

Do song-phrase production rate and song versatility honestly communicate male parental quality in the Gray Catbird?

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ABSTRACT. Sexual selection theory proposes that elaborate male secondary sexual characteristics, including complex song, may increase the attractiveness of males by honestly communicating to females their genetic quality or ability to provide material reproductive resources such as parental care. The Gray Catbird (*Dumetella carolinensis*) is sexually monochromatic, but males sing complex songs during the breeding season while females do not. We tested the hypotheses that song-phrase versatility and rate of song-phrase production are honest indicators of male parental effort. We predicted that both song-phrase versatility and rate of production would be positively correlated with paternal chick feeding rate. Paternal chick feeding rate was not significantly related to song-phrase versatility, but it was positively and significantly correlated with song-phrase production rate. Thus, song-phrase production rate may serve as a more reliable indicator of male parental quality than song versatility in the Gray Catbird.

SINOPSIS. La tasa de producción de frases y la versatilidad del canto comunica honestamente la calidad del cuidado parental en *Dumetella carolinensis*?

La teoría de selección sexual propone que la elaboración de las características secundarias de los machos, incluyendo la complejidad del canto, pueden aumentar su atractivo sexual, comunicando, honestamente a la hembra, su calidad genética y habilidad de proveer recursos de valor reproductivo como el cuidado parental. *Dumetella carolinensis* es sexualmente monocromático, y aunque las hembras no cantan, los machos producen complejas canciones durante la época reproductiva. Se puso a pruebas la hipótesis que la versatilidad de frases en el canto y la tasa de producción de cantos eran un indicador honesto del esfuerzo en el cuidado parental. Se predijo, que los dos patrones previamente mencionados, estaban positivamente correlacionados con la tasa de alimentación a los pichones (esfuerzo) por parte de los machos. Se encontró que la tasa de alimentación a los pichones no estaba significativamente relacionada a la versatilidad del canto, pero sí a la tasa de producción de frases en el canto. Por lo tanto, la tasa de producción de frases en el canto es un indicador más confiable de la calidad de un macho como padre que la versatilidad del canto, al menos en la especie estudiada.

Key words: *Dumetella carolinensis*, Gray Catbird, parental care, sexual selection, song complexity

In some sexually dimorphic species, males have evolved elaborate secondary sexual characteristics such as physical ornaments, energetically expensive visual displays, and song. Sexual selection theory proposes that these traits confer mating advantages only, by either increasing their bearers' ability to compete among each other for access to females or increasing their attractiveness (Darwin 1871; Andersson 1994). Females may prefer males with more exaggerated traits because they honestly communicate their genetic quality and/or ability to provide direct reproductive benefits such as territorial resources, defense, and parental care (Kodric-

Brown and Brown 1984; Hoelzer 1989; Andersson 1994).

Song complexity, as measured by indices such as repertoire size and versatility, appears subject to sexual selection (Catchpole and Slater 1995; MacDougall-Shackleton 1997), and evidence suggests that females may prefer males with larger song repertoires (Catchpole 1980; Baker et al. 1986; Searcy 1992; Searcy and Yasukawa 1996; Buchanan and Catchpole 1997; Neubauer 1999; Reid et al. 2004). Furthermore, song repertoire size has been correlated with various measures of male physical condition (Horn et al. 1993; Catchpole and Slater 1995; Buchanan et al. 1999) and neural development (Szekely et al. 1996; Nowicki et al. 2000). Thus, recent research has provided some

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crucial linkages between song complexity, female choice, and physiological parameters to explain how song could honestly indicate a male's genetic quality or potential to provide breeding resources such as parental care.

However, few studies have directly tested the hypothesis that song complexity is an honest indicator of male parental effort. Parental care provided by males can have a measurable impact on nestling growth and survival (Mock and Fujioka 1990; Markman et al. 1996), and some removal experiments suggest that females may increase their rates of chick feeding in the absence of male parental care, possibly reducing their own long-term fitness (Wolf et al. 1990; Markman et al. 1996). Thus, in species with biparental care, epigamic traits that allow females to compare males' potential capacity for parental care should be favored by intersexual selection (Mountjoy and Lemon 1997).

Although Buchanan and Catchpole (2000) observed a positive relationship between song complexity and paternal chick feeding rates in Sedge Warblers (*Acrocephalus schoenobaenus*), two other recent studies have failed to detect such a correlation (Mountjoy and Lemon 1997; Rinden et al. 2000). These studies quantified song complexity by either repertoire size (Mountjoy and Lemon 1997; Buchanan and Catchpole 2000) or versatility (Rinden et al. 2000).

Given these scant and conflicting data, our first objective was to test the hypothesis that song complexity provides an honest indicator of male parental quality. We studied the Gray Catbird (*Dumetella carolinensis*), a species that is highly suitable for testing this hypothesis. First, catbirds are sexually monochromatic, but exhibit pronounced vocal sexual dimorphism. Males produce highly complex song composed of individually distinguishable note clusters (Cimprich and Moore 1995; Kroodsma 1997; A. S. Dolby, pers. obs.), which we refer to as "song-phrases" (Greig-Smith 1982). Second, male parental care seems to play a crucial role in catbird chick development. Males usually contribute at least half of all chick feedings, especially early in the nestling period (Johnson and Best 1982). Third, laboratory evidence indicates that male catbird song does not develop via imitation, but instead is the product of individual improvisation and invention (Kroodsma et al. 1997). This developmental feature

suggests that song complexity in this species is likely to reflect intrinsic attributes of the singer.

We used song-phrase versatility as our index of song complexity. Previous research indicates that catbird song repertoires are at least several hundred song-phrase types in size (Kroodsma et al. 1997). Therefore, it is more likely that females compare males' ongoing degree of repetition rather than monitor and compare thousands of unique song-phrases from multiple individuals.

Additionally, we observed wide variation among males in their overall song-phrase delivery rate. Greig-Smith (1982) found a positive relationship between song phrase production rate and paternal chick feeding rate in Stonechats (*Saxicola torquata*). Furthermore, Hofstad et al. (2002) reported that male Snow Buntings (*Plectrophenax nivalis*), which produce song strophes at faster rates, also feed chicks at higher rates. Perhaps this song feature is also informative to female Gray Catbirds, either independently of, or in concert with, phrase versatility.

We predicted that both song-phrase versatility and production rate would be positively correlated with chick feeding rates by males. Either positive correlation could be attributable to variation in genetic quality and/or physical condition among males, which could affect an array of physiological and developmental attributes that may, in turn, influence delivery of parental care.

METHODS

We conducted our study on the University of Mary Washington campus in Fredericksburg, Virginia, during May–July of 2001–2003. Campus property includes both landscaped grounds containing scattered trees and shrubs and unmanaged eastern deciduous forest fragments bounded by dense vegetation. During early May of each field season, we mist-netted territory-holding adult catbirds and fitted each with a U.S.F.W.S. aluminum band and a unique combination of colored leg bands. Before mated pairs had formed each season, we used a shotgun microphone (Audio-technica) and a Sony TC-D5M cassette recorder to record song samples from banded males. We obtained three to five separate song samples from 17 males (four in 2001, seven in 2002, six in

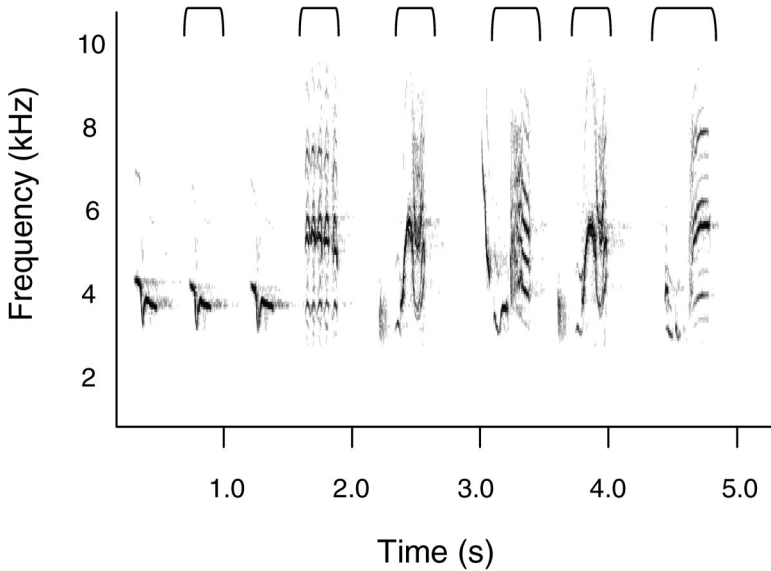


Fig. 1. Sonogram of male Gray Catbird song recorded in Fredericksburg, Virginia. Song-phrases are indicated by brackets.

2003) by regularly visiting each territory. We recorded song between 05:30 and 12:00. Unlike many oscines that breed in the temperate zone, catbirds sing throughout the day, and their song complexity does not decline after the dawn chorus (Cimprich and Moore 1995; A. S. Dolby, pers obs.). We only recorded when males were in full song.

We prepared sonograms (Avisoft-SASLab ProTM) of 1-min samples of continuous song that we randomly selected from each separate recording bout (Fig. 1). Given that males emitted song-phrases at highly variable rates, we based our index of versatility on the first 25 song-phrases per 1-min sample, just under the lower limit for song-phrase production rate for all such samples. Our song versatility index thus consisted of the ratio of unique song-phrases out of the first 25 emitted per sample (e.g., Rinden et al. 2000). We then averaged this ratio for 8–10 min per individual, each recorded on a different day and at different times.

For the same 8–10 min, we also averaged the total number of song-phrases produced (Hofstad et al. 2002). Owing to our ability to identify some of our subjects by their song recordings, we were unable to evaluate sonograms in a fully blind manner. However, we reviewed all sonograms before chick feeding data were collected.

From late May through early July, we located nests belonging to banded pairs, and on either the fifth, sixth or seventh day after chicks hatched, depending on weather conditions, we observed chick feeding for a total of three hours. We conducted observations in 1-h bouts during the morning, mid-day and mid-afternoon, each nest observed during approximately the same hours of the day. We determined that three hours of observation were sufficient to accurately quantify male feeding rates through five to six-hour pilot observations conducted over two days on six nests each. Moreover, our chick feeding observation scheme is consistent with similar studies (Mountjoy and Lemon 1997; Buchanan and Catchpole 2000; Rinden et al. 2000; Hofstad et al. 2002).

For most nests, we observed chick feeding using a Sony VHS Slim CamTM recorder positioned approximately 0.5 m from the nest. Birds habituated to the camera within minutes. A few nests were not positioned favorably for videotaping, and we observed them with binoculars. Observers were positioned about 3 m from nests on sidewalks that consistently carried pedestrian traffic. We found no statistical differences in feeding rates between pairs that were videotaped and those that were observed directly. Only visits during which food was deposited into a chick's buccal cavity were record-

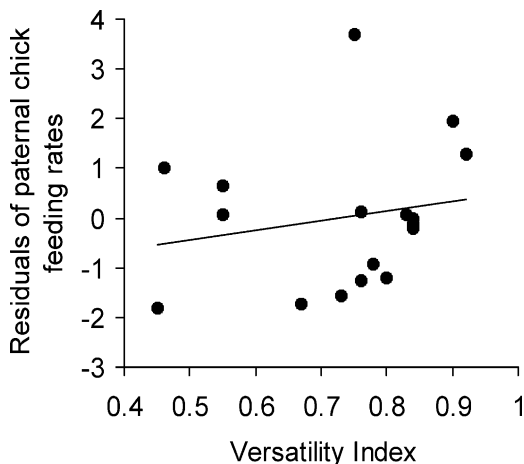


Fig. 2. Nonsignificant relationship between male Gray Catbird song versatilities and residual paternal chick feeding rates after statistical removal of effects of brood size, chick age, female feeding rate, and year (ANCOVA).

ed, but we did not quantify amounts and types of food delivered.

We used ANCOVA for data analysis (General Linear Model, SPSS 11.0 for Windows), a multivariable procedure that allows one to control for extraneous variables that may mask the effects of the dependent variables of interest (Kleinbaum et al. 1988). Hourly chick feeding rates by males was our dependent variable. We entered song-phrase versatility and rate of song-phrase production as covariates. We also entered year, brood size, average chick mass, and maternal feeding rates, to control for these four extraneous variables that may have affected paternal chick feeding rates. Residuals displayed in the figures represent the remaining variation in paternal chick feeding rates after the above four variables were statistically removed. In preliminary treatment of our data, we found no significant interactions among our variables. Thus, we included only main effects in our final analysis.

RESULTS

Paternal chick feeding rates ranged from 3.4–10.0/h ($\bar{x} = 5.8 \pm 1.6$ SD), and males contributed 49% of total chick feedings. Brood sizes ranged from two to five ($\bar{x} = 3.5 \pm 0.7$ SD), and average chick mass per brood ranged from 16.0–26.5 g ($\bar{x} = 19.0$ g ± 1.6 SD). Song-

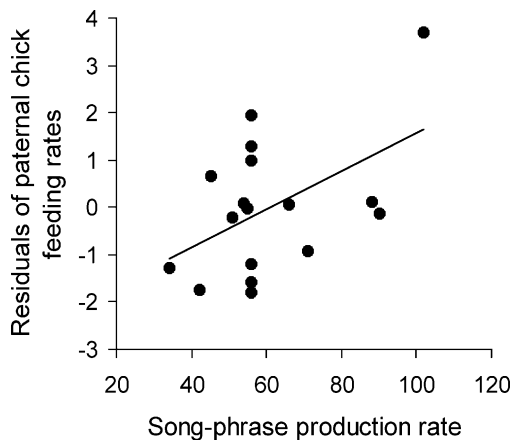


Fig. 3. Significant positive correlation between male Gray Catbird song-phrase production rates and residual paternal chick feeding rates after statistical removal of effects of brood size, chick age, female feeding rates, and year.

phrase versatility averaged 0.7 (± 0.1 SD), while rate of song-phrase production averaged 60.8/min (± 17.8 SD).

We found no correlation between song-phrase versatility and paternal chick feeding rate after controlling for year, brood size, average chick mass, and female feeding rate ($F_{1,9} = 1.2$; $P = 0.29$; Fig. 2). However, paternal chick feeding rate was positively and significantly correlated with song-phrase production rate ($F_{1,9} = 10.6$; $P = 0.01$; Fig. 3). Song-phrase versatility and rate of production were not significantly correlated ($r = 0.35$; $P = 0.17$; Fig. 4). None of the four extraneous variables that we included in our analysis were significant predictors of paternal chick feeding rate (year, $P = 0.10$; chick age, $P = 0.38$; brood size, $P = 0.83$; female feeding rate, $P = 0.84$).

One male had both a noticeably higher chick feeding rate and song-phrase production rate than others, which warranted further scrutiny (Cook's Distance = 1.3; Fig. 2). Although we had no biological rationale for excluding this male from analysis (e.g., proximity to an atypically productive or artificial food supply), to be statistically conservative, we conducted our analysis again without his data point. Excluding this male, the correlation between song-phrase production rate and chick feeding rate remained statistically significant ($F_{1,8} = 5.2$; $P = 0.04$).

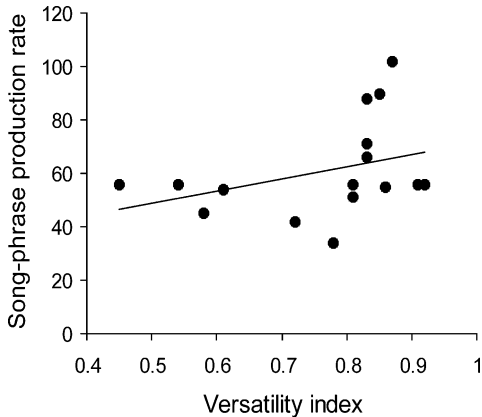


Fig. 4. Nonsignificant relationship between male Gray Catbird song-phrase versatility and production rates.

DISCUSSION

Our data do not support the hypothesis that song-phrase versatility is an honest indicator of paternal chick feeding rate in the Gray Catbird. Similar negative results have been reported by others (Rinden et al. 2000). Our data are, however, consistent with the hypothesis that song-phrase production rate honestly indicates paternal chick feeding effort. Greig-Smith (1982) found that average song-phrase rate by male Stonechats was significantly correlated with the percentage of chick feedings performed by males. Likewise, Hofstad et al. (2002) reported a nonsignificant, but positive relationship between song rate and rates of chick feeding by male Snow Buntings (*Plectrophenax nivalis*). Thus, our results parallel those found for other species.

Because their chicks may be fed more often, females may enhance their fitness by choosing males with faster rates of phrase production. It is possible that their nestlings fledged in better nutritional condition. Such enhanced nutritional condition could increase offspring survivorship during the fledgling period and allow for more successful migration at the end of the breeding season.

Another possible benefit of higher male feeding rates, based upon Nowicki et al.'s (1998) nutritional-stress hypothesis, is that development of male chicks' neural song control nuclei may be improved. This may lead them to sing more complex songs (Nowicki et al. 2000) or

sing at higher rates during adulthood, which could lead to higher mating success. For example, Buchanan et al. (2003) recently found that European Starlings (*Sturnus vulgaris*) sing at reduced rates when presented with unpredictable food supplies during development.

Whether female catbirds actually prefer males with more complex songs or faster rates of song-phrase production has not been tested. Other researchers have used pairing date indicators such as hatching date (e.g., Buchanan and Catchpole 1997), but such reproductive "mileposts" are likely to be determined by a complex combination of factors in addition to pairing date. Nonetheless, in light of our data, females should prefer males with faster rates of song-phrase delivery.

In conclusion, male Gray Catbird song-phrase production rate could act as a signal of paternal quality that females should evaluate when choosing mates. Intersexual selection may therefore be an important force in the maintenance of song quality in catbirds. This conclusion does not exclude the possibility that intrasexual selection also plays a role in the maintenance of Gray Catbird song. Males with higher song-phrase rates or greater song complexity may defend higher quality territories with greater food densities, thus allowing them to feed chicks at higher rates. Finally, in addition to song-phrase production rate, measures of song complexity other than versatility, such as degree of complexity of each phrase type and/or order of phrase presentation (Catchpole and Slater 1995), may also comprise alternative bases for comparison of male song by females.

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