

**SONG RESPONSE TO MALE INTRUDERS AND PROSPECTING  
FEMALES IN THE PIED FLYCATCHER, *FICEDULA HYPOLEUCA***

By

Jayne Lambrou

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## ABSTRACT

Singing in the pied flycatcher, *Ficedula hypoleuca*, was examined in both intra- and intersexual contexts. Song responses to male intruders and prospecting females were investigated by introducing caged conspecific birds into the subjects' territory and recording song immediately prior and after treatment. Syllable repertoire, two measures of strophe diversity, strophe length and syllable switching were analysed using sonograms of the song. Pied flycatchers reduced their repertoire size and tended to increase their syllable switching and shorten their strophe length in response to intruding males. They did not significantly alter their song after encountering a female. Older males switched syllables at a higher rate after a female encounter than did juvenile males. Plumage traits were not correlated to song responses to males or to females. Pied flycatchers did not respond differentially to male intruders and prospecting females when responses to the two sexes were compared. The importance of these findings in relation to the dual function hypothesis of birdsong is discussed.

## 1. INTRODUCTION

Birdsong is often a complex and elaborate signal form that is generally agreed to serve two principle functions (Catchpole & Slater 2008): i) attracting females and stimulating them to mate (intersexual function) and ii) territorial defence (intrasexual function) (Slabbekoorn & Marler 2004). The two are referred to collectively as the ‘dual function’ theory. Whilst signals that have evolved to attract females through sexual selection may be expected to indicate aspects of male quality (for example, nutritional status, territory quality, age), those evolved to deter male competitors may convey location, fighting ability or willingness to escalate (Vehrencamp 2000). It may thus be adaptive to signal differentially to potential mates and male rivals (Collins 2004).

Numerous studies substantiate the occurrence of such differential signalling in passerine birds. Taken together, these suggest that song may vary with inter- or intrasexual function in three principle ways. Firstly, specific song parts such as trills, ‘snarrrs’ and whistles may be associated with particular functions (Rehsteiner *et al.* 1998; Riebel & Slater 1998; Collins 2004; Cramp & Brooks 1992; Naguib *et al.* 2002; Ballentine *et al.* 2004; Dunn & Zann 1996). Secondly, a species may have one or numerous song ‘types’ or ‘modes’ which may be used differentially in certain contexts. This is documented for several species of New World wood warbler (Spector 1991; Beebee 2002; Kroodsma 1988; Kroodsma *et al.* 1984; Kroodsma *et al.* 1989; Wiley *et al.* 1994) as well as an Old World warbler (Catchpole & Leisler 1996), and other passeriforms (Sossinka & Böhner 1980; Nelson & Croner 1991). Lastly, specific characteristics of complex song such as repertoire size or song type switching rate may be used to communicate differentially in certain contexts (Vehrencamp 2000). It is this latter category that this study is focused on.

Song in the pied flycatcher (*Ficedula hypoleuca*) appears to be congruent with the intersexual theory of function of birdsong. Male pied flycatchers cease (or dramatically reduce) singing after mating, with the exception of polygynous individuals seeking second mates (Espmark & Lampe 1993; Lundberg & Alatalo 1992). Higher singing rates (Alatalo *et al.* 1990; Gottlander 1987) and larger repertoire sizes (Lampe & Saetre 1995; Lampe & Espmark 2003) are preferred by female pied flycatchers. However, larger repertoire sizes have also been documented in higher population densities, perhaps indicating a function in intrasexual competition (Lundberg & Alatalo 1992).

The significance of these traits in both intra- and intersexual contexts may be partly due to correlation with male quality in some of them. If such features have associated costs, they may be termed ‘honest signals’ in accordance with Zahavi’s handicap principle (Zahavi & Zahavi 1999) and be sexually selected.

### *1.1 Study species*

Pied flycatchers are intensely studied, small insectivorous passerines (Lundberg & Alatalo 1992). They are migratory, breeding in most of Europe and western Asia and wintering mainly in tropical West Africa. They have a short breeding season and a more constrained time window in which to attract a mate through singing, compared to non-migratory species (Lundberg & Alatalo 1992; Both *et al.* 2006). Females generally arrive at breeding grounds a week or so later than males, though there is some overlap between the sexes (Gottlander 1987).

They are sexually dimorphic in various traits including song (only males sing), size (males are larger) and plumage colour, with the darker plumage in males being more pronounced than in the brownish females (Lundberg *et al.* 1981). Males also have a small

white forehead patch that is absent in females (an exception of this is documented for a Spanish population, Potti 1993). This trait is not sexually selected in Norwegian populations and has been shown to be unimportant in intrasexual competition and unrepresentative of male quality (Dale *et al.* 1999). Males also have larger white wing patches than females (Lundberg & Alatalo 1992).

Plumage colour appears to be particularly important in this species, with darker males typically being more experienced, arriving earlier and defending more nestboxes than brown males (Slagsvold & Lifjeld 1988), and singing more complex songs (Lampe & Espmark 1994). Darker males behave aggressively toward other darkly coloured males but display sexually toward lighter, more female-like males (Saetre 1993; Slagsvold & Saetre 1991).

Pied flycatchers nest in tree holes vacated by woodpeckers or left by fallen branches, but will readily adapt to nestboxes, making them easy to attract to study sites. In natural habitats, nests are usually patchily distributed (Alatalo *et al.* 1982).

They are assumed to be open-ended learners that do not have set song-types (Espmark & Lampe 1993), but recombine syllables in novel ways (Lundberg & Alatalo 1992). Older and more experienced males have more complex song with larger repertoires and higher versatility (Lampe & Espmark 1994). Males sing conspicuously and frequently soon after their arrival at the breeding grounds (Gottlander 1987).

## *1.2 Hypotheses and predictions*

This study addresses the question of whether the song of the pied flycatcher is consistent with the dual function theory by assessing differences in song between inter- and intrasexual contexts.

Song production does not appear to be metabolically costly in relation to the overall daily energy budget in pied flycatchers (Ward *et al.* 2004). With this in mind, along with the

constrained time window males have in which to find a mate, it may be expected that they sing at peak capacity in the pre-pairing period shortly after arriving at breeding grounds. With this assumption, it may be predicted that singing does not change from this maximum state after a conspecific female is encountered. It is thus hypothesized that there will be no significant difference in the song of pied flycatchers before and after encountering a conspecific female.

With the assumption that pied flycatcher song serves a dual function, it is predicted that singing will alter after an encounter with a male intruder. Syllable switching at an increased rate, for example, is considered a conventional aggressive signal in contexts of male-male competition (Vehrencamp 2000). A tendency for song to reduce in length and diversity in intrasexual contexts is documented in many species (e.g. Galeotti *et al.* 1997; Searcy *et al.* 2000) along with an increase in song rate (e.g. Todt & Naguib 2000). Furthermore, it may be possible that, subsequent to encountering an intruder males may alter their song because of the perceived threat of eavesdropping (e.g. Amy & Leboucher 2009). It is therefore hypothesized that i) song length and diversity will reduce after a male encounter ii) syllable switching rate will increase after a male encounter, and iii) song responses to males and those to females will differ from each other.

With consideration of the apparent significance of plumage colour in this species, it is predicted that song responses to male intruders may be correlated with darkness of plumage of the subject. It is hypothesized that darker males will respond to conspecific males with higher syllable switching, a song trait traditionally associated with male aggression, than browner males.

It is also predicted that older and more experienced males will have larger song repertoires and versatility in their responses than younger, inexperienced males.

## 2. MATERIALS AND METHODS

### *2.1 Study site and subjects*

The study was conducted at an established field site at Sinober (59°59'N, 10°38'E) in Sørkedalen near Oslo, Norway. The site consists of mixed coniferous-deciduous woodland provided with approximately 300 nestboxes. On the onset of the breeding season, from the last week of April 2008, the site was monitored daily for new arrivals of pied flycatchers and males were trapped in the nestboxes. They were assigned an age-class: 'adult' (two years old or more) or 'juvenile' (up to one year), based on the amount of white/wear on the tip of the outermost greater wing coverts (after Lundberg & Alatalo 1992). If not already banded in previous years, the birds were fitted with coloured bands fixed in individually unique combinations and numbered aluminium rings to allow individual identification. This was further aided by applying distinctive red markings on the plumage of captured males using a felt pen. Plumage colour was graded for darkness on a scale from 1-7, darkest to lightest (after Drost 1936) and forehead patch height was measured in mm. Biometric data such as body mass and tarsus length was recorded before releasing the birds. A total of 17 of the resident males were used in the subsequent trials.

### *2.2 Trial procedure*

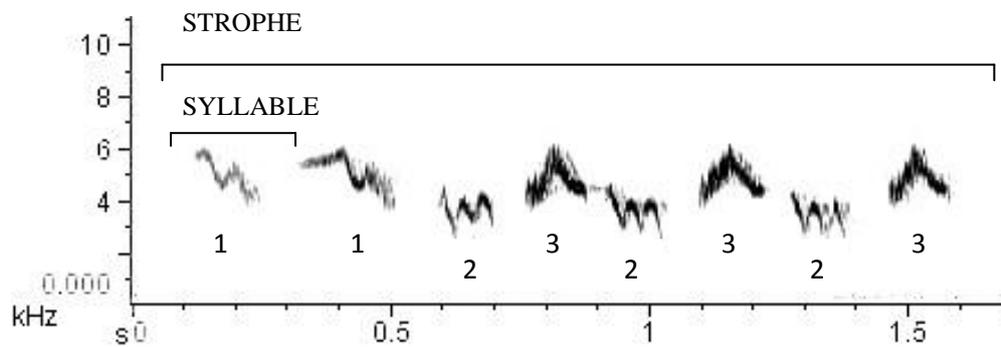
Experiments were conducted prior to pairing and after each male began singing consistently at a nestbox during the period 3–23 May 2008. Females (n=6) were caught in different areas of the study site from focal birds. Male 'intruders' (n=3) were caught at another site approximately 8 km away (Dæli) (Slagsvold 2004), controlling for possible confounding effects that may arise from a subject being presented with a familiar or

neighbouring bird. Treatment males were all adult and of similar colouration (2.5 – 3 on the Drost scale).

For control, each subject's song was digitally recorded (Sound Devices 702, Telinga Pro 6 microphone and headphones) for 25 consecutive strophes (defined below) prior to treatment. Immediately following the control recording, and whilst the focal bird was still in the vicinity, a conspecific male/female was presented in a small wire cage, representing either a male intruder (11 trials) or a prospecting female (15 trials). The cage was set down on the ground 1-2m from the base of the tree housing the relevant nestbox, which was facing the caged bird. The cover of the cage was removed and the observer withdrew to a location from which the focal bird could be observed without obstruction (a distance of 15-40 m depending on local vegetation). After a five-minute period, the treatment bird was covered and removed. As soon as the focal bird resumed singing, it was similarly recorded for the following 25 consecutive strophes. Trials were conducted between 08.00 and 13.00 hrs. Male and female trials on the same subject (n=9) were performed on different days and in random order. Experiments were not conducted in heavy rainfall or in windy conditions.

### 2.3 Song analysis

Song analysis was based on sonograms produced from the digital recordings using bioacoustics software (Raven Pro 1.4, Cornell Laboratory of Bioacoustics) applying a sample rate of 44100 Hz, DFT (discrete Fourier transform) size 256 and a sonogram overlap of 50%. The sonograms were broken down into 'strophes', which are comprised of 'syllables' (Figure 1). Syllables are defined as continuous elements separated from other syllables by more than 0.02 s and less than 1 s. Strophes are comprised of a series of syllables separated by more than 1 s (Eriksen *et al.* 2009; Espmark & Lampe 1993). Each different syllable type was identified and assigned a number (Figure 1).



**Figure 1:** Sonogram of a strophe of pied flycatcher song illustrating eight syllables and three different syllable types

Five variables were then determined for each 25-strophe sample: i) strophe length (s) ii) strophe diversity iii) repertoire size iv) strophe sample diversity and v) syllable switching (Table 1).

**Table 1:** Definitions of the five variables of pied flycatcher song used in the analyses

i)	STROPHE LENGTH	Measured (s) from the start of the first syllable in a strophe to the end of the last syllable
ii)	STROPHE DIVERSITY	Mean of the number of different syllable types per strophe/total number of syllables per strophe
iii)	REPERTOIRE SIZE	Number of different syllable types in 25 consecutive strophes
iv)	STROPHE SAMPLE DIVERSITY	Repertoire size/ the sum of syllables sung
v)	SYLLABLE SWITCHING RATE	Count of consecutive songs that have no syllables in common

#### 2.4 Ethical note

The study was performed under license from the Directorate for Nature Management and the National Animal Research Authority in Norway.

## *2.5 Statistical analyses*

Kolmogorov-Smirnov and Anderson-Darling normality tests determined that data were not normally distributed and only non-parametric statistics were used. Wilcoxon's signed ranks test was used to test for differences in control and response values for the male and female trials separately for the five song variables. This test was also used for comparison of male vs. female trials, both by evaluating the changes in song (subtracting the control values from the responses) and by testing the differences of responses to a male vs. those to a female, for those subjects on which both trials were conducted (n=9). For one bird only 22 strophes were recorded in the male trial, therefore the same number of strophes from the female trial of this individual was used in those analyses where both male and female trials were considered.

Spearman's rank test was used to determine any correlations between the five song variables and i) size of forehead patch and ii) colour grade of the focal bird, for both the male and female trials.

Differences between the song responses of older males and juvenile, inexperienced males were determined using the Mann-Whitney U test.

To control for possible confounding effects of repeat trials, the Mann-Whitney U test was used to compare the responses of subjects that were tested once to those that were tested for a second time. Whilst efforts were made to choose similar male birds to simulate intruders, in terms of plumage and age class, the Kruskal-Wallis test was used to test for differences in responses to the three different birds for all five song variables.

All tests were two-tailed with a significance level of 0.05. Statistical analyses were performed on SPSS statistical software (Release 16.0.1, SPSS Inc. 2007).

### 3. RESULTS

#### 3.1 Response to simulated prospecting females

The singing of males in response to caged females ( $n=15$ ) was not significantly different from the controls for any of the five song variables measured (Table 2A). None of the song variables were correlated with either the colour grade or size of forehead patch of the focal bird. All of the variables had weakly negative  $r_s$ -values when tested with colour (Table 3A). Older males switched syllables at a significantly higher rate in response to a female than did juveniles (Mann-Whitney U:  $n_1=8$ ,  $n_2=5$ ,  $Z=-2.04$ ,  $P=0.042$ ). The other four variables did not significantly change (Mann-Whitney U,  $n_1=8$ ,  $n_2=5$ , NS).

**Table 2.** Mean $\pm$ standard deviation (SD) and Wilcoxon signed ranks  $Z$  and  $P$ -values for five variables of pied flycatcher song, before and after being presented with a caged female (A,  $n=15$ ) and a caged male (B,  $n=11$ ).  $P$ -values stated in bold text are significant, also after sequential Bonferroni correction.

Table 2A: Response to female

Table 2B: Response to male

	Control (mean $\pm$ SD)	Response (mean $\pm$ SD)	$Z$	$P$		Control (mean $\pm$ SD)	Response (mean $\pm$ SD)	$Z$	$P$
<b>Repertoire Size:</b>	27.80 $\pm$ 10.96	26.47 $\pm$ 17.04	-1.00	0.32		27.36 $\pm$ 11.79	17.18 $\pm$ 7.21	-2.94	<b>0.003</b>
<b>Strophe Diversity:</b>	0.50 $\pm$ 0.12	0.48 $\pm$ 0.14	-1.04	0.30		0.48 $\pm$ 0.09	0.47 $\pm$ 0.09	-0.72	0.48
<b>Strophe Sample Diversity:</b>	0.11 $\pm$ 0.04	0.10 $\pm$ 0.06	-1.02	0.31		0.11 $\pm$ 0.04	0.08 $\pm$ 0.03	-2.94	<b>0.003</b>
<b>Strophe Length:</b>	2.13 $\pm$ 0.34	2.06 $\pm$ 0.63	-1.42	0.16		2.09 $\pm$ 0.40	1.87 $\pm$ 0.24	-1.74	0.083
<b>Syllable Switching Rate:</b>	5.53 $\pm$ 5.04	4.87 $\pm$ 3.89	-0.77	0.44		6.18 $\pm$ 5.04	7.45 $\pm$ 5.30	-1.90	0.057

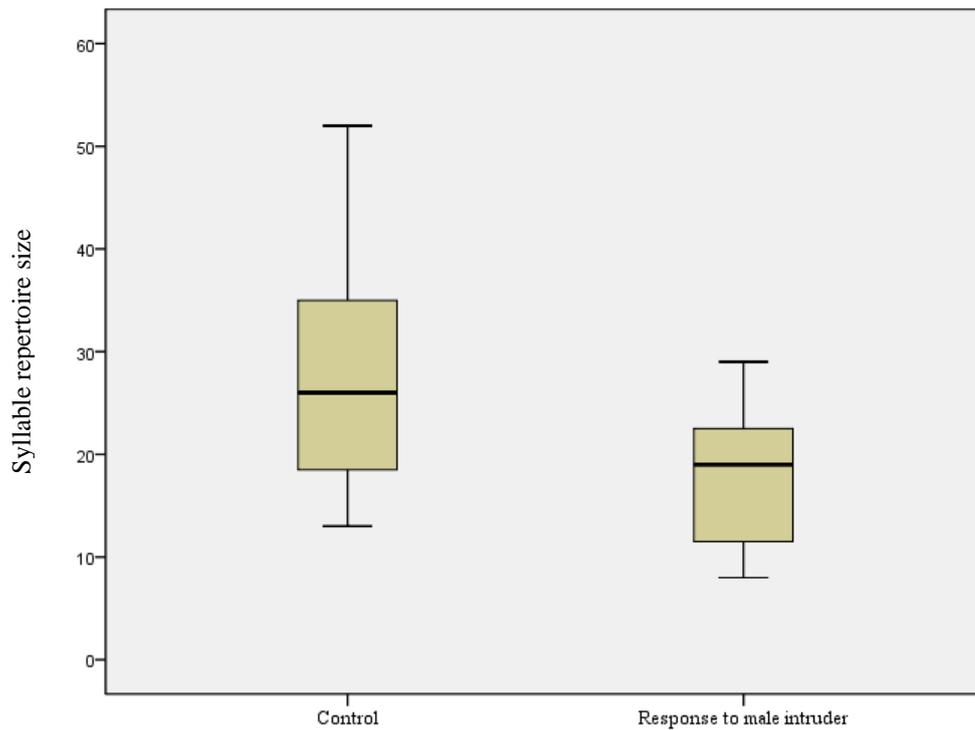
### 3.2 Response to simulated male intruders

Several variables of male song changed in response to a simulated male intruder (Table 2B). Focal birds ( $n=11$ ) significantly decreased their syllable repertoire size (Figure 2) and their strophe sample diversity (Figure 3) in response to a caged male. Syllable switching tended to increase, though this was not significant (Figure 4). Strophe length was highly variable between males (Table 2B) and tended to shorten after a male encounter, though this was not significant. Strophe diversity did not change significantly. The response values for the five song variables were not significantly correlated with the size of the forehead patch or the strength of colour of the focal male (Table 3B). All of the variables had negative  $r_s$ -values when tested with colour, indicating a general trend for song responses to a caged intruder to increase with plumage colour. Positive  $r_s$ -values were generated for all variables when tested with size of forehead patch. Age of focal male had no effect (Mann-Whitney U,  $n_1=8$ ,  $n_2=3$ , NS).

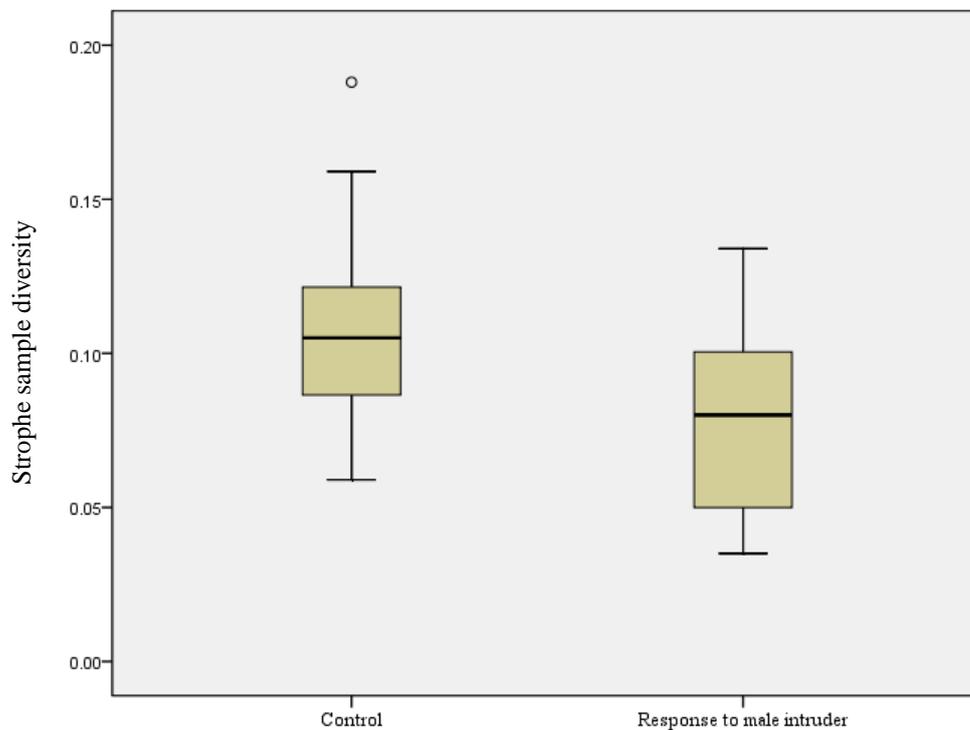
**Table 3.**  $r_s$ -values for Spearman's rank tests of correlation of two plumage traits of male pied flycatchers with five variables of song responses to a conspecific female (A,  $n=15$ ) and male (B,  $n=11$ ). All  $P$ -values were non-significant.

	Plumage colour of focal male		Size of forehead patch of focal male	
	(A)	(B)	(A)	(B)
<b>Repertoire size</b>	-0.21	-0.33	-0.06	0.29
<b>Strophe diversity</b>	-0.19	-0.15	0.02	0.55*
<b>Strophe sample diversity</b>	-0.15	-0.18	-0.12	0.17
<b>Strophe length</b>	-0.11	-0.44	0.09	0.10
<b>Syllable switching rate</b>	-0.13	-0.28	-0.11	0.31

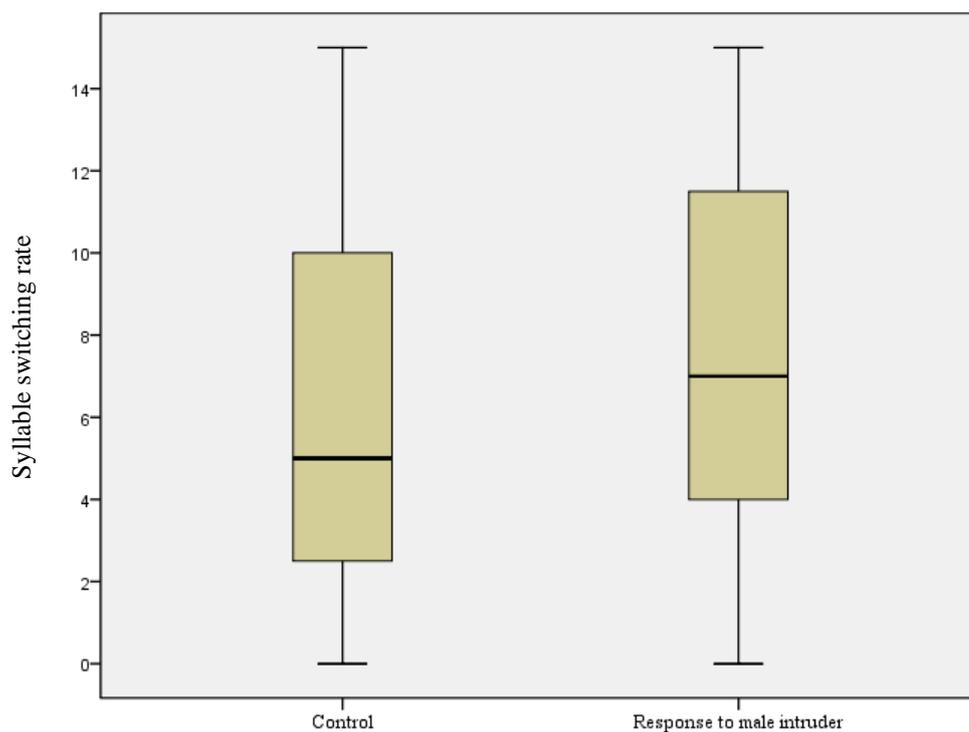
(\* $P=0.077$ )



**Figure 2.** Median number of different syllables in a 25-strophe sample of male pied flycatcher song before and after presentation of a conspecific male intruder



**Figure 3.** Strophe sample diversity (syllable repertoire size/total number of syllables sung) in a 25-strophe sample of pied flycatcher song, before and after being presented with a conspecific male intruder. The circle represents an outlier.



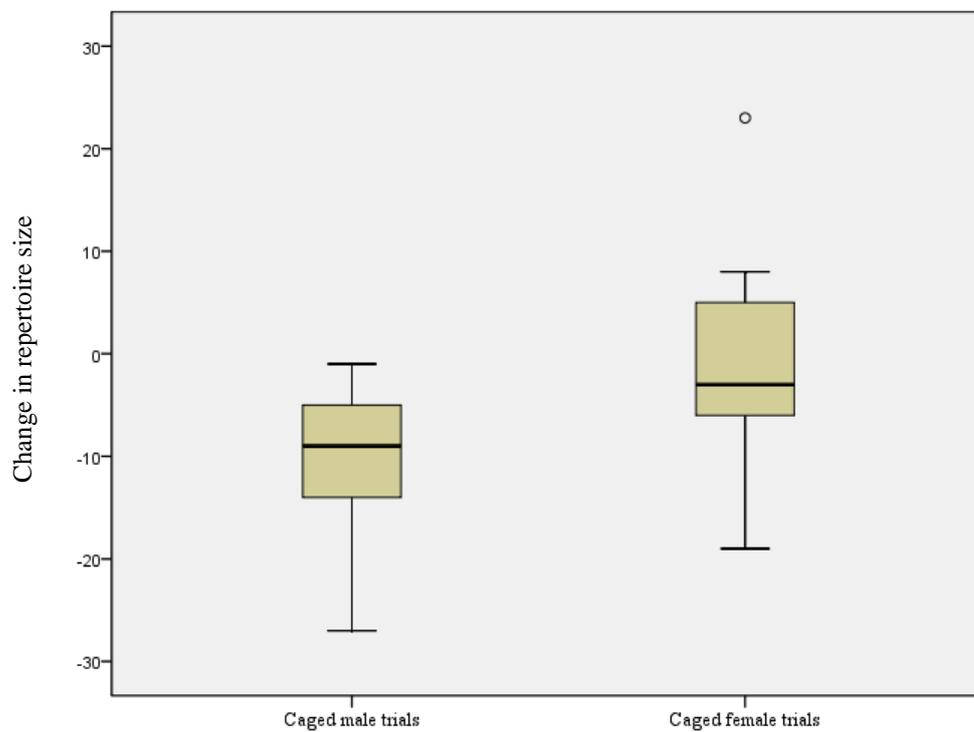
**Figure 4.** Median number of switches of all syllables in consecutive strophes in a 25-strophe sample of pied flycatcher song, before and after being presented with a conspecific male intruder

### 3.3 Response to caged males vs. response to caged females

For the males on which both a male and female trial was performed ( $n=9$ ), there were no significant differences between the responses to caged females and those to caged males (Table 4A). The change in song (response - control) was notably higher for repertoire size in the female trials, though the difference was not significant (Table 4B, Figure 5). This measurement did not differ between male and female trials for the other four song variables.

**Table 4.** Wilcoxon signed ranks *Z* and *P*-values for: (A) The song responses of pied flycatchers (n=9) to a caged a male vs. those to a caged female and (B) The change in song (response – control) after a male encounter vs. that after a female encounter (n=9).

	(A)		(B)	
	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
<b>Repertoire size:</b>	-1.78	0.075	-1.90	0.058
<b>Strophe Diversity:</b>	-0.42	0.68	-0.53	0.593
<b>Strophe Sample Diversity:</b>	-1.72	0.086	-1.42	0.155
<b>Strophe Length:</b>	-1.48	0.14	-1.07	0.286
<b>Syllable Switching Rate:</b>	-0.65	0.51	-1.01	0.313



**Figure 5.** Response-control values for the number different syllables in a 25-strophe sample of pied flycatcher song: female trials compared to male trials

### *3.4 Effects of repeated trials*

There were no significant differences between the song responses of males that had experienced a previous trial and those that had not, both for the male trials (Mann-Whitney U,  $n_1=7$ ,  $n_2=4$ ,  $P=NS$ ) and the female trials ( $n_1=8$ ,  $n_2=7$ ,  $P=NS$ ). There was no significant difference between males tested once and those that were tested in two trials for the remaining five song variables (Mann-Whitney U:  $n_1=8$ ,  $n_2=7$ ,  $P=NS$ ).

### *3.5 Effects of possible differences in male intruder birds*

There was no significant difference between the responses to the three different caged males for all five song variables (Kruskal-Wallis:  $df=2$ ,  $n_1=2$ ,  $n_2=3$ ,  $n_3=6$ , NS).

#### 4. DISCUSSION & CONCLUSIONS

Pied flycatcher song remained unchanged after a female encounter. This is consistent with the hypothesis that they are already singing at full capacity in the pre-pairing period. Pied flycatchers are migratory birds, and as such the selection pressure to breed (due to less time at breeding grounds) may be stronger than that from competition for other resources such as territory (Catchpole 1982; Read & Weary 1992). This is supported in the singing behaviour of the blackcap, *Sylvia atricapilla*. Migratory populations of this species have longer and more complex female-directed warbles than the shorter and simpler song of sedentary populations (Collins *et al.* 2009). Similar findings are documented for the white-crown sparrow and the sedge wren (Nelson *et al.* 1995; Kroodsma *et al.* 1999a; Kroodsma *et al.* 1999b; Kroodsma *et al.* 2002).

This constrained breeding timeframe may be accentuated in the population in this study due to the abundant provision of nestboxes and the associated higher population density. In 'natural' populations, pied flycatcher nests are patchily distributed and tree holes of good quality may be scant (Lundberg & Alatalo 1992). When nestboxes are provided, the population density may increase greatly. The introduction of nestboxes to a site in Swedish Lapland, for example, led to a 75% increase in the bird density of the area (Enemar & Sjöstrand 1972). Availability of nesting sites in natural populations as a constraint is documented for other non-excavator species (e.g. the collared flycatcher, Gustafsson 1988). Whilst an increase in nesting sites via nestbox provision may reduce the selection pressure for traits associated with territory defence, and perhaps lower male intrusion rates, there may be increased competition for attracting a mate due to the higher population density. This may lead to higher selection pressure for intersexual singing. Previous studies involving the effect of nestbox provision in this species have not, however, indicated any detrimental effects in

terms of reproductive success (e.g. Virolainen 1984; Alatalo & Lundberg 1984). Furthermore, 'natural' nest-hole availability may vary with different habitat and vegetation factors. For example, competition for nest-holes was deemed of minor importance in a study of a primeval forest (Wesolowski 2007), whilst competition may be higher in managed forests (such as the site of this study) where dead trees are removed and natural cavities more scarce (reviewed in Newton 1994).

The higher incidence of syllable switching by adult males in response to females (compared to juveniles' response to females) is perhaps only surprising in that it was not accompanied by a significantly higher repertoire. As older males have larger repertoire sizes (Lampe & Espmark 1994), higher syllable switching in this intersexual context may then have been functioning as an amplifier, to 'show off' the older males repertoire (Vehrencamp 2000). A doubtful explanation for the fact that a higher repertoire size was not seen in older males could be that the juveniles' song was not yet fully crystallized. Plastic song often has higher variation than mature, crystallized song (Slabbekoorn & Marler 2004), and migratory birds may persist in this plastic song phase much longer than non-migratory populations, as demonstrated in the white-crown sparrow (Nelson *et al.* 1995; Nelson *et al.* 1996). This may account for higher repertoire values for the younger birds than may otherwise be expected. This is unlikely, however, as there was only one male that showed indication of this in the sonogram analyses, with variable renditions of syllables and most one-year old males can evidently sing typical pied flycatcher song upon arrival at breeding grounds (Lundberg & Alatalo 1992; pers. obs.).

Pied flycatchers did change their singing in response to a male intruder. They reduced their song repertoire, a finding consistent with our predictions and with previous studies of complex singers (e.g. European robin, Hoelzel 1986). As male pied flycatchers may use the song of other males as a cue when locating nest sites (Alatalo *et al.* 1982) (also seen in other

passerines, e.g. European starlings, Mountjoy & Lemon 1991), this reduction may be an intrasexual anti-eavesdropping strategy.

The significance of the difference in strophe sample diversity in response to an intruder should not be overestimated. This variable is a direct function of repertoire size (repertoire size / sum of syllables sung) and the results for the two variables are therefore highly correlated. Whilst this clear reduction in repertoire is fitting with classic male-male singing behaviour (Slabbekoorn & Marler 2004) and consistent with our hypothesis, the perhaps more reliable indicator of song versatility, strophe diversity, did not change.

The slight increase in syllable switching in response to conspecific males may be interpreted as a conventional signal indicating willingness to escalate and/or fighting ability (Vehrencamp 2000), as fitting with our hypothesis. The lack of statistical significance of this phenomenon may be a function of sample size and a re-investigation using a larger sample may be warranted. This may also be the case for the tendency to sing shorter strophes in response to a caged male. Shorter strophe length may also be more pronounced at this study site if a higher population density is assumed, with the associated increased risks from eavesdropping. Shorter song has been employed as an anti-eavesdropping tactic in other species (e.g. the great tit, Peake *et al.* 2005).

Song traits associated with darker, older males (larger repertoire size, higher diversity) are quite different to those traditionally related with intrasexual male singing behaviour (such as more repetitive and less versatile song, Collins 2004). This may have 'cancelled out' any correlation between plumage traits and age of males with regard to responses to intruders, and may partially account for the insignificance.

Whilst males responded differentially to male intruders when compared to their singing before the encounter, there was no real indication of males responding differentially

to males and females, in contrast to our predictions. Males and females did, however, respond differentially *whilst* the intruder/female was present. Caged males elicited alarm calls and aggressive behaviour, whilst the birds responded to caged females with enticement calls and frequent flying to and from their nestbox. These calls and behaviours were not analysed in this study, but may be important in intra- and intersexual signalling.

To conclude, the change of singing behaviour after encountering a male is particularly interesting in this species, when considering the compelling indications from previous studies of the intersexual function of pied flycatcher song. Whilst the syllable switching reported in this study is an example of a song trait serving both as an amplifier in an intersexual context and as a conventional signal in an intrasexual context, the overall lack of difference between responses to males and females is not supportive of a dual function in the song of the pied flycatcher.

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