0.83	0.047	0.83
	Pop. size _{t-1}	4.17	0.041	4.17	0.041
Song versatility	Rel. body cond.	0.0088	0.93	0.0088	0.93
	Pop. size t-1	2.93	0.087	2.93	0.087
Song versatility	Body condition	0.72	0.4	0.72	0.4
	Pop. size _{t-1}	3.39	0.066	3.39	0.066
Song versatility	Arrival order	0.94	0.33	0.94	0.33
	Rel. body cond.	0.011	0.92	0.011	0.92
	Pop. size t-1	3.59	0.058	3.59	0.058
Song versatility	Age (years)	0.45	0.5	0.45	0.5
	Body condition	0.78	0.38	0.78	0.38
	Pop. size _{t-1}	3.32	0.069	3.32	0.069
Song versatility	Age (juv/ad)	0.045	0.83	0.045	0.83
	NDVI	0.035	0.85	0.035	0.85
	Pop. size _{t-1}	4.041	0.044	4.041	0.044
Song versatility	Exp.	0.21	0.65	0.21	0.65
	NDVI	0.0099	0.92	0.0099	0.92
	Pop. size _{t-1}	3.76	0.052	3.76	0.052

The interaction between age (years) and arrival date ($\chi^2=3.87$ df=1 p=0.049), and the interaction between age (juv/ad) and arrival date ($\chi^2=6.051$ df=1 p=0.014) was significant in explaining the variation in song repertoire. The song repertoire was larger in the early arriving males than in later arriving males, with the largest difference in song repertoire with arrival being found in the juveniles (Fig. 3a). However, if the two individuals with large repertoires as juveniles are removed from the data set (Fig. 3b) or the data from when they were juveniles is removed (Fig. 3c), the significance of the interaction between age and arrival date in explaining the variation in the song repertoire disappears (see appendix table E for details).

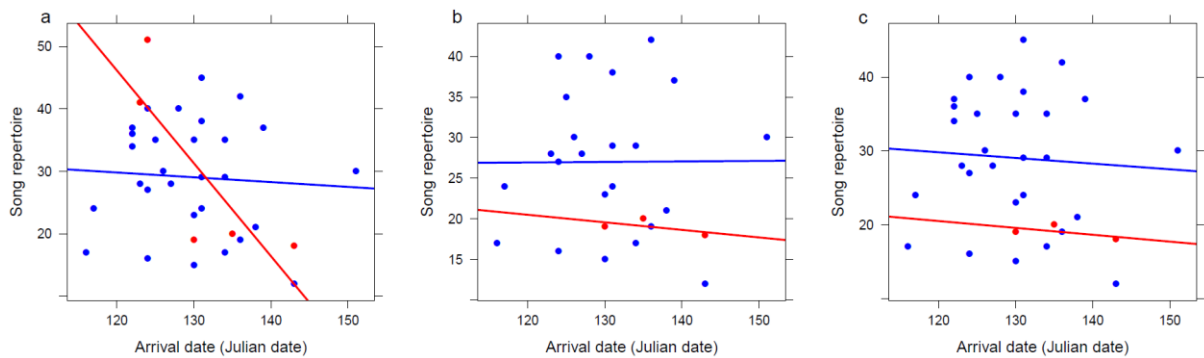


Figure 3: a) the relationship between song repertoire and arrival date grouped by age, with n=10 male pied flycatchers. b) Same as a) but all data of the two individuals with high repertoires as juveniles is removed. c) The two juvenile outliers are removed. Blue are juveniles and red are adults

Although no independent variables were shown to be significant by themselves, some show the same trends as was found by Lampe and Espmark (1994) (fig. 4 and 5). Males with better body condition tended to have a larger song repertoire, but only slightly. There was also a positive trend of song repertoire with wing length. The tarsus length, colour and age shows the opposite trend of what I expected, with browner males, males with shorter tarsus length, and younger males having slightly larger song repertoires. If the two juvenile outlier males are removed from the data set, however, the tarsus length does not show any trends, and darker and older males had the larger song repertoires. Without the two juvenile outlier individuals experienced males tended to have larger song repertoires than inexperienced. The same trends are seen with song versatility as well, except for age that shows a slight positive trend, and tarsus length, colour, and experience showed the same trends for song versatility with and without the two juvenile outlier individuals.

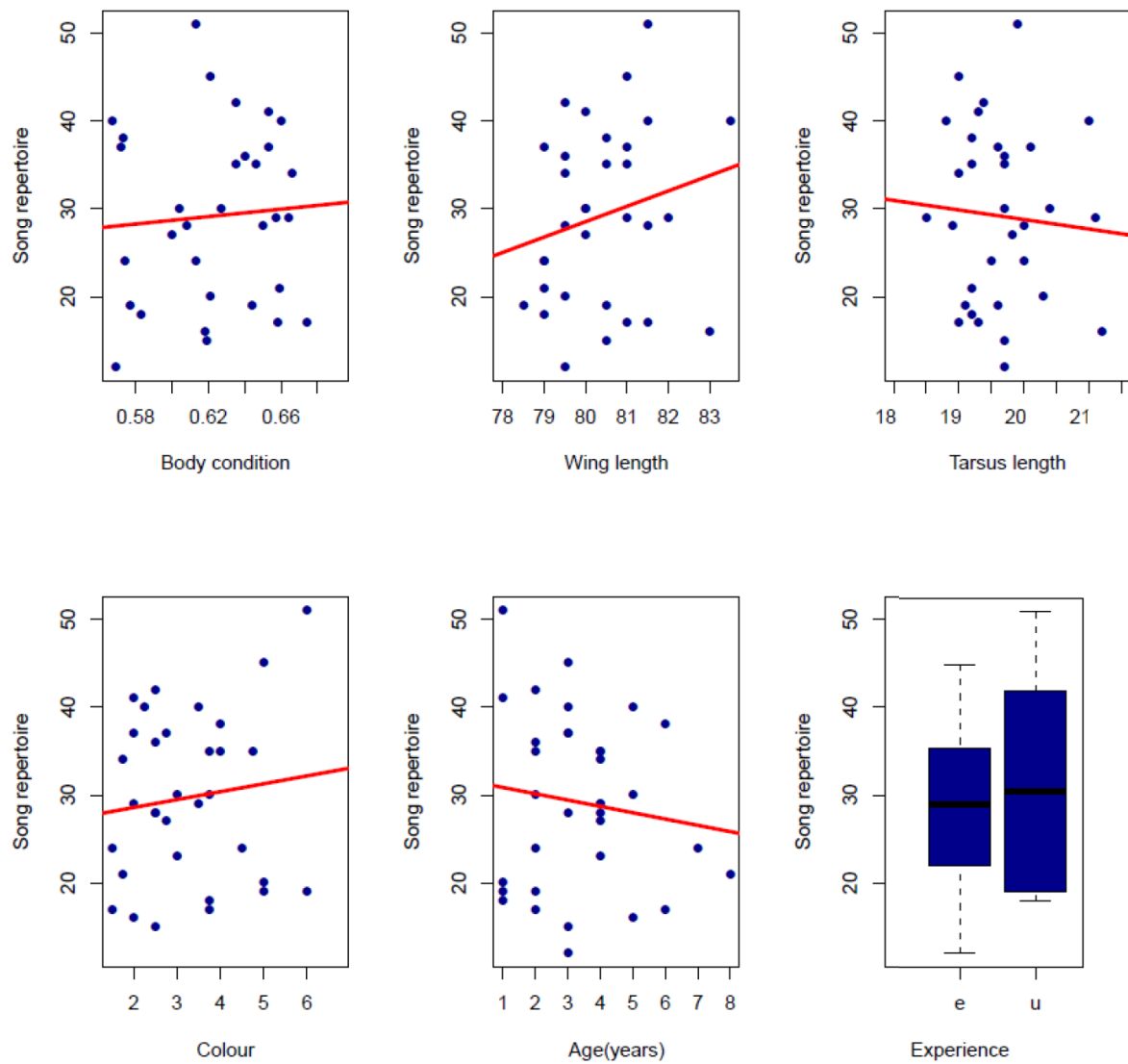


Figure 4: Plots of the song repertoires of the ten male pied flycatchers with different variables.

The males with early arrival tended to have larger song repertoires (fig. 5) and song versatility than later arriving males (see appendix table A and B for details). When the population size of the previous year was large the song repertoire of the males tend to be larger than when the population size was small (fig. 6), the tendency were similar with song versatility (see appendix table A and B for details).

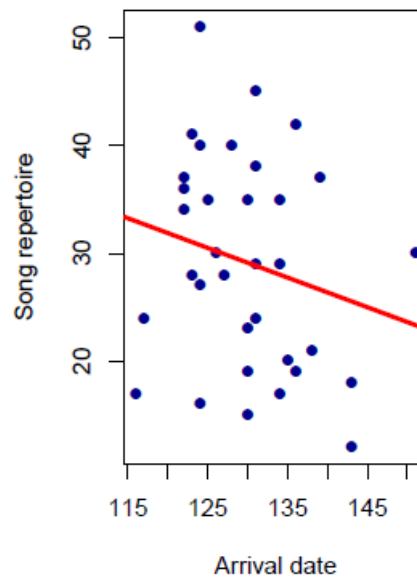


Figure 5: Scatter plot of the ten male pied flycatcher's song repertoires with arrival date.

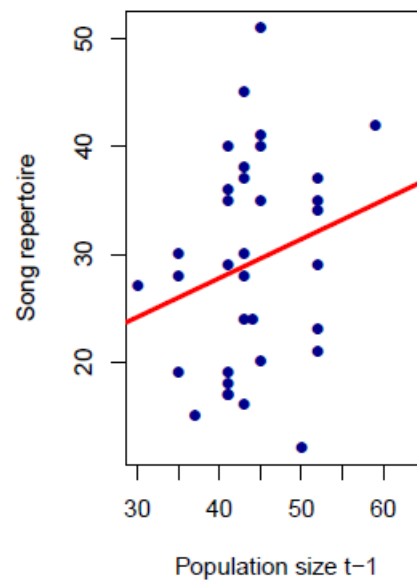


Figure 6: Scatter plot of the ten male pied flycatcher's song repertoire with population size_{t-1}.

The song repertoire did not show any specific trends for the NDVI or the precipitation data, but the song repertoire tended to decrease with higher temperature (fig 7). The trends were similar for song versatility.

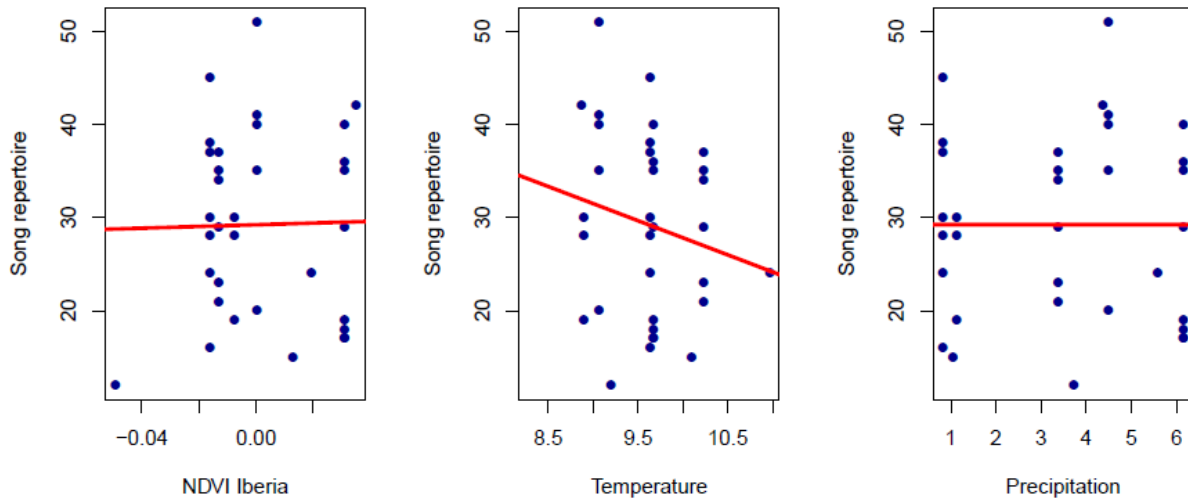


Figure 7: Scatter plots of the ten male pied flycatcher's song repertoires with NDVI, temperature and precipitation.

When looking at the year with the most male song recordings, 2007, the song repertoire tended to be larger for early arriving males, males with blacker plumage colour, longer wings and tarsus, and better body condition (appendix fig. A). Experienced males tended to have larger repertoires than inexperienced males, but there were only one inexperienced male in 2007. The data from 2007 did not include the large juvenile repertoires, and there was only one measurement for each male.

The males in this study showed signs of delayed maturation in some of their qualities (fig. 8). The song repertoire, plumage colour and wing length all seemed to change over the three first years of life, with the song repertoire and wing length increasing from the first to second year, and from the second to the third year of life. The plumage colour seemed to become darker from the first to the second year of life, and also from the second to the third year of life. The increase from first year of life till the third year of life was significant for plumage colour ($\chi^2=10.78$ df=1 p=0.001) and for wing length ($\chi^2=5.72$ df=1 p=0.017) (see appendix table F for details). After the fifth year the males seemed to become browner again. For the eighth year there is only one male who was rather black most of his life. The song repertoire stabilized after the third year and then decreased towards the age of seven and eight, but this

decrease was only from measurements of one male. The wing length also seemed to stabilize after the third year of age. Both the body condition and the tarsus length varied somewhat between the years, with tarsus length staying rather stable.

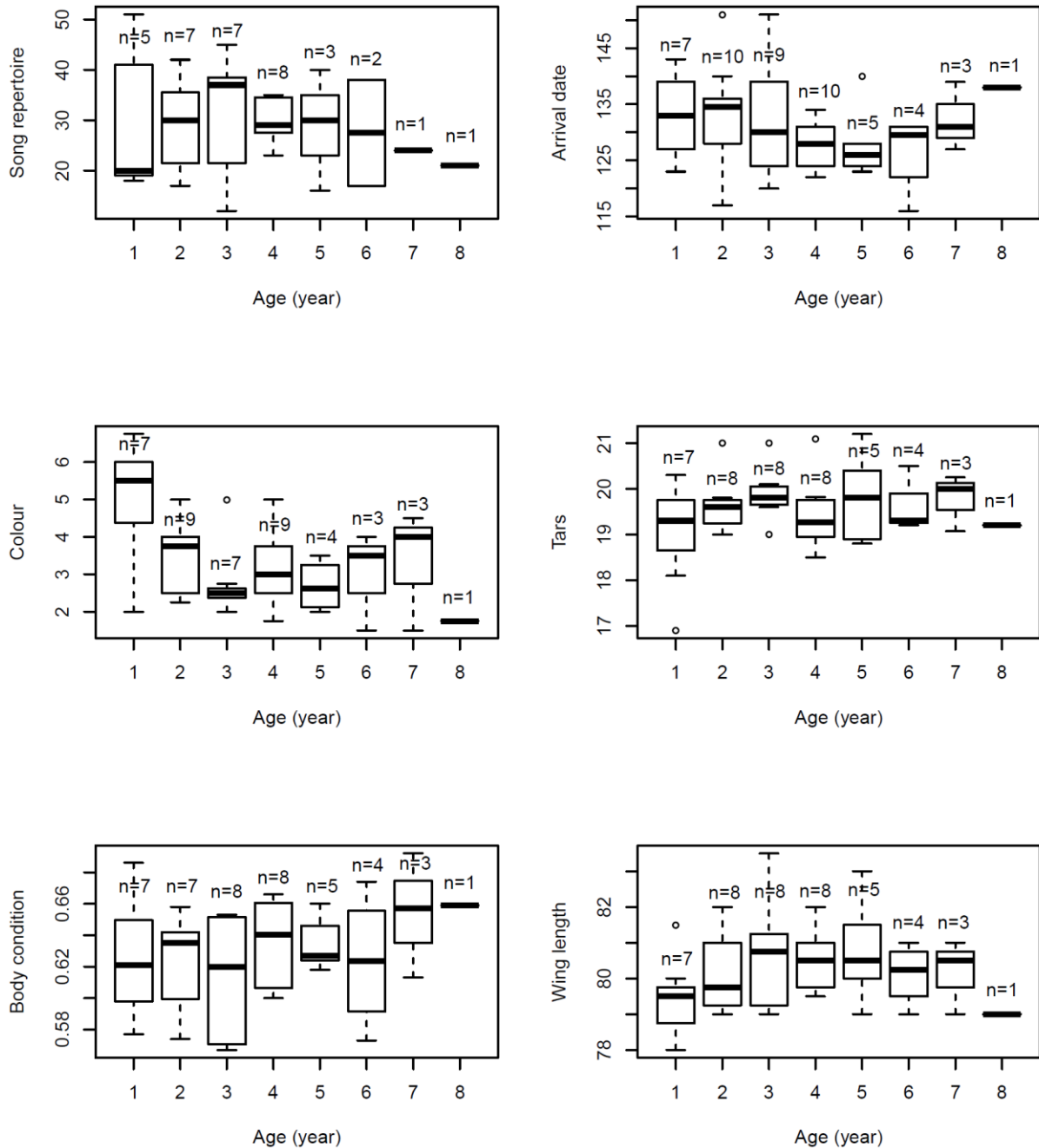


Figure 8: Box plots of different variables over the different ages of the ten male pied flycatchers .

4 Discussion

All the males varied from year to year in their song repertoire and song versatility, but I found that none of the variables tested in my study were significant by themselves in explaining the variation in the song repertoire or the song versatility, only population size_{t-1} tended to be significant for the song versatility. Population size_{t-1} was significant for song repertoire with the added effects of arrival date, and for the song versatility with the added effects of NDVI. The NDVI did not show any specific trends, but both the population size_{t-1} and arrival date showed trends with song repertoire and song versatility. As has been found in previous study of the pied flycatcher (Lampe and Espmark, 1994) the earlier arriving males tended to have larger song repertoires than later arriving males. If the population size_{t-1} were large then the song repertoire tended to be larger. Since the pied flycatcher is most likely an open-ended learner (Eriksen et al., 2011) and the males learn song syllables from other close by singing males (Lundberg and Alatalo, 1992), then the number of males in the breeding area that is singing may suggest how much song a male is able to learn and use for the next breeding season.

The interaction between arrival date and age was shown to be significant in explaining the variation in the song repertoire. The song repertoires of several bird species have been found to correlate with age, e.g. the pied flycatcher (Espmark and Lampe, 1993), the collared flycatcher (Garamszegi et al., 2007), and whitethroats (Balsby and Hansen, 2010), with older males having larger repertoires than younger males. Also the arrival date has been shown to correlate with song repertoire in the pied flycatcher (Lampe and Espmark, 1994), with the early arriving males having larger repertoires than later arriving males. In my study, however, these variables were not significant in explaining the variation in the song repertoire by themselves, but the interaction was. The song repertoire of the males at the time they were juveniles show a large variation with arrival date, with the early arriving males having larger repertoires than the later arriving males, while the adults only show a slight negative correlation with song repertoire and arrival date. The big variation seen in the juveniles is caused by the two males that had very large repertoires as juveniles. Their repertoires were much larger than the other juveniles' repertoires and they also arrived earlier as juveniles than the other males did as juveniles. A possibility is that the two males were adult the first time they were recorded in the study area, since the traits used for aging might not always be as clear. Juveniles may for example be dark in colour, or the light wedge may not be as evident.

This could be a possibility for one of the two males that was rather black, the other male was rather brown. However, the traits that were used for aging are usually very reliable as seen by Lundberg and Alatalo (1992) who were able to determine the age correctly for 90% of 80 individuals. Another possibility for the large juvenile repertoire might be that they still were in a stage between subsong, with undefined syllables, and a crystallized repertoire (Marler and Peters, 1981, Nottebohm et al., 1986). After the first stage of song learning follows a stage where the song shows similar properties as adult song but the syllables are still variable, called plastic song (Nottebohm et al., 1986). Nottebohm et al. (1986) found that canaries had many more syllables in the plastic stage than in fully crystallized adult song. If the two males in my study still were in the plastic stage, which is likely since they had large repertoires with several similar syllables, the song repertoires that were recorded for them were larger than their crystallized repertoire. The song repertoires of both these males decreased between their first and second year of life and many similar syllables became fewer more easily defined syllables. However, in their second year of life they still had song repertoires that were above average for adults that year. It is possible that they were not finished with their song learning, and were therefore more flexible in acquiring larger repertoires. If the two individuals or just their juvenile data were removed from the data set the interaction between age and arrival was no longer significant. This would suggest that the significance seen in the mixed effects models were caused by these two individuals.

Some of the different variables, although not significant, showed trends similar to what has been found in previous studies. Earlier arriving males tended to have larger repertoires than later arriving males, males with better body condition had slightly larger repertoires than those with worse body condition, as was found in a pied flycatcher study by Lampe and Espmark (1994). When looking at only the year 2007, all the variables showed the same trends as have been found previously (Espmark and Lampe, 1993, Lampe and Espmark, 1994). The sample size in my study was rather small and the results are largely affected by the two males with plastic songs, as can be seen with the trend of the song repertoire with plumage colour and age in years. When including the two individuals in the data set, the song repertoire tended to be larger in the browner and the younger males, but without the two individuals in the data set the song repertoire tended to be larger in the blacker and the older males. The song repertoire did not show a positive trend with temperature as was found with singing rate and temperature (Gottlander, 1987). Gottlander (1987) suggested that the effect of temperature on singing rate was caused by the insect availability, which increases with

higher temperature. The males with good body condition and larger repertoires (Lampe and Espmark, 1994) may be better able to sing in colder temperatures than males with poorer conditions and smaller repertoires, this might give the negative trend seen in my study. The NDVI and the precipitation data did not show any specific trends and did not seem to affect either the males' song repertoire or the song versatility.

Several of the variables also showed signs of delayed maturation and some also showed deterioration. The plumage colour, body mass, tarsus length and wing length were shown to have significant delayed maturation in the pied flycatcher in a study by Dale et al. (2002). They also saw that body mass decreased slightly at the age of six, but it was not a significant decrease. The males in my study showed significant delayed maturation in wing length and colour. There was, however, no significant evidence for song repertoire having delayed maturation. These results can therefore not be used to explain correlation between song repertoire and the male qualities. There were signs of deterioration in arrival date, colour and possibly in song repertoire around the age of six years. However, only three males became older than six years, and a fourth males became six years old.

The trends in the song repertoire with the different measures of male quality and the tendency of delayed maturation in the song repertoire and other variables could suggest that the song repertoire might work as a cue for the females of the quality of the males, but none of the variables were significant in my study, but this could be due to small sample size. Because the sample size I have used is rather small the results might be easily affected by variation that would be smoothed out with a larger sample size, as seen with the two individuals with plastic song. With a larger sample size the effect of the two individuals with plastic song might have been smaller. There might also be factors that have not been measured that affect the song repertoire and the song versatility. Since the males most likely are open ended learners (Eriksen et al., 2011) they may learn song from each other during the breeding season when the males sing to attract females. The males who arrive earlier will then have longer time to listen to and learn from the other males than later arriving males. When the late males arrive other males might already have found or will find a partner shortly, and will then decrease or stop their singing activity (Lundberg and Alatalo, 1992, Espmark and Lampe, 1993), and the late arriving males will have fewer males to learn from. And also if there are cold temperatures one breeding season the singing rate will be low (Gottlander, 1987) and there will be less song that the males can learn from than it would be during a warm breeding

season. The males might also learn song from other males during migration that they might use the same spring or the next breeding season. It is therefore possible that differences in time of migration and conditions during migration might affect the learning of syllables from other males. The song of the males might also have been affected by factors that took place just before the recordings as well. If a female have recently visited the nest box of a male he might sing differently than he would if the female were not around. This was, however, not found by Lambrou (2009), but the song repertoire decreased when there had been another male present. The different variables are also inter-correlated, which means it might be difficult to separate the effects of the different variables from each other, and one of the variables may affect one of the other variables. In my study I have only used one recording per male per year, but the song may vary during the breeding season, for example as found by Gottlander (1987) the song activity increases for each day the males' stay unmated. In a food experiment (Krag, 1998) found that males supplied with food increased their song repertoire during the breeding season, while males that were not supplied with food showed a decrease. It may therefore be of future interest to use several recordings for each male per breeding season.

5 Conclusion

Most of the variables I tested in my study were not significant in explaining the variation in the song repertoire or the song versatility of the males. The effects of the population size $_{t-1}$ were significant with the added effects of arrival date for song repertoire and with the effects of NDVI for song versatility. The population size $_{t-1}$ may affect the song of the males, because it might say something about how many males there is in an area that an individual can learn song from. The other variables were not significant in explaining the variation in the song repertoire or song versatility, but some of the variables showed the same trends as in previous findings. The interaction between the arrival date and age was significant for the song repertoire, but most likely only because of the two individuals with plastic song as juveniles. The wing length and the plumage colour were shown to have delayed maturation, but the song repertoire did not, and I can therefore not draw any conclusion from delayed maturation and the correlation between male qualities and the song repertoire. The reasons for why most of the variables were not significant may be that there are other variables that affect the song that were not accounted for in this study, and also the small sample size.

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Appendix

Table A: Results of mixed effects models for the ten pied flycatcher males using individual as random effects. Df = 1 for all tests.

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Age (juv/ad)	0.0042	0.95	0.0051	0.94
Age (years)	0.25	0.62	0.31	0.58
Experience	0.86	0.36	0.22	0.64
Arrival date	0.95	0.33	0.01	0.92
Rel. arrival date	1.86	0.17	0.12	0.73
Colour	7e-04	0.98	0.084	0.77
Wing length	0.87	0.35	0.094	0.76
Tarsus length	0.029	0.87	1e-04	0.99
Body mass	0.13	0.72	0.49	0.48
Rel. body mass	0.13	0.72	0.38	0.54
Body condition	0.16	0.69	0.021	0.89
Rel. body cond.	2e-04	0.99	0.053	0.82
Population size	0.042	0.84	0.58	0.45
Population size _{t-1}	2.2	0.14	2.76	0.096
NDVI Iberia	0.046	0.83	0.18	0.67
Temperature	1.36	0.24	0.25	0.61
Precipitation	0.052	0.82	0.24	0.62

Table B: Results of mixed effects models for the ten pied flycatcher males using individual and year as random effects. Df = 1 for all tests.

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Age (juv/ad)	0.31	0.58	0.0051	0.94
Age (years)	0.2	0.66	0.31	0.58
Experience	0.59	0.44	0.22	0.64
Arrival date	0.84	0.36	0.01	0.92
Rel. arrival date	1.61	0.2	0.12	0.73
Colour	0.043	0.84	0.084	0.77
Wing length	1.098	0.29	0.094	0.76
Tarsus length	0.0017	0.97	1e-04	0.99
Body mass	0.062	0.8	0.49	0.48
Rel. body mass	0.074	0.79	0.26	0.61
Body condition	0.053	0.82	0.38	0.54
Rel. body cond.	0.012	0.91	0.021	0.89
Population size	0.027	0.87	0.58	0.45
Population size _{t-1}	1.89	0.17	2.76	0.096
NDVI Iberia	0.59	0.44	0.18	0.67
Temperature	1.026	0.31	0.25	0.61
Precipitation	0.23	0.63	0.3	0.58

Table C: Results of mixed effects models for the ten pied flycatcher males, with several independent variables and using individual as random effects. Df = 1 for all tests.

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Age (juv/ad)	0.015	0.9	0.0059	0.94
Arrival date	0.94	0.33	0.0087	0.93
Age (juv/ad)	0.0014	0.97	0.0003	0.99
Tarsus	0.025	0.88	0.0017	0.97
Age (juv/ad)	0.0088	0.93	0.0056	0.94
Body condition	0.15	0.7	0.35	0.55
Age (juv/ad)	0.22	0.64	0.1	0.75
Temperature	1.54	0.22	0.34	0.56
Age (juv/ad)	0.0092	0.92	0.022	0.38
Precipitation	0.054	0.82	0.25	0.62
Age (years)	0.42	0.52	0.31	0.58
Arrival date	1.099	0.29	0.029	0.86
Age (years)	0.25	0.62	0.33	0.56
Tarsus	0.027	0.87	0.0	0.99
Age (years)	0.21	0.65	0.41	0.52
Body condition	0.11	0.74	0.44	0.51
Age (years)	0.017	0.9	0.45	0.5
Temperature	1.11	0.29	0.48	0.49
Age (years)	0.38	0.54	0.62	0.43
Precipitation	0.21	0.65	0.64	0.43
Colour	0.013	0.91	0.084	0.77
Arrival date	0.2	0.66	0.0072	0.93
Colour	0.02	0.89	0.011	0.92
Tarsus	0.044	0.83	0.0001	0.99
Colour	0.18	0.77	0.11	0.74
Body condition	0.54	0.63	0.45	0.5
Colour	0.089	0.77	0.0005	0.98
Age (years)	0.23	0.63	0.18	0.67
Arrival date	0.77	0.38	0.0	0.99
Tarsus	0.018	0.89	0.0012	0.97
Arrival date	0.85	0.36	0.0009	0.98
Body condition	0.21	0.65	0.35	0.55
Arrival date	0.79	0.37	0.0001	0.99
Rel. body cond.	0.0034	0.95	0.023	0.88
Arrival date	2.76	0.097	0.29	0.59
Population size _{t-1}	4.047	0.044	2.94	0.087
Arrival date	1.12	0.29	0.011	0.92
NDVI Iberia	0.15	0.69	0.14	0.7
Arrival date	1.11	0.29	0.027	0.87
Temperature	1.41	0.24	0.24	0.62
Arrival date	1.013	0.31	0.031	0.86
Precipitation	0.05	0.82	0.23	0.63

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Rel. arrival date	1.56	0.21	0.21	0.65
Tarsus	0.02	0.89	0.0014	0.97
Rel. arrival date	1.65	0.2	0.23	0.63
Body condition	0.22	0.64	0.37	0.55
Rel. arrival date	1.56	0.21	0.22	0.64
Rel. body cond.	0.0001	0.99	0.025	0.87
Rel. arrival date	3.28	0.07	0.56	0.45
Population size _{t-1}	3.64	0.057	3.14	0.076
Rel. arrival date	2.036	0.15	0.049	0.83
NDVI Iberia	0.041	0.84	0.16	0.69
Rel. arrival date	2.22	0.14	0.059	0.81
Temperature	1.49	0.22	0.26	0.61
Rel. arrival date	1.99	0.16	0.11	0.75
Precipitation	0.0004	0.98	0.29	0.59
Body mass	0.11	0.74	0.35	0.62
NDVI Iberia	0.0006	0.98	0.25	0.61
Body mass	0.1	0.75	0.35	0.56
Temperature	1.15	0.28	0.25	0.6
Body mass	0.11	0.74	0.48	0.49
Precipitation	0.0023	0.96	0.21	0.65
Body condition	0.15	0.7	0.1	0.75
NDVI Iberia	0.0007	0.98	0.2	0.65
Body condition	0.081	0.78	0.18	0.67
Temperature	1.098	0.3	0.23	0.63
Body condition	0.15	0.7	0.39	0.53
Precipitation	0.0	0.99	0.25	0.61
NDVI Iberia	0.056	0.81	0.047	0.83
Population size _{t-1}	2.23	0.14	4.17	0.041
Body condition	0.32	0.57	0.72	0.4
Population size _{t-1}	2.42	0.12	3.39	0.066
Rel. body cond.	0.029	0.87	0.0088	0.93
Population size _{t-1}	1.95	0.16	2.93	0.087
Age (year)	0.32	0.57	0.39	0.53
Arrival date	0.94	0.33	0.0015	0.97
Body condition	0.14	0.71	0.4	0.53
Age (year)	0.84	0.36	0.14	0.71
Arrival date	3.2	0.074	0.21	0.64
Population size _{t-1}	4.4	0.036	2.66	0.1
Age(year)	0.07	0.79	0.46	0.5
Arrival date	1.12	0.29	0.052	0.82
Temperature	1.069	0.3	0.47	0.49
Age (year)	0.57	0.45	0.63	0.43
Arrival date	1.18	0.28	0.071	0.79
Precipitation	0.26	0.61	0.63	0.43
Rel. arrival date	3.0	0.083	0.94	0.33
Rel. body cond.	0.082	0.96	0.011	0.92
Population size _{t-1}	3.4	0.066	3.59	0.058

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Rel. arrival date	1.74	0.19	0.15	0.7
Rel. body cond.	0.0011	0.97	0.033	0.86
NDVI. Iberia	0.02	0.23	0.37	0.54
Rel. arrival date	1.87	0.17	0.15	0.7
Rel. body cond.	0.087	0.77	0.093	0.86
Temperature	1.47	0.23	0.37	0.54
Rel. arrival date	1.72	0.19	0.17	0.68
Rel. body cond.	0.0006	0.98	0.023	0.88
Precipitation	0.0039	0.98	0.15	0.7
Age (year)	0.22	0.64	0.45	0.5
Body condition	0.24	0.62	0.78	0.38
Population size _{t-1}	2.35	0.13	3.32	0.069
Age (year)	0.02	0.89	0.53	0.46
Body condition	0.067	0.8	0.24	0.63
Temperature	0.91	0.34	0.45	0.5
Age (year)	0.22	0.64	0.96	0.33
Body condition	0.044	0.83	0.83	0.36
Precipitation	0.049	0.82	0.91	0.34
Age (juv/ad)	0.0008	0.98	0.005	0.94
Body condition	0.19	0.67	0.32	0.57
Arrival date	0.83	0.36	0.0013	0.97
Age (juv/ad)	0.068	0.79	0.045	0.83
NDVI Iberia	0.044	0.83	0.035	0.85
Population size _{t-1}	2.21	0.14	4.041	0.044
Age (juv/ad)	0.025	0.88	0.0001	0.99
Rel. body mass	0.24	0.62	0.29	0.59
Rel. arrival date	1.72	0.19	0.27	0.6
Age (juv/ad)	0.19	0.66	0.037	0.85
Arrival date	2.82	0.093	0.31	0.58
Population size _{t-1}	4.09	0.043	2.86	0.091
Exp	0.82	0.36	0.24	0.63
Body condition	0.13	0.72	0.28	0.6
Arrival date	1.076	0.3	0.011	0.92
Exp	0.61	0.43	0.21	0.65
NDVI Iberia	0.0021	0.96	0.0099	0.92
Population size _{t-1}	1.91	0.17	3.76	0.052
Exp	1.14	0.29	0.31	0.58
Rel. body mass	0.14	0.71	0.21	0.65
Rel. arrival date	2.23	0.13	0.39	0.53

Table D: Results of mixed effects models for the ten pied flycatcher males, with several independent variables and using individual and year as random effects. Df= 1 for all tests.

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Age (juv/ad)	0.081	0.78	0.0059	0.94
Arrival date	0.71	0.4	0.0087	0.93
Age (juv/ad)	0.16	0.69	0.0001	0.99
Tarsus	0.0	0.99	0.0018	0.97
Age (juv/ad)	0.18	0.67	0.006	0.94
Body condition	0.039	0.84	0.35	0.55
Age (juv/ad)	0.92	0.34	0.12	0.73
Temperature	1.25	0.26	0.37	0.54
Age (juv/ad)	0.9	0.34	0.065	0.8
Precipitation	0.32	0.57	0.35	0.55
Age (years)	0.42	0.52	0.31	0.58
Arrival date	1.02	0.31	0.029	0.86
Age (years)	0.22	0.64	0.35	0.55
Tarsus	0.0019	0.96	0.0004	0.98
Age (years)	0.19	0.66	0.43	0.51
Body condition	0.019	0.89	0.42	0.52
Age (years)	0.039	0.84	0.45	0.5
Temperature	0.84	0.36	0.49	0.48
Age (years)	0.013	0.91	0.71	0.4
Precipitation	0.18	0.67	0.8	0.37
Colour	0.0021	0.96	0.084	0.77
Arrival date	0.13	0.72	0.0072	0.93
Colour	0.047	0.83	0.011	0.92
Tarsus	0.0068	0.93	0.001	0.99
Colour	0.19	0.67	0.11	0.74
Body condition	0.4	0.53	0.45	0.5
Colour	0.23	0.63	0.0005	0.98
Age (years)	0.26	0.61	0.18	0.67
Arrival date	0.76	0.38	0.0	0.99
Tarsus	0.0001	0.99	0.0012	0.97
Arrival date	0.82	0.37	0.0009	0.98
Body condition	0.096	0.76	0.35	0.55
Arrival date	0.76	0.38	0.0001	0.99
Rel. body cond.	0.017	0.9	0.023	0.88
Arrival date	2.54	0.11	0.29	0.59
Population size _{t-1}	3.71	0.054	2.94	0.087
Arrival date	0.57	0.45	0.011	0.92
NDVI Iberia	0.32	0.57	0.14	0.7
Arrival date	1.14	0.29	0.027	0.87
Temperature	1.26	0.26	0.24	0.62
Arrival date	0.78	0.38	0.037	0.85
Precipitation	0.2	0.65	0.29	0.59

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Rel. arrival date	1.48	0.22	0.21	0.65
Tarsus	0.0033	0.95	0.0014	0.97
Rel. arrival date	1.58	0.21	0.23	0.63
Body condition	0.16	0.69	0.37	0.55
Rel. arrival date	1.45	0.23	0.22	0.64
Rel. body cond.	0.0026	0.96	0.025	0.87
Rel. arrival date	3.028	0.082	0.56	0.45
Population size _{t-1}	3.41	0.065	3.14	0.076
Rel. arrival date	1.28	0.26	0.049	0.83
NDVI Iberia	0.3	0.58	0.16	0.69
Rel. arrival date	1.97	0.16	0.059	0.81
Temperature	1.34	0.25	0.26	0.61
Rel. arrival date	1.55	0.21	0.085	0.77
Precipitation	0.26	0.61	0.33	0.57
Body mass	0.06	0.81	0.25	0.62
NDVI Iberia	0.48	0.5	0.2	0.65
Body mass	0.05	0.82	0.34	0.56
Temperature	0.99	0.32	0.25	0.61
Body mass	0.033	0.86	0.42	0.52
Precipitation	0.17	0.68	0.25	0.62
Body condition	0.051	0.82	0.1	0.75
NDVI Iberia	0.49	0.49	0.18	0.67
Body condition	0.017	0.9	0.17	0.68
Temperature	0.94	0.33	0.24	0.63
Body condition	0.02	0.89	0.34	0.56
Precipitation	0.18	0.67	0.3	0.59
NDVI Iberia	0.91	0.3	0.047	0.83
Population size _{t-1}	2.13	0.14	4.17	0.041
Body condition	0.25	0.62	0.72	0.4
Population size _{t-1}	2.3	0.13	3.39	0.066
Rel. body cond.	0.0	0.99	0.088	0.93
Population size _{t-1}	1.75	0.19	2.93	0.087
Age (year)	0.35	0.56	0.41	0.52
Arrival date	0.94	0.33	0.0027	0.96
Body condition	0.034	0.85	0.38	0.54
Age (year)	0.76	0.38	0.14	0.71
Arrival date	3.01	0.083	0.21	0.64
Population size _{t-1}	4.025	0.045	2.66	0.1
Age(year)	0.15	0.7	0.46	0.5
Arrival date	1.22	0.27	0.056	0.81
Temperature	1.015	0.31	0.48	0.49
Age (year)	0.15	0.7	0.77	0.38
Arrival date	0.88	0.35	0.11	0.74
Precipitation	0.091	0.76	0.82	0.37
Rel. arrival date	2.89	0.089	0.94	0.33
Rel. body cond.	0.047	0.83	0.011	0.92
Population size _{t-1}	3.27	0.07	3.59	0.058

Independent variable	Song repertoire		Song versatility	
	χ^2	p	χ^2	p
Rel. arrival date	0.15	0.7	0.15	0.7
Rel. body cond.	0.033	0.86	0.033	0.86
NDVI. Iberia	0.37	0.54	0.36	0.55
Rel. arrival date	1.78	0.18	0.14	0.71
Rel. body cond.	0.092	0.76	0.085	0.77
Temperature	1.36	0.24	0.34	0.56
Rel. arrival date	1.47	0.23	0.14	0.7
Rel. body cond.	0.025	0.87	0.018	0.89
Precipitation	0.2	0.65	0.21	0.65
Age (year)	0.19	0.67	0.45	0.5
Body condition	0.15	0.7	0.78	0.38
Population size _{t-1}	2.15	0.14	3.32	0.069
Age (year)	0.039	0.84	0.57	0.45
Body condition	0.0054	0.94	0.22	0.64
Temperature	0.76	0.38	0.46	0.5
Age (year)	0.028	0.87	1.023	0.31
Body condition	0.013	0.91	0.68	0.41
Precipitation	0.11	0.74	0.95	0.33
Age (juv/ad)	0.054	0.82	0.0055	0.94
Body condition	0.071	0.79	0.32	0.57
Arrival date	0.73	0.39	0.0013	0.97
Age (juv/ad)	0.76	0.38	0.045	0.83
NDVI Iberia	1.065	0.3	0.035	0.85
Population size _{t-1}	1.65	0.2	4.04	0.044
Age (juv/ad)	0.0017	0.97	0.0001	0.99
Rel. body mass	0.21	0.64	0.29	0.59
Rel. arrival date	1.55	0.21	0.27	0.6
Age (juv/ad)	0.11	0.74	0.037	0.85
Arrival date	2.63	0.1	0.31	0.58
Population size _{t-1}	3.79	0.052	2.86	0.091
Exp	0.76	0.38	0.24	0.63
Body condition	0.095	0.76	0.28	0.6
Arrival date	1.073	0.3	0.011	0.92
Exp	0.38	0.54	0.21	0.65
NDVI Iberia	1.15	0.28	0.0099	0.92
Population size _{t-1}	2.06	0.15	3.76	0.052
Exp	1.14	0.29	0.31	0.58
Rel. body mass	0.14	0.71	0.21	0.65
Rel. arrival date	2.23	0.13	0.39	0.53

Table E: Results of mixed effects models for the male pied flycatchers with song repertoire as dependent variable, individual and year as random effects, and the interaction of arrival date and age as independent variable. Df = 1 for all tests

Data set	Independent variables	χ^2	p
All males	Age (juv/ad)	0.016	0.9
	Arrival date	1.08	0.3
	Age (juv/ad):arrival date	6.051	0.014
Without outlier juveniles	Age (juv/ad)	2.24	0.13
	Arrival date	0.14	0.71
	Age (juv/ad):arrival date	0.49	0.48
Without two outlier juvenile individuals	Age (juv/ad)	1.87	0.17
	Arrival date	0.012	0.91
	Age (juv/ad):arrival date	0.22	0.64
All males	Age (years)	0.45	0.5
	Arrival date	1.13	0.29
	Age (year):arrival date	3.87	0.049
Without outlier juveniles	Age (years)	0.0088	0.93
	Arrival date	0.39	0.53
	Age (year):arrival date	1.87	0.17
Without the two outlier juvenile individuals	Age (years)	0.18	0.67
	Arrival date	0.08	0.78
	Age (year):arrival date	0.76	0.38

Table F: Results of mixed effects models for delayed maturation in the ten male pied flycatchers using age in years as independent variable and individual as random effect.

Dependent variable	χ^2	p
Plumage colour	10.78	0.001
Tarsus length	1.13	0.29
Body condition	0.088	0.77
Wing length	5.72	0.017
Arrival date	0.015	0.9
Song repertoire	0.0038	0.95
Song repertoire (without juvenile outlier individuals)	0,86	0,35

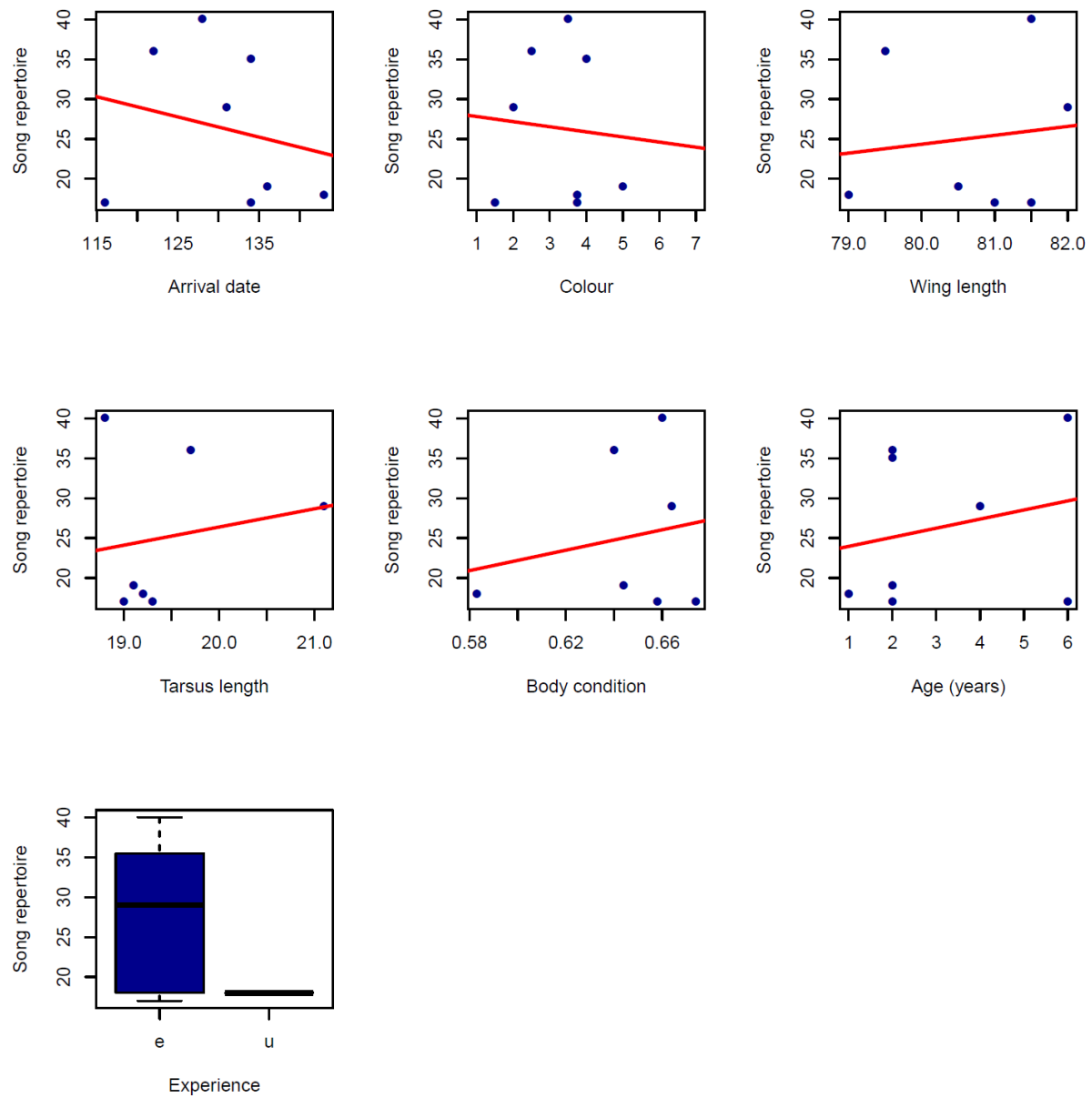


Figure A: Plots of pied flycatcher song repertoire with different variables using only data from 2007 where eight males were recorded.