



# FUNCTIONAL EXPLANATIONS FOR THE USE OF VOCAL MIMICRY IN SONGBIRDS

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## Summary

Songbirds use their song mainly for two purposes: repelling rivals and attracting mates. There is a lot of variation in the song learning process of songbirds. Vocal mimicry is found in many species but its function causes still a lot of debate. In this paper, multiple functional hypotheses are summarised. The main functions can be distinguished into five categories: Avoid competition, avoid predation, forage more efficiently, brood parasitism and sexual selection. The possibility that a songbird gains no advantage out of the mimicry is not excluded as it can arise from mistakenly learning or ecological convergence. Some examples seem to be strong evidence towards one of the hypotheses, but it is not comprehensive as there is clearly a lack of empirical research. Mainly on the development and production is more research needed in order to understand the underlying mechanisms and acquisition of vocal mimicry.

## Introduction

Vocalisation is by many taxa in the animal kingdom used as a way to communicate with each other. A way of communication used by birds is singing. There are typically two main functions described for singing: marking a territory (i.e. repelling rivals) and attracting a mate (Marler & Slabbekoorn, 2004). The first main function is that songbirds mark their territory by singing so that when other birds come into this territory they may be aggressively excluded. This territory defence is in relation to volume. The louder a bird sings, the less chance there is that other birds intrude his territory. The second main reason is to attract a mate. When a male is singing, a females' reproduction and physiology can be stimulated (Brenowitz et al., 1997).

The occurrence of singing behaviour varies between region. In temperate zones, seasonality in song behaviour is found where singing occurs mostly in the breeding season while in the tropics singing occurs more year-round (Brenowitz et al., 1997). Singing behaviour varies also between the sexes. In most studied species, song learning and the associated neural circuit were found to be sexually dimorphic (Brenowitz et al., 1997). Thereby it was thought that in most species, song behaviour is exclusively present within males. However, more and more evidence is found that female song is widespread in songbirds (Odom et al., 2014). In certain tropical species it is even the case that both the male and the female have an equal contribution to the song duet (Slater & Mann, 2004).

In most taxa, vocalisation is developed without a lot of environmental input. Vocalisation is thereby mostly fixed, and learning and adapting upon experience is thus relatively scarce (Seyfarth & Cheney, 2010). However, in for instance three orders of birds a part of their vocalisation is learned: their song (Beecher & Brenowitz, 2005). The most studied order consists of the oscine passerines, or better known as the songbirds. There are globally more than 4000 species of songbirds where a lot of diversity is found in the song learning process (Brenowitz & Beecher, 2005). The difference in song learning must reflect (partly) the differences in the underlying song-learning processes (Beecher & Brenowitz, 2005).

There are early sensitive periods by which song learning is characterised (Brenowitz et al., 1997). Songbirds have innate predispositions for this to learn songs of their own species. However, there is diversity in songbirds in the degree of exposure to species-specific song (Brenowitz & Beecher, 2005). In most species, their song is learned by listening to conspecifics (Marler & Slabbekoorn, 2004). This idea was first seen in Common Chaffinches *Fringilla coelebs*, where they raised the young in two ways: in complete isolation without any song or with recordings of the song of conspecifics. The young that were raised in complete isolation developed very abnormal songs while the young that were raised with recordings of their conspecifics developed a song very similar to that on the recording (Thorpe, 1958). The same

was seen by a study done with Swamp Sparrows *Melospiza georgiana* and Song Sparrows *Melospiza melodia* (Marler & Sherman, 1985). However, there are also species that can learn species-typical songs in complete isolation (Brenowitz & Beecher, 2005), as for example seen in Grey Catbirds *Dumetella carolinensis* and Sedge Warblers *Acrocephalus schoenobaenus* (Kroodsma et al., 1997; Leitner et al., 2002).

The timing of song learning differs between species (Brenowitz & Beecher, 2005). In some species, song learning is restricted to only the first year of their life. These species are called age-limited or close-ended learners. Examples of this are zebra finches or White-crowned Sparrows *Zonotrichia leucophrys* (Brenowitz et al., 1997). The species on the other side of the spectrum can learn songs their whole life, called open-ended learners (Brenowitz & Beecher, 2005). These species still have a similar learning process during their first year but are, in contrast to close-ended learners, able to learn songs at an older age. Example species in this category are Common Starling *Sturnus vulgaris* and Atlantic Canary *Serinus canaria* (Brenowitz et al., 1997). The period when songs are learnt is mainly in a restricted seasonal manner, but there are cases known where species learn songs outside the breeding season. An example of this are Marsh Warblers *Acrocephalus palustris*, where up to 20% of their repertoire can exist of African species that are only found during their migration or on their wintering sites (Garamszegi et al., 2007).

Also in the development of song is variation. The song can be copied from their tutor, and thus fully based on imitation of conspecifics (Marler & Slabbekoorn, 2004). Alternatively, a songbird could use improvisation to create novel songs (Brenowitz & Beecher, 2005), with minimal reference to their tutor. Another option might be that species use the song of their conspecifics as a basis, and then improve the song with novel elements (Beecher & Brenowitz, 2005). Another strategy includes songbirds that copy sounds of heterospecifics or other sounds. This is called vocal mimicry, the copying of songs or calls of other species or environmental sounds (Kelley et al., 2008). Mimicked environmental sounds can be for example a squeaking door by Common Starlings (Hausberger et al., 1991) or the clicking of cameras by a Siberian Rubythroat *Calliope calliope* (Birdguides, 2022). The learning of mimicry may show significant similarities to those seen in song learning (Kelley et al., 2008). Vocal mimicry is found in many songbird species. In this paper, multiple functional hypotheses are investigated for the question: Why do songbirds mimic other species or environmental sounds? Therefore, multiple hypotheses are summarised, provided with examples that support the hypothesis and discussed.

## Results

In this section multiple hypotheses are described for the function explanation of vocal mimicry in songbirds. The main functions can be distinguished into five categories: Avoid competition, avoid predation, forage more efficiently, brood parasitism and sexual selection. Each hypothesis is summarised from literature and provided if present with examples to support the hypothesis. Furthermore, some contradicting finding or shortcomings are discussed. An overview of the hypotheses with provided literature can be found in table 1.

**Table 1:** An overview of the hypotheses with the discussed literature.

Main function	Hypothesis	Mechanism	Supporting cases	Literature
Avoid competition	Beau Geste Hypothesis	False signalling that territory/nest site is taken	-Blue Tit -Red-winged Blackbird	Krebs, 1977 Rechten, 1978 Gorissen & Eens, 2005 Yasukawa, 1981 Haftorn, 1995 Dawson & Jenkins, 1983

				MacDougall-Shackleton, 1997
	Deterrence potential competitor	False signalling that predator/other danger is nearby	-Northern Mockingbird -Burrowing Owl	Dobkin, 1979 Rowe et al., 1986
Avoid predation	Batesian Acoustic Mimicry	Directly scare off predators with predatory signals	-European Jay	Bates, 1862 Curio, 1978
	Attracting species	Attracting more species e.g. to collective mobbing		Fang et al., 2020 Curio, 1978 Caro, 2005
Increase foraging efficiency	Flock forming	Attract more species to form mixed-species flock	-Greater Racket-tailed Drongo	Goodale & Kotagama, 2006 Kotagama & Goodale, 2004 Satischandra et al., 2007 Hino, 1998
	Lure Prey	Luring prey	-Grey Butcherbird -Great Grey Shrike	Pollard, 1930 Lorek et al., 2000 Atkinson, 1997 Carouso-Peck et al., 2021
	Kleptoparasitism	Directly scare off competitors to steal resources	-Fork-tailed Drongo -Blue Jay	Flower, 2011 Ridley & Raihani, 2007 Ridley et al., 2007 Flower et al., 2014 Radford et al., 2010 Aubin & Mathevon, 2020 Flower & Gribble, 2012 Goodale & Kotagama, 2006 Hailman, 2009
Parasitism	Brood parasitism	Mimic host species (mostly begging calls by young)	-Great Spotted Cuckoo -Striped Crested Cuckoo -Common Cuckoo	De Mársico et al., 2012 Langmore et al., 2003 Mundy, 1973 Madden & Davies, 2006
Attract mate	Sexual selection	Reflect qualities by the males		Nowicki et al., 2002 Byers & Kroodsmas, 2009

## 1. Avoid competition

### 1.1. Deter potential competitor with false signal that territory is taken

There is a lot of variation found in the repertoire size of songbirds (Brenowitz & Beecher, 2005). Some species learn a single song, while other species have an extensive repertoire containing heterospecific songs (Beecher & Brenowitz, 2005). This diversity can be even clear within a genus, e.g. in *Acrocephalus* where it is known that Marsh Warblers *A. palustris* mimic more than 100 species while other species mimic fewer species or even lack mimicry at all (Garamszegi et al., 2007). The function of a repertoire size is first discussed by Krebs (1977), where he proposed the Beau Geste Hypothesis. The idea is described that singing a lot of different songs can give the impression to potential intruders that the area is already covered by a substantial number of birds and thus serving as an explanation for the large repertoires that songbirds can have. By mimicking a wide range of heterospecifics, the bird can potentially deter multiple species by the false signal that the area is covered by multiple species (Rechten, 1978). As this potential intruder is territorial (and thus paying close attention to vocal signals) he may move on to find another territory. In this case, the mimicking bird deter his rivals for resources (Kelley et al., 2008). A similar idea is seen when there is competition for nest sites. In this case a species can mimic the vocalisation of their competitor or their competitor's competitor in order to give the false signal that the breeding site is already taken (Dalziell et al., 2014). Gorissen & Eens (2005) described that Blue Tits *Cyanistes caeruleus* mimic sounds of Great Tits *Parus major* (or other competitors of the Great Tit), which might have the reason to be able to compete with the larger and more aggressive Great Tits. When Blue Tits mimic the sounds of great tits by a potential nest site (e.g. nest box), the great tit can deceptively think that the site is already taken by a conspecific and thereby move on.

A study done by Yasukawa (1981) with Red-winged Blackbirds *Agelaius phoeniceus* tested the Beau Geste Hypothesis and found results that are consistent with the prediction for this hypothesis. The hypothesis is however only tested with repertoire sizes of species-specific vocalisation and not in a mimetic context. Therefore it remains unclear why heterospecific mimicry would be more effective as conspecific mimicry, unless competitors pay attention to the number of different species rather than the number of different song types heard in an area (Kelley et al., 2008). One possible explanation for the usage of heterospecific vocalisation rather than species-specific vocalisation in order to mimic high density might be that copying a song is less costly than creating novel songs to increase the repertoire size.

The predictions for the Beau Geste Hypothesis were not met in a study done with coal tits *Periparus ater* (Haftorn, 1995) and a study done with Common Chaffinches *Fringilla coelebs* (Dawson & Jenkins, 1983). Both studies tested predictions for the hypothesis with species-specific vocalisation. Evidence to support the hypothesis in a mimetic context is lacking (Kelley et al., 2008). Macdougall-Shackleton (1997) concluded that it is unlikely that the Beau Geste Hypothesis explains the evolution of repertoires in any species, and thus also in a mimetic context it seems unlikely that the mimicry of multiple species excludes heterospecific competitors (Dalziell et al., 2014) The Beau Geste Hypothesis does also not explain the occurrence of species that copy songs of other species (that are closely related) to seemingly reduce aggression to each other when breeding in the same area. This is seen in great tits that include songs of blue tits in their own repertoire. An alternative to the idea that this is done for reducing aggression to each other, is that it can be done unintentionally. Great tits interact a lot with blue tits and are also closely related, so it may be the case that great tits learn mistakenly the song of blue tits (Kelley et al., 2008).

## 1.2. Deter potential competitors with predatory signals

This hypothesis describes the idea that songbirds mimic predatory or agonistic animals to scare potential competitors. The potential competitor then hears the sounds of their predator and thereby avoids the area and thus does not compete for food or other resources with the songbird that mimics the sound (Dalziell et al., 2014; Kelley et al., 2008). This was first suggested by Dobkin (1979), where he looked at studies of the song of Northern mockingbirds *Mimus polyglottos*. In Northern mockingbirds it was found that the most common mimicked species is the Blue Jay *Cyanocitta cristata* with two different syllables from this species. Dobkin argued that "In fact, because blue jays are highly aggressive nest predators of many passerines, these mockingbirds may be excluding potential competing species from their territories, in part, by acting as vocal mimics of the blue jay." Also a competitor's predator can be mimicked, see in an extensive named example that burrowing owls mimic the 'hiss' of rattlesnakes to deceive their competitor rodents that the burrow is used by rattlesnakes (which is a predator of the rodents) (e.g. Garamszegi et al., 2007; Rowe et al., 1986).

## 2. Avoid predation

### 2.1. Deter potential predators with predatory signal

Building up from the last hypothesis, the same kind of mimicry can also be used in a way to scare off potential predators. By unexpectedly mimicking a songbird can directly scare away a predator. This can be achieved by mimicking sounds that are relevant to the predator, such as territorial sounds of the predator itself or the vocals of a predator's predator (Dalziell et al., 2014). This is kind of the same idea as species that visually resemble a noxious species to deter a predator (Bates, 1862). The first anecdotal evidence was provided by Curio (1978) which consisted of an observation of European Jays that mimicked multiple other species (e.g. carrion crow and blackbird) when disturbed by the observer. This might be done to resemble a whole group of mobbers whereby the birds might try to get rid of the danger.

### 2.2. Attracting more species to avoid predation

Birds are capable of producing different kinds of vocalisation depending on the situation, for example they can use different calls when they find food or see a predator (Marler, 2004). In the presence of a predator, birds regularly use mobbing calls, which are known to attract conspecifics or heterospecifics to react against the potential predator (Fang et al., 2020). Songbirds can mimic the mobbing calls of heterospecifics to attract species which can help to deter a predator (Dalziell et al., 2014). For the mimicking songbird, the predator can be avoided in different ways: dividing the risk with the individuals joining the mobbing (which results in a lower risk for the mimicking bird), confusing the predator with more individuals, by making the predator more conspicuous (where the chance of a surprise attack is lowered) or by attacking collectively the predator (Curio, 1978). Adding up on this, the mimicking bird can avoid the potential predator by attracting more appealing prey (Caro, 2005). Another phenomenon that is described is that if a songbird wants to avoid a predator, it could be beneficial to mimic the sounds that attract another predator, called the 'attract the mightier' hypothesis (Curio, 1978). By this, the second predator can interact with the initial predator and thereby the songbird that is mimicking can escape from the initial predator. This hypothesis is however doubted because species-specific mobbing calls are often enough to attract more individuals (conspecifics but also heterospecifics) in order to collectively chase off the predator (Dalziell et al., 2014).

## 3. Forage more efficiently

### 3.1. Mixed-species flock forming

Another hypothesis for the function of vocal mimicry is to attract other species to form a flock of multiple species, called a mixed-species flock (Goodale & Kotagama, 2006). With mimicking heterospecific vocalisation in combination with conspecific sounds, the impression can be made

that a flock is nearby. This might be attractive for species because it can be advantageous to forage in a flock to have a higher feeding efficiency (i.e. shorter handling time) (e.g. Glück, 1987; Sridhar et al., 2009). One way to achieve this higher feeding efficiency is via the beating effect, that flocks disturb insects that then can be caught (Kotagama & Goodale, 2004) from which the mimicking bird can directly benefit. Another way, although less commonly observed (Satischandra et al., 2007), is with kleptoparasitism where the mimicking bird can steal food directly from the species that is attracted by the false impression that a flock is present (e.g. Goodale & Kotagama, 2006; Hino, 1998). Being in a mixed-species flock can also serve as protection for predators (Morse, 1977). When species joining a flock are better protected, they can reduce vigilance (Sridhar et al., 2009), which might give them more time to forage.

Support for the hypothesis is found with Greater Racket-tailed Drongos *Dicrurus paradiseus*, a species that forage more efficiently when being in a mixed-species flock (Satischandra et al., 2007). Goodale & Kotagama (2006) found that mimicked sounds were most often recorded when the species was not in a mixed-species flock, which is in line with the predictions of the hypothesis. If the drongos are already in a mixed-species flock, mimicking to attract other species is not necessary anymore. Besides that, it was seen that when a recording of drongo vocalisations with mimicry in it was played, the response was twice as high as when the recording was lacking the mimicry. This supports the hypothesis in a way that mimicry is functional, and it is not rather the drongo-specific vocalisation that forms the mixed-species flock.

### 3.2. Luring prey

Pollard (1930) described an observation of Grey Butcherbird *Cracticus torquatus* that mimicked prey species, which appeared to attract them. This was the first time that it was suggested that mimicry can be used by predator species in order to lure their prey. This 'luring prey hypothesis' was further extended with Great Grey Shrikes *Lanius excubitor*, a species that predate on smaller passerines (Lorek et al., 2000). Atkinson (1997) showed that Great Grey Shrikes lure prey species by mimicking them. It was found that small passerines reacted more to playback of the shrike song than to control song (in this case that of an American Robin *Turdus migratorius*) or silence. While doing his study, Atkinson (1997), observed two times a successful attack by the Great Grey Shrike after a period of singing from a hidden spot surrounded by a small flock of passerines. It is also observed that the shrikes mimic the calls of Eurasian Skylarks *Alauda arvensis* which may suggest another observation of prey luring (Lorek et al., 2000).

Given the fact that passerines identify shrikes as predators (Hromada et al., 2002), it probably is more effective to sing hidden than sing from the top of perches (Atkinson, 1997). However, it is not tested if the mimicry is more used when singing from a hidden spot which is expected when the birds use it to lure prey. There are not many songbirds that predate other birds, and it is even suggested that the Great Grey Shrike is with the corvids the only species in Europe that predator on smaller birds (Lorek et al., 2000). Thereby the hypothesis might be a plausible explanation for Great Grey Shrike but gives no function to the mimicry in most species. In addition to that, the hypothesis is so far only supported in one experiment with Great Grey Shrikes (Carouso-Peck et al., 2021; Dalziell et al., 2014).

### 3.3. Scare to steal resources (kleptoparasitism)

Mimicking vocalisation in order to deceive a resource competitor might result in the competitor fleeing. In this case, the mimicking bird can steal food from another species, called kleptoparasitism (Dalziell et al., 2014). Empirical evidence for this hypothesis is provided with a study with Fork-tailed Drongos (Flower, 2011). It was already shown that this species deceptively uses alarm calls to startle pied babblers in order to steal their food (Ridley & Raihani, 2007; Ridley et al., 2007). Flower (2011) showed that the drongo use, besides species-specific alarm calls, heterospecific sounds to deceive pied babblers and also meerkats. The



drongo-specific alarm calls are as effective as the use of heterospecific calls (Magrath et al., 2015), but when using a deception like this frequently, the effect can become less successful (Ruxton et al., 2005). Thereby it is important for the drongo to both use conspecifics and multiple different mimicked alarm calls, in order to increase the chance of success (Flower, 2011). The drongo also switch between alarm calls when they have multiple attempts on a particular species (Flower et al., 2014). Drongos also give alarm calls when there is actually a predator present, making it difficult for the receiver to learn when to react to such calls. With modelling, it is shown that always reacting with the risk to lose sometimes food is the most beneficial way, reducing the evolution of defences against the kleptoparasitism by drongos (Radford et al., 2010), and thereby the effectiveness of the deception by the drongo can be higher when they keep giving honest alarm calls (Aubin & Mathevon, 2020).

Fork-tailed Drongos also kleptoparasite via physical attacks, but it is shown that false alarm calls are more successful and less costly, supporting its functional benefit (Flower & Gribble, 2012). Kleptoparasitisms can also be facilitated by mimicking heterospecific species in order to form a mixed-species flock which higher the chance of stealing food (Goodale & Kotagama, 2006). In an anecdote of Blue Jays mimicking calls of a cooper's hawk, it was suggested that this was used to scare off other jays from a feeder so that the mimicking bird has access to more food (Hailman, 2009). The phenomenon is thus not only used in an interspecific way but also in an intraspecific way shown.

#### 4. Brood parasitism

In brood parasitism, the host species can evolve defences against the parasite species, and thus it can be important for the parasite species to resemble the host more to avoid those defences (Davies, 2000). This mimicry by the parasite species is mostly studied in the egg stage, but is also seen beyond the egg stage (De Mársico et al., 2012). Vocal mimicry of the begging calls of the host species' young may play a role in order to not be rejected. When the begging calls are species-specific, this can result in rejection by the hosts, thus by mimicking the begging calls of the hosts' young, this risk can be lowered (Langmore et al., 2003). Besides that, a host is expected to react to the begging calls of his young in order to give them food and if this is not matched with the begging calls of the host species, it might result in a lowered feeding rate. Also an adult of the parasite may vocally mimic the host, as seen in the viduine-family (Mundy, 1973), to have a higher chance of success of the parasitism.

Mundy (1973) looked at two closely related species of cuckoo: the Great Spotted Cuckoo *Clamator glandarius* and the Striped Crested Cuckoo *C. levaillantii*. In both cases, the fledglings mimicked the sounds of their host species (respectively Pied Crow *Corvus albus* and Arrow-marked Babbler *Turdoides jarinei*). More support is found by Madden & Davies (2006), where they switched fledglings of the Common Cuckoo *Cuculus canorus* from host species. This made clear that the begging call mimicry is not fixed. When cuckoo young from a nest hosted by Reed Warblers were placed in a nest hosted by Dunnocks, they developed begging calls more similar to Dunnocks. Another result was that the difference in begging calls increased the reaction of the host to feed the young. Dunnock hosts reacted more on dunnock-raised cuckoo calls and reed warbler reacted more on reed warbler-raised cuckoo calls, suggesting that this form of vocal mimicry has an adaptive significance. However, there are multiple factors that can serve as a function to elicit enough food. For example stimulation by the palatal papillae (gape stimulation), that can be considered as a supernormal stimulus (e.g. Soler et al., 1995). Because of this, it is hard to say if mimicry of the begging calls is effective.

#### 5. Sexual selection

The first hypothesis with intraspecific communication is about sexual selection. Vocal mimicry can be seen as an indicator for male quality, with only the best males able to learn the song of other species. Females might then show a preference for the males that have an unique song,

which can be achieved by the males by copying the song of heterospecifics (Kelley et al., 2008). This is supported by the nutritional stress hypothesis where it is described that a more complex song is only achieved by songbirds that did well in the critical period to learn songs, thus indicating the qualities of the male (Nowicki et al., 2002). Songs with a lot of mimicry can be seen as more complex songs (i.e. higher repertoire size), and thus provided by a strong male. A shortcoming for this hypothesis is however that when females have a preference for new songs, the male could also improvise and invent songs instead of mimicking others (Kelley et al., 2008). Besides that, it is found that female preference for more complex songs is not widespread and thereby proposed that there is not always sexual selection on this (Byers & Kroodsma, 2009).

## Discussion

The described hypotheses give possible explanations for the existence of vocal mimicry. In all cases, it proposes a function where the mimicking bird gains a certain benefit. The fact that heterospecific mimicry is so widespread and that species often have accurate imitations gives the impression that there must be some kind of functional explanation for this (Kelley et al., 2008). However, the possibility that a songbird gains no advantage out of the mimicry is not excluded. Vocal mimicry may be a result of mistakenly copying the vocalisations of heterospecifics during song learning. One would expect in this case that the vocalisation also contains elements that are similar to their own repertoire. If the sounds are not similar it is not likely that the songbirds take over this vocalisation by accident. Besides that, simple sounds are expected to be more often mimicked than complex sounds and mimicked sounds are common (i.e. often heard) (Kelley et al., 2008).

When vocal mimicry has no functional explanation, it should not be used in a specific context (Kelley et al., 2008) that favours the mimicking bird. However, it is found that Brown Thornbills *Acanthiza pusilla* use different mimicked alarms (from different heterospecifics) in different situations under threat (Igic & Magrath, 2014), thereby suggesting that the mimicked alarm calls have a function rather than that they are mistakenly copied. But this is no evidence for a functional origin of vocal mimicry. An alternative explanation for the context-dependent use of alarm calls may be that the birds are not only mistakenly learning the alarm call, but also the context when it is used (Greenlaw et al., 1998). In addition to that, alarm calls are often given in a stress situation which is known as a moment with strong acquisition of information and long-term storage of it (Rowe, 2002).

Accuracy might also differ when there is no function of the mimicry. If the songbird is by accident copying a heterospecific, it is expected that the accuracy of the mimicry is not very high. When it has a certain function, the accuracy is probably more important. For example seen in Superb Lyrebirds *Menura novaehollandiae* where it is suggested that females have a preference for males that mimic more accurately (Zann & Dunstan, 2008). Thus, there are cases where the expectations of this 'no function hypothesis' are not met. However, the 'no function hypothesis' is not mutually exclusive with the other hypotheses that favour a function for vocal mimicry, which is in line with the study done on 241 European songbirds by Garamszegi et al. (2007). Another possibility is that similarity in vocalisation may be a result of ecological convergence (Dalziel et al., 2014). Some sounds may be more effective causing a selection pressure towards sounds with those functional features rather than copying from heterospecifics.

When heterospecific vocalisation is a result of mistakenly copying, the mistakes are arisen in the learning process of the songbird. As species have different learning processes, this mimicry might be more frequent in some groups of species. For example, close-ended learners are expected to have less heterospecific vocalisation because they have a shorter time span when copying other species can happen (only their first year, see introduction). In contrast, open-ended learners are expected to have more often heterospecific vocalisation in their repertoire

because they have the ability to learn their whole life and thus have more chance to copy other species. This can be directly tested if that's the case.

In this paper, mimicry of all vocalisations of songbirds is discussed. There is however a distinction in the neural circuits between (alarm) calls and songs. This means that mimicry of songs is different from that of (alarm) calls. Due to this, it might be better to treat song mimicry and call mimicry differently when looking at their function. When a songbird mimics a heterospecific the mimicked sound can become part of his repertoire. This can then be copied by conspecifics, making it no mimicry anymore. Thereby it is important to keep the origin of the supposed mimicry in mind. There are examples where the heterospecific sounds are at least partly acquired from other species as the parents are stopped with singing before the eggs are hatched, such as in Marsh Warblers.

Some examples provided seem to be strong evidence towards a certain hypothesis. A problem with this is that it supports mostly just one specific example for only a few species. It still has a value to the functional explanation for vocal mimicry, but it is not comprehensive. There is an overall lack of empirical research. A lot of hypotheses are described for the functional explanation for vocal mimicry, but the supportive evidence is scarce as seen in for example the 'luring prey hypothesis' where it was only tested with one study.

Also development and production of mimicry are important factors in order to say something about its function. For example, research with deafening and captive rearing experiments can gain more understanding of the origin of the mimicry and the underlying mechanisms for the acquisition of it. It also may reveal morphological constraints that some species probably have, as for example seen in Northern Mockingbirds (Zollinger & Suthers, 2004).

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