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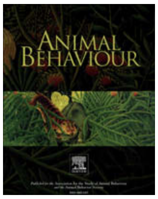

# Female mate choice and songbird song repertoires

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Males of many songbird species use song repertoires that contain multiple song types. A commonly encountered evolutionary explanation for this trait and its recurrent appearance among songbird species is that repertoires have arisen in response to widespread female preference for mates with larger song or syllable repertoires. To assess whether the available evidence supports this hypothesis, we reviewed the literature on the relationship between mate choice and song repertoire size. Our review revealed an array of results that was ultimately inconclusive with regard to the generality of the mate choice hypothesis. Given the ambiguity of these results, we also examined patterns of song use and development and found that some patterns (e.g. overproduction during song ontogeny, repertoires of non-interchangeable songs, hidden repertoires and the prevalence of small repertoires) are at odds with outcomes expected if female preference for larger repertoires were common. We conclude that these cross-species patterns of song use suggest that female preference for larger repertoires is not widespread. We propose that song repertoires have generally arisen not through selection for repertoire size per se, but rather as a by-product of social conditions that favoured the evolution of complex signalling systems.

In many songbird species, each individual's singing includes an array of different song types. The existence of such song repertoires is an evolutionary puzzle, inviting the question of why some songbirds have come to use elaborate collections of songs to perform functions that in other species are accomplished with far simpler and less diverse signals. A possible answer to this question is that song repertoires have arisen in response to sexual selection imposed by female mate choice (Searcy & Yasukawa 1996; MacDougall-Shackleton 1997; Collins 2004). In this view, song repertoires are 'the acoustic equivalent of peacock tails' (Catchpole 1987) and evolved in response to female preference for males with large song or syllable repertoires.

Although the mate choice hypothesis for the evolution of song repertoires is intuitively appealing, its key prediction, that female songbirds prefer mates with larger repertoires, has yet to be conclusively confirmed. This lack of definitive evidence stems not from any lack of diligence on the part of researchers, but is instead due mainly to difficulties inherent in manipulating the vocalizations of male songbirds.

The methodological obstacles that constrain research on the role of bird songs in mate choice are perhaps best illustrated by comparison with investigations of plumage signals. For many plumage signals, researchers can manipulate the signal to assign signal levels to individuals as desired, typically by altering the size and/or colour of feathers (e.g. Griggio et al. 2005; Pryke & Andersson 2005; Westneat 2006; Liu et al. 2007). Investigators are thus able to construct phenotypes in which plumage signals are assigned to breeding males at random with respect to other variable features of the males. The altered phenotypes typically last long enough to allow manipulated males to retain the modified signal throughout the process of mate choice. The ability to manipulate the feathers of living birds thus allows for powerful experimental tests of how plumage signal variation affects female choice of mates.

In contrast, no corresponding method of vocal manipulation has been implemented. The manipulations achieved to date have been limited to muting and other comparatively gross disruptions of male singing (Smith 1979; McDonald 1989; Tomaszycki & Adkins-Regan 2005), and no method for more subtle manipulation has been successfully applied. (Brenowitz et al. 1995 were able to produce marsh wrens, *Cistothorus palustris*, with different repertoires sizes by manipulating the acoustic environments of hand-reared birds, but this method has not been used in a study of song function). Instead, the best available method for isolating the effects of song variation is to divorce the signal from the signaller, typically by replacing singing birds with playback of recorded sounds. In experimental studies of repertoires and mate choice, however, this approach has had the major disadvantage of rendering impossible any observation of effects on actual choice of mates. Instead, investigators have been limited to observation of female behaviours that, it is hoped, serve as indirect proxies of mate choice.

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## REVIEWING THE EVIDENCE

Although direct tests of the effects of song repertoire size on female mate choice are lacking, the bird song literature includes many investigations of effects on putative proxies of mate choice. Despite the necessarily inconclusive nature of such studies, they might collectively reveal a pattern of evidence that would help determine whether the mate choice hypothesis is viable as a broadly applicable explanation for the evolution of song repertories. We therefore examined 47 peer-reviewed papers (see Appendix) that reported on studies of the relationship between female mate choice and song or syllable repertoire size (or closely related measures of song diversity). Although we may have overlooked some papers, we believe that our sample includes most of the published literature in our target category.

### The Key Prediction

Female mate choice can drive the evolution of song repertoire size only if females prefer mates with large repertoires. Thus, the key prediction of the mate choice hypothesis is that female choice of reproductive partners is based at least in part on differences in song repertoire size. The hypothesis also makes additional predictions. For example, it predicts that males with larger repertoires have greater lifetime reproductive success than males with smaller repertoires. It also predicts that repertoire size is heritable. In addition, theory suggests that female preference for large repertories can evolve only if repertoire size reliably reveals aspects of male quality that are beneficial to potential mates (Zahavi 1975; Kirkpatrick & Ryan 1991; Kokko et al. 2003). These additional predictions of the mate choice hypothesis, however, are also consistent with alternative hypotheses for the evolution of song repertoires, and are therefore relevant to the mate choice hypothesis only if females do in fact base mate choice on repertoire size. We therefore limited our review to papers that focus on the connection between repertoire size and proxy measures of mate choice, and we did not consider papers that address the additional predictions.

### Study Outcomes

The studies described in the papers we reviewed fell into two broad categories: (1) experimental laboratory tests of females' immediate behavioural response to playback of stimuli representing song repertoires of different sizes and (2) field observations of correlations between repertoire size and components of male reproductive success that are presumed to reflect the outcome of female choice.

Overall, 25 of 49 studies, involving 15 of 26 tested species, supported the hypothesis that females prefer males that use larger song repertoires, and 25 studies, involving 19 species, failed to support the hypothesis (Table 1). (The 47 reviewed papers yielded 49 studies because two papers each contained reports on two studies, one performed in the laboratory and one in the field. One laboratory study tested multiple species, and results differed by species, so this study is counted in both the 'supported' and 'failed to support' groups). Results differed sharply between laboratory and field studies. Laboratory studies tended to confirm female preference for larger repertoires; of the 22 laboratory studies in our sample, 17 found an effect of repertoire size on an index of female response. In contrast, most field studies failed to detect an effect of repertoire size on the chosen proxy for female choice; only 8 of 27 field studies found an effect.

**Table 1**
Tabulation of 49 field and laboratory studies* of the effect of male song repertoire size on female mate choice

| Response variable† | Number of Studies | Species | Studies also testing other song traits | Studies finding no repertoire effect |
|---|---|---|---|---|
| **Laboratory studies** | | | | |
| Copulation solicit‡ | 13 | 14 | 1 | 2 |
| Operant response | 4 | 4 | 1 | 2 |
| Phonotaxis | 2 | 2 | 2 | 2 |
| Nestbox choice | 2 | 2 | 0 | 0 |
| Egg testosterone | 1 | 1 | 1 | 0 |
| Laboratory subtotal | 22 | 18 | 5 | 6 |
| **Field studies** | | | | |
| First egg date | 5 | 5 | 2 | 3 |
| Pairing date | 8 | 6 | 5 | 5 |
| Harem size | 6 | 5 | 4 | 4 |
| Extrapair paternity | 4 | 4 | 2 | 3 |
| EP young present | 2 | 2 | 2 | 2 |
| Nest initiation date | 1 | 1 | 1 | 1 |
| Mated/unmated | 1 | 1 | 1 | 1 |
| Field subtotal§ | 27 | 16 | 17 | 19 |
| Grand total | 49 | 26 | 22 | 25 |

[*] See Appendix for references and their categorization.

[†] Two laboratory studies and three field studies (see references 26, 30, 36, 40, 47 in the Appendix) that used two measures of female choice were each included in the tabulation only once, in a category selected at random from the two possible categories.

[‡] One copulation solicitation display study (see reference 45 in the Appendix) included four species, and found a repertoire effect for two of those species and no repertoire effect for the other two. This study is counted once in the 'no effect' category.

[§] Twelve field studies included control or statistical adjustment for at least one confounding variable. Nine of these studies included adjustments for territory quality or size.

### Interpreting the results

The collective results of the reviewed studies present a rather puzzling picture, with positive and negative results in equal measure, but with laboratory studies accounting disproportionately for the positive results. What might account for the inconsistency of the overall results, and in particular for the difference between laboratory and field results? We examine several possible explanations below.

### Differences between species

Perhaps the most obvious potential explanation for the mixed results is that females of some species prefer mates with larger repertoires, but that females of other species do not, and different study outcomes simply reflect differences between species. If outcome differences arose from species differences, however, positive outcomes would be expected to be distributed at random across study types (assuming no systematic bias in choice of study species by laboratory or field investigators). Instead, positive outcomes are concentrated in laboratory studies, in a decidedly nonrandom pattern (Fisher's exact test: $P = 0.004$). Also at odds with the interpretation that species' differences account for differences in study outcomes are the results from species that were subjects of multiple studies. Eight of 12 such species yielded both positive and negative results (Table 2); this relatively high level of within-species inconsistency suggests that overall inconsistency in the larger sample should not be attributed to between-species differences.

### Different components of mate choice

If females use different criteria for choosing social and extrapair mates, it is possible that results from laboratory and field studies differ because laboratory and field studies have measured different

**Table 2**
Species represented in more than one study of the effect of repertoire size on female mate choice*

| Species | Laboratory | Field |  | References† |
|---|---|---|---|---|
|  |  | Social mating | Extrapair mating |  |
| Song sparrow | ✓ ✓ ✓ | ✓ × | — | 41, 45, 44, 40, 41 |
| Great reed warbler | ✓ | × × × | ✓ | 11, 9, 16, 23, 24 |
| Sedge warbler | ✓ | ✓ ✓ | × × | 10, 4, 8, 5, 33 |
| Great tit | ✓ | × × | — | 1, 28, 29 |
| Pied flycatcher | ✓ | ✓ | — | 31, 30 |
| Red-winged blackbird | ✓ | × |  | 42, 47 |
| European starling | ✓ × | ✓ ✓ | — | 15, 18, 35, 15 |
| House finch | × | × |  | 36, 34 |
| Willow warbler | — | × | × | 19, 21 |
| Zebra finch | ✓ ✓ × | — | — | 12, 14, 26 |
| Swamp sparrow | ✓ × | — | — | 45, 46 |
| Canary | ✓ ✓ | — | — | 19, 37 |

[*] Each '✓' represents a study that confirmed a repertoire-size effect; each '×' represents a study that tested for but failed to detect such an effect.

[†] Numbers in the 'references' column refer to numbered references in the Appendix. In each row, the left-to-right order of the listed references corresponds to the left-to-right order of the study results represented by the marks in that row.

components of female choice. For example, Marshall et al. (2007) suggest that female sedge warblers, *Acrocephalus schoenobaenus*, use repertoire size to choose social but not extrapair mates, because studies of this species have found a repertoire effect in the laboratory and in field studies of proxies for social mate choice, but not in field studies of extrapair paternity (see Table 2). Conversely, results from the great reed warbler, *Acrocephalus arundinaceus*, are consistent with an interpretation that repertoire size is important in extrapair but not social mate choice (see Table 2). No additional species have been studied in all three contexts (laboratory, social mate choice proxy, extrapair mate choice proxy), and most studied species (17 of 26) have been studied in only one context, so it is difficult to assess whether an interpretation based on differences between social and extrapair choice is viable as a general explanation for inconsistency among studies. However, this interpretation cannot account for instances in which different studies of the same type in a given species yielded contradictory outcomes, as was the case for four species (song sparrow, *Melospiza melodia*; swamp sparrow, *Melospiza georgiana*; European starling, *Sturnus vulgaris*; zebra finch, *Taeniopygia guttata*; see Table 2).

### *Preferences that do not translate to choices*

It is possible that laboratory experiments frequently detected a real, but biologically unimportant, effect. In laboratory tests of female responses to song, subjects are generally isolated and thus do not experience the array of social interactions, sensory stimuli and male signal traits experienced by free-living birds. In such depauperate environments, an experiment might reveal a weak preference or sensory bias that, in natural environments, is unexpressed during mate choice because it is masked by stronger preferences for signal components not presented or varied in the experiment. Alternatively, mate choice under real-world conditions might be constrained in ways that prevent manifestation of preferences revealed in the laboratory (Jennions & Petrie 1997). If laboratory tests on isolated females reveal only weak or constrained biases that do not function in nature, it would be unlikely that the responses observed in the laboratory studies have strong effects on the maintenance of song repertoires.

### *Power of field studies*

If, instead, the repertoire-size effects detected by many laboratory studies are both real and biologically relevant, the frequent failure of field studies to detect such effects may be due to insufficient statistical power. Under this scenario, the reviewed field studies generally failed to detect repertoire effects that were in fact present. However, most of the field studies that failed to find effects of repertoire size but that also considered other song traits did find effects of those other traits (11 of 13 such studies). This result suggests that field studies in general did have adequate power to detect associations between singing and proxy measures of female choice.

### *The file drawer problem*

The tendency of published laboratory studies, but not field studies, to confirm the mate choice hypothesis might reflect artificial inflation of the apparent confirmation rate of laboratory studies. Such inflation would result if laboratory studies were disproportionately affected by publication bias, in which studies with no statistically significant result tend to go unpublished (Rothstein et al. 2005). A tendency for negative results to remain unpublished may be especially strong among studies that test only a single variable, because if that variable has no detectable effect, no other potential effects remain to be reported. Among the studies that we reviewed, most laboratory studies tested only repertoire size (17 of 22 studies; 77%), whereas field studies were less likely to test repertoire size alone (10 of 27 studies; 37%), and to instead consider multiple song traits. Because laboratory studies were less likely than field studies to consider multiple working hypotheses, their collective results may be more likely to reflect publication bias.

### *Validity and interpretability of proxy measures*

The inconsistent results of the reviewed studies may simply reflect the methodological constraints inherent in the study of repertoire size and mate choice. Studies conducted under these inevitable constraints may necessarily yield results that are less reliable and more resistant to unambiguous interpretation than would be ideal.

For example, laboratory studies of the effects of repertoire size rely on measurement of female behaviours that are presumed to be proxy indicators of mate choice, but the degree to which these proxies predict actual mate choice is unknown. The proxy most commonly used in the laboratory-based repertoire-size experiments that we reviewed is the copulation solicitation display (CSD, King & West 1977). Typically, the number of displays performed during or after exposure to taped sounds is taken to be an indicator of female mating preference. In nature, however, the display is not normally associated with mate choice but is instead performed just prior to copulation, well after formation of the social pair bond and (in territorial species) settlement on a territory (see e.g. Mota 1999; Drevon & Slagsvold 2005). (The timing of the display relative to extrapair mate choice is unknown for most species, owing to the usually cryptic nature of extrapair mating). Also, in most species, females in a laboratory setting can be induced to perform the display only if given estradiol implants that substantially increase the subjects' levels of circulating hormone. These females, confined and hormonally abnormal, represent artificial laboratory preparations whose responses may or may not be representative of normal behaviour. The disconnect between the CSD assay and the usual context of CSDs in nature, and the highly artificial nature of the assay suggest that the results of experiments that use CSD to measure female response should be interpreted cautiously.

Alternatives to the copulation solicitation display as an indicator response in female preference experiments have mostly measured indexes of movement towards or proximity to the source of a sound. For example, a few investigators have assessed preference based on simple phonotaxis (e.g. Neubauer 1999) or on the responses of females trained by operant conditioning to trigger a playback selected from among two or more options (Riebel

& Slater 1998). These mate choice proxies seem to us somewhat superior to the copulation solicitation display, because they involve actions at least arguably analogous to those taken during the process of choosing a mate. Again, however, the relationship between phonotaxis in a cage or aviary and actual mate choice is unknown. A mate choice proxy perhaps more closely linked to the actual behaviour was used by Lampe & Saetre (1995) in their study of female pied flycatchers', *Ficedula hypoleuca*, response to taped repertoires of different sizes. The subjects were provided with a choice of two nestboxes, each near a speaker broadcasting a different tape, in which to initiate nest building. To our knowledge, however, nest location has been used to measure response to repertoire size only in this study and in an aviary study of European starlings (Eens et al. 1991), perhaps because few species can be induced to build nests in captivity.

As did the laboratory studies in our sample, the field investigations we reviewed used proxy measurements to assess mate choice. Typically, these proxies were components of male reproductive success that are presumed to reflect the outcome of female choice. For example, in studies of polygynous species, investigators sometimes counted the number of social mates secured by each male in a population. More commonly, investigators measured indicators of the earliness of breeding (e.g. pairing date, egg-laying date, or whether a male was paired or unpaired), under the assumption that desirable males mate before less desirable ones. A few field studies in our sample (6 of 27 studies) measured components of male extrapair reproductive success, under the assumption that male success is determined by female preference. As extrapair paternity (EPP) has been found in more than 90% of tested passerine species (Griffith et al. 2002), its underrepresentation in field studies of singing limits the ability of field studies as a whole to completely capture the relationship between singing and mate choice. On balance, however, the proxies used in field studies seem to us to be more closely tied to actual mate choice than do those used in laboratory studies. Nevertheless, as with laboratory proxies, the validity of the field proxies remains unknown.

### *Study outcomes, summary*

Do the 49 studies we reviewed collectively support the hypothesis that female mate choice favouring males that use larger song repertoires is widespread among songbirds? About half of the studies reported a repertoire-size effect, but the positive findings came disproportionately from laboratory experiments whose results may or may not reflect real-world mate choice, and whose hypothesis confirmation rate is probably exaggerated by publication bias. The more biologically realistic field studies mostly failed to find repertoire effects, but these studies are in general correlative and may therefore lack power. Among species that have been the subject of multiple studies, a few have produced results consistent with a repertoire-size effect, and a few have produced results consistent with the absence of an effect, but most have produced mixed results. These mixed within-species results, especially those in which different studies of the same type reached contradictory conclusions, suggest that results are not in general robust. Methodological limitations inherent in both laboratory and field studies also suggest that findings are best regarded as provisional. Overall, a conservative interpretation of the available evidence is that it does not support a definitive conclusion about the generality of the mate choice hypothesis for the evolution of song repertoires.

## DEVELOPMENT AND USE OF REPERTOIRES

Because the collective results of studies designed to test the effect of song repertoire size on mate choice are equivocal, they do not by themselves resolve the question of whether female mate choice is a broadly applicable general explanation for the existence of repertoires. We believe it therefore useful to interpret the results in light of a broader view of how song repertoires develop and are used. Below, we provide an overview of what is known about aspects of song development and song use that we believe are relevant to the mate choice hypothesis. This overview reveals some patterns that seem to be at odds with the mate choice hypothesis.

### *Prevalence of Small Repertoires*

In most oscine species with song repertoires, repertoire size is small (see Appendix in MacDougall-Shackleton 1997). Indeed, most of the species tested in the papers we reviewed above have modest repertoire sizes. In addition, phylogenetic comparative analyses suggest that loss of song diversity is a common evolutionary outcome in songbird lineages (Irwin 1988, 1990; Price & Lanyon 2004; Price et al. 2007; Cardoso & Mota 2007). The prevalence of small repertoires and the repeated evolutionary loss of song diversity are difficult to reconcile with widespread sexual selection for large repertoires.

Small repertoires persist despite within-population variation in repertoire size that would permit evolution of larger repertoires, if strong selection for such repertoires were present. A seeming absence of selection for larger repertoires is especially apparent in species with single-song repertoires. For example, the vast majority of white-crowned sparrows, *Zonotrichia leucophrys*, use only a single song type, but, in many populations, 1–11% of individuals use two or more types (Chilton & Lein 1996). Yet the uncommon larger-repertoire phenotype has not been swept to high frequency in any known population of white-crowned sparrows. Instead, this sparrow's prevalent song development programme remains one in which song types are systematically removed from the repertoire until only a single type remains (Nelson 2000).

### *Overproduction*

Investigations of oscine song development frequently find that young birds produce a greater variety of sounds than is retained in the crystallized, adult repertoire (e.g. West & King 1986; Hultsch 1991; Nelson 1992a, 2000; Nelson & Marler 1994; Nordby et al. 2007; Liu & Nottebohm 2007). This 'overproduction' (Marler & Peters 1982) during development seems to be a common feature of oscine developmental programmes, and may serve to expand the array of signals available for selective inclusion in crystallized adult singing (Nelson 1992b; Marler 1997). If overproduction is indeed typical of normal song development, then adult songbirds generally use repertoires that are smaller than those that they used earlier in life. If songs discarded during development remain available to adults, adults have the potential to use repertoires larger than the ones they actually use.

There is some evidence that adults do retain the potential to express previously eliminated songs. For example, investigators have induced adult birds to produce song types that had disappeared from their repertoires during development (Hough et al. 2000) or that had been memorized early in life but never produced (Chaiken et al. 1994; Geberzahn et al. 2002). Additional evidence that normal song development may hold song diversity below its maximum potential comes from black-capped chickadees, *Poecile atricapillus*, a species in which males generally use only a single song type. Kroodsma et al.'s (1995) study of chickadee song development showed that, when normal development was disrupted by artificial conditions in the laboratory, adults expressed abnormally large repertoires. In addition, the finding that males in a few, widely dispersed populations of black-capped chickadees have multisong repertoires rather than a single song type suggests that these aberrant populations express a potential that is widespread in the species (Kroodsma et al. 1999a; Gammon & Baker 2004).

Normal development may restrict song diversity in species with larger repertoires as well. Experiments on gray catbirds, *Dumetella carolinensis*, sedge warblers, and canaries, *Serinus canaria*, found that birds deprived of exposure to adult song during development developed larger repertoires than did birds whose acoustic environment included the adult singing typically experienced by wild birds (Kroodsma et al. 1997; Leitner et al. 2002; Leitner & Catchpole 2007). In an experiment in which eggs of wild blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*, were transferred between nests so that offspring of each species were reared by adults of the other species, cross-fostered birds, which experienced abnormal acoustic and social environments, developed larger repertoires than did control birds reared in normal fashion by conspecific parents (Johannessen et al. 2006).

If repertoires had generally evolved under selective pressure to maximize their size, an expected evolutionary outcome might be a developmental process that ensures expression of the maximum possible song diversity. Instead, many songbird species seem to have evolved developmental processes that systematically discard song types and keep expressed repertoire sizes below their potential ceiling.

### *Hidden Repertoires*

If females prefer to mate with males that have larger repertoires, males ought to sing in a fashion that quickly reveals their repertoires to listening females, especially in migratory species in which mate choice is rapid. Singing behaviour that concealed any portion of a male's repertoire would inevitably reduce his reproductive success and would be quickly eliminated by selection. But males of many species, including some with very large repertoires, use their songs in ways that delay revelation of the full repertoire, sometimes for weeks or months. Indeed, some patterns of song use seemingly serve to conceal a male's repertoire from listeners.

A modest form of repertoire-hiding is found in the many songbird species that sing with eventual variety, repeating a particular song type a number of times before switching to a different one. If a male song sparrow, for example, cycles through his repertoire of 10 song types by repeating each type 10 times, on average, before moving to the next type, he is spending 10 times as much time and effort as would be minimally necessary to reveal his repertoire. If females were assessing repertoire size, it seems likely that a large-repertoire male that cycled through his song types as quickly as possible would gain an advantage, and his behavioural phenotype would ultimately replace that of the eventual variety singer. As Wiley (2000, page 864) notes, 'If repertoires are a signal for assessment, it is hard to imagine an advantage in forcing a listener to take longer to make a decision. Listeners should demand immediate variety, and singers should comply'.

The degree of repertoire concealment in species like the song sparrow is limited, compared to species whose singing does not involve systematic cycling through the entire repertoire. Sedge wrens, *Cistothorus platensis*, for example, can have very large repertoires (200–350 song types) and switch types rapidly, but, because some types are sung more frequently than others, the full repertoire is revealed extremely slowly (Kroodsma et al. 1999b). Even after uttering thousands of songs, a male sedge wren is still introducing new types to his performance (Kroodsma et al. 1999c). To choose the male with the largest repertoire size, a female sedge wren would be required to listen continuously to all of the males in her area for days or weeks, a task that would create a seemingly monumental barrier to achieving her goal.

A similar challenge would await a female chestnut-sided warbler, *Dendroica pensylvanica*. A male chestnut-sided warbler has a repertoire of up to 12 song types, but it takes extraordinarily persistent listening to discover his full repertoire (Byers 1995). Almost all of a male's singing consists of two or three preferred types, with song bouts consisting of dozens or even hundreds of repetitions of the same type. Type switches among even the preferred types are infrequent, and the other types are used very rarely (all of the rare types combined account for 15% or less of a male's singing, even though they typically account for at least 75% of his song repertoire). A comparable pattern of singing is found in the bananaquit, *Coereba flaveola*. Most of the 100–400 song types in a male bananaquit's repertoire account for less than 1% of his singing, and investigators must sample singing extensively over the full course of a breeding season to assess repertoires fully (Wunderle et al. 1992).

Males of many species with multisong repertoires conceal repertoire size by using performance patterns that hold portions of the repertoire in reserve over time frames varying from minutes to months. In addition, the repertoires of the species with the largest repertoires are 'hidden' in the sense that their diversity may exceed the ability of listening females to a perceive differences between males. Consider the cognitive challenge facing a female brown thrasher, *Toxostoma rufum*, trying to distinguish between a male with, say, 2000 different song phrases, and a second male with 2020 phrases (Kroodsma & Parker 1977; Boughey & Thompson 1981). The task would seem beyond the capabilities of a female bird under pressure to choose her mate with relative dispatch. Yet, if females were to base mate choice on repertoire size, such distinctions would have to be made by females of the wren, mimid, and other species in which male repertoire sizes climb into the hundreds or thousands.

### *Non-interchangeable Signals*

Male ornaments that arise through female mate choice generally represent the outcome of directional selection for an increase in some quantitative parameter. Female preferences favour male widowbirds (*Euplectes* spp.) with longer tails (M. Andersson 1982; S. Andersson 1992), male junglefowl, *Gallus gallus*, with larger combs (Parker & Ligon 2003), and so on. If song repertoires had evolved by similar means, their growth should have been driven by a similar, simple directional selective pressure, in this case for an increased number of different song types. Such selection favouring the simple accumulation of the largest possible collection of songs, favouring diversity for its own sake, might be expected to yield repertoires of essentially arbitrary, interchangeable signals. Oscine songs, however, do not fit this expectation.

The strongest indication that oscine song repertoires have functions beyond the simple exhibition of accumulated diversity is that, in most repertoire-using species whose song use has been carefully investigated, different song types are not used arbitrarily. Instead, different songs are used in particular circumstances. Song types are not interchangeable, but are used in structured, rule-based patterns.

A good example of structured repertoire use is found in a well-studied population of song sparrows in Washington State, U.S.A. Males in this population use their song types in an ordered series denoting increasing levels of aggression, but a given type's message is not fixed. Instead, the message of a type varies situationally, depending on the composition of the repertoire of the male with which the singer is interacting. Uttering a song type that is not found in a rival's repertoire indicates a lower level of aggression than does using a song that is shared with the rival (Beecher et al. 1996). The highest level of aggression is signalled by use of the same type that the rival is currently singing (Beecher et al. 2000; Burt et al. 2001). A pattern of song use similar to that of the song sparrow has been documented in banded wrens, *Thryothorus* *pleurostictus* (Molles & Vehrencamp 1999, 2001; Vehrencamp et al. 2007).

The behavioural rules governing repertoire use can be complex. Marsh wrens use their repertoires in beautifully intricate 'matched countersinging,' in which a singer selects his songs during rapid-fire vocal duels, with each song in a singer's sequence contingent on the type of the most recent song used by the opponent and on the singer's apparent 'judgment' of the likely type of the opponent's next song (Verner 1976). Similar, if less baroque, type-matching interactions have been documented in a number of other species, including northern cardinal, *Cardinalis cardinalis* (Lemon 1973), western meadowlark, *Sturnella neglecta* (Falls 1985), great tit (Krebs et al. 1981; Falls et al. 1982; McGregor et al. 1992) and rufous bristlebird, *Dasyornis broadbenti* (Rogers 2004).

Song types can also be associated with particular social or behavioural contexts. For example, the repertoires of many species of parulid wood-warblers are partitioned into discrete categories with different contextual associations (reviewed in Spector 1992). A representative example of this parulid singing pattern is found in Grace's warblers, *Dendroica graciae*, in which the song category used depends on time of day, position on territory, mating status and proximity to mates and rivals (Staicer 1989). Similarly partitioned repertoires are found in field sparrows, *Spizella pusilla* (Nelson & Croner 1991), grasshopper sparrows, *Ammodramus savannarum* (Smith 1959), dusky warblers, *Phylloscopus fuscatus* (Forstmeier & Balsby 2002), and superb fairy wrens, *Malurus cyaneus* (Dalziell & Cockburn 2008). Specialized use of particular portions of the repertoire is also seen in duetting species, such as the plain wren, *Thryothorus modestus*, in which certain phrase types serve to initiate a duet, but only if the duetting partner responds with a different, particular phrase type (Mann et al. 2003). Similar patterns of structured song use have been documented in a number of other duetting species (reviewed in Logue 2006).

Overall, a broad view of songbird singing behaviour reveals numerous examples of structured, rule-determined patterns of repertoire use. Singers of many species have been shown to select from among the songs in their repertoire in nonrandom fashion. These findings suggest that oscine songs serve as components of subtle, sophisticated communication systems, not as ornamental displays of variety per se.

### *The Partitioned Repertoires of Wood-Warblers*

The songs and singing behaviour of wood-warblers provide a special case that yields unique insight into the effects of female preferences on male songs. As noted above, many species in the family Parulidae have song repertoires that are partitioned into two categories. Considerable evidence indicates that the categories have distinct functions (reviewed in Spector 1992; see also Weary et al. 1994; Wiley et al. 1994; Byers 1996b; Staicer 1996b; Staicer et al. 2006). 'First Category' songs function in male–female communication in general and mate attraction in particular; unmated males sing far more First Category songs than do mated males. 'Second Category' songs are used mainly for male–male communication, especially in aggressive contexts. Wood-warbler repertoires thus contain one set of songs specialized for use in male–male contests and a second set specialized, at least to some degree, for mate attraction.

In comparing First Category (mate attraction) to Second Category (male–male aggression) songs, one finds that First Category songs are less diverse and less variable. A male yellow warbler, *Dendroica petechia*, for example, has up to 16 Second Category songs, but only a single First Category song (Spector 1991). A male chestnut-sided warbler uses up to 10 Second Category songs, but only one or two First Category songs (Byers 1995). Similar differences in repertoire size between song categories are found in other parulid species (Lemon et al. 1985; Staicer 1989, 1996a; Wiley et al. 1994). In addition, different renditions of a male's First Category songs tend to be more stereotyped than those of his Second Category songs (Staicer 1989; Byers 1995). The form of First Category songs tends to be relatively invariant across long geographic distances and over long periods of time, whereas Second Category songs can show considerable geographic and temporal variability (Kroodsma 1981; Byers 1996a).

In the partitioned wood-warbler communication system, with its unique potential to reveal how songs are shaped by selection for attractiveness to females, the songs presumably optimized for mate attraction are less diverse and less variable than songs that primarily serve other functions. This outcome is the opposite of that expected if selection by female mate choice favoured large repertoires.

### *Song Use and Development, Summary*

Our overview of key aspects of song use and development reveals a pattern of evidence that seems to us inconsistent with widespread presence of female preference for large repertories. Overproduction, hidden repertoires, non-interchangeable signals, stereotyped mate attraction songs, and the prevalence of small repertoires—along with the inconclusive nature of the collective evidence from studies of the relationship between female choice and song repertoires—suggest that female mate choice based on song diversity is rare among songbird species.

## AN ALTERNATIVE HYPOTHESIS FOR THE ORIGIN OF SONG REPERTOIRES

Given the possibility that song repertoires did not in general arise through sexual selection by female mate choice, what alternate scenarios might account for their evolution? We believe that clues about repertoire evolution can be found in the structured patterns of song use that we discussed above. These patterns suggest that vocal communication among songbirds involves complex, contingent interplay among signallers and receivers, in which the signal value of different song types is more significant than is their number. This kind of vocal communication, in which a range of messages is used to manage social interactions with diverse individuals, could engender selection for signal diversity, and thus foster the evolution of song repertoires.

The hypothesis that the evolution of repertoires is in general driven by the advantages of signal modulation does not necessarily make specific predictions about the method by which signal diversity serves to vary signal content. The precise manner in which signal modulation encodes messages differs among species, and in many cases the evolved encoding system will not involve multiple song types (perhaps instead involving variable performance of a single type; see, e.g. Hill & Lein 1987; Liu 2004). In other cases, however, the evolved communication system will be based on modulations that use multiple discrete signals. Once this kind of encoding arises, selection for song repertoires can follow.

One communication system component that is common among songbird species, and that can foster selection favouring individuals with multiple song types, is song type matching. Type matching during interactions between rival males has been documented in many species (reviewed in McGregor 1991; Smith 1991), and has been shown to have signal value in several species (e.g. Burt et al. 2001; Molles & Vehrencamp 2001). Its function may be to direct communication to a particular receiver, to signal a highly aggressive motivational state (Krebs et al. 1981), and/or to facilitate detection of small differences in song performance (Logue & Forstmeier 2008). If, for one of these reasons or some other reason, the ability to selectively type-match rivals is advantageous, then at least two song types (matching and nonmatching) per individual are required, and larger repertoires would be advantageous if individuals interact with multiple territorial neighbours or colony members, each of whom might use different song types. Note that in this circumstance there is an upper limit to beneficial expressed repertoire size, determined by the number of interacting individuals, beyond which further increases in repertoire size provide no additional advantage. (We might, however, find a kind of runaway selection for repertoire size in species, such as the marsh wren, in which rivals engage in contests of serial type matching).

Repertoires might also be favoured when different classes of songs are used in different communication contexts, as occurs in a number of oscine species (see the above section on Non-interchangeable Signals). For example, unmated male American redstarts, *Setophaga ruticilla*, repeat a single song type, but mated males rapidly cycle through multiple song types (Staicer et al. 2006). If advantages accrue to redstart males that advertise their mating status, only males with multisong repertoires can gain those advantages. This benefit of having a repertoire is attained by possessing song diversity sufficient for receivers to perceive two classes of singing, and, again, further benefits would not be expected to accrue to further increases in repertoire size.

More generally, in any song communication system in which signal diversity is used to encode messages, selection for increasingly complex social communication can favour increased song repertoire size. Songbirds may be especially susceptible to this response to selection, because of their specialized, learning-based system of song development. The learning that characterizes this developmental programme tends to remove limits on song diversity by increasing the potential for innovation during development and by allowing components of the song phenotype to be stored in the social environment rather than in the genome. Given this capacity for diversity, the modest repertoire sizes of many species may be a product of the optimal number of beneficial unique messages in a species' signalling systems, rather than the result of directional selection for large repertoires limited by some physiological or mechanical constraint.

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## APPENDIX

### *Annotated Bibliography of Studies Tabulated in Table 1*

Each reference is followed by an annotation that describes how the study was classified in Table 1. F = field study; L = laboratory study; N = tested only repertoire size; O = also tested other song traits; S = supported an effect of repertoire size (or similar measure of song variability); R = rejected an effect of repertoire size; C = field study that controlled for at least one potential confounding variable; (t) = the controlled variables included a measure of territory size and/or quality; VAR = response variable measured as a proxy for female mate choice.

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   [L, N, S, VAR = copulation solicitation display]
2. **Baker, M. C., Bjerke, T. K., Lampe, H. U. & Espmark, Y. O.** 1987. Sexual response of female yellowhammers to differences in regional song dialects and repertoire sizes. *Animal Behaviour*, **35**, 395–401.
   [L, O, S, VAR = copulation solicitation display]
3. **Bell, B. D., Borowiec, M., Lontkowski, J. & Pledger, S.** 2004. Short records of marsh warbler (*Acrocephalus palustris*) song provide indices that correlate with nesting success. *Journal of Ornithology*, **145**, 8–15.
   [F, O, R, VAR = pairing date]
4. **Buchanan, K. L. & Catchpole, C. K.** 1997. Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. *Proceedings of the Royal Society of London, Series B*, **264**, 521–526.
   [F, O, S, C(t), VAR = pairing date]

5. **Buchanan, K. L. & Catchpole, C. K.** 2000. Extra-pair paternity in the socially monogamous sedge warbler *Acrocephalus schoenobaenus* as revealed by multilocus DNA fingerprinting. *Ibis*, **142**, 12–20.
[F, O, R, VAR = extrapair young present/absent in nest]
6. **Byers, B. E.** 2007. Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology*, **18**, 130–136.
[F, O, R, C, VAR = extrapair paternity]
7. **Cardoso, G. C. & Mota, P. G.** 2004. Female serin (*Serinus serinus*) responses to song do not favour the predominant song syntax. *Ethology, Ecology & Evolution*, **16**, 329–338.
[L, N, R, VAR = operant response]
8. **Catchpole, C. K.** 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour*, **74**, 149–166.
[F, N, S, C(t), VAR = pairing date]
9. **Catchpole, C. K.** 1986. Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behavioral Ecology and Sociobiology*, **19**, 439–445.
[F, N, R, C(t), VAR = harem size]
10. **Catchpole, C. K., Dittami, J. & Leisler, B.** 1984. Differential responses to male song repertoires in female songbirds implanted with oestradiol. *Nature*, **312**, 563–564.
[L, N, S, VAR = copulation solicitation display]
11. **Catchpole, C. K., Leisler, B. & Dittami, J.** 1986. Sexual differences in the responses of captive great reed warblers (*Acrocephalus arundinaceus*) to variation in song structure and repertoire size. *Ethology*, **73**, 69–77.
[L, N, S, VAR = copulation solicitation display]
12. **Clayton, N. & Pröve, E.** 1989. Song discrimination in female zebra finches and Bengalese finches. *Animal Behaviour*, **38**, 352–354.
[L, N, S, VAR = copulation solicitation display]
13. **Coleman, S. W., Patricelli, G. L., Coyle, B., Siani, J. & Borgia, G.** 2007. Female preferences drive the evolution of mimetic accuracy in male sexual displays. *Biology Letters*, **3**, 463–466.
[F, O, S, VAR = harem size]
14. **Collins, S. A.** 1999. Is female preference for male repertoires due to sensory bias? *Proceedings of the Royal Society of London, Series B*, **266**, 2309–2314.
[L, N, S, VAR = operant response]
15. **Eens, M., Pinxten, R. & Verheyen, R. F.** 1991. Male song as a cue for mate choice in the European starling. *Behaviour*, **116**, 210–238. Note: paper includes both laboratory and field studies.
[L, N, S, VAR = nest-box choice], [F, O, S, VAR = harem size]
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