

Research



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# Evolving the capacity for socially guided vocal learning in songbirds: a preliminary study

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Socially guided vocal learning, the ability to use contingent reactions from social partners to guide immature vocalizations to more mature forms, is thought to be a rare ability known to be used only by humans, marmosets and two unrelated songbird species (brown-headed cowbirds and zebra finches). However, this learning strategy has never been investigated in the vast majority of species that are known to modify their vocalizations over development. We propose a novel, preliminary evolutionary modelling approach that uses ecological, reproductive and developmental traits to predict which species may incorporate social influences as part of their vocal learning system. We demonstrate our model using data from 28 passerines. We found three highly predictive traits: temporal overlap between sensory (memorization) and sensorimotor (practice) phases of song learning, song used for mate attraction, and social gregariousness outside the breeding season. Species with these traits were distributed throughout the clade, suggesting that a trait-based approach may yield new insights into the evolution of learning strategies that cannot be gleaned from phylogenetic relatedness alone. Our model suggests several previously uninvestigated and unexpected species as likely socially guided vocal learners and offers new insight into the evolution and development of vocal learning.

This article is part of the theme issue ‘Vocal learning in animals and humans’.

## 1. Introduction

Only seven animal taxa are known to contain vocal learners [1]. Seemingly rarer still is the capacity for *socially guided vocal learning* (SGVL) [2], a strategy in which a learner constructs mature vocal forms via contingent reactions to its immature vocalizations from social partners. A key feature of SGVL is *interactivity*, requiring the teacher and the learner to modify their behaviours with respect to each other. In songbirds, interactivity requires the tutor to alter its own behaviour in response to the learner’s plastic song to facilitate their song learning. This differs from other forms of social learning of birdsong, in which learners seek out tutors to imitate, but tutors are not known to provide active feedback on their developing song [3,4] (electronic supplementary material, table S1). Active social guidance is vital for vocal development in human infants, whose immature vocalizations are steered towards more mature forms by contingent responses from their caregivers [5–7]. Currently, SGVL has been demonstrated in only three non-human species: marmosets [8,9], brown-headed cowbirds [10] and, more recently, zebra finches [11,12]. Which other species might use this strategy is unknown, as SGVL has rarely been investigated. Other species with different life histories and ecological niches could elucidate how SGVL evolved, and serve as models for human vocal learning.

The most commonly studied models of vocal learning are oscine songbirds. SGVL, however, is well characterized in only one songbird, the brown-headed cowbird (*Molothrus ater*). The cowbird’s unusual life history as a brood

parasite—the young are raised by other species and never exposed to or given the opportunity to learn from their biological parents—previously led many to believe cowbirds required unique or innate systems of behaviour [13,14]. Cowbird song is used primarily for attracting females, thus female response provides informative social feedback to vocal output during song learning. When juvenile males produce an immature song, female cowbirds selectively respond to arousing song elements. They respond with a ‘wing stroke’, a rapid lateral movement of the wing. Juvenile males are motivated to produce song elements which elicit wing strokes, gradually guiding their song towards a mature form functional for female attraction [10,15].

We recently discovered a similar learning system in the zebra finch (*Taeniopygia guttata*), in which non-vocal contingent visual responses from females affect song outcomes in juvenile males [11,12]. Non-singing female zebra finches learn strong preferences for particular songs [16], and female listeners have long been known to affect male song learning (e.g. [17–19]), but the mechanism by which females influence males was, until recently, unknown. Zebra finch fathers also alter their behaviour in response to the juvenile song in ways that facilitate their learning, by singing contingently on the song of their sons [12] and slowing down their songs [20]. Although previous researchers have searched for contingent feedback behaviours in this species, none were found when zebra finch behaviour was observed [21]. This was likely due to the extremely rapid feedback cues in small birds that may be imperceptible to the unaided human eye, with zebra finch wing strokes often lasting less than 0.3 s. Our observations of bird behaviour in real time are limited by the temporal constraints of human perception, as the human visual system critical flicker fusion rate is about half that of a small bird [22,23]. Thus, interactive social feedback may be a far more ubiquitous learning strategy than previously thought.

Despite their phylogenetic distance, humans, marmosets, cowbirds and zebra finches share several traits that may have given rise to SGVL as a solution to the problem of developing communicative competence. For example, these species are all socially gregarious, ensuring developmental access to social feedback, and all use their learned vocalizations to facilitate and maintain social bonds [5,9,18]. Early in development, each of these species can update their auditory representation of song at the same time they are producing immature vocalizations (electronic supplementary material, figure S1). This overlap may create opportunities for social feedback in response to immature vocalizations to facilitate the learning of new vocal forms [24].

As with any behaviour or developmental trait, vocal learning strategies reflect how each species is adapted to its unique social and physical environment, and shaped and constrained by its evolutionary history [25,26]. Is it possible to determine, from a species’ ecological traits, the likelihood of a vocal learning strategy that incorporates social guidance? We tested the validity of a preliminary evolutionary model that explores the predictive value of several ecological traits. As a demonstration of such an approach, we first identified six ecological and developmental traits across passerines that we hypothesized as foundational to the evolution of SGVL (electronic supplementary material, table S2). Next, using well-studied passerine species, we conducted a literature search for evidence of social influences on vocal

learning and constructed a composite outcome measure of susceptibility to social influences on song ontogeny (electronic supplementary material, tables S3 and S4). We then used a regression model to determine the traits that best predicted the composite outcome measure. The evolutionary model aimed to suggest (i) traits required for a species to evolve the capacity to integrate social feedback into communicative development and (ii) which species are the best candidates for studying the evolution and development of SGVL.

## 2. Methods

### (a) Identifying predictive traits

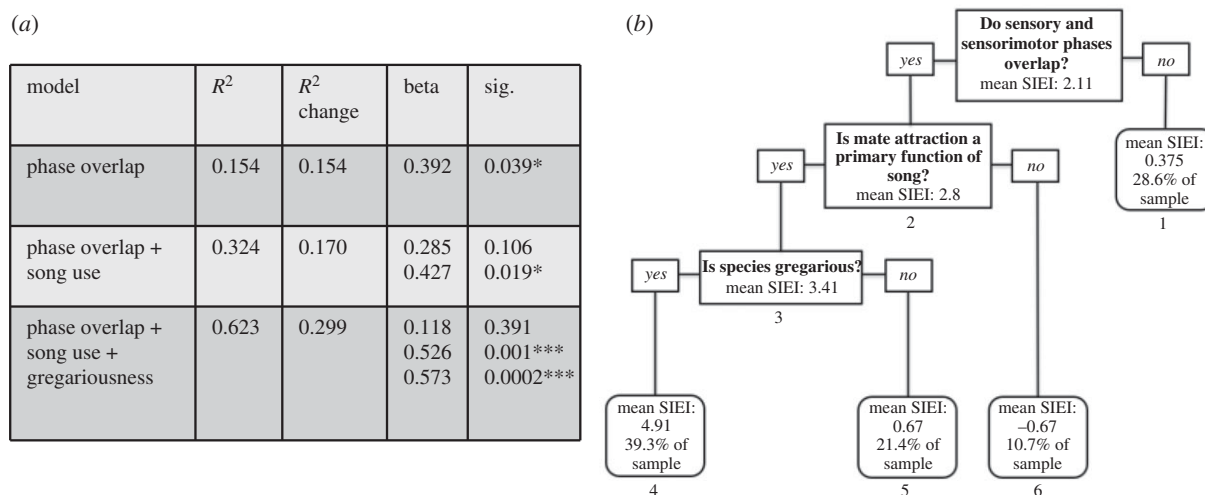
To investigate the prevalence of SGVL among passerines, we constructed an evolutionary model to identify which ecological and developmental traits may predict the presence of SGVL across species. These predictor traits (traits) served as independent variables in our model and were chosen due to their predicted likelihood of giving rise to opportunities for interacting and learning from conspecifics (electronic supplementary material, table S2). We focused on six traits: temporal overlap in sensory and sensorimotor phases of song learning, learning duration, primary function of song, migratory tendencies, gregariousness/flocking tendencies in the non-breeding season and the absence of female song (see electronic supplementary material, Methods).

### (b) Constructing the Social Interactivity Effects Index

SGVL has been directly investigated in only a handful of species. Thus, we conducted an extensive literature search to identify any behavioural, developmental or learning tendencies of a species which indicated the presence or absence of influences of social interaction on vocal learning (electronic supplementary material, table S3). These characteristics included the ability or inability to learn in isolation, to learn from passive playback, to learn via eavesdropping on adult conspecifics or to learn from interactive tutors. Some of the traits that do not grant positive points on the index, such as the ability to learn via eavesdropping, are social, but not socially interactive (electronic supplementary material, table S1). We distilled the findings from the literature search into a composite measure, the Social Interactivity Effects index (index or SIEI), for gauging the likelihood that a given passerine species is a socially guided vocal learner (electronic supplementary material, figure S2). Just as vocal production learning is not a binary trait [4,26], the degree to which species use social influences in vocal production learning likely exists along a spectrum, which the index aims to capture. The index integrated various types of evidence for or against social effects on learning, to produce a single score reflecting the likelihood of social influences on learning for each species. None of the predictor variables (i.e. the traits in electronic supplementary material, table S2) overlapped with the song and learning characteristics used for the construction of the index. The scoring system for the index and values of each learning characteristic are detailed in electronic supplementary material, Methods.

### (c) Species inclusion criteria for regression analysis

To determine which species to include in the regression analysis, we first performed a broad search and analysis of the literature describing the ecological and developmental traits of passerine birds using 1043 papers from the primary literature. Species were only included in subsequent analyses if the literature yielded conclusive information on at least five of the six ecological and developmental traits of interest (electronic



**Figure 1.** Predictive model of SIEI based on predictive ecological traits. (a) Three regression models of traits predicting SIEI score and associated change in  $R^2$  values. The combined model incorporating overlap of the sensory and sensorimotor developmental learning phases, the primary use of song (used for mate attraction or not) and gregariousness (measured by flock size in the non-breeding season) best predicted index scores across species, \* $p < 0.05$ , \*\*\* $p < 0.001$ . (b) Regression tree of model predicting index score from three predictive ecological traits. Mean index score across the total sample was 2.11. Species without temporal overlap between sensory and sensorimotor phases had a low mean index score of 0.375 (node 1), while those with phase overlap had an average index score of 2.8 (node 2). Species for which mate attraction is a primary use of song (node 3, mean index score = 3.41) had significantly higher index scores than those for which territory defence is a main song function (node 6, mean index score = -0.67). Within species whose song functions to attract mates, gregariousness predicted index score. Non-gregarious species (node 5, mean index score = 0.67) had lower index scores than more gregarious species (node 4, mean index score = 4.91).

supplementary material, Methods and tables S3 and S4). This resulted in an initial list of 114 passerine species.

#### (d) Regression tree

We used the package 'rpart' in R software [27] to build our regression model by splitting the dataset into homogeneous subsets of index score using a single predictor variable at each node. The initial result was a large tree incorporating all six ecological trait variables, which could be over-fitted. We therefore pruned the tree to an optimal size using results from eight cross-validations [28] in order to find an optimal trade-off between model complexity and prediction accuracy. For our relatively small sample, we did not choose the minimum cross-validated error, but instead a cross-validated error which was within one standard deviation of the prediction error. This resulted in the best possible model based on cross-validation, a simple tree with three splits (figure 1). Construction of the phylogenetic tree is discussed in electronic supplementary material, Methods.

### 3. Results

#### (a) Relations between individual predictor traits and index score

To determine the traits of primary focus for further modelling, we examined relations between each of the predictor traits and index score and we performed Spearman's rank-order correlations between the index scores of each species and the presence or absence of each predictor trait in those species. We found significant positive correlations between the presence of three traits and index score (presence of sensory/sensorimotor overlap:  $r_s(26) = 0.395$ ,  $p = 0.037$ ; song used primarily for mate attraction:  $r_s(26) = 0.533$ ,  $p = 0.003$ ; flocking in non-breeding season:  $r_s(26) = 0.532$ ,  $p = 0.004$ ).

#### (b) Regression model

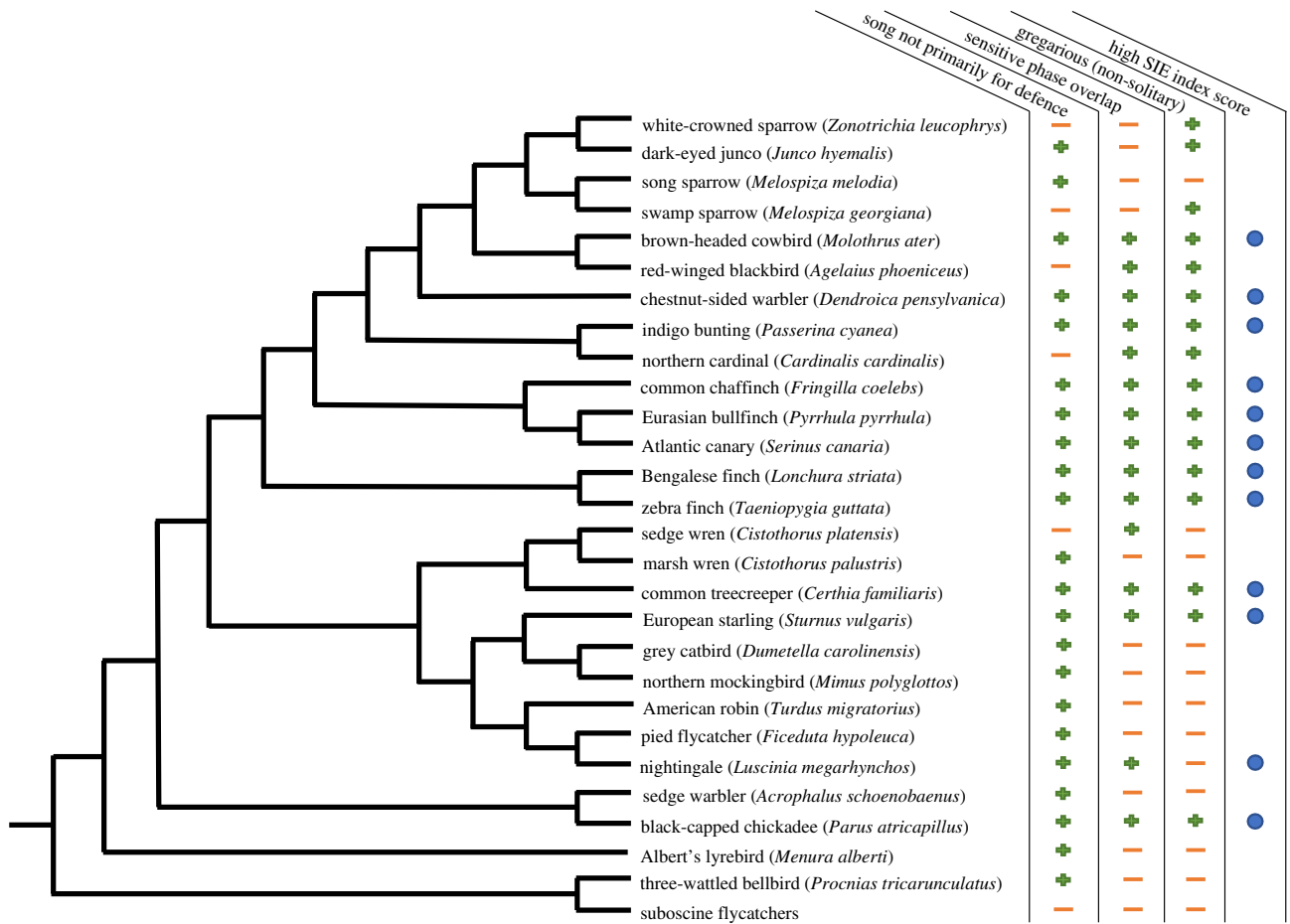
We then modelled the manner in which these traits predicted species with high index scores and conducted regressions to

examine the joint and unique contributions of these traits to index score. Sensory/sensorimotor overlap was in isolation a significant predictor of index score ( $R^2 = 0.154$ ,  $p = 0.039$ ), but adding the traits of primary song use and gregariousness resulted in a stronger model ( $R^2 = 0.623$ ,  $p = 0.0002$ ; figure 1a). A regression tree revealed that primary use of song was the most predictive factor, whereas sensory/sensorimotor overlap, which was present in every species with a high index score but also some with low index scores, is necessary but not sufficient for incorporating social factors into vocal development. Gregariousness was predictive of index score only among species which use song primarily for mate attraction (figure 1b). The model also revealed several traits that did not predict a species' index score. Whether a species was migratory/nomadic or sedentary was not significantly predictive of index value ( $\chi^2_2 = 2.461$ ,  $p = 0.292$ ), nor was the presence or absence of song in females ( $\chi^2_2 = 0.054$ ,  $p = 0.973$ ), or age-limited versus open-ended song learning ( $\chi^2_2 = 0.404$ ,  $p = 0.817$ ).

We found that species with high index scores (above the median of 4) typically shared the three predictive traits. The evolutionary model suggests that, regardless of the position of a passerine within the phylogenetic tree, within our sample sensory/sensorimotor overlap may be necessary for evidence of social influences on song learning, gregariousness is highly predictive of high index scores, and use of song primarily for territory defence is associated with low index scores (figure 2).

### 4. Discussion

Our preliminary model, based on reviews of the songbird literature, suggests that certain ecological traits may predict a strategy of SGVL. We found three traits—gregariousness in the non-breeding season, using song for mate attraction rather than primarily for territory defence, and having developmental overlap between the memorization and practice phases of song acquisition—to be strongly predictive of a given species' SIEI score.



**Figure 2.** Cladistic tree of passerine species included in the final evolutionary model of ecological traits and social learning susceptibility. Twenty-eight passerine species with ecological trait presence (green +) or absence (orange -) for the three primary predictive traits included in the final model (described in §3). From left to right, these are primary use of song not being territory defence (song is used to at least an equal degree for mate attraction); temporal overlap in the sensory memorization and sensorimotor practice phases of song learning; gregariousness, as defined by being non-solitary in the non-breeding season. Blue circles in the final column (far right) indicate high (greater than or equal to 4, above median) scores on the SIEI. This tree is intended to demonstrate relatedness between modern species, but branch lengths are not indicative of actual temporal points of speciation as we were not attempting to determine maximum-likelihood ancestral state reconstruction (see §2). (Online version in colour.)

We emphasize the preliminary nature of these findings due to the scarcity of data on SGVL. This model represents a starting point and call to action for further investigation to refine this theoretical framework. These findings should be interpreted as suggestions to guide future research, not as a definitive statement of the traits from which SGVL emerges. Indeed, our dependent measure, the SIEI, is a proxy for the degree of evidence pertaining to social influences on vocal learning. The literature that comprised our data is incomplete and fragmented, with very few species represented by the in-depth observations that might reveal SGVL. To create our model, we had to categorize the functions of song based on the predominant findings in the literature, but exceptions abound. Furthermore, much of our data are based on laboratory studies and have not yet been validated in the field.

Our model, however, is supported by the presence of SGVL in the brown-headed cowbird and its more recent discovery in the zebra finch, both of which exhibit all three of the predictive traits identified by the preliminary model. These are the only two species in which SGVL is known and are therefore minimal data from which to extrapolate, but they are also the only species in which SGVL has been investigated, suggesting many other currently uninvestigated

species may use SGVL. As more species are studied, we expect that the set of predictive traits in our model will be modified and refined to improve its fit as the available dataset grows larger. Despite this limitation, the strong correlation within our sample between the presence of the three primary traits and index scores suggests that species possessing all three traits are worth investigating further.

The emergence of a SGVL strategy appears to be highly dependent on whether young birds develop an auditory template of their song at the same time they are engaging in immature singing and practice. All sampled species with a high index score also showed temporal overlap of the sensory and sensorimotor periods. These two phases of learning vary widely in their degree of developmental overlap between species [29]. In most seasonally breeding species, including many sparrows, these phases are temporally distinct in laboratory-based studies, with memorized representations of adult song forming during the sensory phase shortly after hatching in the spring, and sensorimotor practice only commencing in the autumn [30]. Sparrows therefore learn to produce whatever was memorized earlier in life, and any social feedback received based on their immature song is unable to alter this auditory template, only potentially reinforce it. However, alternative developmental trajectories

exist in numerous species, including both zebra finches and brown-headed cowbirds, in which the timing of the sensory and sensorimotor periods overlap substantially (electronic supplementary material, table S3 and figure S1). This overlap creates the opportunity for SGVL, in which social feedback to immature song affects the young bird's auditory template of song. However, to our knowledge, the link between this sensitive phase overlap and social influences on vocal learning has never been comparatively investigated.

Similarly, high index scores were only seen in species for which mate attraction was a primary function for song. Given that territorial species tend to learn song via eavesdropping on neighbours [31], and risk aggressive encounters if venturing too near their tutors in the laboratory, interactive social learning may be maladaptive in these species (e.g. [32]). Field studies, however, show that adult song sparrows are tolerant of juvenile learners approaching them [33]. Given recent hypotheses that social interaction could also play a role in territorial species such as song sparrows [34], we call for a closer investigation of the possible role of interactive social feedback in their vocal development. The forms of SGVL thus far discovered involve adult females selectively responding to the immature song of juvenile males [10,12]. This form of learning necessitates song which is ultimately used for mate attraction, as it must generate an arousal response from females to drive learning. Given that females, not males, will be the ultimate judges of the learned song, we suggest that a more adaptive strategy evolved to allow juvenile males to alter their immature song in response to female feedback.

Species with all three predictive traits are distributed in their phylogenetic relatedness, indicating an important role of convergent evolution in the emergence of SGVL (figure 2). It has been speculated that vocal learning strategy in primates might be affected by life-history traits, such as prosociality and cooperative breeding [35,36]. New World primates, especially callitrichids, are more likely to be cooperative breeders than Old World primates, making it difficult to separate traits from phylogeny in this clade. Expanding investigations into avian SGVL beyond closely related species, using clues from shared aspects of life histories, could lead to the discovery of new learning strategies in unexpected clades. The species with high index scores are scattered across the phylogenetic tree, indicating that shared life history has strong predictive power for learning strategy.

## 5. Conclusion

We emphasize that there is no universal vocal learning strategy across species [37]. Social ecology traits such as cooperative breeding have previously been effectively used to predict vocal complexity across species [38], but never to

predict vocal learning strategy. Our model suggests that three traits—gregariousness in the non-breeding season, use of the song for mate attraction rather than primarily for territory defence, and overlap in the sensory and sensorimotor stages of song development—may be predictive of evidence of social influences on song learning. As we have shown, developmental data on SGVL can inform evolutionary models of species ecological traits, and vice versa. Such data are sparse, however, as few researchers have looked for influences of structured social interaction on vocal learning [2].

Our literature search revealed the scarcity of studies examining interactive social influences on vocal learning in a number of otherwise well-studied species, which was a limitation on the amount of data that could be analysed by our model. In the continuing search for those species which, like humans, use SGVL, we must look beyond the handful of traditionally studied species. We must also search beyond those species closely related to cowbirds and zebra finches, focusing on ecological traits predictive of social learning which may have independently evolved. Our evolutionary model predicts that, within our sample, certain passerine species (chestnut-sided warblers, indigo buntings, Atlantic canaries, common chaffinch, Eurasian bullfinch, Bengalese finch, common tree creepers, black-capped chickadees, European starlings, nightingales) are most likely to show evidence of SGVL.

We call for further investigation into these oscines, as the role and mechanisms of SGVL in their vocal ontogeny is currently unknown. Many of these species potentially offer useful parallels to aspects of human speech learning. For example, Bengalese finches [39], black-capped chickadees [40] and European starlings [41] learn songs characterized by a syntax containing probabilistic elements. Also, unlike sparrows and zebra finches, several of these species are open-ended learners like humans (electronic supplementary material, figure S1). In addition to presenting new model systems for the evolution and development of human language, investigating the prevalence of SGVL across vocal learners will offer insights into the evolution of such a socially embedded learning strategy.

**Data accessibility.** All data are included as supplementary material.

**Authors' contributions.** The literature searches and model construction were completed by S.C.P. The manuscript was jointly written by S.C.P. and M.H.G.

**Competing interests.** We declare we have no competing interests.

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