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Quality of song learning affects female response to male bird song

Stephen Nowicki[1*], **William A. Searcy**[2] **and Susan Peters**[1]

[1]*Evolution, Ecology and Organismal Biology Group, Department of Biology, Duke University, Durham, NC 27708, USA*
[2]*Department of Biology, University of Miami, Coral Gables, FL 33124, USA*

Bird song is unusual as a sexually selected trait because its expression depends on learning as well as genetic and other environmental factors. Prior work has demonstrated that males who are deprived of the opportunity to learn produce songs that function little if at all in male–female interactions. We asked whether more subtle variation in male song-learning abilities influences female response to song. Using a copulation solicitation assay, we measured the response of female song sparrows (*Melospiza melodia*) to songs of laboratory-reared males that differed in the amount of learned versus invented material that they included and in the degree to which learned material accurately matched the model from which it was copied. Females responded significantly more to songs that had been learned better, by either measure. Females did not discriminate between the best-learned songs of laboratory-reared males and songs of wild males used as models during learning. These results provide, to our knowledge, a first experimental demonstration that variation in learning abilities among males plays a functionally important part in the expression of a sexually selected trait, and further provide support for the hypothesis that song functions as an indicator of male quality because it reflects variation in response to early developmental stress.

Keywords: bird song; song learning; sexual selection; female choice; indicator mechanism; *Melospiza melodia*

1. INTRODUCTION

The expression of traits used by females as indicators of male quality in the context of mate choice typically reflects both genetic and condition-dependent factors (Andersson 1994; Rowe & Houle 1996). Bird song, which is known to influence female mate choice in many species (Andersson 1994; Searcy & Yasukawa 1996), is unusual as a sexually selected trait because it depends additionally on cultural transmission for its expression (Slater 1989; Catchpole & Slater 1995). The fact that song generally is essential to a male bird's ability to attract and court females, coupled with the fact that the development of song depends on learning, indicates that variation in male learning abilities should affect female choice of mates. As far as we know, this prediction has never previously been tested.

Experiments have demonstrated that males who are prevented from learning produce songs that function poorly, if at all, as signals to females. For example, Searcy *et al.* (1985) showed for both song sparrows (*Melospiza melodia*) and swamp sparrows (*M. georgiana*) that females exposed to songs produced by isolation-reared males respond only minimally, at a level that is statistically indistinguishable from that elicited by heterospecific songs. Searcy & Marler (1987) further showed for song sparrows that females do not respond at all to songs produced by males who are deafened at an early age and thus unable to hear anything during the song-learning period. While experiments such as these demonstrate that song learning is necessary for the expression of a functional signal, they do not address the critical question of whether variation in learning abilities among males in a population results in enough variation in learned features of song to influence female preferences. Knowing whether or not females attend to the quality of song learning, in turn, is important for understanding how sexual selection acts on the expression of song and, more generally, how cultural and biological selection interact in trait evolution (Laland 1994). Understanding how song learning influences female choice also provides insight into the selective forces responsible for the evolutionary maintenance of song learning (Lachlan & Slater 1999) and the mechanisms by which song might function as an indicator of male quality (Gil & Gahr 2002).

A number of song features have been shown to influence female preferences in different songbird species, but three broad categories of features have the most consistent effects (Searcy & Nowicki 2000; Nowicki *et al.* 2002): the amount a male sings (e.g. Kempenaers *et al.* 1997), the size or complexity of his song repertoire (e.g. Hasselquist 1998) and the degree to which the acoustic structure of his songs conforms to species- or population-typical norms (e.g. Searcy *et al.* 2002). Of these categories, only the last is obviously affected by song learning. Repertoire complexity depends on normal song development, of course, and may reflect variation in the development of brain areas associated with song learning (Catchpole 1996; Nowicki *et al.* 1998, 2000, 2002). Available evidence indicates, however, that repertoire size and song complexity are not learned traits *per se* in the sense that they do not depend on copying specific models (Kroodsma *et al.* 1997; Nowicki *et al.* 1999; but see Brenowitz *et al.* 1995). By contrast, the ability to reproduce song elements or other acoustic features that are species- or population-typical clearly depends on song

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[*] Author for correspondence (snowicki@duke.edu).

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learning, as it is only by accurate copying that males can incorporate these details into their songs (Catchpole & Slater 1995). How well males can copy the songs that they are exposed to when young, then, may be the most accessible measure of their song-learning abilities.

We used the solicitation display assay (King & West 1977; Searcy 1992) to compare the response of female song sparrows to songs of males that varied in how well they were learned, measuring the quality of song learning in two ways. First, we compared female responses to male songs that varied in the proportion they included of elements that were recognizable copies of model tutor songs. Song sparrows in the eastern US populations that we study typically develop songs that include 'invented' (i.e. not copied) elements along with material they have copied from models (Marler & Peters 1988; Hughes *et al.* 1998). Songs having a low proportion of copied notes also tend to include elements that are less accurate copies of the models from which they were learned (supporting our assumption that songs with less copied material are poorly learned), so the songs in this comparison differed in average copy accuracy as well. In a second experiment, we compared female responses to male songs that varied solely in their average note-copy accuracy, holding the proportion of copied notes constant. Thus, in this experiment we asked specifically whether the accuracy with which a male copies the material that it learns influences female response. In a final experiment, we compared the responses of females to a set of the field-recorded songs that we used as models in our learning experiment versus their responses to the most completely and accurately learned copies of those songs produced by laboratory-reared birds (i.e. those having a high proportion of accurately copied notes), to determine whether songs of laboratory-reared birds that are well-learned by our measures function as well as songs of wild birds.

2. METHODS

(a) *Stimulus songs*

We obtained songs that varied in how well they were learned from a cohort of laboratory-raised male song sparrows collected from the field in 1999 in the vicinity of Hartstown, Crawford County, PA, USA. Nestlings were collected at three days post-hatch and hand-reared following standard methods (for detailed methods, see Marler & Peters 1987 and Peters & Nowicki 1996), except that subjects were given a restricted amount of food until 18 days post-hatch when they began feeding themselves. This nutritional restriction was part of a separate experiment designed to determine the effects of developmental stress on song learning (e.g. Nowicki *et al.* 2002). All birds contributing songs to the present experiment were from the same restricted-diet treatment group and reared under identical conditions.

Beginning at five days post-hatch, birds were tutored twice daily with a programme of song sparrow songs that had been recorded in the field several years earlier from males in the same population. The tutoring programme included 36 song types sung by 12 different males. Each tutoring session lasted 1 h and included 12 song types presented in 4 min bouts of a single type repeated 24 times, with bouts separated by 1 min of silence. Three sets of 12 song types were rotated in six-week blocks for a total of 18 weeks of tutoring.

We recorded the laboratory-raised males' songs after they had completed song development, and determined song-type repertoires and note-type repertoires by visual inspection of sonograms (300 Hz frequency resolution, 5 ms time resolution, DSP Sona-Graph, model 5500, Kay Elemetrics, Pine Brook, NJ, USA). We then compared the repertoires of laboratory-reared birds with the songs with which they were tutored to identify material that had been copied from these models (for detailed methods see Podos *et al.* 1992; Peters & Nowicki 1996; Nowicki *et al.* 1999). Laboratory-raised song sparrows typically copy parts of songs (ranging from single notes to phrases comprising long strings of notes) and they recombine these copied parts with invented material to form their own song-type repertoires (Marler & Peters 1987; Beecher 1996; Nordby *et al.* 2000); this same pattern is observed in the field in eastern US populations (Marler & Peters 1988; Hughes *et al.* 1998). For each learned song type, we determined the proportion of notes that were recognizable copies of model song notes, providing one measure of the quality of song learning (figure 1). Copied notes may vary, however, in how closely they match the models from which they were learned. As a second measure of the quality of song learning, we used spectrographic cross-correlation (SCC) (Clark *et al.* 1987; Nowicki & Nelson 1990; Beeman 1999) to quantify how closely copied notes matched model notes (20 kilopoints s^{-1} sample rate, 128 pt fast Fourier transform, SIGNAL v. 3.1 sound analysis software, Engineering Design, Belmont, MA, USA). The average SCC between copy notes in a song and the models from which they were learned (with scores ranging from 0–1.0) was calculated.

(b) *Female solicitation assays*

Twenty female song sparrows were captured as breeding adults in May and June 2001 at the same sites from which we previously had obtained nestling males and where we had recorded the songs used to tutor those males. All females were given a subcutaneous implant of 17-β-estradiol in silastic tubing of 1.96 mm outside diameter and containing 8–10 mm of hormone seven days before testing began (for detailed methods, see Searcy 1992 and Searcy *et al.* 1997). Each female was housed singly in a sound attenuation chamber (AC-1, Industrial Acoustics, Bronx, NY, USA). We played songs through a loudspeaker (DSM-Monitor, Nagra/Kudelski, Cheseaux, Switzerland) located just outside the chamber at a rate of six songs $\min^{-1}$ for 3 min, at an amplitude of 78 ± 2 dB SPL at 1 m. The chamber door of the female being tested was opened to permit her to hear the test songs and her response was videotaped through the open chamber door. We used the number of solicitation displays performed during 3 min of playback as the sole response measure (Searcy *et al.* 1997; Nowicki *et al.* 2001).

(c) *Experimental design*

Using a within-subjects design, female response to contrasting song stimulus pairs was compared in three separate experiments.

In experiment 1, we compared female response to songs having a high proportion of copied notes (HPC songs), (mean ± s.e. = 98 ± 1%, range = 89–100%, $n = 10$ songs recorded from five males) with songs that had a low proportion of copied notes (LPC songs) (29 ± 11%, 0–78%, $n = 10$ songs recorded from five males). Because songs with a low proportion of copied notes in our sample of learned songs also tended to include more poorly copied notes, HPC and LPC songs also differed in note-copy accuracy as measured by SCC (0.69 ± 0.02, 0.57–0.87 versus 0.54 ± 0.07, 0.33–0.69).

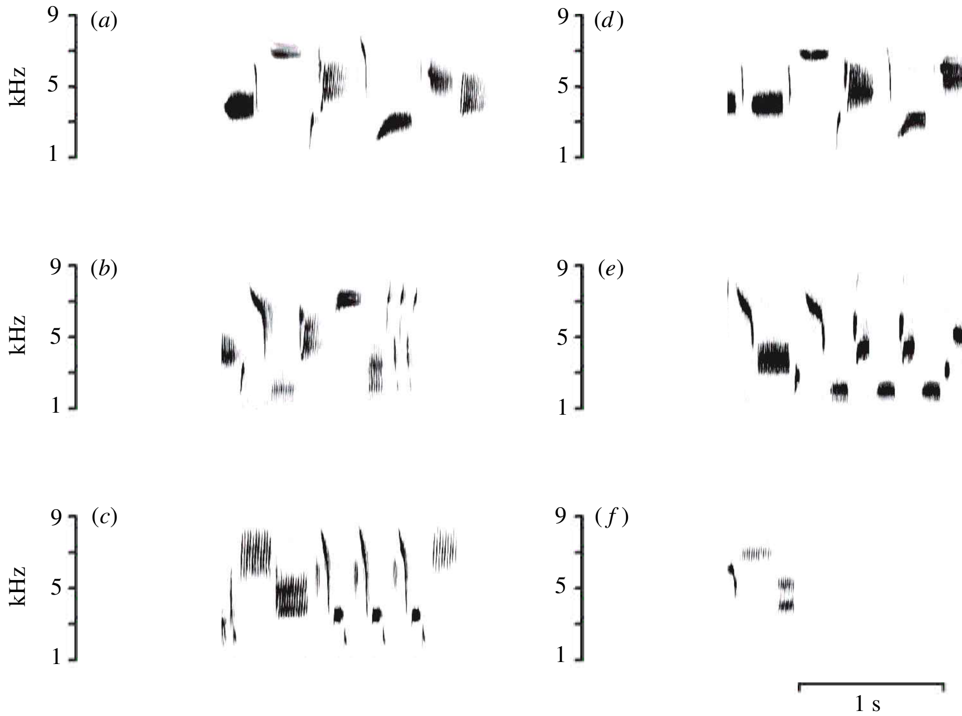

Figure 1. Examples of model songs (*a*–*c*) used to tutor young males in the laboratory and learned songs (*d*–*f*) subsequently produced by these males. Learned song (*d*) best matches the model song (*a*) and includes a high proportion of notes that have been accurately copied, typical of HPC, HSCC and copy songs in experiments 1, 2 and 3, respectively. Learned song (*e*) best matches the model song (*b*) and includes a lower proportion of notes that have been less accurately copied, typical of LPC songs in experiment 1. Learned song (*f*) best matches the model song (*c*) and includes a high proportion of copied notes, but these notes are inaccurately copied, typical of LSCC songs used in experiment 2. Songs (*a*–*c*) are typical of the model songs used in experiment 3. Note that songs having a high proportion of copied notes may include notes that have been copied from several different models; such an example is not shown here.

In experiment 2, we compared female responses to songs having a high average note-copy accuracy as measured by SCC (HSCC songs) (0.71 ± 0.01, 0.65–0.78, $n = 10$ songs recorded from six males) with songs having a lower note-copy accuracy (LSCC songs) (0.59 ± 0.02, 0.44–0.64, $n = 10$ songs recorded from five males); in this experiment, all songs included a high proportion of copied notes that was the same for the two sets of songs (95 ± 2%, 80–100% versus 96 ± 2%, 86–100%). Seven of the HSCC songs in experiment 2 were the same as HPC songs used in experiment 1.

In experiment 3, we compared female response to field-recorded model songs (model songs) ($n = 10$ songs recorded from seven males) with learned songs having a high proportion of accurately copied notes (copy songs) ($n = 10$ songs recorded from five males). The learned songs in this experiment were the same as the HPC songs used in experiment 1, and the models were those tutor songs from which the largest proportion of material in the learned songs was copied.

The 20 females were tested in all three experiments, with a one-day break between the end of one experiment and the beginning of the next. The same songs were used as HPC songs in experiment 1 and as copy songs in experiment 3, and seven of these songs also were used as HSCC songs in experiment 2; for this reason, we assigned stimulus sets such that no individual heard the same song type in more than one experiment. Model songs used in experiment 3 were recorded from the same population in which females were captured, but 6–8 years before the tests we report here were done. Because song sparrows rarely if ever live this long in the field (Nice 1937), we deem it highly unlikely that test subjects were familiar with any of the males from whom we obtained model songs.

In experiments 1 and 2, individuals were each tested twice with one pair of contrasting stimuli (e.g. one HPC song versus one LPC song). The two songs of a stimulus pair were tested on one day, with at least 3 h between tests to minimize habituation, and then tested again two days later. The order of stimuli in a pair was counterbalanced among subjects on the first day of testing and reversed on the second, and individual female responses were averaged across the two days. In experiment 3, females were only tested once with each stimulus pair, again with presentation order counterbalanced among subjects. For all three experiments, we determined statistical significance (two-tailed) using a Wilcoxon's matched pairs signed ranks test on the mean response of the two subjects per stimulus pair. We thus used as our sample size the number of contrasting stimulus pairs ($n = 10$ in all cases) to avoid pseudoreplication (McGregor *et al.* 1992).

3. RESULTS

(a) *Experiment 1*

Female song sparrows performed significantly more displays to HPC songs than to LPC songs (Wilcoxon's signed ranks test, $Z = -2.814$, $p = 0.005$; figure 2*a*). All 10 HPC songs were responded to at least once, but only four of the 10 LPC songs elicited a response; for all the contrasting stimulus pairs, the average response was higher to the HPC song than to the LPC song. Of the 17 individual

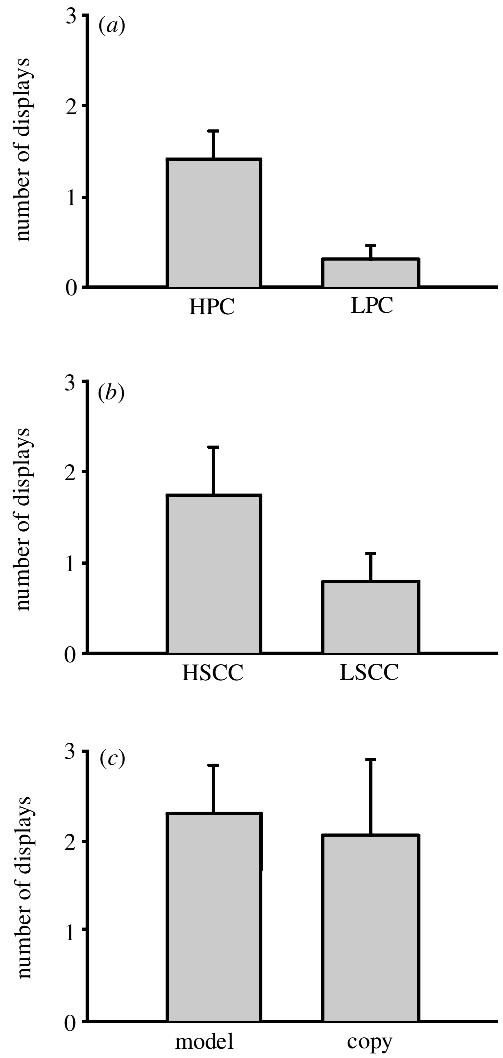

Figure 2. Number of solicitation displays given in response to playback of (*a*) HPC songs versus LPC songs ($p = 0.005$), (*b*) HSCC songs versus LSCC songs ($p = 0.035$) and (*c*) model songs versus copy songs (n.s.).

females that responded to any stimuli, only one responded more strongly to the LPC song that they heard than to the HPC song. Thus, we conclude that songs with a higher percentage of accurately copied notes—that is, songs with more material that has been learned with greater accuracy from model songs—function better to elicit female sexual response than songs with fewer copied notes that are less accurately copied.

(b) *Experiment 2*

Females also performed significantly more displays in response to HSCC songs as compared with LSCC songs ($Z = -2.106$, $p = 0.035$; figure 2*b*). Nine out of 10 HSCC songs elicited at least a minimal response as compared with seven out of 10 LSCC songs, and the average response was higher to the HSCC song for eight out of the 10 contrasting stimulus pairs. Of 14 subjects that responded to any stimuli, nine responded more strongly to the HSCC song that they heard than to the LSCC song. We conclude that songs with more accurately copied notes—that is, songs with material that more accurately matches the model song material as measured by SCC—also function better to elicit female sexual response than songs that have been less accurately copied when the proportion of identifiable copies is held constant.

(c) *Experiment 3*

Female response to well-learned songs of laboratory-reared birds, defined as songs having a high proportion of accurately copied notes, did not differ significantly from response to model songs from which the copied songs were learned ($Z = -0.845$, $p = 0.398$; figure 2*c*). Eight out of 10 model songs elicited at least a minimal response as compared with nine out of 10 copy songs; average response was higher to the model song for five contrasting stimulus pairs, higher to the copy song for three pairs and equal in the remaining two cases. Out of 15 subjects that responded in this experiment, seven responded more strongly to the model song than to the copy song, five showed the reverse preference and three showed no preference. We conclude that songs produced by our laboratory-reared males function as well as the songs recorded from wild males in the field if those songs are well-learned, according to our measures of learning quality.

4. DISCUSSION

Our results show that female song sparrows attend to variation in how well male songs have been learned, measured both in terms of the amount of learned versus invented material incorporated into songs and in terms of the precision with which learned material has been copied, with females soliciting more to those songs that have been better learned by these measures. This finding indicates that female birds may assess potential mates based on the quality of song learning, in much the same way as females in some species have been shown to assess males based on the size of their song repertoires or on the amount that they sing (Searcy & Yasukawa 1996). Earlier work had demonstrated that song learning is necessary for males to develop functional songs (Searcy *et al.* 1985; Searcy & Marler 1987), but only to the extent of showing that males who do not learn anything produce songs that are almost completely non-functional. In our experiments, all of the stimuli were learned, species-typical, population-specific songs. Females did not discriminate between the well-learned songs in our sample and model songs (figure 2*c*), demonstrating that our laboratory learning paradigm yields copied songs in the best cases that do not differ functionally from songs recorded from the wild. When comparing the strength of response with songs that differed in how well they had been learned, however, females responded significantly more strongly to those songs that had been learned better (figure 2*a*,*b*). To our knowledge, these results provide a first experimental demonstration that variation in learning abilities plays a functionally important part in the expression of a sexually selected trait.

Our results also provide support for a novel mechanism by which females may gain information about male quality through song. Nowicki *et al.* (1998) suggested that song may function as an indicator of male quality because of the developmental costs associated with song learning (see also Catchpole 1996; Buchanan 2000; Nowicki *et al.* 2000, 2002; Gil & Gahr 2002). Developmental stress due to undernourishment is often experienced by nestling and young fledgling birds (Lack 1954; Ricklefs 1983; Starck & Ricklefs 1998). The 'nutritional stress hypothesis' proposes that such stress will have an adverse effect on the development of brain structures responsible for song learning and production, leading to variation in song-learning abilities among males. Females mating with males that have learned better will be choosing mates, on average, which fared better in the face of stresses experienced early in life and who are thus likely to be phenotypically, and perhaps genotypically, superior (Nowicki *et al.* 2002).

Most discussions of how song might function as an indicator of male quality have focused on repertoire size as the relevant cue to females (e.g. Buchanan *et al.* 1999; Buchanan & Catchpole 2000; Møller *et al.* 2000; Nowicki *et al.* 2000). Obviously, the ability to learn songs is necessary to develop a repertoire of species-typical songs, and variation in learning abilities may correspond to *how much* an individual male can learn (i.e. how many syllable or song types). However, evidence that song learning *per se* affects repertoire size is mixed: male marsh wrens (*Cistothorus palustris*) tutored with a much smaller number of song types than they would normally encounter in the field develop correspondingly smaller repertoires (Brenowitz *et al.* 1995), but the number of song types heard when young does not affect adult repertoire size in catbirds (*Dumetella carolinensis*) (Kroodsma *et al.* 1997) and early experience does not influence the expression of within-song-type variation in song sparrows (Nowicki *et al.* 1999). Nutritional differences in early post-hatch development have been shown to cause lasting differences in brain size in the swamp sparrow, including the volume of nuclei responsible for song learning and production (Nowicki *et al.* 2002), and a number of studies have shown a correlation between repertoire size and 'brain space' across species (Székely *et al.* 1996), between populations (e.g. Canady *et al.* 1984) and among individuals within a population (Airey *et al.* 2000). There is disagreement, however, as to whether repertoire size is functionally limited by the size of song system nuclei (reviewed in Bolhuis & Macphail 2001; Gil & Gahr 2002).

By contrast, how well an individual male reproduces the song models that it attempts to copy clearly is the result of song learning. Numerous song-learning experiments have demonstrated that early exposure to particular song models leads to remarkably precise reproduction of the acoustic features of those models later in life (Catchpole & Slater 1995). Nowicki *et al.* (2002) have shown recently that nutritional stress incurred early in life affects the precision with which young swamp sparrows copy model songs, by the same measure as used in experiment 2 of the present study. If early stress affects both the precision of song learning and the quality of phenotypic development, the female preferences for precisely learned songs, as demonstrated here, may aid females in acquiring mates of superior quality.

Females must have a reference in order to assess how well a male has learned its songs. Our females were taken as adults from the same population where we obtained male nestlings and where we had recorded the model songs with which these males were tutored. Riebel (2000) recently demonstrated in zebra finches (*Taeniopygia guttata*) that early exposure to a particular male's songs leads to a lasting preference for those songs in the context of an operant conditioning task. Similarly, field studies have shown that early exposure to song can influence a female's choice of mate (McGregor & Krebs 1982; Grant & Grant 1997). Presumably, then, the females in our experiments had learned song characteristics typical of their population. Further work is needed to determine how and when females learn these characteristics, and the extent to which variation in female learning influences their ability to discriminate well-learned and poorly-learned songs.

Lachlan & Slater (1999) correctly point out that most hypotheses proposed for the function of song learning, such as habitat-matching, neighbour-matching or assortative mating, lack generality inasmuch as they can be applied to some but not all species. Their 'cultural trap' hypothesis, which describes the evolutionary consequences of the interaction between genetic predispositions for song recognition and patterns of cultural transmission of song, stands as the only truly general hypothesis for the evolutionary maintenance of song learning in songbirds, albeit a non-adaptive one. Given the ubiquitous importance of song for attracting females and stimulating their courtship (Catchpole & Slater 1995), our finding that female birds attend to the quality of song learning indicates an alternative, adaptive hypothesis for the evolutionary maintenance of song learning through its role in sexual selection by female choice. Whether our hypothesis is as broadly explanatory as that of Lachlan & Slater (1999) remains to be tested.

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