

SONG LEARNING IN OSCINE
SONGBIRDS

*Tutor choice, timing, and the relationship with sexual
imprinting*

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1. LIST OF PAPERS

PAPER I

Eriksen A, Slagsvold T. Mother-mediated tutor choice – an experimental study on song acquisition in wild great tits. Manuscript.

PAPER II

Eriksen A, Lampe HM, Slagsvold T. Song learning and sexual misimprinting in cross-fostered great tits. Manuscript.

PAPER III

Eriksen A, Lampe HM, Slagsvold T. 2009. Interspecific cross-fostering affects song acquisition but not mate choice in pied flycatchers, *Ficedula hypoleuca*. *Animal Behaviour* 78: 857-863.

PAPER IV

Eriksen A, Slagsvold T, Lampe HM. 2011. Vocal plasticity – are pied flycatchers, *Ficedula hypoleuca*, open-ended learners? *Ethology* 117: 188-198.

2. ABSTRACT

Birdsong is a species-specific signal that is used in mate attraction and intrasexual competition. This thesis concerns song acquisition in two oscine songbird species, the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*. It addresses questions such as how free-living songbirds choose their song tutors and whether learning of foreign songs can take place in adult birds, and it looks into the relationship between song learning and sexual imprinting. This was done using a method of experimental, interspecific cross-fostering, in which eggs were swapped between nests of different species. Great tits were cross-fostered to blue tits *Cyanistes caeruleus*, and pied flycatchers were cross-fostered to great tits and blue tits.

In oscine songbirds, young males have to learn their song from adult conspecifics, and a mechanism is needed to ensure that they choose song tutors of the right species. Early laboratory studies proposed the existence of an innate auditory template facilitating the recognition and memorization of conspecific song. However, in a number of species, males reared by heterospecifics have been found to copy songs of the foster species and thereby become mixed singers. To account for such heterospecific song learning, it has been suggested that familiarization with the social father before independence guides the choice of song tutors. However, under natural conditions, young males may grow up without a social father. A study on captive zebra finches *Taeniopygia guttata* has demonstrated effects of the social mother on song learning. Based on this finding, I propose a mechanism of mother-mediated tutor choice, suggesting that experience with the social mother as well as the father guides the choice of song tutor in oscine songbirds. Great tits cross-fostered to blue tits include blue tit song in their repertoires. They also get sexually misimprinted, and occasional heterospecific pairs are formed between cross-fostered great tits and cross-fostered blue tits. I tested the hypothesis of mother-mediated tutor choice by letting great tits grow up with a blue tit foster mother and a great tit foster father. Males of this treatment included blue tit song in their repertoires. To control for the possibility that the males had learned the blue tit song directly from their cross-fostered fathers, we also recorded song from great tit males that were reared by conspecifics, but whose fathers had been cross-fostered to blue tits. None of these males sang blue tit song, suggesting an effect of the social mother. However, cross-fostered great tit males mated to blue tits may sing more blue tit song than those mated to great tits. Our samples were too small to separate between heterospecific song learning resulting from

mother-mediated tutor choice and from exposure to blue tit song in the repertoire of the father.

Song learning shares a number of characteristics with sexual imprinting. I investigated the relationship between these two processes in great tits. I exposed cross-fostered great tit males to playback of great tit song and blue tit song inside their territory. Males that showed sexual interest in blue tit females were more likely to respond with blue tit song to playback than males that showed interest only in conspecific females. This suggests that different degrees of misimprinting may have parallel effects on song learning and sexual preferences in cross-fostered great tit males. Furthermore, the response to territorial intruders seemed to be affected by social interactions: Cross-fostered males currently associated with blue tits increased their response to playback of blue tit song whereas males currently associated with great tits increased their response to playback of great tit song through the season.

I also studied the effect of social rearing condition on song learning in pied flycatchers. Cross-fostered pied flycatchers do not seem to get sexually misimprinted. However, I found that pied flycatcher males reared by blue tits or great tits became mixed singers, uttering a combination of pied flycatcher song and the foster species' song. Furthermore, males reared with nest mates of the foster species included tit song in a higher proportion of strophes than did cross-fostered males reared with conspecific nest mates. Hence, in pied flycatchers, growing up with heterospecific foster parents and nest mates caused a mixed choice of song tutors without affecting their mate preferences.

Some songbird species are open-ended learners and retain the ability to learn new songs throughout their lives. However, to demonstrate that a species is a true open-ended learner, it is necessary to make sure that the elements learned as adults have not been heard and possibly memorized by the birds at an early age. I performed a playback experiment to test whether the pied flycatcher is a true open-ended learner. I exposed pied flycatcher males to playback of song containing syllables that were unknown to the study area. Among the 20 subjects, one yearling and two older males had learned a foreign syllable type, supporting the hypothesis that pied flycatchers are true open-ended learners. Pied flycatcher song is believed to serve mostly for mate attraction, and possible functions of adult song learning are to increase the repertoire size and to increase syllable sharing with neighbours. The subjects showed no increase in either of these parameters after the treatment. An alternative adaptive value of adult song learning in pied flycatchers may rather be to pick up particularly attractive song elements.

3. GENERAL INTRODUCTION

Birdsong is quite a remarkable phenomenon, both for its beauty and complexity, but also owing to its important role in the social lives of songbirds. For generations, naturalists have been asking questions about its function, evolutionary history, physiological and neurological mechanisms, and the process by which individual birds acquire the ability to sing. The latter question is the main focus of this thesis. Using an experimental approach in natural conditions, I will address questions such as how free-living songbirds choose their song tutors and whether learning of foreign songs can take place in adult birds, and I will look into the relationship between song learning and sexual imprinting.

3.1. The functions of birdsong

Male song is an important intra- and intersexual signal that functions in female attraction and territory defence. In oscine passerines, also called ‘true songbirds’, it has been suggested that long, complex songs and larger repertoires generally serve the former function, whereas small repertoires of song types are more likely linked to the latter (Catchpole and Slater 2008).

When choosing a social or extra-pair mate, oscine females may pay attention to a number of different song parameters, such as repertoire size (e.g. Lampe and Saetre 1995; Buchanan and Catchpole 1997; Reid et al. 2004; but see review by Byers and Kroodsma 2009), song rate (Gottlander 1987), consistency in pitch and timing (Byers 2007), and particular, ‘sexy’ syllable types (Vallet and Kreutzer 1995). Some of these parameters may reflect the age, experience, or genetic quality of the singing male (Espmark and Lampe 1993; Lampe and Espmark 1994; Balsby and Hansen 2010; Nicholson et al. 2007); information which may serve as an indicator to prospecting females about whether the male is likely to provide direct benefits, such as good parental abilities or access to a good territory, or indirect benefits in the form of ‘good genes’ for the offspring (Kirkpatrick and Ryan 1991; Collins 2004). By eavesdropping on singing interactions between territorial neighbours, females may make direct, immediate comparisons of potential partners and make reproductive decisions based on the males’ relative vocal performance (Otter et al. 1999; Mennill et al. 2002; Logue and Forstmeier 2008).

Birdsong also has an important function in male-male interactions. Holding a territory can be crucial for successful mating and breeding, and when a male has occupied one, he can

save valuable energy by defending it with song rather than constantly chasing off rivals (Catchpole and Slater 2008). The presence or absence of song in a territory can be essential for whether it gets invaded. This has been demonstrated experimentally, both by muting territorial males (e.g. Peek 1972), and by replacing territorial males with a speaker playing back recordings of song (e.g. Krebs et al. 1978). In the latter case, the repertoire size of the playback may be of importance for its effectiveness at repelling invading males (Krebs et al. 1978). Overlapping and matching each other's songs are believed to be ways for rivals to escalate territorial contests (Catchpole and Slater 2008). Evidence from interactive playback experiments have been taken to suggest that temporally overlapping the songs of a rival is perceived as a threatening signal (e.g. Naguib 1999; Poesel and Dabelsteen 2005), and that increasing levels of overlap is perceived as increasingly aggressive (Naguib and Kipper 2006). However, whether overlapping is actually an aggressive signal is currently being debated (Searcy and Beecher 2009; Naguib and Mennill 2010; Searcy and Beecher 2011). Matching is another way of addressing a specific rival. A male can *repertoire match*, i.e. use a song type that is shared between the two birds, or more aggressively, he can *song type match*, i.e. reply with the particular song type that the rival is singing. Different levels of song matching have been reported in a number of species, although there are also species that do not song match at all (for a review, see Catchpole and Slater 2008). For those that do, having a repertoire of song types of which some are shared with each territorial neighbour is advantageous (Beecher et al. 2000; Wilson et al. 2000; Beecher and Brenowitz 2005). Song sharing can be related to survival, territory tenure, and mating- and breeding success (Payne et al. 1988; Beecher et al. 2000; Wilson et al. 2000), and selective use of memorized songs to increase sharing with neighbours has been found in a number of species (Nelson 2000; Franco and Slabbekoorn 2009; Kiefer et al. 2010). If during a singing contest a male does not have a complete match of the rival's song type in his repertoire, he may respond with a partially matching song type (Anderson et al. 2005) or with the closest song type that he has (Burt et al. 2002). Matched countersinging can thus provide successively more precise assessment of the rival, from just matching a song type or parts of a song type, to matching a song type in addition to various temporal parameters (McGregor et al. 1992).

A striking feature of birdsong is its species specificity (Becker 1982). Birdwatchers can easily learn to identify different species by song, and in some cases, the song can be the most evident feature to distinguish between closely related species that lack other obvious species-specific traits. Given that birdsong is an important intraspecific signal for mate attraction and intrasexual competition, it is reasonable to assume that one function of its

species specificity is for the birds to be able to easily recognize conspecific rivals and potential mates. Indeed, zebra finch *Taeniopygia guttata* females are able to distinguish between songs of two different subspecies, preferring that of their own (Clayton 1990), and playback of species-specific song is frequently and effectively used to attract and catch male birds for banding (Catchpole and Slater 2008). However, some species, such as the superb lyrebird *Menura novaehollandiae*, are known for performing accurate mimics of a large variety of heterospecific sounds (Beecher and Brenowitz 2005; Kelley and Healy 2011). Heterospecific vocal mimicry has been reported from field studies of a number of different species (e.g. Thorpe 1958; Lundberg and Alatalo 1992; Haavie et al. 2004; Osiejuk et al. 2004; Gorissen et al. 2006; Garamszegi, Eens et al. 2007). In some of these species, vocal mimicry seems to have an adaptive function, such as repelling heterospecific territorial intruders (e.g. Gorissen et al. 2006) or attracting a female when these prefer large and complex song repertoires (Kelley and Healy 2011). However, in the majority of cases, vocal mimicry seems to have no function, but rather results from learning mistakes (Garamszegi, Eens et al. 2007; Kelley et al. 2008). Such mistakes can appear if female preferences for large repertoires result in males being less selective in what songs they will copy, and they can remain if they do not include fitness costs, such as reduced effectiveness at signalling species identity (Garamszegi, Eens et al. 2007).

Hence, birdsong is a complex signal that needs to be performed in the proper, species-specific way to ensure that it serves its purpose effectively. How do young birds acquire this skill? In many bird species, such as most sub-oscine passerines studied to date (e.g. Kroodsma 1984; Kroodsma 1989; but see Kroodsma 2004), the songs are innate. However, genetically encoded behaviour takes generations to adjust through natural selection. In contrast, oscine songbirds along with parrots (Psittaciformes) and certain species of hummingbirds (Apodiformes) and toucanets (Piciformes), learn their song (Moore 2004). Learning allows individuals to quickly adapt their song to the environment, e.g. by learning the songs that are common among territorial neighbours in a specific area (for a review of possible benefits of song learning, see Catchpole and Slater 2008).

3.2. *Oscine song learning*

Song learning in oscine songbirds has been extensively studied (for reviews, see Hultsch and Todt 2004; Catchpole and Slater 2008), although much of what is known comes from studies of captive birds. The exact pattern of song learning differs between species, but the

ontogenetic development of song can generally be divided into two stages: an early *sensitive phase*, or memorization phase, and a *motor phase* in which the male develops his own vocal skill based on the memorized songs (Hultsch and Todt 2004). The sensitive phase is a time window, often starting around the time of fledging, in which memorization is facilitated by an increased sensitivity to song (e.g. Thorpe 1958; Marler 1970; Slater and Ince 1982; Böhner 1990; Chaiken et al. 1994; Nordby et al. 2001; Roper and Zann 2006). The timing of the sensitive phase varies among species, and it often coincides with times when adults are vocally active (for a review, see Hultsch and Todt 2004). There is also some flexibility within species with respect to the duration of the sensitive phase, as males that are kept from hearing song early in life often show a prolonged ability to memorize songs (Nottebohm 1989; Slater et al. 1993). The motor phase starts with a period of *subsong*, which consists in sequences of soft, rambling sounds that lack defined syllables (Nottebohm 1972; Marler and Peters 1981; Hultsch and Todt 2004; Roper and Zann 2006). Subsong gradually merges into *plastic song*, in which the vocalizations become gradually more stereotyped as the bird starts practising songs that were memorized during the sensitive phase (Marler and Peters 1981; Hultsch and Todt 2004). Finally, during the *crystallization phase*, the song fully develops into the stereotyped, species-specific song of an adult songbird (Marler and Peters 1981; Todt and Geberzahn 2003; Hultsch and Todt 2004).

In a natural environment in which songbirds are exposed to an array of acoustic stimuli, young males need a mechanism to make sure that they learn the songs of the right species. Marler (1970) suggested that this is ensured through the existence of an innate auditory template, predisposing birds to selectively recognize and memorize conspecific song. Some laboratory studies have provided support of this hypothesis by showing that birds reared in isolation had a preference for learning conspecific song over heterospecific song (e.g. Marler 1970; Marler and Peters 1977; but see Baptista and Petrinovich 1984). However, there is large variation among species in how selective males are with respect to copying song that fits constrained species-specific parameters (for a review, see Beecher and Brenowitz 2005), and as pointed out above, heterospecific mimicry has been reported in a number of species. Experiments on captive zebra finches (Clayton 1988, 1989) and free-living great tits *Parus major* and blue tits *Cyanistes caeruleus* (Johannessen et al. 2006) have demonstrated that when reared by heterospecifics, these species will learn heterospecific song from the foster species as well as their own species' song. An extreme case is that of the brood-parasitic indigobird *Vidua chalybeata*. In this species, the males learn the songs of the species they grow up with and use this song to attract conspecific females that were reared by the

same foster species (Payne et al. 1998). Such cases of extensive heterospecific song learning cannot be accounted for by the auditory template hypothesis. Böhner (1990) proposed a different hypothesis that can account for more of the variation in song tutor selection: Before independence, young males get familiarized with the general features of the song of their social father, and after independence, they learn the details of their song from adult males of which the song resembles that of the young males' social father.

3.3. Questions addressed in the thesis

PAPER I and II in this thesis use the study population of interspecifically cross-fostered great tits that was studied by Johannessen et al. (2006). In this population, experimental, interspecific cross-fostering between great tits and blue tits has been carried out since 1995 in order to assess the effect of early learning on different behavioural traits (Slagsvold et al. 2002). Allowing great tits to be reared by blue tit foster parents and vice versa has been shown to affect a number of behaviours, such as aggressive response (Hansen and Slagsvold 2003; Hansen et al. 2008), social dominance (Hansen and Slagsvold 2004), sexual preferences (Slagsvold et al. 2002), foraging (Slagsvold and Wiebe 2007, 2011), and song (Johannessen et al. 2006). The cross-fostered birds get sexually imprinted on the foster species, resulting in occasional heterospecific pairings between great tits and blue tits (Slagsvold et al. 2002). Furthermore, great tit males reared by blue tit foster parents become mixed singers, with repertoires consisting of a combination of great tit and blue tit song types (Johannessen et al. 2006).

The use of blue tit song by cross-fostered great tit males is probably due to a mixed choice of great tit and blue tit song tutors. Possible tutors for male songbirds are the social father (Millington and Price 1985; Clayton 1987; Böhner 1990; Zann 1990; Mann and Slater 1995), neighbours to the natal territory (McGregor and Krebs 1982; Wheelwright et al. 2008), and neighbours to the males' own breeding territory (McGregor and Krebs 1982; Langmore 1999; Liu and Kroodsma 2006; Wheelwright et al. 2008). The hypothesis presented by Böhner (1990) can explain how cross-fostered males may choose song tutors of the foster species through an early familiarization with the foster father's song. However, such a mechanism requires experience with the social father before independence. In the wild, this is not always the case, as males may die or desert the nest to become polygynous (Lifjeld and Slagsvold 1989; Cockburn 2006; Van Dijk et al. 2007), leaving the female alone to care for the young. PAPER I proposes a hypothesis of mother-mediated tutor choice to complement the

hypothesis of Böhner (1990), suggesting that familiarization with the social mother as well as the father may guide song tutor choice. Clayton (1988) demonstrated that zebra finch males that were reared in the laboratory by a zebra finch foster father and a Bengalese finch *Lonchura striata* foster mother, and then given a male tutor of each species, would copy songs of both species. This suggests that also the mother plays an important role for the development of song tutor preferences. In PAPER I, the hypothesis of mother-mediated tutor choice is tested in the field by analyzing the songs of great tit males growing up with a great tit foster father and a blue tit foster mother. Great tits growing up with conspecific parents, but whose father was initially cross-fostered, serve as controls.

Existing evidence from indigobirds, zebra finches and great tits (Böhner 1990; Payne et al. 1998; Johannessen et al. 2006) suggests that experience with the social parents affects whom male songbirds perceive as potential song tutors. This gives clear associations to a different process, namely sexual imprinting. Sexual imprinting is a process by which species-specific characters learned during an early sensitive phase lay the basis for the individual's sexual preference (Immelmann 1972; Irwin and Price 1999). With a clear parallel to song learning, during the sensitive phase for sexual imprinting, experience with the parents affects who are perceived as potential mates (Irwin and Price 1999). The similarities between song learning and sexual imprinting are numerous (for a review, see Baptista et al. 1993), a fact that has been given much attention. In 1992, a conference was dedicated to the parallel between these two learning processes, resulting in an entire issue of the Netherlands Journal of Zoology the following year (see ten Cate, Slater et al. 1993). Both song learning and sexual imprinting occur through exposure to a stimulus during an early sensitive phase (Baptista et al. 1993). A natural question is therefore whether the timing of the sensitive phases for the two processes overlap in time, and as a result, whether the young males focus their attention on one stimulus that becomes the model for both their song tutor choice and their mate preference. This question was addressed by ten Cate, Vos et al. (1993) in a study on zebra finches. They found that the sensitive phase for song learning and sexual imprinting did overlap in time. Nevertheless, zebra finches seem to use the father as the main model for song tutor choice and the mother as a model for sexual imprinting (ten Cate, Vos et al. 1993; but see Clayton 1988). PAPER II in this thesis looks into the relationship between song learning and sexual imprinting in cross-fostered great tit males. In great tits, interspecific cross-fostering affects both song learning and mate preferences. However, the cross-fostered males show large individual variation in both the degree to which they prefer heterospecific mates and the degree to which they sing heterospecific song. PAPER II investigates whether

this variation may be due to different degrees of imprinting that have parallel effects of on both song and sexual preferences. Such individual variation in imprinting may result from differences in the level of parental care, as has been found in cross-fostered zebra finches (Bischof and Clayton 1991; Oetting et al. 1995). We also look into the ontogeny of the use of heterospecific song, suggesting that the apparent individual variation may reflect changes in the use of blue tit song through the lives of cross-fostered great tits. This may result from an own-species bias (Marler 1970; Immelmann 1972; Marler and Peters 1977) or positive feedback from conspecifics rather than heterospecifics (ten Cate 1984; ten Cate and Mug 1984), both predicting a decrease in the use of blue tit song with age. Alternatively, changes in the use of blue tit song through the life of cross-fostered males may result from changing mating associations between years, predicting a shift towards the species with which the male is currently associated.

To what degree can the findings from the cross-fostered great tits and blue tits be generalized to other songbird species? The method of interspecific cross-fostering has been used on a different songbird species, the pied flycatcher *Ficedula hypoleuca* (Slagsvold 2004). Despite earlier propositions that sexual imprinting is probably present in all species showing song learning (ten Cate, Vos et al. 1993), Slagsvold (2004) found no indication that pied flycatchers reared by great tits and blue tits got sexually misimprinted. Furthermore, later studies have revealed that the preference for conspecific mates may be genetically determined in this species (Saether et al. 2007). Nevertheless, pied flycatchers in sympatry with the closely related collared flycatcher *F. albicollis* copy collared flycatcher songs, thereby becoming mixed singers (Haavie et al. 2004; Qvarnstrom et al. 2006; Vabishchevich and Formozov 2010). PAPER III presents results from song analyses of pied flycatcher males cross-fostered to great tits and blue tits in the field, investigating whether altered social-rearing conditions affect the tutor choice of this species, despite the lacking effect on mate preference.

The time during which songbirds are able to acquire new songs varies among species (for reviews, see Beecher and Brenowitz 2005; Kipper and Kiefer 2010). Some songbird species, the *closed-ended learners*, are unable to achieve new songs after the crystallization phase in their first breeding year (Thorpe 1958; Nordby et al. 2002). In contrast, *open-ended learners* can keep adding new elements to their repertoire throughout their lives (Nottebohm et al. 1986; Chaiken et al. 1994), enabling males to learn song elements from new neighbours and thus potentially increase their repertoire size and song sharing. Adult song learning is the focus of PAPER IV. Beecher and Brenowitz (2005) make the case that it is harder to

demonstrate that a species is a closed-ended learner than demonstrating that it is not, because it only takes one bird to show that learning can take place beyond the first year. They illustrate their point with the great tit. This species was believed to be an age limited learner until it was observed that great tit males would add song types to their repertoires after experience with new neighbours (McGregor and Krebs 1989). However, after a song element has been heard and memorized by a male, it may stay concealed in his hidden repertoire without being sung for a long time (Chaiken et al. 1994). Therefore, showing that a species is a true open-ended learner is challenging, especially in the field, because it requires the knowledge that new elements in the repertoire of a male have not been heard and memorized by the bird early in life. Although circumstantial evidence for adult song learning exists from field studies on e.g. great tits (McGregor and Krebs 1989) and pied flycatchers (Lundberg and Alatalo 1992; Espmark and Lampe 1993), studies conducted outside the laboratory often lack the necessary information about previous exposure to the 'new' song elements. PAPER IV presents results from a field experiment in which pied flycatchers were presented with playback stimuli that included song elements that were foreign to the study area, testing the hypothesis that the pied flycatcher is a true open-ended learner.

4. SPECIES AND STUDY SITE

The focal birds in this thesis were great tits and pied flycatchers. We used blue tits as foster species for the cross-fostered great tits, and both great tits and blue tits were used as foster species for pied flycatchers. All three species are territorial, hole-nesting passerines that feed on insects and readily breed in nest boxes. Only the female builds the nest and incubates the eggs, but normally both parents feed the young. The great tit and the blue tit weigh about 17–19 g and 10–11 g, respectively. The species share some of the characteristics of their plumage colouration, with carotenoid-based yellow underparts (Partali et al. 1987) and greenish backs, although the black head and chest stripe of the great tits differs from the blue markings of the blue tits (PLATE 1). In great tits, the sexes can be told apart by the much more pronounced chest stripe and shiny head of the male, whereas the blue tit sexes differ in the brightness of the blue markings, although much of the variation is in the UV spectrum which is invisible to humans (Andersson et al. 1998). Great tits and blue tits were previously both considered members of the genus *Parus*, and although they have been separated into different genera (Gill et al. 2005), their ecology is quite similar, with similar food, habitat and nest site preferences. Both sexes of both species defend a resource territory during the breeding season, and during autumn and winter, great tits and blue tits occur together in mixed-species flocks. Great tits are socially dominant to blue tits (Haftorn 1993). Both species are generally socially monogamous with similar levels of extra-pair paternity (approximately 30% of nests containing extra-pair young in our study population; Johannessen et al. 2005), although some blue tits engage in polygynous matings (Kempnaers 1994). Great tits and blue tits are not known to hybridize under natural circumstances.

The pied flycatcher is intermediate in size to great tits and blue tits, with adult body weight averaging 12–13 g (Lundberg and Alatalo 1992). Pied flycatchers are sexually dimorphic (PLATE 1), and in contrast to the tits they are migratory and solitary, performing long-distance migrations to wintering grounds in tropical Africa (Lundberg and Alatalo 1992). Breeding site fidelity is generally high, with up to approximately 50% return rate and breeding dispersal distances of 100–200 m recorded for pied flycatcher males in Scandinavia (Nyholm and Myhrberg 1983; Slagsvold and Lifjeld 1990). The males arrive at the breeding grounds in our study area in late April, after which the females arrive to choose among available males and nest sites. After having attracted a mate, many pied flycatcher males occupy a second nest box and try to attract another female (Lundberg and Alatalo 1992). Polygynous males usually only provide paternal care at the primary nest (Lifjeld and

Slagsvold 1989). Pied flycatcher females on the other hand seem to be more faithful than the tits, with extra-pair young occurring in < 10 % of the nests (Lifjeld et al. 1991; Rätti et al. 2001; Slagsvold et al. 2001).



PLATE I Great tit (upper left), blue tit (upper right) and pied flycatcher (lower right) females on their nests, and a pied flycatcher male (lower left). Photo: Tore Slagsvold (lower left) and Ane Eriksen

Great tits, blue tits and pied flycatchers are all oscine passerines with song repertoires. However, the way their song elements are organized during song bouts differs, and so does the terminology that is most commonly used in song studies of these species. In great tits, each *song* typically consists of several repetitions of a short phrase of two or three *notes* (FIG. 1a; Krebs 1976). Songs can be assigned to distinct *song types* based on the number, type and patterning of notes in the repeated phrases (McGregor and Krebs 1982). The size of the repertoires of individual males varies between two and eight song types (Krebs et al. 1978; Johannessen et al. 2006), and despite some variation in e.g. the number of notes, the same song types can be recognized in the repertoires of different males (McGregor and Krebs 1982). During a song bout, a male typically repeats a song type for several times before switching to a different song type (Krebs 1976). Blue tits also have song types that they organize in to bouts in a similar way, and they have repertoire sizes that are comparable to those of great tits (Doutrelant et al. 2000; Johannessen et al. 2006). However, some blue tit song types contain a *trill*; a series of rapidly repeated identical notes (Doutrelant et al. 2000).

Whereas blue tit untrilled song types often have similar syntax to great tit song, trilled blue tit songs often contain one long phrase rather than short, repeated phrases, and their syntax therefore differs from that of great tit song (FIG. 1b; Doutrelant et al. 2000).

Pied flycatchers do not organize their song into discrete song types. The basic song unit is the *figure* or *syllable*, which are continuous elements or groups of elements separated from other syllables by more than 0.02 s (Espmark and Lampe 1993). These are organized into *strophes* (FIG. 1c) that are separated from other strophes by more than 1 s (Espmark and Lampe 1993) and equivalent to *songs* in great tits and blue tits. Each pied flycatcher male has a repertoire ranging from < 10 to probably > 100 different syllable types. These are continuously recombined in each strophe in a song bout, and although some syllables frequently occur together in phrases, successive strophes are rarely identical (Lundberg and Alatalo 1992).

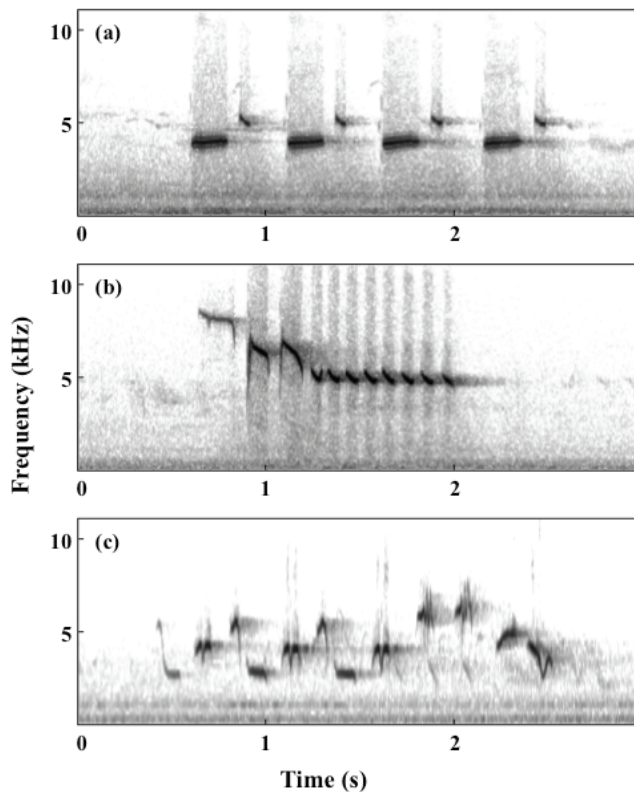


FIGURE 1 Sonograms of a two-note great tit song (a), a trilled blue tit song (b) and a pied flycatcher strophe containing 12 syllables and 7 different syllable types (c).

The great tit studies were carried out in a 1.6-km² nest box plot at Dæli (PLATE II, 59°55'N, 10°32'E) in Bærum. The study area is located on a south-facing slope that is part of a larger woodland area dominated by deciduous trees with some patches of conifers, interspersed with farmland and settlements. The nest box plot contains approximately 500 wooden nest boxes that are placed on the tree trunks about 1.5 m above the ground. About 60-90 great tit pairs and 80-140 blue tit pairs breed in the boxes each year along with a similar number of pied flycatchers and a few nuthatches (*Sitta europea*) and coal tits (*Periparus ater*). Due to the surplus of provided nest boxes, each year only very few great tit and blue tit pairs are found breeding in natural cavities. European sparrowhawks (*Accipiter nisus*), pygmy owls (*Glaucidium passerinum*), cats (*Felis catus*) and weasels (*Mustela erminea*) are the main predators on tits in the area.

We studied pied flycatchers in a similar, 0.6-km² nest box plot at Sinober (59°59'N, 10°38'E) in Sørkedalen near Oslo. Situated about 7 km from the Dæli study site, Sinober is a mixed coniferous woodland with patches of deciduous trees and has been provided with close to 300 nest boxes.



PLATE II Dawn at Midtfelset, Dæli study site. Photo: Ane Eriksen

5. GENERAL METHODS

We monitored the great tits, blue tits and pied flycatchers in the study areas from early spring to the end of the nestling period. Starting in February-March at Dæli, and at the time of arrival of the first pied flycatchers in April-May at Sinober, we recorded the identity of resident birds, their nest box ownership, mating status, and onset and progression of breeding. During nest building and egg laying, all nest boxes were visited regularly (at least every third day). We determined the onset of egg laying assuming that a female lays one egg per day, and hatching date was calculated using a weight curve of chicks of known age. At day 15 (tits) and 13 (pied flycatchers) post hatching, all nestlings were weighed and banded with a numbered metal ring for later identification. In addition, great tits and blue tits received coloured plastic bands indicating year and treatment. From late August to early December, we caught adult and juvenile great tits and blue tits by mist netting. Local recruits were then given unique combinations of colour bands. Immigrants were given a numbered metal ring and a colour ring indicating the year and age of first capture. We weighed the captured birds with a spring balance and measured their wing and tarsus length. Pied flycatchers, and tits that had avoided mist netting in the fall, were trapped in nest boxes and banded with unique colour combinations in spring.

We performed experimental, interspecific cross-fostering during the incubation period. Great tit eggs were placed in blue tit nests, and pied flycatcher eggs were placed in great tit and blue tit nests. The number of eggs assigned to each cross-fostered nest was chosen so that the feeding demands would not exceed those of the natural broods of the foster species. When great tits were cross-fostered, the entire blue tit clutch was substituted with 4-6 great tit eggs depending on the original clutch size. Hence, the great tits growing up with blue tit foster parents had conspecific nest mates. When a cross-fostered individual was found breeding with a conspecific, the nest was left unmanipulated to assess any second-generation effects of the cross-fostering. Sometimes a cross-fostered great tit and a cross-fostered blue tit were breeding together, and in the majority of cases the great tit was the male and the blue tit was the female. Previously, when nests of a great tit male and a blue tit female have been left unmanipulated, all hatching chicks have been blue tit, demonstrating that the females had copulated with male blue tits (Slagsvold et al. 2002; PLATE III). For this thesis, nests of heterospecific pairs were given great tit eggs in order to assess the effect of each individual parent on the one species that so far seems to be the most strongly affected by cross-fostering

(e.g. Slagsvold et al. 2002; Johannessen et al. 2006). Control and cross-fostered nests were visited and disturbed the same number of times to control for disturbance.



PLATE III Mixed blue tit and great tit pair; here feeding blue tit chicks. Photo: Tore Slagsvold

We used two different treatments for cross-fostered pied flycatchers, a whole brood treatment and a mixed brood treatment (PLATE IV). In the whole broods, all the host eggs were removed, and replaced with 4-8 pied flycatcher eggs. In the mixed broods, one or two pied flycatcher eggs were added to the clutch of tit eggs, allowing the pied flycatchers to grow up with heterospecific nest mates as well as foster parents.



PLATE IV Pied flycatcher chicks growing up in blue tit nests. The photo to the left shows a mixed brood where one pied flycatcher chick is reared together with three blue tit chicks, and the photo to the right shows a whole brood with two pied flycatcher chicks. Photo: Tore Slagsvold

Cross-fostering was performed under license from The Directorate for Nature Management and from the National Animal Research Authority in Norway. Males of the following treatments were used as focal individuals in this thesis:

GREAT TITS

- *Immigrants*: not born in the area, but assumed to have been reared by their own, conspecific parents.
- *Controls*: unmanipulated local recruits, reared by their own, conspecific parents.
- *Cross-fostered males*: reared by blue tit foster parents.
- GT_XBT_X *males*: reared by a cross-fostered great tit foster father and a cross-fostered blue tit foster mother.
- BT_XGT_X *males*: reared by a cross-fostered blue tit foster father and a cross-fostered great tit foster mother.
- GT_XGT *males*: reared by their own, conspecific parents, but the father had initially been cross-fostered.

In the last three categories, the first acronym indicates the species of the foster father whereas the second acronym indicates the species of the foster mother (GT = great tit, BT = blue tit). The subscript X indicates whether the foster parent was cross-fostered. The great tit mothers of the GT_XGT males could be either cross-fostered or controls.

PIED FLYCATCHERS

- *Controls*: immigrants or local recruits, reared by their own, conspecific parents.
- *Cross-fostered males*: reared by great tit or blue tit parents.
 - o *Whole broods*: with only conspecific nestmates.
 - o *Mixed broods*: with nest mates of the foster species.

6. RESULTS

6.1. Mother-mediated tutor choice in great tits (PAPER I)

Do both foster parents play a role for the misdirected song tutor choice of the cross-fostered great tit males? To ensure that young males choose tutors of the right species, early studies proposed the existence of an innate template facilitating the recognition of conspecific song. Other studies have suggested that experience with the father guides the choice of song tutors. In PAPER I, we proposed a hypothesis of *mother-mediated tutor choice*, suggesting that experience with the mother as well as the father guides the choice of song tutor. Effects of the mother on song learning have been demonstrated in captive zebra finches (Clayton 1988).

Due to the sexual misimprinting resulting from the cross-fostering, occasional pairs are formed between blue tits and great tits (Slagsvold et al. 2002; PLATE III). This provided a unique opportunity to test our hypothesis, as studying the song of males reared by such mixed pairs would make it possible to tease apart the effect of each individual parent. Consistent with the hypothesis of mother-mediated tutor choice, great tit males reared by a great tit male and a blue tit female ($GT_{\times}BT_{\times}$ males) included blue tit song in their dawn repertoires and in their responses to playback. $GT_{\times}BT_{\times}$ males responded equally strongly to caged great tit and blue tit males, but they all mated with conspecific females and showed no obvious signs of being sexually misimprinted. To control for the possibility that $GT_{\times}BT_{\times}$ males had learned blue tit songs directly from their cross-fostered great tit fathers, we recorded song from males reared by great tits, but whose fathers had initially been reared by blue tits ($GT_{\times}GT$ males). None of these males sang blue tit song. Where available, we also analyzed recordings of the subjects' fathers. There was a positive relationship between the proportion of blue tit song in the dawn song of fathers and sons. However, the two fathers of $GT_{\times}GT$ males of whom we obtained song data were recorded to sing blue tit song, both at dawn and as response to playback, without this resulting in their sons singing blue tit song. Our results are consistent with the hypothesis of mother-mediated tutor choice as well as learning through experience with the father, but our samples are too small to separate between these two mechanisms. Given that the hypothesis of mother-mediated tutor choice will receive empirical support from future studies, we suggest that young songbird males select song tutors based on experience with their mother as well as their father to ensure correct song tutor choice even in the absence of a father.

6.2. Song learning and sexual imprinting in cross-fostered great tits (PAPER II)

In great tit males, interspecific cross-fostering affects the acquisition of both song (Johannessen et al. 2006) and sexual preference (Slagsvold et al. 2002). In PAPER II, we explored the relationship between these two processes in a playback experiment. We presented subjects sequentially with blue tit and great tit playback and recorded whether the subject responded with song, and whether the response song was a blue tit or a great tit song type. Consistent with previous findings, the response to blue tit playback relative to great tit playback was higher in cross-fostered males than in controls. Furthermore, many of the cross-fostered males, but not the controls, frequently responded with blue tit song to the playback. We also recorded whether the cross-fostered males had shown repeated interest in blue tit females, and whether they were associated with blue tits or great tits during the year of the trial. We analyzed the cross-fostered males' response to playback in binomial generalized linear mixed models, testing the following hypotheses: (1) The variation in the degree to which individual males perceive blue tits as song tutors potential mates results from different degrees of imprinting that has parallel effects on song learning and sexual imprinting. Consequently, cross-fostered males with a preference for blue tit females also sing more blue tit song and respond more strongly to blue tit playback. (2) The use of and response to blue tit song is affected by age with a gradual shift towards conspecific song due to social feedback. (3) The degree to which cross-fostered great tit males use and respond to blue tit and great tit song is affected by social interactions, resulting in a shift towards song types of the species to which the male is currently mated.

Cross-fostered great tit males that had shown an interest in blue tit females had a marginally higher likelihood of responding with blue tit song to playback. Although not conclusive, this finding is consistent with the first hypothesis. We found no general decrease in response to or use of blue tit song with age, but we did find an effect of social interactions. Cross-fostered males currently associated with blue tits increased their response to blue tit song whereas males currently associated with great tits increased their response to great tit song through the season. This was probably due to repeated interactions with sexual rivals that were conspecific to the resident female during the breeding season. Finally, the subjects showed heterospecific song matching on the species level, responding more frequently with blue tit song to blue tit playback than to great tit playback.

6.3. Song learning and mate choice in cross-fostered pied flycatchers (Paper III)

In PAPER II, we studied the relationship between song learning and sexual imprinting in cross-fostered great tit males. In PAPER III, we wanted to find out to what degree these findings can be generalized to other songbird species. We recorded the song of pied flycatchers that had been experimentally cross-fostered to blue tits and great tits in the field. In contrast to great tits that get sexually misimprinted when reared by blue tits (Slagsvold et al. 2002, PAPER II), pied flycatchers reared by heterospecifics were shown in a previous study to mate normally with conspecifics, and they did not show any signs of being sexually imprinted on the foster species (Slagsvold 2004). In PAPER III however, we found that similarly to great tits, the cross-fostering did affect the song acquisition of pied flycatchers. Flycatcher males reared by blue tits or great tits became mixed singers, uttering a combination of pied flycatcher song and the foster species' song. Furthermore, the cross-fostered flycatchers changed their frequency range and increased the number of syllables per strophe, and their song thus became intermediate between controls of their own species and the foster species. There seemed to be an additional effect of siblings. Cross-fostered males growing up with nest mates of the foster species had a higher proportion of strophes containing tit song than cross-fostered males growing up with conspecific nest mates (PLATE IV). Hence, in pied flycatchers, growing up with heterospecific foster parents and nest mates causes a mixed choice of song tutors without affecting their mate preferences. Mate choice and song acquisition thus depend on different proximate mechanisms in this species.

6.4. Adult song learning in pied flycatchers (Paper IV)

In PAPERS I-III, we focused on the significance of early learning for song acquisition in great tits and pied flycatchers. However, some songbird species are open-ended learners and maintain the ability to learn new songs throughout their lives. Earlier studies have provided circumstantial evidence suggesting that this may apply to pied flycatchers. However, to demonstrate that a species is a true open-ended learner, it is necessary to make sure that the elements that the adult males learn have not been heard and possibly memorized by the birds at an early age.

In PAPER IV, we performed a playback experiment to test whether pied flycatchers are true open-ended learners. We played back recordings of unfamiliar pied flycatcher song inside the territories of pied flycatcher males for one week. The stimulus recordings contained foreign song elements that had not previously been recorded in our study area, and were therefore most likely unknown to the subjects. Among the 20 subjects, one yearling and two older males had learned a foreign syllable type, supporting the hypothesis that pied flycatchers are true open-ended learners. Pied flycatcher song is believed to serve mostly for mate attraction, and possible functions of adult song learning are to increase the repertoire size and to increase syllable sharing with neighbours. However, our subjects showed no increase in either of these parameters after the treatment. On the contrary, the repertoire size decreased from before to after the playback. An alternative adaptive value of adult song learning in pied flycatchers may rather be to pick up particularly attractive song elements.

7. GENERAL DISCUSSION

7.1. Mechanisms for mixed tutor choice

The findings in PAPER I, II and III of this thesis, along with previous findings by Johannessen et al. (2006), demonstrate that great tits and pied flycatchers reared by heterospecific foster parents become mixed singers, uttering a combination of their own species' song and the foster species' song. Hence, both conspecifics and males of the foster species are perceived as acceptable song tutors. The fact that the repertoires of tits and flycatchers reared by two heterospecific foster parents still contained conspecific song suggests that a conspecific bias may exist, possibly through an innate template as described by Marler (1970). However, together with studies reporting heterospecific song learning in interspecifically cross-fostered zebra finches (Clayton 1988, 1989) and brood-parasitic indigobirds (Payne et al. 1998), the results from tits and flycatchers cannot be explained by an innate auditory template alone. Böhner (1990) proposed the hypothesis that young zebra finch males get familiarized with the song of the social father before independence, and later choose song tutors with similar songs. The hypothesis was supported by Payne et al. (1998) in their study of indigobirds, and is consistent with the findings by Johannessen et al. (2006) for great tits and blue tits.

However, the mother may also play a role in song tutor choice, as demonstrated by Clayton (1988) for captive zebra finches. From the findings in PAPER I, it may seem that both the mother and the father can have independent effects on the song learning of free-living great tits as well. Consistent with our hypothesis of mother-mediated tutor choice, $GT_{\times}BT_{\times}$ males as well as $BT_{\times}GT_{\times}$ males were recorded to sing blue tit song (PAPER I). This is, to our knowledge, the first evidence that mothers may affect the song tutor choice of wild songbirds. However, our results do not allow us to determine whether the $GT_{\times}BT_{\times}$ males learned the blue tit song through mother-mediated tutor choice or from exposure to blue tit song in the repertoires of the fathers. Great tits have been shown previously to learn song from natal year- and breeding year neighbours, but not from their social father (McGregor and Krebs 1982), and the $GT_{\times}GT$ males did not include any great tit song in their repertoires, suggesting an effect of the social mother. However, a reasonable question is whether cross-fostered great tit males mated with a blue tit female sing more blue tit song than the ones mated with a conspecific. In PAPER II, we did not find a generally higher occurrence of blue tit song from males currently associated with blue tits, but we did find a marginally higher occurrence of blue tit song from males that had shown sexual interest in blue tits. In PAPER I, there was a

positive relationship between the proportion of song containing blue tit elements in the dawn song of fathers and sons, suggesting an effect of blue tit song in the fathers' repertoires. However, the two fathers of GT_XGT males of which we obtained song data included blue tit song, both at dawn and as response to playback, without this resulting in their sons singing blue tit song. It is possible that hearing blue tit song from the father only affects the song learning of great tit males if it occurs in combination with additional blue tit stimuli, such as one or both of the parents being blue tit. Some female great tits and blue tits do occasionally sing (Garamszegi, Pavlova et al. 2007), raising the possibility that the GT_XBT_X males may have learned blue tit song from their mothers. However, this seems unlikely considering that singing females are observed very sporadically in our study site, and it probably happens too infrequently to account for the blue tit song found in the repertoires of five out of seven GT_XBT_X males. The results of PAPER I are inconclusive, primarily because the samples of both GT_XBT_X males and GT_XGT males were very small. This was mainly because the pairing success of cross-fostered great tit males is generally very low (Slagsvold et al. 2002).

Unfortunately, the experiment in PAPER I could not be repeated for pied flycatchers. This was because tits could not be successfully cross-fostered to pied flycatchers, as they would not survive the nestling period (T. Slagsvold, unpublished data). In addition, the apparent lack of sexual imprinting in pied flycatchers (Slagsvold 2004; Saether et al. 2007) makes it unlikely that mixed pairs between tits and flycatchers would occur, even if tits could fledge from pied flycatcher nests. We therefore do not know the role of each individual parent for song tutor choice in pied flycatcher males. However, this would be an interesting species for testing the hypothesis of mother-mediated tutor choice, because males that become polyterritorial may only provide parental care at the primary nest (Lifjeld and Slagsvold 1989). Hence, nestlings from secondary nests may get little or no experience with their father, making mother-mediated tutor choice advantageous. Although nestlings from primary nests may get more visual experience with the father, the opportunity to familiarize with his song is limited also in these nests, because males sing very little after pairing (Gottlander 1987; Espmark and Lampe 1993).

Given that the hypothesis of mother-mediated tutor choice will be supported by future studies, we suggest two possible mechanisms through which it may take place: through a preference for learning songs either from males that physically resemble the mother, or from males that show sexual interest in females resembling their mother. The former may occur if sexual dimorphism does not hamper the use of a female model (the mother) for the recognition of a male stimulus (song tutor). This is unlikely to be a problem in great tits and

blue tits as the sexual dimorphism is mainly limited to the size of the chest stripe in great tits and the degree of UV reflectance in blue tits (Andersson et al. 1998). Zebra finches have pronounced sexual dimorphism, with colourful markings that are only present in males (ten Cate, Vos et al. 1993), yet males reared by a heterospecific foster mother and a conspecific foster father still learned songs from heterospecific males (Clayton 1988). As a second mechanism for mother-mediated tutor choice, we suggest that young males may pay attention to adult males' behaviour towards their social mother and develop a tutor preference for males showing sexual interest in her or in females resembling her. In zebra finches, males singing female-directed song have been found to be more attractive song tutors than males singing undirected song (Roper and Zann 2006). If such a preference exists in great tits, GT_XBT_X males may develop a tutor preference for males directing their song towards females that fit the image to which the young male is familiarized. Due to the species of the resident female, GT_XBT_X males may experience frequent intrusions by blue tit males to their natal territory, and may thus get more exposed to blue tit song. If this increased exposure to blue tit song was the reason for the GT_XBT_X males learning blue tit song, such a mechanism would also be mother-mediated, but with the tutor preference resulting from the high exposure to blue tit song rather than familiarization with the mother.

Laboratory studies have previously identified sibling effects, or group effects, on song learning in chaffinches *Fringilla coelebs*, zebra finches, and white-crowned sparrows *Zonotrichia leucophrys* (for a review, see Baptista et al. 1993). In an experiment in which interactions between white-crowned sparrow siblings were unrestricted while those between pupil and tutor were limited, the songs of siblings showed greater similarity to each other than to the songs of the tutor (Cunningham and Baker 1983). However, Baptista et al. (1993) claimed that sibling effects on song learning only influence variation within species, and they predicted that a sibling effect would be difficult to demonstrate in the field. In cross-fostered great tits and blue tits, no sibling effect was found on the use of blue tit song (Johannessen et al. 2006), although growing up with siblings of the foster species did affect species recognition (Slagsvold and Hansen 2001; Hansen and Slagsvold 2003). In pied flycatchers, the effect of the cross-fostering on the song was stronger for males from mixed brood than for males from whole broods (PAPER III). That is, cross-fostered males growing up with nest mates of the foster species had a higher proportion of tit song in their repertoires than those growing up with conspecific nest mates. Despite the small sample size, PAPER III may thus provide the first evidence of a sibling effect both on song learning in the field, and on heterospecific song learning in general. Although we do not have data on the degree of song

sharing between the cross-fostered pied flycatcher subjects and their siblings, it seems that the presence of heterospecific siblings may have increased the familiarization with the foster species and hence the preference for heterospecific song tutors.

7.2. Song learning and sexual imprinting

Consistent with previous studies (Slagsvold et al. 2002; Johannessen et al. 2006), many of the cross-fostered great tit males studied in PAPER II were found to sing blue tit song in response to playback, and many associated mainly with blue tits during the breeding season. There was large individual variation in the use of blue tit song, and in contrast to previous findings from zebra finches (Clayton 1988), we found a positive relationship between the use of blue tit song and the apparent preference for blue tit females. Although the relationship was only marginally significant, it suggests that varying degrees of misimprinting may have parallel effects on song and sexual preferences. However, as the relationship between mate preference and the use of blue tit song by cross-fostered great tits was not very strong, much of the variation in the use of blue tit song by cross-fostered great tits has yet to be explained. In contrast to zebra finches (Clayton 1988), we found no evidence that great tit males reared by mixed species pairs developed a sexual preference for heterospecific females (PAPER I). Although we did not conduct mate choice experiments, this suggests that one heterospecific parent is not enough for great tit males to get sexually misimprinted. Pied flycatchers differ from both great tits and zebra finches in that their sexual preferences are not affected by heterospecific cross-fostering (Slagsvold 2004). Hence, sexual imprinting is not present in all species showing song learning, and as pointed out by ten Cate, Vos et al. (1993), it is not a necessary precursor for song learning in young songbirds.

In contrast to the strong effect of the cross-fostering on some great tit males, other cross-fostered males only responded to playback with great tit song, and some mated with conspecific without showing a noticeable interest in blue tits. This suggests that there is a varying degree of own-species bias in the development of both song tutor preferences and mate preferences, which is comparable with the mixed tutor choice and mixed mate preference of zebra finches that grow up with one or two heterospecific foster parents (Clayton 1988, 1989). An own-species bias may result from the behaviour of the foster parents (Clayton 1988). When zebra finches are reared by Bengalese finches, the consolidation of their heterospecific mate preference is affected by how much they have been fed by the foster parents (Bischof and Clayton 1991; Oetting et al. 1995), and when reared by heterospecifics, zebra finch males generally receive less parental care than normal (ten Cate

1982). If this is also the case for great tits reared by blue tits, variation in the degree of parental care received from the foster parents may account for some of the variation in song and mate preference in cross-fostered great tit males.

7.3. Vocal plasticity and adult song learning

A number of songbird species, including closed-ended learners, have been shown to modify the use of their repertoires in response to social factors such as territorial neighbours (e.g. Baptista and Morton 1988; Nelson 2000; Kipper and Hultsch 2006; Franco and Slabbekoorn 2009). In PAPER II, we investigated whether cross-fostered great tit males would modify their use of blue tit song as a result of interactions with conspecifics and heterospecifics. We did not find evidence for changes in the use of blue tit song that could be attributed to the age or the mating associations of the subjects. However, we did find an effect of social interactions on the likelihood that a cross-fostered great tit male would respond to great tit or blue tit playback with song. Males currently associated with blue tits increased their response to blue tit song whereas males currently associated with great tits increased their response to great tit song through the season (PAPER II). In our study area, 30% of control broods of both species have been found to contain at least one nestling sired by an extra-pair male (Johannessen et al. 2005). Thus, male intruders of the same species as the resident female constitute a serious threat to the fitness of the resident male. Exposure to intruders that were conspecific to the resident female may thus have made the subjects more responsive to the song of this species.

True adult song learning differs from changes in the use of already acquired song elements. As Beecher and Brenowitz (2005) pointed out, it only takes one bird to demonstrate that a species is an open-ended learner. However, due to the challenge of determining the time of memorization of new elements, true adult song learning has previously been demonstrated in very few species, and only in laboratory studies where the exposure to different vocal stimuli can be carefully monitored (Chaiken et al. 1994; Todt and Geberzahn 2003). PAPER IV in this thesis provides the first evidence for true adult song learning from a field experiment. After a one-week playback treatment, three out of 20 subjects had copied a foreign syllable type that had never previously been recorded in the study area. We had predicted that the functions of adult song learning might be for males to increase their repertoire size or the song sharing with territorial neighbours. However, neither of these ideas were supported by our findings, as the syllable sharing with the playback stimulus repertoires had not changed, and the subjects' repertoires had decreased rather than increased. It is

possible that the function of adult song learning in pied flycatcher males is to increase their repertoire size, but that the increase does not become apparent until the following spring. If that is the case, learning from territorial neighbours may be one of the means by which repertoire sizes increase with age and breeding experience in pied flycatcher males (Espmark and Lampe 1993; Lampe and Espmark 1994). An alternative is that adult song learning enables pied flycatcher males to copy syllable types that females find particularly attractive. Particular phrases that increase the sexual response in females have been found in canary *Serinus canaria* song (Vallet and Kreutzer 1995), although it is not known whether pied flycatcher song contains such 'sexy syllables'.

It is currently not known whether great tits are true adult song learners. In a field study, McGregor and Krebs (1989) found that great tit males would add song types to their repertoires after experience with new neighbours. However, the study seemed to lack information about previous exposure to the new song types. Unfortunately, the song of the great tits at the Dæli study site has not been studied as persistently as that of the pied flycatcher population at Sinober. Hence, we did not have the necessary information to test the song learning ability of adult great tit males.

7.4. The functions of song

A number of studies of great tits and pied flycatchers suggest that the main function of song differ between the two species, both because of the timing of the peak in song activity and because of the response to the song by conspecifics. The seasonal peak in great tit song activity takes place after pairing (Krebs et al. 1978), suggesting that great tit song is related to territorial behaviour rather than mate attraction (Krebs 1976). Neighbouring great tit males usually share some song types, and matched countersinging between neighbours is common (Krebs 1976). Furthermore, when territorial males are replaced by a speaker playing great tit song, the territories take longer to be occupied by new settling males compared to control areas without song, and the effectiveness of the playback at repelling settling males is affected by repertoire size (Krebs et al. 1978). Larger repertoires may reduce habituation in the listener, and thus maintain the effectiveness of the song as a territorial signal (Krebs 1976). However, also great tit females may pay attention to male song. Baker et al. (1986) found that hormone-induced great tit females displayed more to playback sequences of three to five song types than to sequences of only one or two song types. Males with larger repertoires do not seem to pair earlier (McGregor et al. 1981). However, McGregor et al.

(1981) found a positive relationship between repertoire size and the likelihood that a great tit male would survive and breed in later years. This suggests that great tit song may play a role in attracting extra-pair mates. Great tits continue singing at high levels during egg laying and incubation (Amrhein et al. 2008), and females' visits to the territories of neighbouring males during the peak fertile period has been found to be affected by the outcome of singing interactions between the territorial male and an interactive playback stimulus (Otter et al. 1999; but see Otter et al. 2001).

Cross-fostered great tits defend their territories against blue tit intruders (Hansen and Slagsvold 2003). When responding to simulated territorial intrusion, cross-fostered great tits match the song of the intruder on the species level (PAPER II), suggesting that the blue tit song in the repertoires of these great tit males may serve to repel blue tit males from their territories. Great tits in a Belgian population have been shown to use heterospecific song type matching to defend their territories against blue tit intruders (Gorissen et al. 2006), and thus the behaviour of the cross-fostered Norwegian great tits is not without parallel in unmanipulated populations. An additional benefit of heterospecific song in the repertoires of cross-fostered great tit males may be to attract extra-pair mates if there are cross-fostered blue tit females in the neighbourhood.

In pied flycatchers, the main function of song seems to be female attraction rather than male-male competition. In contrast to great tits, pied flycatcher males sing at high levels before pairing, but their singing activity decreases substantially after obtaining a mate (Gottlander 1987; Espmark and Lampe 1993). On the other side, pied flycatcher females are attracted to male song (Eriksson and Wallin 1986) and seem to prefer males with large repertoires (Lampe and Saetre 1995). In pied flycatchers, repertoire size is correlated with breeding experience, body mass, and territory quality (Lampe and Espmark 1994, 2003), and can thus provide relevant information to prospecting females.

The cross-fostered pied flycatchers studied in PAPER III did not increase the size of their repertoires compared to controls through early heterospecific song learning, nor did the subjects of PAPER IV increase their repertoires within the season by learning foreign syllable types as adults. Furthermore, even though adult song learning may contribute to the larger repertoires found in older and more experienced males (Espmark and Lampe 1993; Lampe and Espmark 1994), pied flycatcher males frequently drop syllable types from their repertoire over time (Espmark and Lampe 1993). Hence, they never expose their complete lifetime syllable repertoire within the time frame that prospecting females have available to choose their mate. This may suggest that other constraints than the number of memorized syllable

types limit a male's expressed syllable repertoire at a given time, or that here are trade-offs between repertoire size and other song parameters that are relevant to prospecting females. A possible function of adult song learning in pied flycatchers is to enable males to pick up particularly attractive syllable types. Two of the males that picked up a foreign syllable type from the playback in PAPER IV had been exposed to the same playback stimulus recording, and these males both picked up the same foreign syllable type. This may be taken as circumstantial evidence that there is some agreement about which syllable types are attractive and worth learning.

8. CONCLUDING REMARKS

Together with previous findings from heterospecifically reared songbird males, the findings in this thesis suggest that song tutor choice in oscine songbirds cannot be attributed to one single mechanism. The fact that male songbirds reared by heterospecific foster parents learn both conspecific and heterospecific song (e.g. Clayton 1988; Johannessen et al. 2006; PAPERS I, II and III) corroborates the existence of a conspecific bias (Marler 1970), but it also lends support to the idea that familiarization with the social father affects who are perceived as song tutors (Böhner 1990; Payne et al. 1998). Furthermore, the findings of PAPER I are consistent with the hypothesis of mother-mediated tutor choice, suggesting that song tutor choice is affected by familiarization with the mother as well as the father, and they thus add to previous findings from the laboratory (Clayton 1988). However, the findings in PAPER I might also result from experience with blue tit song in the repertoires of the fathers. Finally, in the familiarization process that shapes the song tutor preferences of young males, siblings may play an additional role to that of the foster parents (PAPER III). These different mechanisms are not mutually exclusive, and although different factors may prevail in different species, they probably all play a role in shaping the song tutor preferences of wild songbirds.

The relationship between song learning and sexual imprinting differs between the species studied to date. Zebra finches and great tits show both song learning and sexual imprinting (Clayton 1988; ten Cate, Vos et al. 1993; Slagsvold et al. 2002; Johannessen et al. 2006). However, in zebra finches, one heterospecific foster parent can be enough to cause sexual misimprinting (Clayton 1988), whereas great tits have only been found to get sexual misimprinted when both foster parents were heterospecifics (Slagsvold et al. 2002, PAPER I). PAPER II found a positive relationship between the use of blue tit song and the apparent preference for blue tit females in cross-fostered great tit males; a relationship that has not been found in cross-fostered zebra finches (Clayton 1988). Although the relationship was only marginally significant, it suggests that varying degrees of misimprinting, resulting from e.g. variation in parental care, may have parallel effects on song and sexual preferences in great tit males. Pied flycatchers differ from both great tits and zebra finches in that they do not seem to show sexual imprinting (Slagsvold 2004; Saether et al. 2007). Hence, sexual imprinting is not present in all species showing song learning, and it is not a necessary precursor for song learning in young songbirds.

In order to determine whether a songbird species is a true open-ended learner, it is necessary to ensure that novel song elements added to the repertoire of an adult were not heard and possibly memorized earlier in life. This has so far not been achieved for great tits. PAPER IV revealed an ability to learn foreign syllable types in adult pied flycatcher males. The function of adult song learning in this species may be to increase the repertoire size and thus their attractiveness to females, although no repertoire increase was found within the breeding season. Alternatively, adult song learning may enable pied flycatchers to pick up particularly attractive syllable types from breeding neighbours.

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COMPILATION OF PAPERS (I-IV)

