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Review

Why is birdsong so repetitive? Signal detection and the evolution of avian singing modes

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Abstract

Signal repertoires, such as the song type repertoires of many songbirds, are thought to play a role in male mating success, with females preferring larger male repertoires over smaller ones. Yet, in many songbird species, males sing in a way that does not readily reveal their repertoire sizes by repeating each song type multiple times before switching to the next. Here I describe a potential explanation for such signal redundancy, based on the predictions of signal detection theory as it applies to intersexual communication during mate choice. According to this idea, a female's response threshold to male mating signals (i.e., her 'choosiness') should select for male signal features that elicit favorable female responses (i.e., that are more 'detectable'). Males can increase the detectability of their signals by producing them with higher redundancy, as well as by increasing their intensity and distinctiveness. Thus, in species with relatively high female response thresholds to males, such as taxa in which the sexes associate only briefly during breeding, males are expected to produce mate attraction signals that are especially stereotyped and repetitive. High signal stereotypy is also expected to be associated with features within signals that are relatively extravagant. Phylogenetic studies of a songbird group with a wide range of mating patterns, the oropendolas and caciques (family Icteridae), provide evidence consistent with these evolutionary predictions. Singing modes in this group have become more repetitive in some lineages along with the evolution of polygynous mating systems, even as various features within songs have become more extravagant.

Keywords

bird song, communication, mating systems, redundancy, sexual selection, signal detection theory.

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1. Introduction

The evolution of extravagant traits by sexual selection, particularly male traits used in mate attraction, has long been a central focus of evolutionary biology (Cronin, 1991; Andersson, 1994). Complex and exaggerated features, such as the elaborate trains of peacocks (Petrie, 1994), are thought to have evolved because they are preferred by females over less elaborate features and thus confer mating advantages to males that exhibit them (Darwin, 1871; Fisher, 1930; Kirkpatrick & Ryan, 1991). In animal communication systems, female choice presumably explains many extravagant features in the mate attraction displays of males, such as predator-attracting components in the calls of some frogs (Ryan, 1985, 1997; Akre & Ryan, 2011), the brightly colored dewlap used in anoline lizard displays (Fleishman, 1992; Fleishman & Pallus, 2010), and the diverse song type repertoires of many oscine passerines, or songbirds (Searcy & Yasukawa, 1996; Searcy & Nowicki, 2005; Catchpole & Slater, 2008).

While the presence of extravagant display features has been well studied, another common characteristic of these signals, their stereotypy, has received comparatively little attention. Yet, this characteristic might be an equally important aspect of signal evolution. Mate attraction displays in a wide variety of taxa, including those mentioned above, are often performed in a highly stereotyped and repetitive manner, and examples include acoustic, visual and even electrical signals (Bradbury & Vehrencamp, 2011). Furthermore, in species that exhibit different signaling patterns in different social contexts, displays used specifically in the context of mate attraction are usually less variable and more repetitive than are signals directed at individuals other than potential mates (e.g., Spector, 1992; Kroodsma, 1999).

Signaling patterns can range in organization from highly stereotyped, in which a signal is repeated with high levels of precision, to highly versatile, in which a diversity of different signals are presented in series with little repetition of any particular signal type. A common presumption, especially in studies of at least some songbirds (e.g., song sparrows, *Melospiza melodia*; red-winged blackbirds, *Agelaius phoeniceus*), is that female choice favors diversity in male displays (Searcy & Yasukawa, 1996). Indeed, evidence from various well-studied songbird species suggests that females prefer males with larger song repertoires and that repertoire size is associated with male fitness (reviewed by Catchpole & Slater, 2008). Yet, surprisingly few male songbirds sing in a way that advertises their repertoire sizes. Rather, in many species, males repeat each of their song types multiple times before switching to the next. This suggests that signalers might be under two competing selection pressures: selection for large repertoire sizes and selection to produce each signal type with high stereotypy (Nowicki et al., 2002; Searcy & Nowicki, 2005). Such signal stereotypy is common in animal mate attraction displays, yet few studies have presented a testable explanation for its existence.

Here, I present a potential explanation for the widespread evolution of repetitive singing patterns in songbirds, based on previous discussions of signal evolution by Wiley (1983, 1994, 2000a) suggesting that choosy females should favor the evolution of male signals that are highly stereotyped and redundant. These predictions are based on signal detection theory, as it applies to intersexual communication during mate choice.

2. Mate choice as a signal detection problem

In the study of animal communication, signal detection theory is most often applied to communication in noisy environments, such as in situations where signals degrade during transmission (Wiley & Richards, 1982) or are masked by other stimuli (Klump, 1996; Wollerman & Wiley, 2002; Slabbekoorn, 2004; Luther & Wiley, 2009). All forms of communication occur in the presence of some form of background noise (Wiley, 2006). However, this model can also be applied effectively to communication during mate choice, as the difficulties faced by male signalers are largely the same (Wiley, 1994, 2000a). In both cases, there is a less than certain probability that a receiver will respond favorably to a male's signal, in the former case because of environmental interference and in the latter case because of a female's fastidiousness in choosing a mate. For displaying males, these situations (environmental noise during transmission and 'neural noise' due to female choosiness) are effectively identical and should favor the evolution of similar modifications in signal design to improve receiver response (Wiley, 1983, 1994, 2000a).

When considering the evolution of mating signals, it is important to recognize that male signalers and female receivers have different interests (Searcy & Nowicki, 2005). Females seek reliable information about male quality as potential mates, either by direct assessment or through more indirect means (Wiley & Poston, 1996; Wiley, 2000a), whereas males often seek to attract females regardless of quality (Wiley, 1983; Krebs & Dawkins, 1984). Selection favors females who respond only to optimal males and males who successfully elicit favorable responses (e.g., copulations) from females. The underlying assumption of signal detection theory is that communication under natural conditions is never noise-free and that receivers therefore make mistakes (Wiley, 1983, 1994, 2000a, 2006, 2013). In the context of mate choice, this implies that a female receiver faces inescapable trade-offs between two kinds of error: choosing to mate with a suboptimal male (a false alarm) or failing to respond to the signals of an optimal male (a missed detection). It is impossible for females to minimize both of these types of error simultaneously; consequently, they must evolve thresholds of response based on the probabilities and relative costs of each (see Figures 1 and 2 in Wiley, 2013, this issue). The higher the response threshold, the lower the responsiveness of a female to male signals and thus the choosier she is.

For a female, the consequences of mating with a suboptimal male can include less assistance in raising offspring, less than optimal genes for her progeny, or even no progeny at all. Missing an opportunity to mate with an optimal male, on the other hand, has far less serious long-term consequences, especially when the cost of additional searching is low. Females are therefore expected to evolve response thresholds that minimize false alarms in order to reduce the potential for costly mistakes in mating, even when such thresholds increase the probability of missed signal detections (Wiley, 1994). Females that have less time for making their choices or limited information about males should evolve even higher thresholds of response so as to minimize costly false alarms. As a result, these females also ignore more signals from potential mates, provided this does not cause them to miss their window for successfully breeding. In contrast, when females have ample time and multiple cues for assessing the qualities of potential mates, the probabilities of both types of error are relatively low and therefore female response thresholds to male signals should be relatively low as well.

To counteract female choosiness, optimal males should evolve signals that are more ‘detectable,’ in other words, ones that increase the probability of eliciting favorable responses in females. Highly detectable signals allow females more opportunity for assessing signal features and thus reduce the difficulty in discriminating between optimal and suboptimal males. Features that increase detectability include (1) increasing a signal’s intensity, (2) increasing a signal’s contrast with irrelevant stimuli and (3) increasing the temporal or spatial stereotypy, or redundancy, of a signal (Wiley & Richards, 1982; Wiley, 1983, 1994). All of these signal features are favored in the presence of factors that reduce the probability of a receiver response, whether these factors include environmental noise, signal degradation over distance, or the response thresholds of choosy females. Therefore, when females use some attribute of a male's signal as a cue in assessing his quality as a potential mate, increased choosiness in females should favor the evolution of increased intensity, distinctiveness, and stereotypy in signal production by males.

The first two of these adaptations, high intensity and distinctiveness, are potentially costly to signalers and are well-documented as targets of female choice (Kirkpatrick & Ryan, 1991; Endler, 1992; Andersson, 1994; Ryan, 1997; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). Signal stereotypy, in contrast, has been largely ignored in studies of sexual selection, possibly in part because the costs of this feature are not as readily apparent. Nevertheless, when considering mate attraction as a signal detection problem, all three of these adaptations are expected to evolve in response to choosy females, not necessarily because they provide information about male quality but because they increase a display's chance of eliciting a response from a choosy female, and thus its effectiveness in obtaining mating opportunities (Wiley, 1994). Decreasing the variability and increasing the repetition of a signal are known to enhance its effectiveness in communication by reducing ambiguity and by allowing receivers more than one opportunity for detection and assessment (Wiley & Richards, 1982; Wiley, 1983). The evolution of stereotypy in signals is therefore closely related to the classic ethological concept of ritualization (Cullen, 1966; Wiley, 1994).

A further consequence of selection for stereotypy is that it may enhance a female's ability to compare multiple renditions of a signal type from the same male. Repeating a signal with high precision is presumably more difficult than repeating the same signal with high variability, so signal consistency might provide useful information to females about a male's abilities. High consistency in song type performance is known to be correlated with aspects of male quality in some songbirds (Byers, 2007; Botero et al., 2009). Furthermore, if selection causes the signals of different males to converge on a common, species-specific pattern (e.g., Wiley, 1973; Byers, 1996; Kroodsma, 1996, 1999), high stereotypy might benefit females by providing a common standard by which males may be compared (Zahavi, 1980).

3. Signaling patterns and sexual selection

Female response thresholds to male signals should be strongly influenced by the time and information available to females during mate choice (Wiley, 1994). Although measuring such factors in a species may not always be feasible, we can still make some predictions about the relative response thresholds of females based on other species characteristics. For example, in sedentary, socially monogamous species in which both sexes provide parental care, females probably have ample opportunities for assessing males and avoiding costly errors in mate choice. Response thresholds to male signals in these species are therefore expected to be relatively low. The difficulty of detecting optimal males, and the consequent probability of error, presumably increases when females have little time to make their choices or when they have little experience with potential mates, for example, when mate choice occurs shortly after arrival at breeding grounds after migration (Wiley, 1983). Females should encounter even greater problems when their previous experience with male signals is limited, for instance, when the sexes associate only during mating and when young are reared by females alone (Wiley, 1994). In these species, females should evolve higher thresholds of response to males so as to minimize costly mistakes. In short, females of species with less interaction between the sexes are expected to be choosier, and hence less responsive to male signals, than females of species with long-term associations between the sexes (Wiley, 1994).

Species with relatively brief male–female interactions, such as animals that breed at display sites (e.g., leks), have no male parental care, or have relatively short breeding seasons due to seasonal migration, generally exhibit male secondary sexual traits that are more intense and conspicuous (i.e., extravagant) than species with long-term associations between the sexes (Darwin, 1871; Wiley, 1983; Andersson, 1994). As described above, brief male–female relationships are also the situations in which we expect females to evolve higher thresholds of response to male signals and thus to be choosier during mate choice (Wiley, 1994, 2000a). Consequently, we predict that male mating signals in these species should be more stereotyped and repetitive. In songbirds, for example, we should expect males of migratory and/or polygynous species to produce songs with higher stereotypy, and hence lower versatility, than males of sedentary, monogamous species.

This prediction is in direct contrast to the idea that increased female choosiness favors the evolution of greater diversity in male signaling patterns rather than greater redundancy, which is a common presumption in studies of songbirds that produce more than one song type (Catchpole & Slater, 2008). Moreover, because female choosiness is predicted to decrease, rather than increase, the apparent complexity of a male trait (signal versatility), the evolution of signal stereotypy appears superficially to be a striking exception to the general pattern of sexual selection favoring extravagance. It should be emphasized, however, that the predictions of signal detection theory do not contradict the idea that female choice favors exaggerated and expensive features in the design or production of signals. Producing a sequence of diverse signal types is not necessarily any more costly to a signaler (and might even be less costly physiologically, e.g., Lambrechts & Dhondt, 1988) than repeating only one signal type from that same signal repertoire.

It could be argued that stereotypy itself might be an extravagant feature in some cases, especially if a display is highly complex (Wiley, 1973, 1983). As mentioned above, the ability to repeat a complicated motor pattern with high precision should require a greater degree of skill than performing the same motor pattern with more variability, and might therefore require long-term practice or special developmental mechanisms (Nowicki et al., 2002; Botero et al., 2009). Such ‘temporal symmetry’ in signal production is thus analogous to spatial symmetry (i.e., fluctuating asymmetry) in morphological features, which is thought to reflect male developmental homeostasis and to be used by females of some species in assessing potential mates (Møller & Swaddle, 1997). Therefore, in at least some cases, female preferences are expected to favor the evolution of distinctive signals that are extremely stereotyped. The strut display of the male sage grouse, *Centrocercus urophasianus*, might represent such an example (Wiley, 1973).

A certain degree of stereotypy should also be favored when a number of different displays must be learned, such as in birds that sing multiple song types. Nowicki et al. (1998) have argued that sexual selection favors the ability of male songbirds to learn repertoires of diverse song types because this ability indicates greater learning capabilities in general and thus might indicate good genes for a female’s offspring. The quality of vocal learning, however, might reveal just as much about a male’s developmental history as the quantity of song types learned (Nowicki et al., 2002). That is, learning many patterns in a careless way presumably requires no more neural capacity than learning one pattern with high precision. Thus, in the end, the stereotypy of each song in a male's repertoire might be just as important as how many songs are learned for indicating his quality (Byers, 2007; Botero et al., 2009).

In summary, we should expect the evolution of relatively repetitive mate attraction signals: (1) in species characterized by relatively brief interactions between the sexes, as occurs in many polygynous or itinerant taxa with little or no male parental investment beyond mating and (2) when male signals include features that are especially intense and distinctive (i.e., extravagant) due to female choice. Although such associations should be universal in animal communication systems, songbirds provide an especially useful model system for testing these ideas.

4. Signaling patterns in songbirds

The diversity of acoustical signals used by a particular songbird species can be enormous; however, the patterning of these signals during display is usually relatively invariant within species (Catchpole & Slater, 2008). Oscine songbirds are somewhat unusual among animals in that individuals often have a number of distinct, apparently functionally-redundant signals (song types) used during communication with rivals and potential mates (Collins, 2004). These vocal repertoires can range in size from just a few song types (e.g., Krebs et al., 1978) to thousands of distinct songs (Kroodsma & Parker, 1977). Furthermore, and perhaps more interestingly, species with similar repertoire sizes can nevertheless differ dramatically in the species-specific modes with which these signals are presented, from highly versatile to highly repetitive. This variation among songbird taxa allows us to investigate the selective forces on signal organization in a way not possible in most other animals (Read & Weary, 1992).

Songbird singing modes can be placed into one of three categories of signal organization, representing points along a continuum: (1) immediate variety, in which a sequence of distinctly different song or syllable types is presented with little to no immediate repetition of the same sound pattern (e.g., ABCDE...); (2) eventual variety, in which a sound pattern is repeated a number of times in a stereotyped fashion before another type is introduced (e.g., AAA...BBB...); or (3) no variety, in which only a single song pattern is sung. Even closely related songbird species can differ a great deal in the temporal redundancy of their signals (Price & Lanyon, 2004).

The fact that so many songbird species sing with eventual, rather than immediate, variety is one of the remaining unsolved puzzles in the study of bird song (Wiley, 2000b). Song repertoires are widely thought to have evolved under the influence of intersexual selection (Searcy & Yasukawa, 1996; Nowicki et al., 1998), and evidence supports this idea by showing that males with larger repertoires often have higher fitness (Catchpole & Slater, 2008). Yet, if repertoire size is indeed assessed by females during mate choice, why do the males of so many species appear to hide this trait by performing their songs with eventual variety? What is the advantage for a male in repeating each song type in his repertoire several times and thus taking longer than necessary to reveal his repertoire size? This paradox strongly suggests selection for stereotypy in these signals.

Even more intriguing are the vocal organizations of songbirds that use different singing modes in different contexts. Song in most passerine species appears to serve dual functions for both female attraction and territorial defense against rival males (Collins, 2004). In some species, however, different singing patterns may be used in each context, which allows us to separate the effects of inter- and intrasexual selective factors on vocal organization (Spector, 1991, 1992; Wiley et al., 1994; Byers, 1996; Kroodsma, 1996, 1999; Molles & Vehrencamp, 1999). For example, some North American warblers (family Parulidae) have two distinct singing modes: one in which several different song types are sung in sequence (immediate variety) and one in which a single song type is repeated with high stereotypy (eventual or no variety) (Spector, 1992). The first, more versatile mode of singing is often used during male–male interactions, whereas the second, more redundant mode is thought to play a role in attracting females (Spector, 1991, 1992; Byers, 1996), though each mode may have multiple functions in communication (Wiley et al., 1994; Beebee, 2004). Similar two-mode song systems appear to have evolved independently in at least two additional songbird lineages (Kroodsma, 1999), which suggests that the selective forces involved might be general ones. Moreover, in a wide variety of songbird species, males use relatively stereotyped vocalizations to attract females but then transition to more variable, lower amplitude sounds ('quiet song') after the female approaches (Dabelsteen et al., 1998). These patterns not only indicate selection for stereotypy in mate attraction signals; they also suggest competing selection for versatility in signals used in some other contexts, such as close-range courtship or interactions between counter-singing males.

5. Comparative studies of singing patterns

Previous comparative studies of the consequences of sexual selection on birdsong have focused primarily on comparing the vocal repertoire sizes of males rather than comparing their signaling patterns (Kroodsma, 1977; Catchpole, 1980, 2000; Catchpole & McGregor, 1985; Loffredo & Borgia, 1986; Irwin, 1990; Shutler & Weatherhead, 1990; Read & Weary, 1992; Garamszegi et al., 2005). Vocal repertoires are often expected to be larger in polygynous species than in monogamous species (Catchpole & Slater, 2008), yet comparative studies have provided little conclusive support for this prediction. For example, Read & Weary (1992) found that larger song repertoires are associated with male parental care and that polygynous taxa produce songs that are more complex (i.e., that include a larger diversity of syllables), but they found no clear relationship between mating system and song type repertoire size. Interestingly, however, Read & Weary (1992) showed that both song complexity and song repertoire size are higher in species that migrate, which presumably have less time for mate selection than do sedentary taxa (Catchpole, 1980).

In one of the few comparative studies to focus on closely related passerines within a monophyletic group, Catchpole (1980) showed that polygynous warblers of the genus *Acrocephalus* sing shorter songs and have smaller repertoires of syllables (the elements combined to produce a song) than their monogamous congeners. Mapping these results onto a more recent molecular-based phylogeny for this genus (Helbig & Seibold, 1999) suggests that this relationship between polygyny and decreased syllable diversity has evolved at least twice in this group (J.J.P., unpubl. data). Although Catchpole (1980) did not report any measures of song stereotypy in his study, the fact that polygynous males have smaller syllable repertoires with which to compose their songs suggests that, if anything, vocalizations are more stereotyped in these species than in monogamous taxa. Catchpole & McGregor (1985) provide a similar example in the genus *Emberiza*, in which polygynous species exhibit smaller vocal repertoires than monogamous taxa.

Relatively few previous comparative studies have included descriptions of signaling modes in their analyses (i.e., whether males sing with immediate, eventual, or no variety). Among those that have, evolutionary trends in this trait are often difficult to interpret because studies lacked well-supported phylogenies (Kroodsma, 1977; Irwin, 1990) or were based on data from a variety of sources and obtained using heterogeneous methods (Read & Weary, 1992). Indeed, to my knowledge only one previous investigation, Read & Weary's (1992) comprehensive survey of 165 passerine species, suggests any ecological correlates with singing mode. Their analysis indicates that males who provide less parental care tend to sing with eventual or no variety, whereas males who invest more in offspring are more likely to sing with immediate variety. In other words, birds with relatively brief associations between the sexes tend to sing in a more repetitive manner. Although this trend is consistent with the predictions outlined above, Read & Weary's (1992) results were based on broad categories of behavior inferred from the literature, which were insufficient to allow comparisons to be made within genera. With no such within-clade comparisons, it is difficult to rule out the confounding effects of phylogeny (Felsenstein, 1985; Harvey & Pagel, 1991).

6. Singing patterns in oropendolas and caciques

More recent studies of vocal evolution in the oropendolas (*Psarocolius*, *Ocyalus*) and caciques (*Cacicus*), a monophyletic group within the New World blackbird family (Icteridae), are among the few to examine songbird signaling patterns using a robust molecular-based phylogeny (Price & Lanyon, 2002b, 2004). Oropendolas and caciques are found from Mexico to northern Argentina, and all are non-migratory, year-round residents in these areas (Jaramillo & Burke, 1999). Species differ dramatically, however, in their breeding systems and degrees of sexual size dimorphism (Robinson, 1986; Webster, 1992; Jaramillo & Burke, 1999), from territorial species that are monogamous and sexually monomorphic (e.g., *Cacicus solitarius*) to some of the most extreme examples of female-defense polygyny and sexual size dimorphism known in birds (e.g., *Psarocolius montezuma*: Webster, 1994). Polygyny has evolved from monogamy multiple times in this clade, based on molecular relationships (Price & Lanyon, 2002a). Although details of the mating behaviors of some species are poorly known (Robinson, 1986; Jaramillo & Burke, 1999), we can assume that the sexes interact for much briefer periods in highly polygynous taxa, in which males spend much of their time displaying and females alone provide parental care, than in other taxa that breed as year-round territorial pairs. Species in this clade also exhibit a diversity of species-typical singing modes, ranging from highly repetitive (repeating a single song type many times in succession) to highly versatile (producing a variety of different song types during a singing bout).

Thus, this is an excellent group for exploring the evolutionary relationship between mating systems and oscine song organization.

Scott Lanyon and I have examined the evolution of a variety of acoustic and behavioral features of these birds' species-specific displays (Price & Lanyon, 2002b, 2004; Price, 2009; Price et al., 2009). To reconstruct historical changes in traits, we converted display measures into discrete characters by plotting means and standard errors for taxa and then dividing these measures into states where error bars did not overlap (more detailed methods are in Price & Lanyon, 2002b, 2004). Characters were then mapped onto a DNA-based phylogenetic tree to identify unambiguous changes. For example, we measured song versatility in each species as the mean number of distinct song types occurring during the production of eight consecutive songs (Figure 1, right side), then mapped discrete character states for this measure onto the phylogeny (Figure 1, left side), which showed that singing patterns have changed at least three times in the clade. Historical changes in a variety of other acoustic traits have been reconstructed using similar methods (Price & Lanyon, 2004).

Our reconstructions of signal organization in the oropendolas and caciques have revealed several interesting patterns. First, and perhaps most surprisingly, we found that monogamous, sexually monomorphic species in this group tend to switch song types relatively frequently with immediate variety, while the most polygynous, sexually size dimorphic species often sing highly stereotyped songs with eventual variety (Figure 1; Price & Lanyon, 2004). Song versatility has decreased at least two separate times along with the evolution of polygyny, once in *Psarocolius oseryi* and once in the ancestors of a clade including the rest of the *Psarocolius* genus. Furthermore, independent contrast analyses (Felsenstein, 1985) suggest that song versatility is negatively associated with degree of sexual size dimorphism ($F_{1,20} = 3.76$; $r^2 = 0.16$; $p = 0.067$), which reflects degree of polygyny as measured by mean harem size (Webster, 1992). The one unambiguous increase in song versatility, in *Cacicus uropygialis* (Figure 1), was associated with a decrease in sexual size dimorphism. Based on our tree, the stereotyped and repetitive displays of polygynous taxa appear to have evolved from much more versatile modes of singing in monogamous ancestors (Price & Lanyon, 2002b, 2004).

We also found that, in species with highly repetitive singing modes (e.g., *Cacicus sclateri*, *P. oseryi* and the *Psarocolius* clade), various acoustic features within songs have evolved to become relatively extravagant (Figure 1).

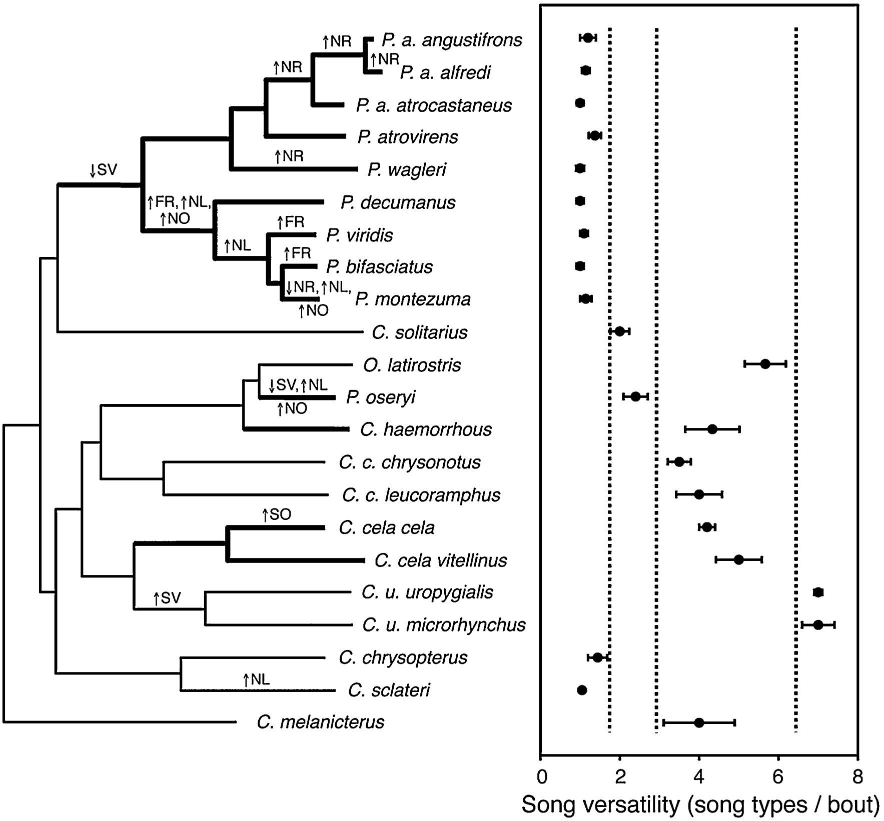

Figure 1. Evolutionary changes in several song features reconstructed on branches of the oropendola–cacique molecular phylogeny (shown on the left, from Price & Lanyon, 2004). Arrows and character abbreviations on the tree indicate increases (up arrows) or decreases (down arrows) in song versatility (SV), frequency range (FR), note repetition rate (NR), maximum note length (NL), note overlap (NO) and song output (SO). Thicker branches indicate polygynous lineages, based on measures of sexual size dimorphism (Price & Lanyon, 2004). Mean (± SE) measures of song versatility (number of song types per bout of eight songs) for each taxon are shown on the right, with vertical dotted lines indicating where measurements were divided into discrete character states for reconstructing historical changes.

These features include dramatic increases in frequency range, rapid note repetition rates, long continuous sounds, and the production of two different sounds simultaneously (i.e., overlapping notes). Changes in one or more of these song characters occurred in polygynous lineages more often than expected by chance (concentrated changes test: $p = 0.033$; Price & Lanyon, 2004). Studies of other songbird species have provided evidence for similar song features as potential targets of female choice (King & West, 1983; Allan & Suthers, 1994; Vallet et al., 1998; Forstmeier et al., 2002; Gil & Gahr, 2002; Ballentine et al., 2004).

It is particularly interesting that many of the species that sing with high versatility and that lack extravagant song features (e.g., *C. solitarius*, *C. uropygialis*) are also species in which females are known to sing as much as males (Price et al., 2009), a trait that is relatively common in tropical, sedentary birds with long-term, male–female relationships and convergent sex roles (Price, 2009). As described earlier, females in such species presumably have ample opportunities and multiple cues for assessing males and avoiding costly errors in mate choice (Wiley, 1994), so we should expect these females to have relatively low response thresholds for male signals. Consequently, there should be relatively little selection for males to produce signals that are especially extravagant or repetitive. Some of these species perform their songs as coordinated male–female duets (Jaramillo & Burke, 1999), further suggesting that male songs play a comparatively minor role in mate attraction in these taxa. In contrast, evidence suggests that the extravagant, repetitive songs of at least some polygynous oropendolas play a role in advertising male attributes (Price et al., 2006).

7. Conclusion

Signal detection theory predicts that increased female choosiness favors male signals that are more redundant, as well as more intense and distinctive. Moreover, high levels of female choosiness are expected to occur when the sexes tend to interact relatively briefly, as in many polygynous mating systems. Our studies of oropendolas and caciques support these predictions by showing that the patterning of song types during male displays has become more repetitive along with the evolution of polygyny, while at the same time some acoustic features within songs have tended to become more extravagant. This is consistent with previous comparative work showing that species with less male parental investment tend to sing more repetitive songs and that polygynous species have songs that are more complex (Read & Weary, 1992).

The ideas presented here are significant in addressing mechanisms of signal evolution relevant to all animal communication systems. Such mechanisms may explain a variety of signaling patterns previously not fully understood, such as the evolution of highly stereotyped and repetitive mate attraction displays in many taxa. In particular, these ideas address the paradox of why many birds with song repertoires appear to hide this trait by repeating each song type many times, thus taking longer than necessary to reveal their repertoire sizes. Stereotypy is a common characteristic of animal signals that has been largely ignored in previous research (but see Botero et al., 2009 for an exception).

Future research should investigate whether or not the patterns described here are widespread in songbirds and other taxa. Other species characterized by short male–female interactions during mate choice, such as long-distance migrants with short breeding seasons, should also be expected to exhibit singing modes that are relatively repetitive in comparison to those of year-round territorial pairs. Research should focus on females as well. The evolution of female mating preferences, like the evolution of male signals, should have a basis in signal detection theory (Wiley, 2000a). A major assumption of the predictions outlined above for male signaling patterns is that females are choosier in species in which males and females interact relatively briefly. This assumption could be tested by measuring female responses to the songs of conspecific males to see if, for instance, females of highly polygynous species tend to be less responsive than their monogamous congeners. Conducting standardized playback experiments with estradiol-implanted females might be an effective way to investigate this possibility (e.g., Searcy, 1992). Comparing the levels of female preference as well as the 'detectability' of male displays using phylogenetic comparative methods could provide interesting new insights into to the coevolution of preferences and traits.

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