



REVIEWS

Vocal mimicry in songbirds

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Baylis (1982, *Acoustic Communication in Birds*, Academic Press) decried the serious lack of experimental verification for the various hypotheses proposed to explain vocal mimicry in songbirds. With few exceptions, our understanding of the function and acquisition of this fascinating behaviour seems to have scarcely progressed. We examine the proposed functional explanations and supporting evidence, and summarize advances made since Baylis's (1982) review. We conclude that there is no compelling evidence to support any of the functional hypotheses but, rather, that almost all of the data concerning song mimicry are consistent with the learning mistakes hypothesis, whereby birds learn simple and common sounds, frequently using them in inappropriate contexts. Additionally, many apparently mimicked sounds are calls, not songs, which themselves may not be learned by the models. It is plausible that many examples of call mimicry are, in fact, due to evolutionary convergence.

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Vocal learning may be broadly split into two categories: copying of conspecifics and copying of heterospecifics or other sounds. In this review we focus on vocal mimicry, the copying of the vocalizations of another species or an environmental sound, specifically in songbirds, the most widely documented group. Twenty-six years ago, Baylis (1982) wrote an extensive review of vocal mimicry in songbirds, outlining possible functional explanations. It seemed likely then that there might be more than one such explanation for the existence of vocal mimicry but there were too few appropriate data to be sure. The purpose of this review is to revisit those functional explanations in light of the data that have been produced since 1982.

Functional explanations for vocal mimicry are inherently attractive given the complexity and accuracy of some of the mimicry. Additionally, there are many anecdotes in which birds are described as having used mimicry in a seemingly appropriate context. For example, egg collectors at nests of great bowerbirds, *Chlamydera*

nuchalis, have reported hearing mimicry of cats, dogs and whistling kites, *Haliastur sphenurus* (a local raptor species) and this has been interpreted as an attempt by the nesting female to intimidate the approaching human (Frith & Frith 2004). However, as we will show, such interpretations do not explain the mimicry of other sounds and their use in other contexts by great bowerbirds or almost all other songbird mimicry.

Throughout this review we focus entirely on data published subsequent to Baylis's (1982) review, as in that review no consensus as to the importance of one functional explanation over another was reached. These data involve fewer species than the data in a recent comparative review by Garamszegi et al. (2007) but are geographically more widespread, and the detail allows us to examine mimetic structure and the context in which mimicry is used.

We think it helpful to distinguish between calls and songs, although the distinction is somewhat arbitrary and there is no universal definition in the literature (Spector 1994). Here, we define calls as being simple, short, and produced by both males and females throughout the year in particular contexts, for example alarm, threat and so on (Catchpole & Slater 1995). Importantly, it is usually considered that they are not learned (although

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see Vicario et al. 2002) and that a brain pathway (with nuclei located in the midbrain) different from that involved in song is used in their production (Seller 1981). We define songs as, typically, long, complex, and largely produced by males for reproductive and territorial purposes (Marler 2004). They are usually learned either in early juvenile development or, in some cases, acquired throughout the bird's lifetime and a complex of brain nuclei in the forebrain is involved in learning and production.

Another distinction is that between mimicry via learning and mimicry caused by convergence over generations, as the processes involved in sound acquisition are entirely different. True vocal mimicry is typically considered to be the acquisition of sounds within an individual's lifetime, and, as such, must be learned. The learning mechanisms involved in mimicry are not the focus of this review, although they may show significant similarities to those seen in song learning (Beecher & Brenowitz 2005). In contrast to true vocal mimicry, there is another process by which birds arrive at sounds that are very like the vocalizations of heterospecifics. Evolutionary convergence is likely to be seen between closely related species or result from the occurrence of similar selection pressures, where a common form of vocalization is favoured. This process is the result of the genetic effects of selection accumulating over time and one in which learning plays no part. There is a third instance of mimicry, often termed vocal convergence or vocal matching, in which an individual changes its vocalization to match that of another (see below). This type of matching is usually a response to conspecifics rather than to heterospecifics and is not the convergence we describe above (Gahr 2000). As such, we have not included instances of vocal matching among conspecifics in this review.

FUNCTIONS OF HETEROSPECIFIC VOCAL MIMICRY

A number of possible functional explanations for vocal mimicry have been suggested, which fall into two major categories: (1) interspecific communication, for avoidance of threats and/or competitors; and (2) intraspecific communication, either in a sexual context or for social affiliation. Two common assumptions in all of these hypotheses are that mimicry is a separate category of sounds from calls and songs, and it is used in preference over other sounds in specific contexts.

INTERSPECIFIC COMMUNICATION

The Beau Geste Hypothesis

By singing many different types of (species-specific) song, an individual may give a false impression that many individuals inhabit a territory and so deter potential intruders. Krebs (1977) originally proposed this Beau Geste hypothesis to explain the occurrence of large, species-specific song repertoires and Rechten (1978) suggested that it may apply to vocal mimicry, particularly for territorial birds. By mimicking the vocalizations of a wide range of heterospecifics, birds may reduce the

chance that competitors for food or other resources enter their territory, especially if these potential intruders are themselves highly territorial and thus pay close attention to vocal signals.

In the 1970s there was anecdotal evidence that some species incorporate heterospecific mimicry into their territorial advertisements, perhaps acting to deter heterospecific competitors (Curio 1978). Not only has there been no subsequent support for the hypothesis in the context of species-specific vocalizations (Yasukawa 1981; Dawson & Jenkins 1983; Haftorn 1995), it is also unclear why heterospecific song would be more effective at deterring potential competitors than conspecific song, unless competitors pay attention to the number of different species heard in an area. Without evidence to support this hypothesis in either a species-specific or mimetic context, this seems an unlikely explanation for the occurrence of mimicry (MacDougall-Shackleton 1998).

The Beau Geste hypothesis also does not explain the occurrence of species (usually closely related) including sounds like those of heterospecifics in their own songs, seemingly so as to reduce aggression over territory boundaries (Baptista & Catchpole 1989). For example, great tits, *Parus major*, may include blue tit, *Cyanistes caeruleus*, songs (which sound significantly different) in their own vocalizations (Gorissen et al. 2006). There are at least two possible explanations for this kind of mimicry: first, because of competition for resources, mimicry has arisen so as to lower interspecific aggression, an idea that is similar to vocal matching of group members seen in parrots (Wright et al. 2005). Alternatively, it could be that great tits, because they interact so frequently with blue tits, mistakenly learn blue tit song. Discrimination between these two would be possible if the use of heterospecific mimicry leads to a reduction in aggressive interactions with these heterospecifics. Other instances seem best explained by copying of an inappropriate tutor as occurs when individuals are isolated or when allopatric species occasionally overlap (Helb et al. 1985).

Batesian Acoustic Mimicry

Dobkin (1979) suggested that mimics may deter competitors or potential predators by copying the vocalizations of animals that are predatory or agonistic, in a manner akin to that of a palatable species attempting to avoid predation by visually resembling a noxious species (Bates 1862). Competitor species may perceive a threat from an apparent predator, avoid entering the territory of the mimic, and thus not compete for resources. The intended audience may also include potential predators that are deterred from attacking the mimic by the threat of encountering another predator (Vernon 1973; Dobkin 1979), or are perhaps confused as to the identity of their proposed prey by the conflicting acoustic signals coming from the mimic (Harcus 1977; Curio 1978). We consider that the identification of mimicry of predators with Batesian mimicry in the coloration pattern context has caused some unnecessary confusion in that visual mimicry comes about through evolutionary convergence and not

learning. None the less, the predictions are that vocal mimics should learn predator vocalizations and then use those sounds in response to the presence of a predator or a competitor.

There have been no compelling experimental data collected in the past 26 years that support or refute this hypothesis. One possible example comes from the Australian magpie, *Gymnorhina tibicen*, which mimics potential nest predators, the barking owl, *Ninox connivens*, and the boobook owl, *Ninox novaeseelandiae* (Kaplan 1999). However, not only are there no data on the context in which these sounds are used, but, given the diversity of sounds that magpies mimic, it would seem that Batesian mimicry is not the most parsimonious explanation for the mimicry of these two owls. Australian magpies can have a considerable mimetic repertoire, a very small proportion of which is mimicry of predatory species (other mimicry includes rosellas, *Platycercus* spp. lapwings, *Vanellus* spp. lyrebirds, *Menura* spp.). Call convergence in this species might be ruled out if there is considerable between-individual variation in repertoire content. However, if they learn these sounds from conspecifics (not yet known) they would be not considered to be true vocal mimics (copying from heterospecifics or the environment).

Another Australian species that mimics aggressive or predatory species is the spotted bowerbird, *Chlamydera maculata* (Coe 2005). However, as mimicry is commonly produced in bouts along with nonpredatory models such as grey-crowned babblers, *Pomatostomus temporalis*, and yellow-throated miners, *Manorina flavigula*, it seems unlikely that the mimicry would be an effective deterrent for potential predators. Additionally, although one might expect this kind of deterrent to be effective only when the mimic is hidden from view, spotted bowerbirds frequently vocalize (including mimicry of predators) from conspicuous perches.

Experimental manipulations demonstrating that signalers give mimetic calls of predators or agonistic species when their territory, nest or safety is threatened, and that receivers respond to mimicry as if to vocalizations by a genuine predator, would provide compelling evidence that mimicry is used as an acoustic aposematic signal (i.e. appropriate response to a specific context). In an apparent experimental test of the Batesian mimicry hypothesis, burrowing owl, *Athene cucularia*, hisses (claimed to be mimicry of rattlesnake rattles) were played to ground squirrels, *Spermophilus beecheyi*, eliciting more avoidance behaviour from ground squirrels sympatric with rattlesnakes than from rattlesnake-naïve ground squirrels (Rowe et al. 1986). Playback of rattlesnake noise elicited a stronger response from the ground squirrels than did the owl hiss, but it is not clear whether the owls naturally use this hiss in a defensive response to rattlesnakes, a potential nest predator, or whether it functions to deter ground squirrels from competing for nest burrows. Importantly, this is not vocal mimicry as the hisses are not learned; rather, it appears that the hisses are a modified juvenile begging call and are the result of call convergence (Owings et al. 2002).

In our view, then, while there is a possibility the Batesian mimicry hypothesis may explain some of the components of the mimetic repertoire of some species, for most species' mimicry this is an implausible hypothesis. It is also clear how very few quantitative data exist that document the natural context in which mimicry is used.

Attracting a Third Species

Mimics might benefit by inducing mobbing of their own predators or competitors by individuals of one or more other species. Alternatively, alarm calls, including apparently mimetic ones, may attract a second predator, possibly coming in search of injured prey, giving the caller a chance to escape during the ensuing contest with the first predator (Curio 1978; Hogstedt 1983). While this might explain the use by phainopeplas, *Phainopepla nitens*, of mimicry of heterospecific alarm calls when distressed (e.g. when captured in mist nets) as it can elicit mobbing by heterospecifics, it does not fit with the stronger mobbing response evoked by playback of the phainopepla's own alarm calls (Chu 2001a, b). At the very least, this seems an inefficient use of mimicry. Eastern towhees, *Pipilo erythrophthalmus*, will also substitute their own alarm calls with mimicry of heterospecific alarm calls when disturbed. It is not yet clear what benefit is gained by doing this as behavioural responses of heterospecifics and conspecifics were not investigated (Greenlaw et al. 1998).

Greater racket-tailed drongos, *Dicrurus paradiseus*, insert calls thought to be mimicry of alarm calls of heterospecific flockmates alongside their own mobbing calls (Goodale & Kotagama 2006a). They also use apparently heterospecific alarm calls in alarm situations, but this is done only as they increase the number of their own alarm notes and not all of the calls used are alarm calls. As phainopeplas also include nonalarm calls in stressful situations alongside alarm calls, it is possible that this less-than-perfect matching of context to the use of specific mimicry is due to a lack of our understanding of the context. However, there is no evidence that the drongos preferentially use heterospecific calls in alarm situations. There is also no evidence, yet, that they learn these calls in spite of these calls being labelled as heterospecific mimicry. Unusually, however, drongos do mimic songs of heterospecifics although these are relatively uncommon and are used inappropriately, that is, in the same contexts as the alarm calls.

As drongos' feeding efficiency is higher when they forage within a flock (comprising conspecifics and heterospecifics) than when foraging alone, Goodale & Kotagama (2006b) proposed that these birds use nonalarm mimetic sounds to attract other birds to form flocks. Indeed, playbacks of drongo nonalarm mimicry were more likely to attract other birds than were playbacks without mimicry although the species attracted tended not to be those species being mimicked (Goodale & Kotagama 2006b). Until there are substantive data on the context in which drongos themselves produce nonalarm calls, these playback data, while consistent with the attraction of a third species hypothesis, do not demonstrate that the drongos use

mimicry in a context-specific way, that is, only using mimicry appropriate to a specific situation.

Facilitating Brood Parasitism

Brood parasites face discrimination by their hosts and are commonly rejected at the egg stage, driving the evolution of visually mimetic eggs (Davies 2000). Hosts may also discriminate against brood parasite nestlings, perhaps noting the differences in begging calls that they give. To counter this, brood parasite nestlings might have been selected to produce begging calls very like those of their host young. For example, nestling Horsfield's bronze-cuckoos, *Chrysococcyx basalis*, may be accepted by superb fairy-wrens *Malurus cyaneus*, which reject shining bronze-cuckoo chicks, *C. lucidus* (Langmore et al. 2003). Horsfield's bronze-cuckoo chicks have a similar begging call to that of the superb fairy-wren chicks, both of which differ from the begging call of shining bronze-cuckoo chicks. The chicks of this latter species have a begging call very like that of the chicks of their usual host, the thornbill, *Acanthiza* spp. (Langmore et al. 2003). This may be mimicry by direct copying, especially if the parasite is raised alongside host young, so gaining an opportunity for learning the host chicks' begging calls (Redondo & Dereyna 1988). However, as this similarity in vocalization has also been described for cuckoo species that eject the host's young and are raised alone, it is likely that this is not vocal mimicry but call convergence (McLean & Waas 1987; Madden & Davies 2006).

Vocal mimicry has been demonstrated in another brood parasite, the village indigobird, *Vidua chalybeata*, which parasitizes and mimics the songs of the red-billed firefinch, *Lagonosticta senegala*. Female indigobirds mate with males that mimic the song of their host species. When indigobirds were experimentally foster-reared by Bengalese finches, *Lonchura striata*, they developed songs similar to those of their new foster parents, despite being able to hear and see firefinches, their usual host (Payne et al. 1998). Irrespective of host species, indigobird males did not copy songs directly from their host parents (unless isolated with them after fledging) but from other adults of the foster species or other indigobirds mimicking the same foster species. Learning host songs may occur in two stages: early life when the general features of host song are learned from parents, and a later developmental period when songs are learned from nonparents. This example does appear to be one of learning and the implication is that these mimicked songs are used to attract conspecific females.

In summary, with the exception of some brood parasites, none of the functional explanations for mimicry in an interspecific context has yet been strongly supported. In all cases, it appears that the birds either do not produce mimicry relevant to the appropriate context or, if they do, they are not very good at doing so. There is also no compelling evidence to suggest that the models mimicked are specifically chosen for later use in a particular context. Finally, there is almost no evidence for learning of vocalizations in any of these studies and thus no support for vocal mimicry itself.

INTRASPECIFIC COMMUNICATION

Sexual Selection

A wide variety of models mimicked might be explained by sexual selection, as mimetic vocalizations could provide an honest indicator of male quality (Zahavi 1975), with only the best males being able to learn and give accurate renditions of mimicry (Loffredo & Borgia 1986; Nowicki et al. 2002). Alternatively, females might show a preference for novelty, which could be achieved by a male by incorporating heterospecific song into his display (ten Cate & Bateson 1988). However, if females were interested only in repertoire size we would expect high levels of improvisation or invention.

The occurrence of mimetic sounds in the courtship displays of several bowerbird species is consistent with mimicry playing a role in mate choice. For example, a satin bowerbird, *Ptilonorhynchus violaceus*, male may include mimicry of up to five sympatric bird species alongside species-specific vocalizations in his courtship display. While older males tended to produce longer and higher-quality bouts (of mimicry of laughing kookaburra, *Dacelo novaeguineae*, calls, spectrograms assessed by eye) than did younger males, in only 1 of 2 years in which mimicry was quantified did mimetic duration and quality result in higher mating success (Loffredo & Borgia 1986). More recently, and using a more sophisticated method of assessing accuracy of mimicry (spectrographic cross correlation), male satin bowerbird mimetic accuracy of both kookaburra and Lewin's honeyeater, *Meliphaga lewinii*, calls was correlated positively with mating success and accuracy was correlated positively with repertoire size (Coleman et al. 2007). However, these satin bowerbirds mimicked only five species, two of which featured only rarely in the vocal displays, suggesting that much potential for expanding repertoire was not being used. The possibility that satin bowerbird females prefer sounds that are physically difficult for males to produce (rather than a large repertoire) has not been investigated (as is the case in canaries, *Serinus canaria*: Vallet & Kreutzer 1995).

There is some evidence that quality of mimicry is correlated with male age in the satin bowerbird (Loffredo & Borgia 1986), which might lead to female preference for vocalizations that are complex and difficult to mimic. However, male satin bowerbirds mimic calls and not songs, and the calls they mimic do not appear to be very complex. There has been no explicit demonstration of learning although this has been implied for the more distinctive sounds, such as the laughing kookaburra-like noises that the bowerbirds produce. If these sounds are learned, it is not clear whether they are learned from the models or from conspecifics. Mimetic ability provides an indicator of male age in superb lyrebirds, *Menura novaehollandiae*, as subadults produce less accurate mimicry and have smaller repertoires than adults (Zann & Dunstan 2008). Although these data are consistent with mimicry playing a role in mate choice, alternative hypotheses cannot be excluded without explicitly testing the relationship between mating success and variation in mimetic quality and/or repertoire size.

In the only other species for which there has been an investigation into the relationship between mimicry and mating success, male black-browed reed warblers, *Acrocephalus bistrigiceps*, sing long, complex songs but do not achieve higher mating success (as measured by pairing date) when the mimetic component (syllables rather than whole songs) of their repertoire is higher (Dowsett-Lemaire 1979; Hamao & Eda-Fujiwara 2004).

In sum, then, the only data supporting the sexual selection hypothesis have come from bowerbirds and these are not especially compelling as yet. To determine that mimicry is preferentially used as a different and additional cue in female choice, both learning of sounds and specific benefits to using mimicry in displays still need to be demonstrated.

Social Affiliation

The ability to match vocalizations of conspecifics for social cohesion has been reported in several species of birds and is likely to be prevalent in the taxa that learn their vocalizations (Hile et al. 2000; Vehrencamp et al. 2003; Cortopassi & Bradbury 2006). Robinson (1991) suggested that lyrebirds, *Menura* spp., might use vocal mimicry in this kind of way, too, for maintaining contact in the dense rainforest in which they live. However, the value of using mimicry, rather than species-specific calls, to maintain contact is unclear. It may be that certain types of song transmit especially well in certain habitats and that it is more cost effective to copy these from the environment than it is to establish them as part of a species-specific repertoire. Structural adaptation for maximum transmission in each particular habitat appears to be the most suitable explanation for satin bowerbird vocalizations and, as Albert's lyrebirds, *Menura alberti*, mimic the calls of local satin bowerbirds, they may also produce effectively transmitted sounds (Nicholls & Goldizen 2006; Putland et al. 2006). However, this fails to explain why the lyrebirds mimic many more environmental sounds than just the most efficient call type. Importantly, models do not respond to lyrebird mimicry and there are, as yet, no data on the response by lyrebirds to mimicry produced by conspecifics.

LEARNING

In 26 years, then, almost no significant evidence supporting any of the functional hypotheses for vocal mimicry has been produced. Any of the data that do appear somewhat consistent with the predictions of one hypothesis or another are not convincing even for the hypothesis they have been invoked to support. And yet, the widespread existence and degree of accuracy of heterospecific vocal copying surely needs some kind of explanation. There is, however, one hypothesis that is consistent with almost all of the instances of vocal mimicry in songbirds.

Hindmarsh (1984) suggested that, at least in the European starling, *Sturnus vulgaris*, avian vocal mimicry may be a result of mistakes made during song learning and therefore the mimicry serves no function. If mimicry is indeed a collection of sounds mistakenly picked up during

song learning (during imprinting in some cases), rather than a result of specific context-dependent learning, we would expect one or more of the following: (1) mimetic repertoires to contain notes that are similar to the species-specific repertoire; (2) simple sounds to be mimicked more often than expected by chance; (3) mimetic repertoires should contain sounds that are commonly heard; (4) mimicry is not always used in the appropriate context.

In one of the few studies to test the predictions of more than one hypothesis, mimicry in robin chats, *Cossypha* spp., is consistent with several predictions that come from the learning mistakes hypothesis: robin chats are more likely to mimic simple songs and do not mimic significantly more predators or competitors (Ferguson et al. 2002). There was no correlation between model prevalence in the acoustic environment and presence or absence in the mimetic repertoire: many species that were commonly heard at study sites were never mimicked and several mimicked models were never heard at that site. However, the mimetic repertoire of the black-browed reed warbler (see above) does seem to be a reflection of the sounds of the common birds in its environment rather than of any specific group of species (Hamao & Eda-Fujiwara 2004), as is that of the marsh warbler, *Acrocephalus palustris* (Dowsett-Lemaire 1979).

There is at least one prediction that follows from the learning mistakes hypothesis that could readily be tested: we would expect to hear mimicry often being used in inappropriate contexts. However, tests of the potential predictions will have to wait until we know more about what and how sounds are learned, and in what context. For example, while it seems plausible that sounds that are similar to species-specific vocalizations are more likely to be learned in error than are dissimilar sounds, there is, as yet, little relevant evidence. The plausibility of such an idea is enhanced by findings such as the learning by song sparrows, *Melospiza melodia*, of swamp sparrow, *Melospiza georgiana*, songs if the swamp sparrow syntax is edited to have a similar syntax to song sparrow conspecific songs (Marler & Peters 1988).

If mimicry is a result of making mistakes during song acquisition, then mimicry acquisition should be confined to the stages at which normal song learning occurs (Hindmarsh 1986). This should be relatively straightforward to examine in closed-ended learners. With a relatively limited window of opportunity, closed-ended learners might also be expected to have small mimetic repertoires. Open-ended song learners, however, which modify their species-specific song repertoires after their first year of life, have greater opportunities to learn new sounds and may, then, learn more heterospecific songs by mistake.

The mimicry of alarm calling or of vocalizations of predatory species might also be explained through mistaken learning. This is because learning about any particular individual, location, object or event is always affected by the motivational state of the learner, which itself is affected by stress. Although high acute stress (which itself may be good or bad) may make it difficult to recollect remembered information at the time, it is often correlated with good acquisition of information and long-term

retention of that information (Rowe 2002). Hearing predators or alarm calls of other prey species is likely to increase stress levels acutely and may lead to enhanced uptake of lots of information pertinent to that instance. Not only would this lead to learning the specific sound, it may also lead to learning the context in which that sound was heard (Greenlaw et al. 1998). Such one-trial learning of complex information is the hallmark of learning to avoid unpalatable prey, imprinting, snapshot memory and, indeed, all episodic memory. Later production of a sound learned in a specific context may be expected to occur when the context is reproduced or when the animal is stressed. This would explain all of the apparent intentional insertion of mimicked alarm calls into alarm calling and mobbing in the appropriate context. As the neural structures underlying alarm call production are significantly different from those operating in song learning, it may also be the case that mimicry of song or complex sounds differs significantly in other ways from that of alarm calls.

Vocal learning may, in some cases, be the result of operant conditioning, whereby there is gradual acquisition in response to a reward (C. ten Cate, unpublished data). Mimicry by parrots such as Alex seems best explained in this way (Pepperberg 1981). Until we know more about the context in which mimicry is acquired, we cannot determine whether or not it is gradual or the result of a one-trial episode. Either of these explanations could lead to the apparent complexity of any one mimicked sound, or both may be involved, which might explain the observation of an Australian magpie mimicking a kookaburra 2 days after hearing a single call, and adding to its repertoire duetting kookaburras when exposed to these at a later date (Kaplan 1999).

Understanding the acquisition of mimicry could help to address associated questions such as choice of models. For example, reports of sedentary starlings mimicking species that are found many miles away seem best explained by the mimicry passing from one starling to another (Hausberger et al. 1991; P. J. B. Slater, personal communication). This process may also maintain mimetic calls across many generations, but not always: starlings in New Zealand, introduced in the 19th century, are proficient mimics, but their mimetic repertoire does not contain calls from any nonintroduced European birds (Hausberger et al. 1991). Once a mimicked sound is part of a bird's repertoire it may then be learned by a conspecific as part of the overall species-specific repertoire and, as such, would no longer be mimicry. Marsh warblers cease singing before their young hatch and repertoires are learnt entirely from heterospecifics, copied from species at both their European breeding grounds and Africa, where they overwinter (Dowsett-Lemaire 1979). Local mimetic 'dialects' of Albert's lyrebirds indicates vocalizations are learned directly from models, although the stereotyped sequence of different models produced during a mimetic bout suggests this component of mimicry is transmitted between conspecifics.

As yet we do not know whether any selectivity of model is accompanied by auditory or physiological constraints on models that are mimicked. Bill and vocal tract morphology are likely to limit the rate of syllable

repetition and hence the type of models that a species is able to mimic (Podos 2001). For example, birds use both sides of the syrinx independently during song production, and mockingbirds, *Mimus polyglottus*, that produce more accurate mimicry use an identical motor pattern to their model species (Zollinger & Suthers 2004). When mimicking songs with notes outside their frequency range, mockingbirds either substitute a note within their frequency range, or omit the note. When notes are omitted, other notes in the sequence are lengthened, so that the song is identical in duration to the model song, as if in recognition that song duration is important. When mimicking songs with high syllable repetition rates such as the canary's, mockingbirds cluster notes into discrete groups because of pauses for inspiration but, again, maintain the overall song length. In mockingbirds, at least, there may be physiological constraints on the accuracy of mimetic songs. By investigating these questions in other mimics, we would be able to examine whether species with smaller mimetic repertoires are physiologically constrained in the models that they mimic, or whether they have other constraints acting upon them. Captive rearing and deafening experiments can also provide valuable insights into the development and production of mimicry. As with species-specific song production, the roles of tape and live tutors and the importance of auditory feedback can be investigated (Kroodsma et al. 1997).

Conclusions

Twenty-six years on and we are no closer to determining even a single function for vocal mimicry. While this may, in part, be because of the relative paucity of work, there is only one study that has been carried out in this time that offers any credible support for the proposed functional hypotheses (indigobirds mimicking firefinches in a mate choice context). This view is consistent with the main outcome of a recent comparative analysis of vocal mimicry in western Palaearctic songbirds (Garamszegi et al. 2007): there was no significant support for any of the proposed functional hypotheses but, importantly, those authors concluded that research effort is the best predictor of the existence of vocal mimicry. We would add to this by concluding that future research effort should be directed towards determining the mechanisms underpinning the acquisition of mimicry and contexts of use.

Just as the following questions have been useful guides for directing research in song learning generally, we suggest that effort should be put into addressing them in the context of vocal mimicry. Is mimetic learning an open process with the potential for acquiring new vocalizations throughout an individual's life, or is it restricted to specific periods? Does learning depend on refinement of sounds after repeated exposure, or can a sound be mimicked after a single hearing? Does an individual increase its quality or repertoire size as it ages, thus providing information about its status? Do mimics learn directly from model species, indirectly from conspecific mimics or a combination of both? In what contexts is mimicry produced? Answers to these questions would help us go a long way to understanding just what avian

vocal mimics are doing and the extent of their cognitive capabilities.

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