

From nestlings to adults

Song perception and function in the pied flycatcher

Lan Ma



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Academic dissertation for the Degree of Doctor of Philosophy in Ethology at Stockholm University to be publicly defended on Monday 15 June 2026 at 13.00 in Vivi Täckholmsalen (Q-salen), NPQ-huset, Svante Arrhenius väg 20.

Abstract

Sexual signals and preferences play a central role in mate choice, sexual selection, and reproductive isolation. When such traits are learned rather than genetically fixed, maintaining their accuracy and alignment becomes a major evolutionary challenge, raising the question of how learned mating traits remain sufficiently stable to function in communication and reproduction. Birdsong is one such trait. In songbirds, songs are acquired through social learning, and successful song development depends on young individuals attending to, discriminating, and learning from appropriate acoustic models. Understanding how early song responses arise, what shapes tutor-related biases, and whether adult song reliably reflects broader aspects of male quality is therefore important for explaining the development and evolution of learned sexual signals.

In this thesis, I investigate these questions in the pied flycatcher (*Ficedula hypoleuca*), focusing on early song discrimination and the information content of adult song. In Chapter I, I examine whether nestlings discriminate between their social father's song and that of an unfamiliar local male. I show that 13-day-old nestlings respond more strongly to their social father's song, indicating that nestlings can distinguish socially familiar from unfamiliar conspecific songs at an early age.

In Chapter II, I test whether nestlings respond differently to simplified short songs versus longer complex songs played back from either their social father or an unfamiliar male. Nestlings showed stronger postural begging responses to shorter songs regardless of familiarity, suggesting that both early auditory experience and intrinsic acoustic salience contribute to early song responsiveness.

In Chapter III, I investigate whether early discrimination of paternal song reflects inherited predispositions or early auditory experience using an embryonic cross-fostering experiment in the wild. Nestlings reared by genetic or foster parents were exposed to songs from their social father, genetic father, and an unfamiliar male. Nestlings showed no differential begging responses to the three treatments. As begging was strongly influenced by nestling condition, these results suggest that playback assays may underestimate auditory discrimination when nestling motivation is low, and the data remain inconclusive about the relative contributions of experience and predisposition.

In Chapter IV, I shift to adult sexual signalling and test whether song complexity predicts cognitive ability in breeding males, using a novel foraging task and a detour reaching task. Contrary to the hypothesis that preferred song traits signal cognitive quality, I find no consistent positive relationship between song complexity and cognitive performance. The traits most strongly linked to female preference were unrelated or negatively related to task performance, suggesting that song complexity is unlikely to serve as a straightforward indicator of cognition.

Together, these findings shed new light on how learned sexual signals emerge, are shaped during development, and are maintained in natural populations.

Keywords: *bird song, vocal learning, song discrimination, early auditory experience, cross-fostering, sexual selection, song complexity, cognition, pied flycatcher.*

Stockholm 2026
<http://urn.kb.se/resolve?urn=urn:nbn:se:su:diva-254633>

ISBN 978-91-8107-662-2
ISBN 978-91-8107-663-9

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ISBN print 978-91-8107-662-2

ISBN PDF 978-91-8107-663-9

Cover image:

Printed in Sweden by Universitetservice US-AB, Stockholm 2026

To curiosity, and to the
joy of not yet knowing.

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I **Lan Ma**, Samyuktha Rajan, Fanny Linn-Kraft, Mario Gallego-Abenza, David Wheatcroft. Nestling pied flycatchers, *Ficedula hypoleuca*, recognize the songs of their social fathers. *In preparation*.
- II **Lan Ma**, Samyuktha Rajan, Fanny Linn-Kraft, Mario Gallego-Abenza, David Wheatcroft. Do nestling songbirds prefer simple songs? *In preparation*.
- III **Lan Ma**, Mario Gallego-Abenza, Miriam Kuspiel, David Wheatcroft. Nature or nurture in recognition of paternal song by pied flycatcher nestlings. *In preparation*.
- VI **Lan Ma**, Mario Gallego-Abenza, Miriam Kuspiel, Samyuktha Rajan, David Wheatcroft. Song complexity and cognitive ability are not consistently related in the pied flycatcher (*Ficedula hypoleuca*). *In preparation*.

Candidate contributions to thesis articles*

	I	II	III	IV
Conceived the study	Substantial	Substantial	Substantial	Substantial
Designed the study	Substantial	Substantial	Substantial	Substantial
Collected the data	Substantial	Substantial	Substantial	Substantial
Analysed the data	Substantial	Substantial	Significant	Significant
Manuscript preparation	Substantial	Substantial	Substantial	Substantial

***Contribution Explanation**

Minor: contributed in some way, but contribution was limited.

Significant: provided a significant contribution to the work.

Substantial: took the lead role and performed the majority of the work.

On bird song and listening

Birdsong is one of the first signs of spring. Long before the trees leaf out, the dawn chorus fills the air, and for many people, it is their first point of contact with the natural world. We notice birdsong because it is beautiful, because it is loud, and because it seems to come from nowhere and everywhere at once. More than two centuries ago, Gilbert White observed that “as long as there is any incubation going on there is music.” Yet we rarely stop to ask what that music sounds like from the other side, from the perspective of a young bird hearing song for the very first time.

For a nestling songbird, the world begins in darkness. Eyes closed and confined to a nest cup, it has no way of seeing who is around or where it is. What it can do is listen. The songs and calls of its parents are among the earliest and most consistent sounds it encounters, arriving with every feeding visit, every territorial defence, and every quiet interval in between. Long before a nestling is old enough to sing itself, it is already immersed in an acoustic environment shaped by the adults that raise it.

This matters because in songbirds, song is not innate but learned. Like any learned behaviour, what is eventually produced depends on what was experienced early in life. A young bird must somehow identify the right sounds to attend to, distinguish them from the many other sounds in its environment, and later reproduce something recognisable from memory. How does it know what to listen to? Does it already possess some bias toward the sounds of its own species, or does it build that knowledge entirely through experience? And once a male has developed his song, does that song tell us, or a female choosing a mate, anything meaningful about who he is?

These are old questions in the study of birdsong, and they have no single answer. Song learning varies enormously across species, and the mechanisms that guide it are still not fully understood. This thesis takes a small step toward understanding them by asking what young birds can hear before they can sing, what shapes the sounds they attend to, and whether the songs adults produce carry information beyond their melody.

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Sexual signals and reproductive isolation

Sexual selection has produced an extraordinary diversity of ornaments and signals across animal taxa, from the elaborate tail feathers of peacocks to the complex courtship dances of birds-of-paradise. These signals serve two broadly recognized functions: attracting mates and competing with rivals for access to mating opportunities (Andersson 1994). In many species, females choose mates based on the expression of specific signal traits, while males use the same or related traits to establish and defend territories against competitors (Searcy and Nowicki 2005). The evolution and maintenance of these signals is therefore shaped by both intersexual and intrasexual selection, with direct consequences for individual reproductive success. More broadly, sexual selection has long been viewed not only as a driver of trait elaboration within populations, but also as a process that can contribute to divergence between populations when signals and preferences evolve in concert (Andersson 1994; Moran et al. 2020; Mendelson and Safran 2021; Schield et al. 2024).

Signal divergence between populations or species is now widely recognized as one of the key mechanisms through which reproductive barriers arise. When populations become geographically isolated, differences in sexual signals and associated preferences can accumulate through divergent selection, sexual selection, or genetic drift (Coyne and Orr 2004; Price 2008). If these populations later come into secondary contact, individuals that preferentially mate with partners bearing familiar signal traits will avoid costly hybridization, while those that fail to discriminate may produce offspring of reduced fitness (Lachlan and Servedio 2004). In this way, divergence in sexual signals can function as a pre-mating barrier, limiting gene flow between populations and reinforcing reproductive isolation. This logic has been particularly important

in discussions of incipient speciation, where behavioural isolation may arise before strong post-mating barriers are established (Uy et al. 2018).

The importance of signal divergence for species boundaries is well illustrated in systems where closely related species coexist. In túngara frogs (*Engystomops pustulosus* and relatives), females choose mates based on species-specific features of male advertisement calls, and acoustic divergence between sympatric species is a primary mechanism maintaining reproductive isolation (Ryan and Rand 1993). In Lake Victoria cichlids, closely related species that coexist in the same waters differ primarily in male nuptial colouration, and females preferentially mate with males matching their own species' colour. When experimental lighting conditions obscure these colour differences, females fail to discriminate and hybridization increases dramatically, demonstrating that signal divergence alone can be sufficient to maintain species boundaries (Seehausen et al. 1997). These examples highlight a general principle: when signals and preferences are aligned, they can effectively prevent hybridization even in the absence of strong post-mating barriers.

However, for signal based reproductive isolation to be maintained, the signals themselves must remain sufficiently distinct and the associated preferences sufficiently strong. This requirement raises a fundamental challenge when signals are not genetically fixed but instead acquired through learning during development, a challenge that is the focus of the next section.

The challenge of learning

Not all sexual signals are genetically fixed. In many animal taxa, mating signals, preferences, or both are acquired through learning during develop-

ment (Verzijden et al. 2012). Mate preferences can be shaped by sexual imprinting in birds and fish (Irwin and Price 1999; Verzijden et al. 2005), and signals themselves can be socially transmitted, as in the acoustic displays of cetaceans and songbirds (Catchpole and Slater 2008; Garland and McGregor 2020). Learning makes the signalling system flexible, as individuals can adjust their signals to match the local social environment, improving communication with neighbours, competitors, and potential mates (Beecher and Brenowitz 2005). Socially transmitted traits can also change more rapidly than genetically encoded ones, potentially accelerating cultural divergence between isolated populations (Lachlan and Servedio 2004).

Yet these same properties create vulnerabilities. When signals are learned, individuals may acquire inappropriate models by copying the wrong species, the wrong population, or low quality variants, leading to mismatches between what is signalled and what receivers prefer (Slabbekoorn and Smith 2002). If individuals from divergent populations come into contact and learn from one another, previously accumulated signal differences can erode within a single generation, effectively reversing the process of divergence (Olofsson et al. 2011). Whether learned signals promote or undermine reproductive isolation therefore depends critically on what individuals learn, from whom, and when during development. These questions require a system in which learning mechanisms can be studied in detail.

Birdsong provides precisely such a system. In the three major avian clades capable of vocal learning (oscine songbirds, parrots, and hummingbirds) mating songs are acquired through social imitation rather than inherited as fixed motor patterns (Catchpole and Slater 2008). Among these, oscine songbirds have been studied most extensively, owing to their elaborate songs, specialized vocal control musculature, and well-characterized neural circuitry for song learning and production (Bolhuis et al. 2010). Song serves two broadly recognized functions in songbirds, attracting mates and mediating competition

among rivals, both of which impose strong selection on song structure and performance. Although female song is widespread and ancestral in songbirds (Odom et al. 2014), this thesis focuses primarily on species in which only males sing, as is the case in the pied flycatcher like most temperate bird species.

In the context of mate attraction, females attend to multiple dimensions of male song. At the broadest level, song content conveys species identity: females preferentially respond to conspecific over heterospecific songs, and in species with geographic song variation, to songs of the local population over foreign ones (Searcy et al. 2002; Danner et al. 2011). Beyond species or population identity, females also evaluate song performance traits that may indicate individual male quality. Females in many species prefer males that sing more frequently or for longer durations, that produce larger repertoires, that perform physically demanding song features such as rapid trills at wide frequency bandwidths, or that sing familiar songs (Catchpole and Slater 2008). In swamp sparrows (*Melospiza georgiana*), females show stronger solicitation responses to songs approaching the upper limit of vocal performance, suggesting that song traits constrained by production ability serve as honest indicators of quality (Ballentine 2004). In songbirds such as zebra finches (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata domestica*), females develop preferences for their father's song through early auditory experience, and these preferences can co-emerge with sexual preferences in adulthood (Riebel 2000; Fujii and Okanoya 2022).

Song also functions prominently in intrasexual competition. Playback and removal experiments have demonstrated that song alone is sufficient to maintain territorial boundaries: when a territory owner is removed but its song continues to be broadcast, rival intrusions are delayed or prevented (Krebs 1977; Nowicki, Searcy and Hughes 1998). Beyond simple occupancy signalling,

males modulate their singing behaviour during territorial encounters. Behaviours such as song type matching, frequency matching, and song overlapping have been interpreted as graded aggressive signals, although their reliability as predictors of attack varies across species (Searcy and Beecher 2009). In song sparrows (*Melospiza melodia*) and swamp sparrows, low amplitude "soft songs" have been shown to reliably predict imminent aggression, functioning as honest threat signals (Searcy and Nowicki 2006; Ballentine et al. 2008).

Because song is learned, culturally transmitted, and simultaneously under selection from both female choice and male competition, it offers an ideal framework for investigating how learned sexual signals develop, how they are maintained despite the potential for disruption, and what information they carry about the signaller. The remainder of this introduction examines these questions in turn.

How song learning works

The process of song learning

Since the pioneering work of Thorpe, who demonstrated that chaffinches (*Fringilla coelebs*) raised in acoustic isolation develop only rudimentary songs lacking species-typical structure (Thorpe 1954), and Marler, who showed that geographic variation in chaffinch song reflects cultural rather than purely genetic differences (Marler 1952), the study of song learning has become central to understanding how vocal signals develop and diversify.

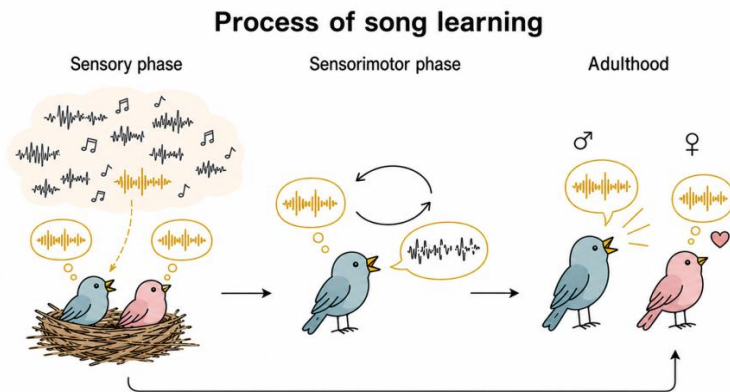


Figure 1. Schematic of the two-stage process of song learning in songbirds, from the sensory phase in early life through the sensorimotor phase to adult song. The figure depicts a species in which only males sing, as in the pied flycatcher.

The song learning process is typically described in two stages (Marler 1970, Figure 1). During the sensory phase, which begins early in life and often co-

incides with a species-specific sensitive period, juveniles listen to nearby singing adults and form an internal auditory representation of the songs they hear, commonly referred to as the auditory template (Marler 1970; Soha 2017). The onset and duration of the sensory phase vary across species and can be modulated by experience: juveniles exposed only to heterospecific songs, for instance, may retain sensitivity to conspecific song input for longer than those raised with conspecific tutors (Brainard and Doupe 2002). During the subsequent sensorimotor phase, juveniles begin to vocalize. Early vocalizations are quiet, unstructured sounds known as subsong, comparable to babbling in human infants (Brenowitz et al. 1997). Through repeated practice and self-monitoring, these are gradually refined into more structured plastic song and eventually crystallize into stable adult song that matches the memorized template (Konishi 1965; Marler 1970). Auditory feedback is critical throughout this process: juveniles deafened after memorization but before crystallization produce severely degraded songs, demonstrating that birds must hear themselves to refine their output (Konishi 1965).

The sensorimotor phase of song learning depends on a set of specialized brain nuclei collectively known as the song system. The vocal control region HVC plays a central role in song production and sensory integration, while RA (the robust nucleus of the arcopallium) serves as the primary motor output, and Area X and LMAN (lateral magnocellular nucleus of the anterior nidopallium) form part of a basal ganglia–thalamo–cortical loop involved in vocal variability and learning (Nottebohm et al. 1986; Mooney 2009). These song control nuclei undergo rapid growth during early post-hatching development and are among the most striking examples of experience-dependent neural plasticity in vertebrates (Nottebohm F et al. 1986). Crucially, the development of these nuclei is highly sensitive to environmental conditions during early life, such that early-life stress can leave lasting effects on adult song, an idea

I return to when discussing what song complexity may signal about male quality.

What shapes song learning

Young songbirds do not simply copy every sound they hear. The outcome of song learning is shaped by an interplay between innate predispositions and social experience, with their relative contributions varying across species and contexts.

Innate predispositions toward species-typical song features have been demonstrated across a range of songbird species. In classic isolation experiments, birds reared without exposure to adult tutors still produce songs retaining basic species-specific structure, although these songs are abnormal compared to those of wild-reared birds (Konishi 1965; Marler 1970). When exposed to a mixture of conspecific and heterospecific songs, juvenile swamp sparrows selectively memorize and reproduce only conspecific elements (Marler and Peters 1977). Cross-fostering studies reinforce this pattern: pied flycatchers raised by blue tits (*Cyanistes caeruleus*) incorporate some foster parent song elements but retain a predominantly conspecific song repertoire (Eriksen et al. 2009), and pied flycatcher eggs translocated between populations develop songs that partially resemble their ancestral population even when raised entirely in a foreign acoustic environment (Rajan et al. 2024). Within-species predispositions have also been documented at the population level: white-crowned sparrow (*Zonotrichia leucophrys*) juveniles show a preference for learning their own subspecies' song over that of a foreign subspecies (Nelson 2000). Such predispositions may have a genetic basis rooted in the auditory processing regions of the brain, potentially linking inherited neural architecture to selective attention during early song learning (Wheatcroft and Qvarnström 2015). These findings indicate that songbirds are not blank

slates but arrive with perceptual or cognitive biases that filter what they attend to and memorize.

At the same time, social experience profoundly shapes what birds learn. Laboratory experiments in white-crowned sparrows demonstrated that juveniles learn more effectively from live tutors than from tape recordings, and that social interaction can extend the sensitive period beyond its normal closure (Baptista and Petrinovich 1984). In zebra finches, the presence of a singing tutor activates specific midbrain neurons that trigger dopamine release in song control areas, providing a neural mechanism through which social context facilitates learning (Tanaka et al. 2018). Field studies in song sparrows show that juveniles preferentially learn from adults that sing frequently and interact actively with other territorial males, even without direct contact with the juvenile (Beecher 2017). Social interaction with females can also influence learning outcomes: in zebra finches, the presence of a female improves the accuracy with which juveniles match their tutor's song (Carouso-Peck and Goldstein 2019).

Predisposition and experience do not operate independently. In zebra finches, innate perceptual biases and early acoustic experience jointly determine song learning outcomes, with neither factor alone sufficient to explain the full pattern of adult song (ter Haar et al. 2014). More broadly, predispositions appear to function as filters rather than rigid constraints: they bias learning toward relevant models but can be modulated, and in some cases overridden, by sufficiently strong social input (Beecher and Brenowitz 2005). Understanding how these factors interact during development is essential for explaining why songs remain population typical despite the flexibility inherent in vocal learning.

When and from whom: timing and tutor selection

The outcome of song learning depends not only on what biases a young bird brings to the process, but also on when learning occurs and which individuals serve as models. Both factors ultimately determine what songs a male produces as an adult, and therefore play a central role in the transmission and evolution of song culture.

Species differ markedly in the developmental window during which they are receptive to song input. In closed-ended learners such as zebra finches and white-crowned sparrows, the sensitive period is restricted to the first weeks or months of life, after which song structure becomes largely fixed (Marler and Tamura 1964; Immelmann 1969). Songs heard during this early window shape the individual's lifelong repertoire, regardless of subsequent acoustic experience. In these species, accurate song learning depends critically on the quality and timing of early social and acoustic experience. At the other extreme, open-ended learners such as canaries (*Serinus canaria*), European starlings (*Sturnus vulgaris*), and nightingales (*Luscinia megarhynchos*) retain the capacity to acquire or modify songs throughout adulthood, often in association with seasonal cycles of neural plasticity in the song control system (Nottebohm et al. 1986; Chaiken et al. 1994; Hultsch et al. 2004). In these species, song learning may be closely tied to changes in social environment, competitive context, or breeding opportunities, enabling males to adjust their songs to local conditions or new neighbours.

The identity of the tutor is also consequential for song outcomes. In some species, the father is the primary model. This pattern is best documented in zebra finches, where sons copy their father's song with high fidelity in both captive and wild populations (Clayton 1987; Zann 1990). It is also a classic feature of Darwin's finches (*Geospiza* spp.), where the close resemblance of sons' songs to their fathers' has been linked to assortative mating and the

maintenance of species boundaries (Grant and Grant 1996). Father based learning is most likely when the sensory phase begins early and ends before dispersal, limiting the juvenile's exposure to alternative models (Catchpole and Slater 2008). Learning from the father under these conditions may be adaptive because paternal song provides an early, stable, and locally appropriate template from a male that has already bred successfully, reducing the risk of acquiring socially ineffective or heterospecific songs when alternative tutors are unavailable (Catchpole and Slater 2008). Learning from the father may also benefit from higher quality social interaction compared to passive exposure to more distant singers (Beecher and Burt 2004).

In other species, neighbouring territorial males serve as the primary tutors. In song sparrows, juveniles learn most of their repertoire from natal year neighbours and subsequently adjust it to better match breeding year neighbours after territory settlement (Beecher et al. 1994; Nordby et al. 2007). Learning from neighbours promotes local song sharing, which can facilitate territorial interactions through mechanisms such as song type matching and the maintenance of "dear enemy" relationships (Beecher et al. 2000). From an evolutionary perspective, neighbour tutoring promotes local conformity and the maintenance of dialects, while still allowing for limited innovation when individuals integrate elements from multiple neighbours. Evidence from Savannah sparrows (*Passerculus sandwichensis*) suggests that tutor selection can be stage dependent rather than exclusive. Juveniles initially learn from a combination of their social father and nearby natal year neighbours, but later incorporate or preferentially retain song types from breeding year neighbours after territory settlement (Wheelwright et al. 2008; Williams et al. 2013). This mixed strategy allows young males to acquire species typical song early while retaining flexibility to adjust their repertoire to the local social environment encountered at settlement.

Together, the timing of the sensitive period and the identity of the tutor shape what songs are acquired, how faithfully they are transmitted across generations, and how much variation accumulates within and between populations. Despite extensive study, however, identifying the precise tutors that juveniles learn from in natural populations remains difficult, particularly when adult songs do not closely resemble those of any candidate model (Beecher and Brenowitz 2005). One way to address this challenge is to focus on the earliest stages of development, when the acoustic and social environment of a nestling is still limited and more readily characterized.

The nestling period: early song experience and discrimination

Early life stages are critical for song learning in birds. The sensory phase, during which juveniles form auditory memories of the songs they hear, coincides with a period of heightened neural plasticity in the song control system, particularly in regions such as HVC and RA that govern song production and imitation (Brainard and Doupe 2002). Disruption of auditory input during this period leads to highly abnormal songs, impairing communication and reproductive success (Konishi 1965; Nelson and Marler 1994). It was long presumed that an innate auditory template helps young birds identify appropriate conspecific models at the onset of learning, with acoustic experience before the post-fledging sensory phase assumed to play little role (Marler 1970; Soha 2017). However, growing evidence indicates that sensitivity to acoustic stimuli begins earlier than previously recognized, with relatively well-established effects during the nestling stage and more contested evidence for learning during embryonic development (Colombelli-Négrele et al. 2012; Katsis et al. 2018), raising the question of what role this early period plays in shaping subsequent song learning.

Playback experiments across several species have demonstrated that nestlings discriminate among vocal stimuli well before fledging. In several songbird species, nestlings respond more strongly to conspecific than heterospecific song and to local than foreign dialects (Nelson and Marler 1993; Nelson 2000; Shizuka 2014; McFarlane et al. 2016; Wheatcroft and Qvarnström 2017; Hudson et al. 2019; Hudson et al. 2020; Schroeder and Ramage-Healey 2021; Wheatcroft et al. 2022; Schroeder and Podos 2023). These findings indicate that nestlings are not passive receivers of acoustic input but are already extracting and responding to biologically relevant features of the songs around them. Whether this early discrimination reflects innate predispositions, early auditory experience, or their interaction remains an open question, one that is difficult to resolve because genetic background and acoustic environment are typically confounded in the wild.

Beyond species and population level discrimination, the ability to distinguish among individual conspecific males is of particular interest. The social father represents a uniquely relevant acoustic model: as a male that has survived and attracted a mate locally, his song provides a cue to traits that are both species-typical and locally successful. Early familiarity with the father's song could bias subsequent learning toward acoustically similar models, providing a proximate mechanism through which local song traditions are maintained. Evidence from zebra finches supports this logic: juvenile males respond more strongly to their father's song than to unfamiliar male songs, and the strength of this early preference predicts later song copying accuracy (Rodríguez-Saltos et al. 2023). Moreover, early learned preferences need not remain restricted to a single familiar exemplar but can generalize to acoustically related songs (Wei et al. 2022), suggesting that familiarity with one tutor could shape responses to a broader range of relevant models. Whether nestlings discriminate between familiar and unfamiliar conspecific songs remains largely untested outside the zebra finch system. *This raises a central question*

addressed in Chapter I: do nestlings respond differently to their social father's song than to the song of an unfamiliar local male?

If nestlings do discriminate in favour of their father's song, an immediate question follows: what underlies this ability? Early discrimination could reflect inherited perceptual biases that direct attention toward particular acoustic features independently of experience, or it could arise from auditory learning during the nestling period. These two mechanisms are not mutually exclusive, and their relative importance may differ depending on the level of discrimination. In many wild passerines, fathers sing much less after pairing, and nestlings may hear as many or more songs from neighbouring males as from their own father (Labra and Lampe 2018), complicating any simple experience based account. Disentangling genetic and experiential contributions requires experimental designs that dissociate the two. *Whether early discrimination of the father's song reflects auditory experience during the nestling period or inherited predispositions is the focus of Chapter III.*

A closely related question concerns what version of the father's song nestlings are actually exposed to during this period. In many species, males shift their singing behaviour after pairing, producing shorter, simpler songs with fewer syllable types compared to the complex songs used during mate attraction (Espmark and Lampe 1993). Nestlings are therefore exposed primarily to a simplified version of the father's song rather than the full complex repertoire. If these simplified songs share key acoustic features with the complex songs used in adult contexts, they could serve as an accessible entry point for recognizing and later learning more elaborate conspecific songs. Alternatively, nestlings may respond more strongly to short songs simply because simpler acoustic input is inherently easier to process, a possibility consistent with findings in zebra finches, where excessive exposure to abundant song models reduces learning efficiency (Tchernichovski et al. 1999). *This raises the question addressed in Chapter II: do nestlings respond differently to short and*

long versions of conspecific songs, and does this response depend on song familiarity?

Why complex song

The preceding sections have focused on how nestlings perceive and respond to song during early development. But early song experience shapes what males eventually produce as adults, and an equally important question is what the resulting song communicates to receivers. As discussed previously, females in many songbird species are attracted to males that sing more, sing longer, or produce larger repertoires. But why should females prefer these traits? For such preferences to evolve and be maintained, the song traits females attend to must reliably indicate some aspect of male quality from which females gain direct or indirect benefits (Searcy and Nowicki 2005). Unlike a single ornament such as a brightly coloured patch, however, song is a complex, multidimensional signal, and different components may be constrained by, and therefore advertise, different aspects of quality (Gil and Gahr 2002).

Some song traits appear to signal current condition or competitive ability. Song output, for example, is constrained by time and energy budgets: because singing and foraging are largely incompatible, sustained singing represents an opportunity cost that only males in good condition can bear (Berg et al. 2005). Song performance traits such as trill rate are constrained by physical limits on vocal production, meaning that songs approaching the upper performance boundary may honestly reflect neuromuscular capacity (Podos 1997). Song can also reflect age and breeding experience: repertoire size and song diversity tend to increase with age in a range of passerines, making these traits potential indicators of survival ability (Gil et al. 2001; Kiefer et al. 2006; Motes-Rodrigo et al. 2017). Additionally, song has been linked to health and immune state: males with larger repertoires can show reduced stress responsiveness

and stronger immune function (Pfaff et al. 2007; MacDougall-Shackleton et al. 2009), and experimental parasite exposure can reduce song complexity later in life (Spencer et al. 2005).

Among the various dimensions of song, song complexity, broadly defined as the diversity of acoustic elements within and across a male's songs, has received particular attention as a sexually selected trait. Measures of complexity include repertoire size (the number of unique syllable types a male produces), versatility (the diversity of syllables within individual songs), and syllable switching rate (how frequently a male changes between song types). Meta analyses indicate that song complexity is positively associated with mating success overall, though the strength of this relationship varies across species and is stronger in species with larger average repertoires (Soma and Garamszegi 2011; Robinson and Creanza 2019).

What aspect of male quality might song complexity signal? One influential framework is the developmental stress hypothesis. As discussed in Section 4, the song control nuclei undergo rapid growth during the early post-hatching period and are highly sensitive to environmental conditions during this window. Across a range of species, early-life stressors including nutritional restriction and parasite infection have been shown to reduce the volume of song control nuclei and impair subsequent song development (Spencer et al. 2003; Buchanan et al. 2004; Nowicki and Searcy 2004; Spencer et al. 2005; MacDonald et al. 2006; Peters et al. 2014). Under this framework, song complexity serves as an honest signal of developmental condition: only males that experienced favourable early-life conditions can sustain the neural investment required to produce complex songs (Nowicki, Peters and Podos 1998; Nowicki and Searcy 2004).

Extending this logic, if the developmental stressors that constrain song system growth also affect other neural structures, then song complexity might

additionally reflect cognitive ability, a latent quality that females cannot easily assess through direct observation but that may confer benefits such as enhanced foraging efficiency, better predator detection, or improved parental care (Cole et al. 2012; Cauchard et al. 2017; Griesser et al. 2023). The possibility that females use learned signals to assess cognitive traits in potential mates has attracted growing theoretical and empirical interest (Boogert et al. 2011). Consistent with this reasoning, nutritional deficits during early life impair spatial memory in Western scrub jays (*Aphelocoma californica*) and association learning in European starlings (Pravosudov et al. 2005; Farrell et al. 2016), suggesting that song and cognition may share a common developmental vulnerability. At the species level, comparative evidence also supports a link: species with larger vocal repertoires have larger brains and perform better on problem-solving tasks (Audet et al. 2023).

However, at the individual level, which is the scale most relevant to sexual selection and mate choice, the evidence is mixed, with positive, negative, and null associations reported across different species, song traits, and cognitive tasks (reviewed in Searcy and Nowicki 2019). Whether this inconsistency reflects domain-specific effects of developmental stress, methodological differences among studies, or a genuine absence of a general relationship remains unresolved. Field based tests of this hypothesis remain rare, particularly in species where song complexity is demonstrably preferred by females. *Whether song complexity reliably predicts cognitive ability at the individual level in the wild is the question addressed in Chapter IV.*

The pied flycatcher

The pied flycatcher (*Ficedula hypoleuca*) is a small, insectivorous passerine that migrates annually between breeding grounds across temperate Europe and Western Asia and wintering areas in sub-Saharan Africa (Lundberg and

Alatalo 2010). The species is sexually dimorphic in the breeding season, with males bearing a distinctive black and white plumage pattern and females a more cryptic brown colouration (Lundberg and Alatalo 2010). Pied flycatchers nest readily in artificial nest boxes, a trait that has made them among the most widely studied songbirds in Europe.

Males return to the breeding grounds in late April and establish territories by singing near suitable nest sites. Females arrive shortly after and choose mates based on a combination of song, plumage, and territory characteristics (Lampe and Espmark 1994; Sirkiä and Laaksonen 2009; Lundberg and Alatalo 2010). Pied flycatcher song is complex relative to many European passerines. Songs are composed of discrete acoustic units called syllables (Figure 2), which are the basic building blocks of song structure. Males produce large repertoires that can exceed 50 unique syllable types (Lampe and Saetre 1995; Eriksen et al. 2009). Song complexity can be characterized along multiple dimensions, including repertoire size (the total number of unique syllable types), syllable switching rate (how frequently consecutive songs contain non-overlapping syllable types), and versatility (the proportion of unique syllable types within individual songs) (Lampe and Espmark 1994; Motes-Rodrigo et al. 2017; Labra and Lampe 2018). Females prefer males with larger repertoires and higher versatility in both laboratory and field settings (Lampe and Saetre 1995; Lampe and Espmark 2003; Sirkiä and Laaksonen 2009), and song complexity correlates with indicators of condition including body mass and plumage brightness (Lampe and Espmark 1994). These properties make the pied flycatcher a strong system for testing whether song complexity signals cognitive ability, the question addressed in Chapter IV.

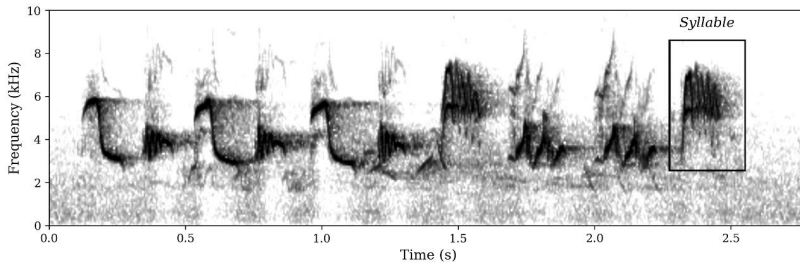


Figure 2. Spectrogram (frequency–time representation of the sound wave) of a pied flycatcher song. The black rectangle highlights one syllable, the basic acoustic unit of song.

After pair formation, males reduce their singing substantially, shifting from long, complex songs to shorter bouts with fewer syllable types (Espmark and Lampe 1993). This means that nestlings hear primarily a simplified version of their father's song during the nestling period rather than the elaborate songs produced during mate attraction, a feature of the species' biology directly relevant to Chapter II.

Songs are socially learned, and available evidence suggests that song acquisition may be shaped by experience both early in life and again around the first breeding season (Labra and Lampe 2018). Sons share more syllables with their social father than with neighbouring males, though the majority of adult syllables are unique and cannot be traced to any identified tutor (Labra and Lampe 2018). Some evidence suggests that pied flycatchers may be open-ended learners capable of acquiring new elements throughout life (Eriksen et al. 2011), though support for this remains weak. Tracking song acquisition longitudinally in wild pied flycatchers is difficult, as most nestlings disperse on migration and few return to breed at their natal site. The incomplete knowledge of tutor identity in this species underscores the importance of studying early auditory experience, when the acoustic environment is more limited and better characterized, a point central to Chapters 1 through 3.

The pied flycatcher's breeding range partially overlaps with that of the closely related collared flycatcher (*Ficedula albicollis*), which diverged within the last two million years (Qvarnström et al. 2010). Cross-fostering experiments between the two species show that nestlings discriminate conspecific over heterospecific song even when raised by the other species, indicating a strong genetic component to species-level song discrimination (Wheatcroft and Qvarnström 2017). Songs also vary geographically across pied flycatcher populations (Wheatcroft et al. 2022). Both nestlings and territorial males respond more strongly to local than to foreign songs, suggesting that song variation at the population level is perceived and acted upon by receivers (Wheatcroft et al. 2022; Gallego-Abenza et al. 2025).

A key methodological approach in studying early song discrimination in this system is the playback experiment combined with measurement of nestling begging responses. Nestlings respond to acoustic stimuli with begging calls of varying intensity, from low-intensity audible calls to high-intensity postural begging calls accompanied by forward or upward body movements (Wheatcroft and Qvarnström 2017). These responses provide a quantifiable behavioural assay for auditory discrimination in pre-fledging birds that cannot yet produce song. The approach has been used to demonstrate species-level discrimination by day 11 (Wheatcroft and Qvarnström 2017), population-level discrimination by day 12 (Wheatcroft et al. 2022), and, in this thesis, individual-level discrimination by day 13 (Chapter I). However, begging is also strongly influenced by nestling condition and hunger: well-fed, heavier nestlings may show reduced begging motivation independently of their capacity for auditory discrimination. This sensitivity of the assay to motivational state is an important consideration when interpreting results, particularly in Chapter III.

The pied flycatcher's complex and sexually selected song, its early onset of auditory discrimination, the limited understanding of how song learning proceeds during early development, and the availability of established playback methodology together make it well suited for the questions addressed in this thesis: how early song responses arise and what shapes them during development, and whether the song traits that adults produce carry information about cognitive ability.



Figure 3. A male pied flycatcher during the breeding season.

Chapter summaries

In this thesis, I investigate the development and function of a socially learned mating signal, song, in the pied flycatcher. Focusing on early life, I explore how nestlings respond to paternal song, what mechanisms underlie early song discrimination, and whether the structure of the songs nestlings hear shapes their responses. Shifting to adulthood, I ask whether the complexity of song that males produce carries information about their cognitive ability. Below are summaries of each chapter; please refer to the full articles for further details and citations.

Chapter I

Pied flycatcher nestlings discriminate conspecific songs from heterospecific songs (Wheatcroft and Qvarnström 2017) and songs of their local population from those of foreign populations (Wheatcroft et al. 2022). While genetic factors have been shown to influence species-level discrimination, the mechanisms underlying population-level recognition remain unclear. One possibility is that early exposure to the social father's song facilitates discrimination of locally typical songs. A necessary first step in evaluating this hypothesis is to establish whether nestlings can recognize their father's song at all. *Can nestling songbirds discriminate between their social father's song and that of an unfamiliar conspecific male from the same population?*

I conducted playback experiments on 13-day-old nestlings from 26 clutches, broadcasting songs of the social father and a local stranger male and quantifying begging responses. Nestlings produced significantly more high-intensity postural begging calls in response to their social father's songs than to stranger songs (Figure 4), while low-intensity begging calls did not differ between treatments.

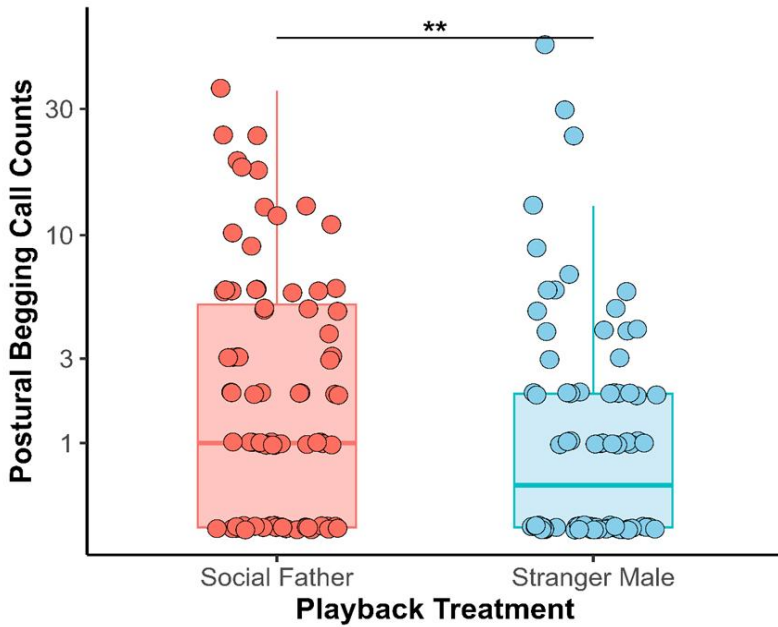


Figure 4. Song discrimination of nestlings. Nestlings respond stronger toward social father songs than unfamiliar male songs. Y-axis is the number of postural begging calls (log-transformed) produced by individual nestlings. Significance score is from post hoc test. ** $P < 0.005$. For clarity, nestlings who did not produce postural begging calls in either treatment were excluded from this figure, but all individuals were included in statistical analyses.

These results provide evidence that pied flycatcher nestlings recognize their social father's song before the onset of sensory learning, highlighting an early mechanism that may shape later song learning. Such recognition could support cultural inheritance in song transmission and potentially reinforce pre-mating isolation between populations.

Chapter II

Chapter I established that nestlings recognize their social father's song. However, the songs used in that experiment, and in all previous playback studies on pied flycatcher nestlings, were complex songs recorded during the pre-pairing stage. In practice, nestlings are unlikely to hear these complex songs, because males shift to producing shorter, simpler songs after pairing (Espmark and Lampe 1993). This raises the question of what version of paternal song nestlings actually learn from, and whether the simplified songs they hear during the nestling period play a role in shaping their responses to more complex songs encountered later. *Do nestlings respond differently to simplified short songs versus complex long songs, and does this depend on whether the songs come from a familiar or unfamiliar male?*

I confirmed that male pied flycatchers sing significantly fewer syllables per song during the nestling stage than during the early breeding stage. I then conducted playback experiments on 13-day-old nestlings from 42 clutches, presenting both short and long versions of songs from either the social father or a local stranger male.

Nestlings showed stronger postural begging responses to short songs than to long songs, and also responded more strongly overall to songs from their social father than to songs from a stranger male (Figure 5). No interaction was found between song length and song origin.

These findings suggest that both early auditory experience with simplified paternal songs and intrinsic acoustic salience contribute to early song responsiveness. Simplified songs heard during the nestling stage may therefore serve as an accessible entry point for recognizing and later learning more complex conspecific songs.

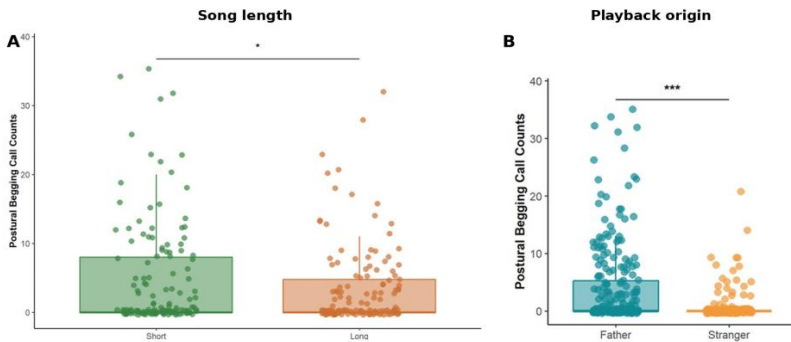


Figure 5. Nestlings' begging responses to song length and playback origin. (A) Postural begging responses to short and long male songs. (B) Postural begging responses to playbacks from social fathers and unfamiliar local males. Individual data points represent responses of individual nestlings. Significance scores are from post hoc tests. * $P < 0.05$, *** $P < 0.001$. For clarity, nestlings that maintained silence during the entire experiment were excluded from the figure but were included in statistical analyses.

Chapter III

The finding in Chapter I that nestlings discriminate in favour of their father's song raises an immediate question about the mechanism underlying this ability. Early discrimination could arise from auditory experience with the father's song during the nestling period, from inherited perceptual predispositions, or from their interaction. In the wild, these alternatives are difficult to disentangle because genetic background and early acoustic environment are typically confounded. *Does early recognition of the father's song reflect auditory experience during the nestling period, inherited predispositions, or their interaction?*

To test this, I used an embryonic cross-fostering experiment in which eggs were transferred between nests before hatching, so that nestlings were reared

either by their genetic parents or by foster parents. At 13 days of age, nestlings were exposed to playback of songs from their social father, their genetic father, and an unfamiliar local male.

Contrary to the results in Chapter I, nestlings in this experiment did not show differential begging responses to the three song treatments (Figure 6). The interaction between song treatment and offspring status (genetic versus cross-fostered) was therefore uninformative for distinguishing between experience-based and inherited mechanisms. However, heavier nestlings showed reduced postural begging, suggesting that low motivation constrained behavioural expression. Nestlings in this experiment were significantly heavier than those tested in the years when Chapter I was conducted, supporting a motivational explanation for the null result.

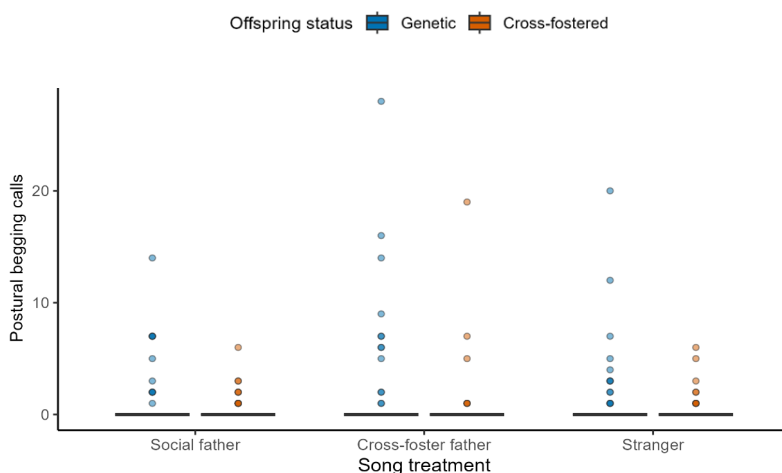


Figure 6. Postural begging responses of genetic and cross-fostered pied flycatcher nestlings to three song treatments. Blue: genetic offspring of the nest pair; orange: cross-fostered nestlings. Neither song treatment nor the Treatment \times Offspring status interaction significantly affected postural begging responses. $N = 483$ observations from 161 nestlings in 28 nests.

These results suggest that begging-based playback assays may fail to detect auditory discrimination when nestlings are in good condition, and the data remain inconclusive about whether early father-song recognition is shaped primarily by auditory experience, inherited predispositions, or their interaction.

Chapter IV

Chapters I through III focused on how nestlings perceive and respond to song during early development. In Chapter IV, I shift to the adult stage and ask what information song carries about the signaller. Song complexity has been hypothesized to signal cognitive ability, a latent quality that females cannot easily assess through direct observation but that may confer indirect benefits. However, empirical support for this hypothesis at the individual level remains inconsistent across species and study contexts (reviewed in Searcy and Nowicki 2019). *Does song complexity reliably predict cognitive ability in wild breeding males?*

I recorded songs from territorial males and measured four complexity variables (mean versatility, versatility SD, syllable switching rate, and repertoire size) that captured largely independent dimensions of song structure. The same males were then tested on a novel foraging task and a detour reaching task during the nestling provisioning period.

Contrary to the prediction that preferred song traits signal cognitive ability, repertoire size and syllable switching rate, the complexity measures most consistently linked to female preference in this species, both negatively predicted success on the novel foraging task. Within-individual variability in versatility (versatility SD), a previously unstudied song dimension, positively predicted detour reaching success. No other association survived correction for multiple comparisons, and cognitive performance showed no consistent cross-task associations.

These findings suggest that the song traits females attend to in pied flycatchers do not reliably signal cognitive ability, and that female preference for complex song is more likely maintained through its role as a multicomponent honest signal of overall male quality.

Conclusions and Future Directions

This thesis has approached birdsong from two connected perspectives: development and function. The first three chapters ask how early song discrimination arises during the nestling period, a stage when song learning has traditionally been assumed to matter little. The fourth asks what adult song complexity may signal once song has fully developed. Taken together, the chapters argue that understanding learned sexual signals requires attention to both ends of the life course.

One central conclusion is that the nestling period should not be treated as a passive prelude to later song learning. Pied flycatcher nestlings discriminate among biologically relevant song stimuli before fledging, including between their social father's song and that of an unfamiliar local male (Chapter I), and between short and long songs (Chapter II). These responses suggest that early auditory processing begins well before overt song production and may channel subsequent learning by shaping familiarity and attention. At the same time, Chapter III shows that identifying the mechanism behind such early discrimination is not straightforward: begging-based assays can be strongly influenced by motivational state, meaning that null responses cannot always be taken as evidence of absent discrimination.

A second conclusion is that song complexity should not be assumed to signal every desirable aspect of male quality simply because it is developmentally costly and sexually selected. In pied flycatchers, the complexity traits

most strongly linked to female preference did not positively predict cognitive performance (Chapter IV). This does not diminish the importance of song as a sexual signal, but refines our understanding of what it may convey. Song complexity may function as a multicomponent indicator of developmental history and overall condition without serving as a specific cue of cognitive ability.

These findings open several avenues for future research. Most immediately, the inconclusive result of the cross-fostering experiment highlights the need for approaches that are less dependent on begging motivation. Physiological or neural measures of auditory responsiveness, such as immediate early gene expression in auditory brain regions following song exposure, could provide more sensitive assays of discrimination that are not confounded by hunger or condition. Beyond methodology, the acoustic basis of individual-level discrimination remains unknown. Identifying which features of song encode individual identity, whether spectral, temporal, or combinatorial, would clarify what nestlings are actually extracting from the acoustic environment. It would also be valuable to test whether nestlings can discriminate among unfamiliar individuals, for instance by exposing them to a tutored stranger song during the nestling period and then presenting playback of multiple unfamiliar males. Such an experiment would establish whether early discrimination reflects a general capacity for individual recognition or is restricted to familiarity with one particular singer. Whether father-song recognition arises from experience or inherited predispositions also remains unresolved. If the mechanism turns out to be primarily experiential, it would be relatively straightforward to explain through acoustic familiarity. However, if inherited predispositions play a role, this would raise deeper questions, since individual-level song differences arise largely from each male's own learning history, and how such individually variable, experience-dependent traits could become genetically encoded is far from obvious. Resolving this question will likely require converging evidence from manipulative, neurobiological, and genomic approaches.

These questions about early discrimination naturally lead to a broader puzzle: how early perceptual biases relate to later song production. One of the most intriguing findings emerging from work in this system is the apparent disconnect between early song preference and adult song output. Nestlings respond preferentially to their social father's song, yet adult males produce repertoires that largely do not match their father's (Labra and Lampe 2018). What happens between these two stages? Understanding how early perceptual biases are transformed, overridden, or integrated during the sensorimotor phase and territory establishment would shed light on how cultural transmission operates across the full developmental trajectory of song learning. Longitudinal studies tracking individual males from the nest through to their first breeding season, while challenging in migratory species, would be particularly informative. A related question is whether the strength of early father-song discrimination predicts later learning outcomes. In zebra finches, the intensity of early preference for the father's song predicts song-copying accuracy (Rodríguez-Saltos et al. 2023). Testing this in a wild population with more complex and variable songs would reveal whether early discrimination functions as a reliable predictor of learning ability, or whether its influence is diluted by the many additional tutoring experiences encountered after fledging. It would also be informative to examine nestlings' natural responses to their father's song during routine nest visits: do they beg in response to song as they do to feeding cues? If so, whether such begging evolved primarily to solicit food or additionally to enhance auditory learning would be a fascinating question at the intersection of parent-offspring communication and vocal development.

Closely related is the question of what role simplified songs play in this developmental process. Chapter II shows that nestlings respond more strongly to short than to long songs, but whether this reflects a functional role of simplified songs in facilitating learning remains open. Do short songs improve

learning efficiency by providing a more tractable acoustic template that scaffolds the acquisition of more complex songs encountered later? And are the simplified songs males produce after pairing merely a byproduct of declining testosterone and reduced territorial motivation (Silverin 1998), or do males actively adjust their singing to benefit their offspring? This question connects to a broader and rapidly developing area of research on active teaching in songbirds (Chen et al. 2016; Taylor 2021), where tutors have been shown to modify their behaviour in ways that facilitate juvenile learning. Whether pied flycatcher fathers do something similar, and whether such behaviour is better understood as teaching or as an incidental consequence of changed hormonal state, would be a productive direction for future work.

Turning to the adult stage, the finding that preferred song traits do not reliably signal cognitive ability raises the question of what, precisely, females gain from preferring complex songs. One possibility, consistent with the developmental stress hypothesis, is that complexity reflects early-life condition and developmental history rather than any single cognitive capacity. More broadly, if cognitive ability does confer benefits such as better foraging efficiency or predator avoidance, females may assess it through other channels entirely, such as direct observation of male behaviour during courtship or territory defence, rather than through song. Alternatively, females may not need to assess cognitive ability independently if it is already captured by territory quality or other condition-dependent traits. Chapter IV also identified within-individual variability in versatility (versatility SD) as a novel dimension of song complexity that positively predicted cognitive performance. This measure captures consistency versus flexibility in singing style, a dimension orthogonal to conventional measures such as repertoire size. Whether versatility SD is perceived by females, and whether it carries signalling value in mate choice or territorial contexts, remains untested. Including such fine-grained measures of within-individual variation alongside conventional complexity

metrics could provide a richer picture of what song communicates in species with large and variable repertoires.

Closing remarks

This thesis set out to ask what song means to a pied flycatcher at different moments in its life: first as a nestling hearing its father's voice, and later as a breeding male whose own song is judged by mates and rivals. What I found is that the early chapters of this story are richer than previously appreciated. Nestlings are already listening, already distinguishing, already responding selectively to the acoustic world around them, days before they take their first flight. At the same time, the later chapters resist easy interpretation. Complex songs are clearly important to females, but they do not seem to advertise cognition in any straightforward way. Perhaps the most honest summary is that song, like most biological signals, resists being reduced to a single message. It is shaped by genes, by experience, by condition, and what it communicates depends as much on who is listening as on who is singing. I hope this work has opened a few new questions worth pursuing, and that others will find reason to listen as closely as I have tried to.

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Swedish Summary

Fågelsång är ett av de första vårtecknen. Långt innan löven kommer tillbaka fyller gryningskören luften, och de flesta av oss lägger märke till den utan att tänka närmare på vad som faktiskt pågår. Bakom dessa sånger döljer sig en av de mest anmärkningsvärda inlärningsprocesserna i djurvärlden. Tättningar, däribland svartvita flugsnappare, föds inte med kunskapen om hur de ska sjunga. Unga fåglar måste i stället lyssna på vuxna individer, lägga det de hör på minnet och så småningom forma sin egen röst för att efterlikna förebilden. Sång befinner sig därför i en ovanlig korsning: den formas av gener, av erfarenhet och av den sociala omgivningen, och den spelar en central roll i hur fåglar lockar partners och försvarar revir.

Den här avhandlingen ställer frågan om vad sång betyder för en svartvit flugsnappare vid två olika tidpunkter i livet. De första tre kapitlen handlar om boungar, fåglar som bara är några dagar gamla, fortfarande i boet, med ögonen knappt öppna och flera veckor från att själva börja sjunga. Det fjärde kapitlet flyttar fokus till vuxna hannar, vars sånger bedöms av honor under häckningssäsongens få veckor.

Ett vanligt antagande har länge varit att sånginläringen börjar först när den unga fågeln lämnar boet. Men allt fler studier tyder på att boungar redan lyssnar och redan skiljer mellan ljuden runt omkring sig. I kapitel 1 visar jag att 13 dagar gamla flugsnapparungar reagerar starkare på inspelningar av sin egen fars sång än på sången från en obekant hane från samma population. Det innebär att ungarna kan känna igen en enskild individs röst långt innan de själva försöker sjunga, ett resultat som pekar på en tidigare underskattad roll för boungeadiet i sångens utveckling.

Kapitel 2 frågar vilken sorts sång ungarna faktiskt får höra från sin far. Efter parbildningen slutar svartvita flugsnapparhannar att producera de långa,

utsmyckade sånger som de använde för att locka en hona, och övergår i stället till kortare och enklare versioner. Jag fann att ungar reagerar starkare på dessa korta sånger än på långa, oavsett vem som sjunger dem. Förenklade sånger kan därför fungera som en tillgänglig ingång, lättare att bearbeta och lättare att minnas, som hjälper unga fåglar att rikta uppmärksamheten mot de mer komplexa sånger de senare kommer att möta i livet.

Kapitel 3 frågar var den tidiga igenkänningen kommer ifrån. Är den inlärd genom erfarenhet i boet, eller finns det en medfödd benägenhet att reagera på faderns röst? För att ta reda på det genomförde jag ett experiment ute i fält där jag bytte ägg mellan bon, så att vissa ungar växte upp hos sina genetiska föräldrar och andra hos fosterföräldrar. Tyvärr blev ungarernas reaktioner i det här experimentet för svaga för att ge ett tydligt svar. De ungar som testades var tyngre och bättre matade än de som ingick i tidigare år, och välmatade ungar tigger helt enkelt mindre. Experimentet visade sig vara en värdefull metodologisk lärdom: beteendebaserade test av hörsel förmåga hos boungar är beroende av att fågeln är tillräckligt motiverad för att överhuvudtaget reagera.

Kapitel 4 går vidare till det vuxna stadiet. Honor av svartvit flugsnappare företrar hannar som sjunger komplexa, varierade sånger, och en inflytelserik tanke har varit att sångens komplexitet skulle kunna avslöja något om hannens kognitiva förmåga, alltså att en hane som sjunger bra också tänker bra. Jag testade detta genom att spela in vilda hannars sånger och sedan låta samma hannar utföra två kognitiva uppgifter: ett nytt födosöksproblem och en omvägsuppgift. Resultaten gav inte stöd för hypotesen. De sångegenskaper som är mest attraktiva för honorna var inte kopplade till bättre kognitiv prestation, och i vissa fall var de kopplade till sämre prestation. Sångens komplexitet hos svartvita flugsnappare verkar förmedla något om hannens allmänna kondition och utvecklingshistoria, men inte specifikt hur smart han är.

Tillsammans gör de fyra kapitlen en enkel poäng: en sång är inte ett enda budskap utan flera, och vad den förmedlar beror lika mycket på vem som lyssnar som på vem som sjunger. Boungar hör en tidig, förenklad version av sin fars röst och använder den för att börja orientera sig i en akustisk värld. Flera år senare bedöms samma fåglars sånger av honor, men honorna lyssnar troligen efter ledtrådar om hannens övergripande kvalitet snarare än efter någon enskild dold egenskap. Att studera båda ändarna av denna utvecklingsbåge, lyssnaren såväl som sångaren, är nödvändigt om vi vill förstå hur inlärda signaler som sång formas, vidmakthålls och förs vidare.

Acknowledgements

The work in this thesis would not have been possible without a great many people, and these few pages are my attempt to thank them properly.

First and foremost, to my supervisor, **David Wheatcroft**. I could not have hoped for a better supervisor. You have been warm, encouraging, and brilliant in equal measure, and the rhythm of your supervision has suited me perfectly. Talking with you is like striking a match in a dark room: when I bring half-formed ideas, you find the angle I had missed, and I leave almost every conversation thinking more clearly than when I walked in. I am also still quietly impressed by what I saw of you in the field: while I was struggling for hours with that tutoring setup just to follow a protocol, it kept dawning on me that you were the one who had built the whole thing from scratch years ago. Beyond academia, you are a deeply decent person, and your kindness, both in and out of work, has mattered more than you probably know. Thank you, David, for everything.

To the Wheatcroft lab, my coauthors and my companions through these years. **Sam**, thank you for being there before me. Being the second PhD student in the group has meant that at every step of the way there has been someone a little ahead, lighting the path. You are like the sun in any room, generously shining on everyone, and the department itself feels warmer and more connected because of you, and I have quietly relied on that warmth more than you know, finding through you a way into a place that might otherwise have felt much larger. Beyond that, I have always been struck by your mind: the breadth of your scientific curiosity, the ease with which you move between questions, the brilliance you carry without ever wearing it heavily. The naan you made, the taste of food we shared, and the understanding of being Asian women in Europe together made these years richer. The summers at Tovetorp would not have been half as bright without you. **Mario**, you are the hardest-

working person I know, and being in the team with you has felt like sailing with someone who has read the wind before — even in the worst weather, somehow we are safe. Your tortilla has been, half-seriously, one of the things I looked forward to about each field season. I am still struck by the strangeness of how one person can hold both such softness for other people and such fierce curiosity for the natural world; that combination has quietly shaped how I want to be in this work. **Miriam**, thank you for being so kind and so attentive, even at the times when I was bad at attending to myself. You have brought clarity, structure, and a way of thinking that I have learned a great deal from, and at the same time, the board games, the theatre evenings, the sense that work and joy are not separate things. **Fanny**, thank you for being the calm older-sister presence of the field season, the one who made the lists, made the plans, and made the decisions. And thank you for bringing the dog, which has functioned as essentially free therapy for the rest of us. **Christian**, thank you for the talent that turned my cognitive experiment from sketch to reality, and for the conversations, the party spirit, and the Swedish midsummer traditions you brought to Tovetorp. **Elena** and **Alice**, working with you in the field and in the lab was a quiet pleasure of efficiency and good company. **Damon**, your passion for wildlife and the beautiful photos that come from it have always impressed me. **Julia**, thank you for the time we spent together on great tits.

Beyond my own lab group, I've been lucky to be part of a department that has felt both supportive and inspiring. **Niclas**, my co-supervisor, thank you for the wisdom and the carefully considered advice you offered as I designed my cognition experiments. Your expertise opened up a perspective that strengthened the work in ways I could not have managed alone. **Cilla** and **Emily**, thank you for your thoughtful guidance through my follow-up meetings, both on the science and on the questions of life that surround it. Cilla, I have especially enjoyed our conversations about warblers, flycatchers, and nearby wildlife, and I am grateful to you and **Sven** for letting us clutter in your beautiful garden

with poles and cameras for experiments. **John**, thank you for your generous comments on my chapters and the humor and happiness you bring to department events. **Love**, thank you for your steadying and clear-eyed advice in the moments when I was anxious about what came next. **Rhonda** and **Mafalda**, thank you for the careful questions and incisive comments during my half time seminar.

To all the students and postdocs of the department, too many to name: thank you for the kitchen chats, the seminar discussions, the corridor hellos, and everything else that has made these corridors feel less like a workplace and more like a community.

To all the students and postdocs of the department, too many to name: thank you for the kitchen chats, the seminar discussions, the corridor hellos, and everything else that has made these corridors feel less like a workplace and more like a community. **Kathi**, master of toast, my go-to person for anything and everything in the department, thank you for your endless kindness and willingness to help; the PhD council has felt so warm and well-organised under your hand. **Victor**, thank you for the Thai boxing lessons and the fun you brought to midsummer. **Loke**, your talent in coding and statistics, your generosity in answering questions you must have been asked a hundred times before, and your unwavering devotion to Bayesian over frequentist methods will all stay with me. **Bella**, your laughter has been one of the best sounds in the office, and your eye for decoration has turned our shared room into a place I have genuinely enjoyed coming to. **Chloe**, the best office mate I could have asked for: I have been quietly inspired by your whiteboard brainstorms, by the way you hold a dozen tasks at once without dropping any of them, and by the simple, contagious energy of you walking back into the office after exercise. **Edana**, thank you for being my housemate when I first landed in Stockholm, for showing me the way into the department, for the quiet, restorative evenings we shared after dinner, and for opening my eyes to the charm of ballet. **Philip**,

so kind, so genuine; talking to you has always left me feeling lighter than before. **Anna**, you are sweetness itself, and I have loved every chance to learn about insects from you. **Alex**, the wild heart of the department, the spirit of every party. **Chenyu**, I have always admired the way you stand up against what is unfair, and it has been nice to share the small, particular joy of being cat mums together. **Rubie**, the unscheduled moments when we have run into each other in the building outside of office hours have been small, quiet pleasures of these years, a reminder that someone else was also still here, still going. Thank you also for your eye for the cute and the beautiful in the smallest things. **Mina**, it has simply been lovely to know you, to share lunches and seminars and the occasional precious game night. **Lennart**, thank you for the fancy dinners at your place with Miriam, and for a calm attitude toward things that has been quietly steadying. **Marion**, every game night has been better for your laugh, your conversation, and your small tricks at the table. And to **Maxence, Ingo, Kevin, Gua, Priscilla, Tilly, Marianne, Lea, Lars, Michael, and Julie**, thank you all for being part of what has made this department such a good place to be.

To the friends who came into my life during my master's years in Sweden, and whom fate, kindly, returned to me during my PhD: thank you for the gift of finding you again. **Zhe**, we have shared so many happy hours together that I have lost count, from the absurd ritual of carrying our laptops on holiday and solemnly swearing to get work done in the hotel room (and almost always failing), to the long, quiet stretches of online co-working that have made the lonely parts of writing feel less lonely. **Leyi**, my sweet travel companion, I am always already looking forward to wherever we are going next. And to **Jinci**, who arrived later but no less luckily, thank you for the countless shared dinners, the easy, winding conversations, and the chaos of frantic Overcooked sessions that have made for some of the most joyful evenings of these years.

You are also, for the record, the best customer a cook could ask for, always generous with compliments and somehow always the one washing the dishes.

And finally, to my family. **Mom**, thank you for being the steady support behind me, the reason I have been able to take whatever adventures I wanted without ever having to worry about the ground beneath my feet. **Dad**, you have simply been there, and the stubbornness and curiosity I inherited from you have been quietly important forces in my academic life. And to my cat, **Big White**, the reason I have come to know both love and responsibility in their fuller forms; watching you on video calls has been some of the most soothing moments of these years.