



Montezuma oropendolas modify a component of song constrained by body size during vocal contests

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Physical constraints on animal signals can influence how challenging they are to produce, which in turn can provide potentially important cues about the condition or quality of a signaller. Some components of a signal are often more challenging to produce than others, however, and we expect animals to modify those elements that are especially costly so as to give high-intensity and demanding displays only when necessary. We found that Montezuma oropendolas, *Psarocolius montezuma*, modify a particular component of their songs during vocal contests, the lowest peak frequency (LPF). Songs that overlapped other males' songs during interactions at nesting colonies had slightly but significantly lower LPFs than did the same song types produced when singing alone. Other components of song, in contrast, did not change. We also provide evidence that the production of loud, low-frequency notes in this species is constrained by body size, based on a negative bounded relationship between mean measurements of LPF and tarsus length across 102 species and subspecies of New World blackbirds (Icteridae), the songbird family to which the Montezuma oropendola belongs. Measures of LPF in the songs of Montezuma oropendolas fall near the lower limit of what members of the family produce. Taken together, our results suggest that low-frequency notes in these birds might constitute an honest signal of competitive ability during male–male interactions.

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Songs of male songbirds are known to function in both mate attraction and competition with other males over territories and mates (Catchpole & Slater 1995). Individual variation in songs can have important consequences for reproductive success, so signal design is likely to be strongly influenced by sexual selection (Andersson 1994). Based on current theory, features of song used in inter- and intrasexual advertisement should be subject to some constraint to constitute stable, honest indicators of quality (Kodric-Brown & Brown 1984; Grafen 1990; Gil & Gahr 2002). For features constrained by a performance limitation, such as sounds that are limited in some way by morphology (Podos 1997), performing near this biomechanical limit should be especially challenging for a singer, and individuals should modify these elements of song conditionally based on perceived levels of competition and the potential payoffs of an interaction (e.g. Maynard Smith & Parker 1976; Wagner 1992; Kreutzer et al. 1999;

Cynx & Gell 2004). During highly competitive interactions, for example, such as close-range, male–male contests over mating opportunities, individuals should invest more in their displays and thus should produce more extravagant signals. In situations with less potential immediate benefit, however, such as while a male is singing alone, we expect less demanding versions of these sounds.

The Montezuma oropendola, *Psarocolius montezuma*, provides an extreme case of sexual selection in a songbird. This Neotropical member of the New World blackbird family (Icteridae) has a harem-defence polygynous mating system, in which males compete intensely for access to sexually receptive females at nesting colonies (Webster 1994). It is also one of the most sexually size dimorphic of all birds, with adult males having more than twice the body mass of females (Webster 1997). Larger males tend to have higher ranks in dominance hierarchies than do smaller males, and male rank is closely associated with mating success (Webster 1995). Thus, large body size, as well as other male morphological features presumably important in courtship and competition for mates, appears to be a product of strong sexual selection (Webster 1992, 1997).

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Several factors suggest that the songs of male *Montezuma oropendolas* are subject to strong sexual selection as well. These vocalizations consist of loud, elaborate cascades of notes often accompanied by a dramatic visual display in which the singer bows forward on a branch, often until hanging nearly upside down. Songs are produced frequently during the breeding season, especially by dominant males defending harems, and they appear to be important in male competitive interactions (Jaramillo & Burke 1999). At large colonies, singers often overlap the songs of other males with their own by beginning a song before their opponent's song is complete (personal observation); in many cases these songs occur almost simultaneously. Overlapping an opponent's song is thought to be a more aggressive signal than producing songs that do not overlap those of other males, based on studies of a variety of other songbird species (black-capped chickadees, *Poecile atricapillus*: Mennill & Ratcliffe 2004; great tits, *Parus major*: Langemann et al. 2000; European robins, *Erithacus rubecula*: Dabelsteen et al. 1997; nightingales, *Luscinia megarhynchos*: Naguib 1999). Vocal overlapping could have importance for male competitors in disrupting the courtship signals of other males (Webster & Robinson 1999; Todt & Naguib 2000), and might have additional importance in conveying information about contestants both to each other and to nearby receptive females (Mennill et al. 2002).

Evidence of past selection on *Montezuma oropendola* song comes from phylogenetic comparative studies of the entire oropendola group (genera *Psarocolius* and *Ocyalus*), in which the evolution of various vocal features was reconstructed using robust molecular phylogenies (Price & Lanyon 2002, 2004). Reconstructed changes in song indicate that vocalizations have changed recently and relatively dramatically in the *Montezuma oropendola*. Far more evolutionary changes have occurred in the recent ancestors of this species than in any other oropendola lineage (Price & Lanyon 2002), and many changes have resulted in song features that are probably costly for singers to develop or perform, such as broad frequency ranges and long continuous sounds (Price & Lanyon 2004).

Sounds that are challenging to produce, because of mechanical limitations of the vocal tract or other physical constraints, could provide useful information to listeners about a singer's quality or motivation and thus could have important consequences for reproductive success (Gil & Gahr 2002). Recent studies indicate that features of bird song produced near such performance limits are more attractive to females and more effective in repelling competing males than features that are produced well below these limits (Drăgănoiu et al. 2002; Forstmeier et al. 2002; Balentine et al. 2004). If any such physically constrained song features are important in mating success among male *Montezuma oropendolas*, we predict that singers will produce versions that are especially challenging when the potential benefit to the signaller is high, such as during intense competitions between males at nesting colonies.

In this study we show that male *Montezuma oropendolas* modify a particular aspect of their songs during

male–male contests: the lowest peak frequency (LPF). Songs produced during vocal overlapping situations at colonies have lower peak frequencies than do the same song types produced by males singing alone. We also provide evidence that the production of loud, low-frequency notes in song is constrained by body size, based on our finding of a negative bounded relationship between these variables across the entire family Icteridae. Measures of LPF in the songs of *Montezuma oropendolas* fall near the lower limit of what members of the family produce. This song component therefore might constitute a physically limited, and thus honest, signal of male size and competitive ability during male–male interactions.

METHODS

Study Species and Song Analysis

The *Montezuma oropendola* is a large, colonial-nesting songbird found in lowland rainforest habitats from southern Mexico to the Canal Zone of Panama (Howell & Webb 2000). It is one of the largest and most polygynous members of the oropendolas and caciques (genera *Psarocolius*, *Ocyalus* and *Cacicus*; Webster 1992; Jaramillo & Burke 1999), a monophyletic subgroup of the New World black-bird family (Icteridae). Other major clades in this family are the orioles, grackles and allies, meadowlarks and allies, and the monotypic cup-nesting species *Amblycercus holocercus* (Lanyon & Omland 1999). Male *Montezuma oropendolas* have more than twice the body mass of females (Webster 1997). The sexes do not differ in plumage coloration, but adult males have brightly coloured, swollen facial wattles and elongated outer primary feathers not found in females or juvenile males.

The mating system of *Montezuma oropendolas* is harem-defence polygyny, a system common in mammals but rare in birds (Webster 1994). Females nest colonially during the dry season in trees separated from the surrounding forest canopy (Skutch 1954). Males compete intensely for breeding positions at these nesting colonies and form linear dominance hierarchies in which high-ranking males are able to physically exclude others from nest-building females. Subordinate males excluded from a colony tree frequently perch in nearby trees and display (i.e. sing) as females fly to and from the colony. Top-ranked males obtain virtually all observed copulations and, based on genetic studies, father the majority of young (Webster 1994, 1995). Male body size is positively associated with dominance rank, indicating that size is an important factor in competition for mates (Webster 1997).

Montezuma oropendola song consists of a series of loud, harmonically rich notes that shift up and down in sound frequency. The range of these frequency shifts and the overall sound amplitude increase steadily during a song, normally ending with a loud sweeping whistle. Songs can easily be heard from a distance of 150 m (Jaramillo & Burke 1999). Spectrographic analysis reveals that a song consists of continuous sound (>2 s) without any apparent pauses. Spectrograms also reveal that each song includes

a series of low-frequency notes (400–600 Hz) that often appear to be produced at the same time as the higher-frequency notes described above (Price & Lanyon 2002). As in other oropendola species, males typically repeat a particular song type several times a minute for many minutes before switching to another type (Price & Lanyon 2004). We observed no instances of males switching song types twice in the same recording session, even in continuous recordings over 9 min long.

Songs of male *Montezuma oropendolas* were recorded by M. S. Webster during the 1988 and 1989 breeding seasons (January to May) at nesting colonies near the La Selva Biological Station in Costa Rica (10°26'N, 83°59'W). Colonies were spaced 1 km or more apart. All recordings were made using a Uher reel-to-reel tape recorder and a Sennheiser directional shotgun microphone. Most males in these colonies had previously been captured, measured and individually marked with unique combinations of coloured leg bands (see Webster 1994, 1995, 1997). Unbanded males were often identifiable by individually distinctive facial wattles. Whenever possible, the observer identified individual singers on tape immediately following each recorded song. When two or more songs occurred contemporaneously at a nesting colony, individuals were identified on tape as either the first male or second male in the interaction, except when songs were simultaneous. Throughout this paper, we refer to songs produced contemporaneously by males as 'overlapping', and songs that did not overlap the songs of other males on tape as 'nonoverlapping'. Overlapping songs always occurred while males were in close proximity to each other (<5 m), typically at a colony tree, whereas nonoverlapping songs were generally produced while a singer was not near other singing males, often away from the colony tree. We have deposited these recordings at the Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.

We digitized recordings at 44.1 kHz using SoundEdit 16 (version 2, Macromedia, San Francisco, California, U.S.A.), then generated spectrograms of songs using Raven sound analysis software (version 1.1, Cornell Laboratory of Ornithology). No components of songs appeared above 10 kHz in preliminary inspections of spectrograms, so we down-sampled our files to a sampling frequency of 22.05 kHz for our analysis (discrete Fourier transform, DFT = 512 samples; frequency resolution = 61.9 Hz; time resolution = 23.2 ms; 50% frame overlap). Songs that were indistinguishable by visual inspection of onscreen spectrograms and by ear were classified as the same song 'type', and those that differed were classified as different song types. Song types were generally highly stereotyped and thus easy to distinguish. From these spectrograms (over 700) we identified song types that had been recorded both during a song contest (i.e. overlapping another song in spectrograms) and while that same male was singing alone. Only songs in which the identity of the singer was clearly confirmed on tape were included in the analysis. Males in our study did not appear to share any song types (see below). In total we included 25 different song types produced by 15 males (mean = 1.67, range 1–5 song types per male).

We used Raven to measure several spectrogram features of each song type, which were then compared between two contexts: (1) songs that overlapped other songs during contests and (2) the same song types produced by males singing alone. These spectrogram features were initially selected to reflect aspects of song shown in previous studies to have changed in the recent evolutionary ancestors of this species (Price & Lanyon 2002, 2004). The lowest and highest peak frequencies of songs, ranges of frequency shifts and durations of continuous sounds all differ markedly between *Montezuma oropendolas* and other closely related taxa (see appendix in Price & Lanyon 2002). The individual who made measurements of spectrograms in our study (S. M. E.) was at the time blind to any particular hypotheses about vocal changes during contests.

The lowest peak frequency (LPF) and highest peak frequency (HPF) to occur in each song were identified by eye and then confirmed using measurements of single power spectra (i.e. spectrogram slices in Raven). These features represented the time-specific peak amplitude with the lowest and highest sound frequency, respectively, during a song. Initial measurements of LPF revealed differences between songs that were relatively small, so we confirmed our measurements of this feature using spectra with higher frequency resolution (DFT = 2048 samples; frequency resolution = 15.5 Hz; time resolution = 92.9 ms). We also measured the maximum frequency shift (MFS) in each song, defined as the greatest change in peak frequency occurring in less than 20 ms. As in previous analyses (Price & Lanyon 2002, 2004), a peak frequency was defined as the frequency with the highest power at any selected time during a song. We chose to measure peak frequencies rather than the lowest and highest frequencies visible in spectrograms to control for variation in the signal-to-noise ratio among recordings. Moreover, because the peak frequency at any particular moment in a song is a product of both the syrinx and the variety of other structures associated with avian sound production (e.g. orientation of the vocal tract, beak gape, etc.; Nowicki & Marler 1988; Westneat et al. 1993; Lambrechts 1996; also see Fitch 1999), we considered this to be a more physiologically meaningful measure of performance than would be measurements of just lowest and highest apparent frequencies.

Measuring song duration (SD) was more problematic, because *Montezuma oropendola* songs begin with relatively low-amplitude notes that were sometimes masked by background noise in our spectrograms. To avoid this problem, yet still be able to compare the length of a particular song type in different contexts, we selected a clearly identifiable point in the middle of a song, typically the beginning of a loud note, and measured the duration (i.e. delta time) from this point to the end of the song. This same point was then used in all subsequent duration measurements of that song type. Reverberation of sounds in forested habitats can tend to make notes appear longer in spectrograms, which might have caused us to overestimate this measurement. However, most tape recordings were conducted under similar environmental

conditions and so were probably equally affected by environmental distortion.

For each song type, we measured several examples that overlapped another song in spectrograms (mean \pm SE = 2.52 ± 0.28) and several that did not overlap other songs (mean \pm SE = 5.80 ± 0.75). We then used these measures to calculate a mean value for each feature in each context. Features identified in nonoverlapping songs were usually easy to find in the same song types in overlapping situations. Features that were masked by an overlapping song or by other sounds were not included in the analysis. For those males that contributed more than one song type, we calculated within-male mean values so that each male was represented in our analysis only once. Values were compared between contexts for all 15 males using a Wilcoxon signed-ranks test, two tailed.

Low-frequency Notes and Body Size

Sound frequency varies negatively with body size in birds (Wallschläger 1980; Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Laiola & Rolando 2003), which suggests that size might limit a male songbird's ability to produce loud, low-frequency notes. That is, small individuals might be unable to produce frequencies as low as can larger individuals. To investigate this possibility, we examined the relation between lowest peak frequency and relative body size across the entire New World blackbird family (Icteridae). This passerine group includes species with a wide range of male sizes, reflected in mean tarsus lengths (21–57.5 mm: Webster 1992; Jaramillo & Burke 1999). We were unable to obtain enough measurements of body size for the *Montezuma oropendolas* recorded in this study to allow a similar intraspecific comparison. In total, we measured the LPF (following methods outlined above) of the songs of 102 icterid taxa including the *Montezuma oropendola*, constituting 92 of the 97 described species in the family and all recognized genera (Sibley & Monroe 1990). We then plotted mean LPF against mean measurements of male tarsus length for these same taxa.

We obtained tape recordings of icterid songs from a variety of sources, including the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology and several commercially available cassette tapes (Coffey & Coffey 1984, 1989; Parker 1985; Peterson 1990; Moore 1993, 1994, 1997; Elliot et al. 1997; Hardy et al. 1998; source information available from the authors upon request). Multiple recordings from different geographical areas by different recordists were available for most species. We attempted to maximize the independence of our samples by analysing only one relatively undistorted example of each identified song type and only three or fewer representative song types from each recording (see Price & Lanyon 2004 for a detailed description of song sampling methods). In all we measured 1–27 representative song types from each species or subspecies (mean \pm SE = 5.32 ± 0.49), in addition to the 50 measurements made of *Montezuma oropendola* songs, to produce a single mean measurement for each of the 102 icterid taxa.

We used mean measurements of male tarsus length as an indicator of relative body sizes of taxa, based on previous evidence that tarsus length is a good general indicator of overall body size in birds (Rising & Somers 1989; Webster 1992). Mean tarsus measures for all 102 taxa were obtained from Webster (1992) and from Jaramillo & Burke (1999). In species with multiple subspecies, we used tarsus measurements from the same subspecies from which we had obtained song recordings whenever possible.

To investigate how body size might limit the lowest peak frequency of song, we estimated the lower limit of LPF in relation to tarsus length in the Icteridae following the statistical methods of Blackburn et al. (1992) and Podos (1997). If size acts as a constraint on the production of low sound frequencies but does not limit the production of other frequencies, small species should be limited to relatively high LPFs, whereas larger species should have the ability to produce lower LPFs as well as high LPFs. Furthermore, we expected that only some species, presumably those influenced by selection for low sound frequencies in their songs, would have mean LPFs near this lower limit. To investigate the relation between body size and minimum mean LPF, we binned taxa into 5-mm increments based on tarsus measurements (20–25 mm, 25–30 mm ...55–60 mm) and selected the taxon with the lowest mean LPF in each bin. A linear regression through these minimum values was then used to calculate the lower boundary of LPF for the family. (See Podos 1997 for an example of this method used in investigating another potential physical constraint on bird song production.)

We evaluated the statistical significance of this relationship using independent contrast analysis (Felsenstein 1985) as implemented in CAIC (Version 2.0; Purvis & Rambaut 1995). This method allowed us to incorporate phylogeny into our comparisons to control for statistical nonindependence in our data set caused by shared history among taxa (Harvey & Pagel 1991). Phylogenetic relationships and branch lengths for this analysis were taken from the molecular phylogeny of Price & Lanyon (2004).

RESULTS

Song Contests in *Montezuma Oropendolas*

Male *Montezuma oropendolas* have repertoires of complex song types that are generally stable in acoustic structure, even in recordings made many months apart. Although some of the song types included in our study had similar acoustic features, none were identical. Moreover, we found no evidence that different males share any song types. Males overlapped the songs of other males with their own songs (Fig. 1), but individuals were never observed matching the particular sound patterns of their opponents, as documented in some other songbirds (Todd & Naguib 2000; Vehrencamp 2001; Mennill & Ratcliffe 2004). The stereotypy of these song types was illustrated by the fact that most of our measurements did not differ in overlapping and nonoverlapping songs

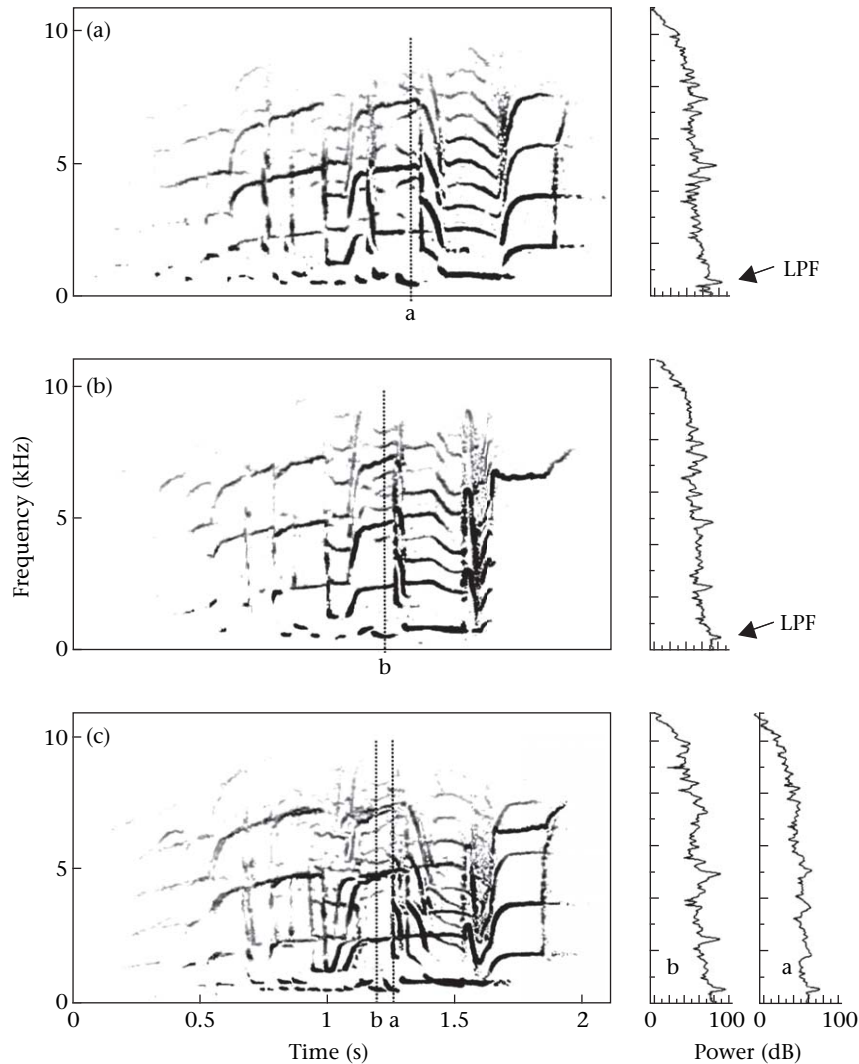


Figure 1. Sound spectrograms (left) and power spectra (right) showing (a) a typical song by a lone male Montezuma oropendola, (b) a different song type by another male and (c) the same two song types overlapped by these males during a song contest at a nesting colony. Vertical dotted lines on spectrograms indicate where power spectra were calculated to measure lowest peak frequencies (LPF, indicated on top two power spectra).

(Fig. 2a). Highest peak frequency, maximum frequency shift and our measure of song duration differed between song types but were virtually unchanged in versions of the same song type in these two contexts (Wilcoxon signed-ranks test: $N = 15$; HPF: $Z = -0.03$, $P = 0.97$; MFS: $Z = -1.31$, $P = 0.19$; SD: $Z = -0.91$, $P = 0.363$).

Unlike these other song measures, the lowest peak frequency of a song type differed consistently depending on context. Songs that overlapped other males' songs had slightly but significantly lower LPFs than the same song types produced while singing alone (Wilcoxon signed-ranks test: $Z = -2.10$, $N = 15$, $P = 0.035$; Fig. 2b). Measurements of LPF were also strikingly similar across different song types: standard errors were smaller for mean LPFs (overlapping song: $SE = 10$ Hz; nonoverlapping songs: $SE = 9$ Hz) than for mean highest peak frequency ($SE = 487$ Hz and 467 Hz, respectively). Decreases in LPF were found regardless of whether an overlapping song

occurred first, last or simultaneously in reference to another male's vocalization. The order of overlapping songs likewise did not appear to vary with male rank, although this was based on a limited sample of 15 males, none of which was the top-ranking male at a colony during the study.

Interspecific Relationship Between LPF and Tarsus Length

A plot of mean LPF against tarsus length for all 102 icterid taxa, while not evaluated for statistical significance due to uncertainties about phylogeny (Harvey & Pagel 1991), suggested that this song measure tends to decrease with increasing body size across the family (Fig. 3a). The lower-bound regression for these points had a negative slope ($Y = -0.011X + 1.026$; Fig. 3b) and approached

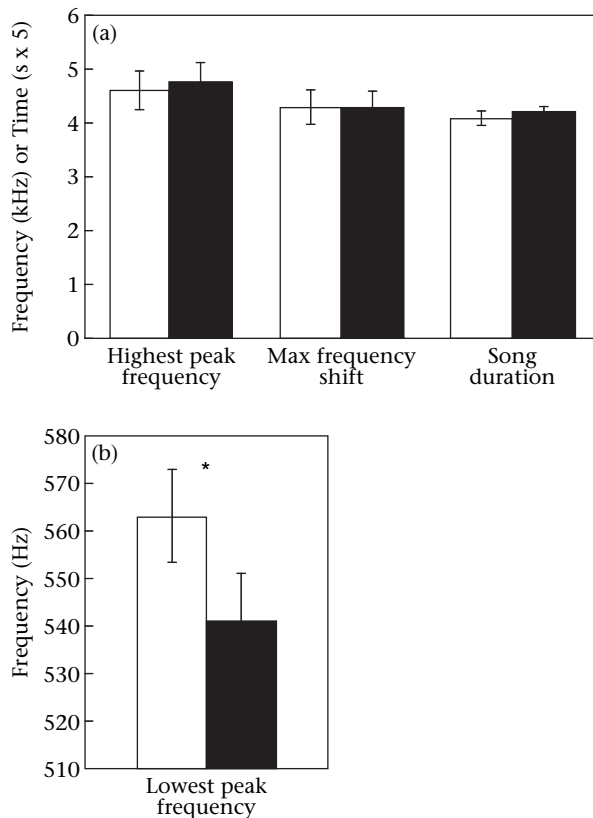


Figure 2. Means \pm SE of (a) highest peak frequency, maximum frequency shift, song duration and (b) lowest peak frequency in overlapping (■) and nonoverlapping (□) songs. Axes are scaled differently to show differences in lowest peak frequency. * $P < 0.05$.

statistical significance in an independent contrast analysis ($F_{1,6} = 5.33$, $r^2 = 0.47$, $P = 0.06$). Interestingly, most of the points along this lower boundary represented polygynous members of the oropendola–cacique clade (filled circles in Fig. 3a), including the Montezuma oropendola (filled triangle). All 10 species and subspecies in the genus *Psarocolius* (Jaramillo & Burke 1999), including taxa that are distantly related based on molecular analyses (Price & Lanyon 2004), fell along the lower-bound regression line, as did several cacique taxa. Only one species not included in the oropendola–cacique clade, the brown-headed cowbird, *Molothrus ater* (Fig. 3a, lower left unfilled circle), had a mean LPF along this lower boundary.

DISCUSSION

Male Montezuma oropendolas consistently decreased the lowest peak frequency of their songs when these vocalizations overlapped those of other males. Other measures of song, in contrast, did not differ consistently between overlapping and nonoverlapping contexts, which suggests that changes in LPF were due to male behaviour rather than differences in other factors (e.g. sound transmission properties). Males decreased the lowest peak frequencies of their songs regardless of which song occurred first in an overlap, suggesting that changes in sound frequency

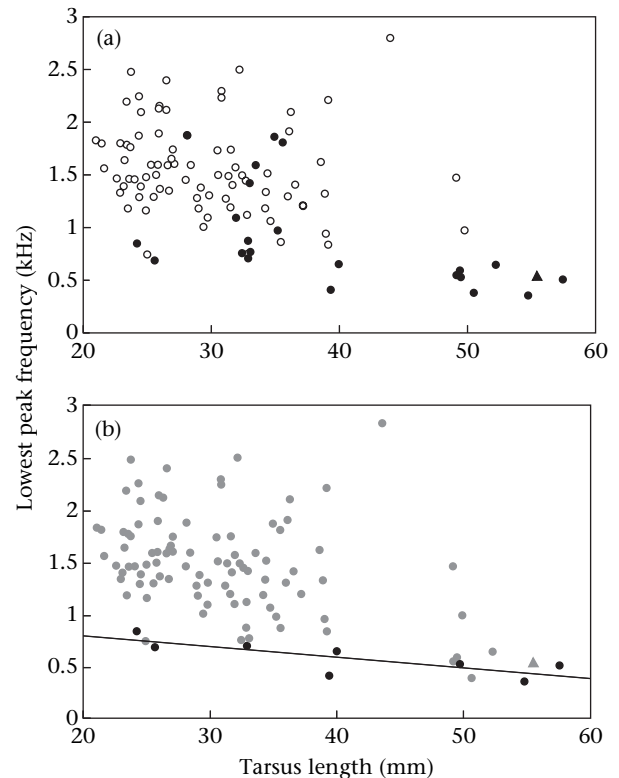


Figure 3. Mean lowest peak frequency (LPF) of songs plotted against mean tarsus length for the Montezuma oropendola (triangle) and 101 other taxa in the family Icteridae (circles). (a) Taxa in the oropendola–cacique clade (filled circles and triangle) in relation to other icterid taxa (open circles). (b) Lower-bound regression ($Y = -0.011X + 1.026$) indicating the lower limit for LPF in the family, with taxa used in the calculation marked in black and other taxa included in grey for reference.

resulted from the presence of nearby contemporaneously singing males rather than from who overlapped whom during the encounter. Indeed, most overlapping songs were nearly simultaneous (Fig. 1).

Comparing the mean lowest peak frequency of Montezuma oropendolas to those of other icterids shows that songs in this species are near the lower limit of what members of the family produce. The negatively sloped lower boundary in the relationship between LPF and tarsus length (Fig. 3b) suggests a physiological low-frequency limit in the production of loud (i.e. 'peak') notes and, further, that this low-frequency limit is higher for smaller than for larger birds. Taken together, these results imply that the low-frequency notes in Montezuma oropendola songs are constrained by body size and thus could function as an indicator of size during male–male contests (Gil & Gahr 2002). Such a cue would probably be useful in this species, because body size is an important factor in male reproductive success (Webster 1997). Intraspecific comparisons to investigate whether low-frequency notes actually do reflect body size in Montezuma oropendolas will be needed to confirm this idea.

Our findings are consistent with previous comparative studies showing a negative relation between body size and the sound frequencies used by birds in their songs

(Wallschläger 1980; Ryan & Brenowitz 1985; Tubaro & Mahler 1998; Laiola & Rolando 2003). The specific causes of this relation are not clearly understood, but likely factors that covary with body size and mass could include dimensions of the syrinx and vocal tract resonances (Lambrechts 1996; Fitch 1999). A relation between sound frequency and body size has been shown in other taxa as well; for instance, the dominant sound frequency in the calls of many frog species reflects body mass and is used by competing males in assessing an opponent's size (Davies & Halliday 1978; Wagner 1989, 1992).

A similar physical constraint on bird song has been demonstrated in species of the family Emberizidae, in which singers face a performance trade-off between trill rates and frequency bandwidths of trilled songs due to mechanical limitations of the vocal tract (Podos 1997, 2001). Songs with features near this physical limit are more challenging to produce, and evidence suggests that such indicators of performance can have important consequences for male mating success (Drăgănoiu et al. 2002; Ballentine et al. 2004). A low-frequency limit on the production of loud, low notes in Montezuma oropendola songs would indicate that these sounds are similarly constrained and, further, that songs with lower LPFs produced in overlapping situations are closer to this physical limit than are songs produced in other contexts. The surprising lack of variation in LPF across different song types by different males (apparent as relatively small error bars in Fig. 2b) suggests that this aspect of song has been pushed to its physiological limit by strong directional selection.

Several possibilities might explain why Montezuma oropendolas overlap the songs of other males at nesting colonies. Overlapping could function to disrupt or impair the courtship signals of another male by masking that male's sounds, an effective tactic if vocal displays are important in the assessment of male quality (Todt 1981; Todt & Naguib 2000; Mennill & Ratcliffe 2004). Such disruptions would be especially important at larger colonies, where multiple males compete at close range for access to receptive females (Webster & Robinson 1999). However, although males in our study often altered the timing of their songs in overlapping situations, we found little evidence that singers attempt to avoid song overlapping by truncating their songs or by stopping singing altogether, as found in some other species (nightingales: Naguib 1999; great tits: Langemann et al. 2000; black-capped chickadees: Mennill & Ratcliffe 2004).

Our finding that males modify the structure of their songs in overlapping versus nonoverlapping situations suggests another potential reason for song-overlapping behaviour. Superimposing songs might allow potentially important components of these vocalizations, such as sounds that reflect condition or body size, to be more readily compared between opponents. This would be akin to other male displays in which a physical attribute that reliably reflects competitive ability is lined up by individuals at close range for direct comparison during a contest (Maynard Smith & Parker 1976). Examples include comparisons of antler or eye stalk spans during contests in some fly species (Wilkinson & Dodson 1997) and comparisons of body size during the 'parallel walk' in red

deer, *Cervus elaphus* (Clutton-Brock et al. 1979). Like physical features that are positioned near each other spatially, sounds that are closely spaced in time might provide advantages for competing male oropendolas in allowing contestants to scrutinize vocal differences at a level not possible when songs are timed further apart. Such comparisons could also have importance for other individuals nearby, including receptive females (Mennill et al. 2002). Unlike some other polygynous icterid species (e.g. boat-tailed grackles, *Quiscalus major*: Poston 1996), female Montezuma oropendolas appear to play an active role in determining the fertilization success of males (Webster 1995).

If lowering LPF is important for male success during contests, one might ask why male oropendolas do not sing songs with the lowest possible LPF at all the times. The metabolic costs of bird song are probably not restrictive (Oberweger & Goller 2001), and it is unclear whether producing low-frequency notes is any more energetically expensive than producing sounds of other frequencies (e.g. Wagner 1992). However, birds singing near their mechanical limits probably face trade-offs involving more than just energetic costs, such as decreases in consistency or problems in sound transmission, so that 'pushing the limit' with LPF may result in decreased performance in other key aspects of song. Such mechanistic hypotheses are not mutually exclusive and any might lead to males using lower LPF only under social conditions where it is required (i.e. song contests).

At least one other species is known to alter the sound frequencies of its displays during contests, much as male Montezuma oropendolas do. In Blanchard's cricket frogs, *Acris crepitans blanchardi*, a species in which the dominant frequency of calls correlates negatively with body size, males actively lower the dominant frequency of their calls during male-male competitions (Wagner 1989). The extent to which a male frog alters his sound frequency is independent of body size, yet it appears to provide reliable information about male fighting ability, suggesting that frequency-lowering behaviour reflects male condition or motivation (Wagner 1992). If, as Wagner (1992) suggested, lowering the dominant frequency of a call is a physiologically expensive behaviour in these frogs, perhaps lowering the LPF of a song in Montezuma oropendolas is similarly demanding and serves a similar function. In other signals known to be condition dependent, such as roaring rate in red deer, males perform versions of their displays during contests that are especially physiologically costly (Clutton-Brock & Albon 1979; Clutton-Brock et al. 1979). These signals provide reliable information about the competitive abilities of opponents, thereby allowing animals to avoid potentially costly fights that they are unlikely to win (Maynard Smith & Parker 1976).

Our finding that other oropendola and cacique species have low mean LPFs like those of Montezuma oropendolas (Fig. 3a) suggests that selection for loud low-frequency notes might be an evolutionarily conserved aspect of song in this clade (Price & Lanyon 2002). All nine congeners of the Montezuma oropendola (genus *Psarocolius*) included in our study have mean LPFs along the lower limit for icterids and all are also among the most sexually size

dimorphic species in the family (Webster 1992; Jaramillo & Burke 1999). This relation is noteworthy because one species, the casqued oropendola *Psarocolius oseryi*, is not a close relative of its congeners based on molecular analyses (Price & Lanyon 2004), so the evolution of both low-frequency notes and high sexual size dimorphism in these distantly related birds appears to have arisen convergently. Low-frequency notes also appear to have evolved independently in the brown-headed cowbird, an icterid in the grackles and allies clade (Lanyon & Omland 1999). Studies of brown-headed cowbirds by King & West (1983) showed that the low-frequency notes in male song ('low-frequency modulator' or LFM) influence a song's attractiveness to females. Although similar studies have not been conducted for oropendolas or caciques, our results suggest that low-frequency notes may similarly influence male dominance rank and/or mating success in these species.

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