



## Canyon wrens alter their songs in response to territorial challenges

Lauryn Benedict\*, Anne Rose, Nathaniel Warning

School of Biological Sciences, University of Northern Colorado, Greeley, CO, U.S.A.

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Many animals use low frequency and harsh sounds in aggressive contexts. Low frequencies are correlated with body size in some species, and thus can provide an indication of fighting ability. Because of this, low frequencies and harsh sounds may also indicate aggressive intent and motivation to attack. We tested for facultative adjustment of vocal behaviour in canyon wrens, *Catherpes mexicanus*, by using playbacks to simulate territorial intrusions. Thirteen territory-holding wrens were exposed to playback of typical conspecific songs which did not include harsh elements. Territory holders increased song rate in response to simulated intrusions, altered song type usage and altered some song sound frequency parameters. Birds singing in response to playbacks did not adjust the highest frequencies or the frequencies with maximum power in their songs, but they significantly lowered the lowest song frequencies and were more likely to append harsh notes to the ends of their songs. Results match predictions of the motivation-structural hypothesis, and suggest that canyon wrens alter their songs in multiple ways when faced with conspecific territorial intrusion.

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Animals in aggressive contests often signal before fights occur. If individuals can accurately inform opponents of superior fighting ability and motivation to attack, then they might win contests while avoiding physical conflict (Maynard Smith & Price 1973). Thus, the properties of aggressive signals should convey information about an individual's likelihood of winning contests. Because birdsong is used to establish territories and repel intruders, it provides an excellent model system within which to examine signal properties indicating individual quality and aggressive intent (Gil & Gahr 2002). Multiple existing hypotheses couple song structure with aggressive function (Searcy & Beecher 2009). By measuring song properties and assessing how birds alter song structure in contest situations, researchers can gain insights about how animals signal aggressive intent.

Evidence suggests that birds signal quality or aggressive intent in multiple ways (reviewed in: Searcy & Beecher 2009; Cardoso 2012). In this study we tested predictions of the motivation-structural hypothesis, which observes that many animals use low-frequency, harsh sounds to signal aggression (Morton 1977). In several animal species, receivers show increased alertness in response to noisy, broadband sounds (Blumstein & Récapet 2009; Blumstein et al. 2012). Harsh sounds may be particularly effective in

aggressive contests because their nonlinear structures are arousing to animal sensory and neural processing systems, making these sounds difficult to ignore (Fitch et al. 2002). Harsh, noisy sounds are also very different in acoustic structure from many appeasing or friendly sounds and, therefore, may be easily recognizable as aggressive signals (Morton 1977). Low-frequency sounds may be particularly effective in aggressive contests because birdsong frequency is associated with body size such that larger species produce lower frequencies (Wallschläger 1980; Ryan & Brenowitz 1985; Bradbury & Vehrencamp 2011). Within some, but not all, species, larger individuals produce lower-frequency sounds, providing the opportunity for conspecific receivers to gain information relevant to the sender's fighting ability (Galeotti et al. 1997; Hardouin et al. 2007; Cardoso et al. 2008; Forstmeier et al. 2009; reviewed in Patel et al. 2010). Low-frequency song can also be correlated with dominance and aggressive behaviour (Galeotti et al. 1997; Price et al. 2006; Geberzahn et al. 2009).

Although a variety of birdsong features may signal individual quality, the majority of studies have found that lower vocalization frequencies are associated with aggression (Cardoso 2012). This trend is most evident among nonpasserines and among passerines whose vocalizations indicate body size (reviewed in Cardoso 2012). Nonpasserine vocalizations are relatively fixed and, consequently, many studies have related interindividual differences in vocalization structure to individual quality (approximated from body condition, dominance and other measures; i.e. Mager et al. 2007; Marks et al. 2010). Facultative adjustment of vocal signals by a single individual is also possible and seems to occur in the black

\* Correspondence: L. Benedict, University of Northern Colorado, School of Biological Sciences, 2480 Ross Hall, Campus Box 92, 501 20th Street, Greeley, CO 80639, U.S.A.

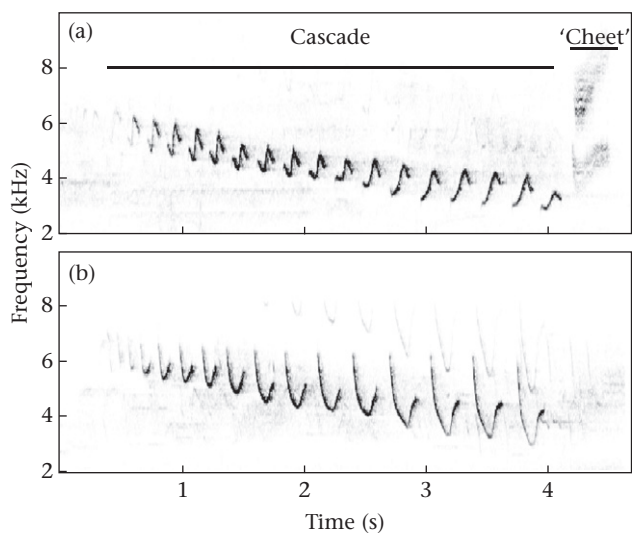
E-mail address: [lauryn.benedict@unco.edu](mailto:lauryn.benedict@unco.edu) (L. Benedict).

coucal, *Centropus grillii*, where females decrease song frequencies in response to playback of conspecific song (Geberzahn et al. 2009). Passerines are most likely to show more facultative adjustment of song features because they learn songs and because vocal repertoires are typically larger than among nonpasserines (Catchpole & Slater 2008). A good example of facultative song adjustment in passerines come from Montezuma oropendolas, *Psarocolius montezuma*, which use lower lowest peak frequencies of song during overlapping song contests (Price et al. 2006). Some species may also adjust their singing behaviour by changing song type usage. Banded wrens, *Pheugopedius pleurostictus*, preferentially use song types that contain harsh rattle or buzz notes during aggressive contests (Trillo & Vehrencamp 2006).

Although aggressive behaviour has been linked with low-frequency song and harsh notes among multiple passerine species, experimental studies of facultative adjustments of song frequency are lacking. We tested aggressive responses of canyon wrens, *Catherpes mexicanus*, to simulated territorial intrusion using conspecific song playbacks. Canyon wrens sing to defend territories using multiple song types that are delivered with eventual variety (Kroodsmma 1977). All song types consist of a cascade of similar descending frequency-modulated notes (Fig. 1). Birds sometimes append one or more harsh ‘cheet’ notes to the end of the typical song. Because of this song structure, we were able to test for facultative alteration of the basic song frequency parameters, as well as differential use of song types and addition of harsh cheet notes in simulated territorial contests.

## METHODS

We conducted playback experiments on 13 canyon wren territories in Larimer County, CO, U.S.A. during 5–14 July 2011. Territories were identified in May and June, and we confirmed that canyon wrens sang consistently in those locations by visiting each site at least twice before conducting playbacks. Birds were not individually marked, but all territories were separated by at least 0.6 km, and we repeatedly observed individuals at each site simultaneously, making us confident that all focal birds were different individuals. We conducted playbacks late in the breeding season to ensure that simulated intruders would be viewed as territorial challengers rather than threats to a male’s paternity.



**Figure 1.** Spectrograms illustrating canyon wren song types: (a) type 3; (b) type 5. Both song types show a descending cascade of frequency-modulated notes. Type 3 song ends with a cheet syllable.

Female canyon wrens do sing, but their song is relatively infrequent and distinctively different from male song (Jones & Dieni 1995; A. Rose & L. Benedict, unpublished data). For this study we focused our analyses on male song only.

All 13 trials were conducted between 0630 and 0915 hours Mountain Standard Time (MST). Each trial lasted 121 min and included 1 h of preplayback recording and observation, 1 min of playback and 1 h of postplayback recording and observation. We began each trial at a site on the focal territory where the resident bird had most often been observed to sing. We spent 1 h observing and continuously recording natural singing behaviour using either a Sennheiser MKH 20 microphone with a Telinga 24-inch parabolic reflector, or a Sennheiser MKH-70 shotgun microphone connected to a Marantz PMD 670 solid-state digital recorder. Recordings were made in mono at a sampling frequency of 48 kHz and a rate of 768 kb per second per channel. We continued to record through the 1 min playback period and for an additional 1 h postplayback period. In addition to capturing song features, observers dictated information about focal subject behaviour into the microphones.

Playbacks were broadcast from a portable speaker (Radio Shack model 277-1008) held by the experimenter while standing in a central location on the subject’s territory. All playback files were used only once and were broadcast at a sound level of 80 dB at 0.3 m (measured using a Radio Shack Sound level meter, model no. 33-2055). Playback files were constructed from 13 recordings obtained from the Macaulay Library of Natural Sounds. Recordings came from Texas ( $N = 5$ ), Arizona ( $N = 4$ ), California ( $N = 2$ ) and Mexico ( $N = 2$ ). Playback files were made by selecting the best-quality sound recordings from those available, making sure not to use multiple files from the same location or files that were obtained using playback to the recorded bird. From each file we chose the song that was loudest and least overlapped by background noise as our playback song. We used some songs with no cheet notes on the end ( $N = 5$ ), and for the remaining songs we removed cheet notes ( $N = 8$ ). Before using this approach, we verified that the birds regularly sang the same song types with and without cheet notes (A Rose & L. Benedict, unpublished data). We removed cheet notes from all stimuli to ensure that any observed increase in the use of cheet notes by focal subjects was not a result of the presence of cheet notes in playbacks. Playbacks were constructed in Syrinx (J. Burt, University of Washington, Seattle, WA, U.S.A., [Syrinxpc.com](http://Syrinxpc.com)). On the noisier files we filtered out background noise and all sound at frequencies below 1 kHz. Sound at 1 kHz is below the lowest song frequencies and this filtering allowed us to remove low-frequency noise. We then created a 1 min playback with silence surrounding five copies of the same song at times 10, 20, 30, 40 and 50 s. This approximates a natural rate and style of canyon wren song (A. Rose & L. Benedict, unpublished data). Playback files included a mix of local and foreign song types and were randomly assigned to focal subjects.

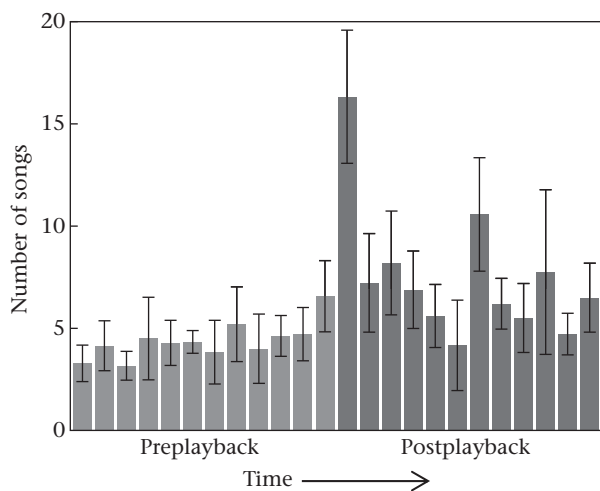
To assess facultative adjustment of song behaviour, we measured time and frequency parameters from 690 songs delivered before and after playback. Recordings were analysed using Raven Pro 1.3 Sound Analysis Software (Cornell Laboratory of Ornithology, NY, U.S.A.). Recordings were visualized as Hanning type spectrograms with a discrete Fourier transform of 512 samples, a frequency resolution of 11.7 Hz, and a time resolution of 5.33 ms. One of us (L.B.) took the following seven measurements from all songs recorded during each trial: song length, song lowest frequency, song highest frequency, frequency range, frequency with maximum power, number of syllables in the cascade and number of cheet notes. All measurements (except the last) were taken on the descending cascade of notes and excluded frequency and time parameters for cheet notes, which were appended variably to different songs. We also assigned all songs to type by eye. Canyon

wrens share a number of song types that are easy to discriminate on spectrograms (A. Rose & L. Benedict, unpublished data). Following the motivation-structural hypothesis, we predicted that song low frequencies would decrease and the number of cheet notes would increase following playbacks. We also predicted that birds would use song types with more low-frequency or harsh elements following playbacks. We made no predictions relative to duration measurements, changes in high frequencies or frequencies with maximum power.

We compared the total number of songs sung by each individual during preplayback and postplayback periods using a repeated measures *t* test. To examine how song parameters changed following playbacks, we first qualitatively determined the time period for which song rate remained elevated following playbacks (see Results, Fig. 2). We then compared song parameters from all songs sung during the preplayback period to song parameters from all songs sung during this portion of the postplayback period. To do so we constructed linear mixed models for each of the seven variables measured from spectrograms using the standard least squares method with preplayback versus postplayback as a fixed factor. We included bird identity and song type as random factors to account for variation in individuals' tendency to respond and in their use of different song types before and after playback. To assess the overall use of different song types pre- versus postplayback, we used a Cochran–Mantel–Haenszel test, which performed a single chi-square analysis on all songs recorded from all individuals while accounting for bird identity. We also broke down the results by song type and used linear mixed models to test for changes to song low frequency and number of cheet notes for each of the five most commonly recorded song types. These models included pre- versus postplayback as a fixed factor and bird identity as a random factor. All statistics were performed in JMP, v.9 (SAS Institute Inc., Cary, NC, U.S.A.). All procedures were conducted in accordance with the University of Northern Colorado Institutional Animal Care & Use Committee (Protocol No. 1105C).

## RESULTS

During the 1 h prior to playback, canyon wrens sang an average  $\pm$  SD of  $27.83 \pm 18.35$  songs. During the 1 h following playback, they sang an average of  $53.15 \pm 35.33$  songs. This represents a significant increase in song rate (repeated measures *t* test:



**Figure 2.** Mean  $\pm$  SE song rate for 13 canyon wrens prior to and following playback of conspecific song. Each bar represents the average number of songs given during a 5 min block. Light grey bars: song rates for 1 h prior to playback; dark grey bars: song rates for 1 h following playback.

$t_{12} = 2.82, P = 0.016$ ). Figure 2 shows the average number of songs delivered during 5 min blocks through the duration of the trial. Song rates were highly elevated during the first 5 min period following playback. For the first 20 min postplayback (blocks 1–4), average song rate remained elevated relative to preplayback rates, although not significantly so during minutes 6–20. Song rates were elevated in other postplayback periods, and birds may have continued to sing aggressively in response to playback for more than 1 h following simulated intrusion, but song rates were relatively low during the 21–30 min following playback, and these songs may not have reflected a strong aggressive response. We therefore chose to include only songs delivered in the first 20 min following playback in our analyses of song type usage, cheet note usage and song time/frequency parameters.

Linear mixed models run on all song types combined for each measured variable indicated that, following simulated conspecific territorial intrusion, canyon wrens did not alter the highest song frequencies or the frequencies in their songs with maximum power (Table 1). They did, however, significantly lower the lowest song frequencies, creating larger song frequency ranges (Table 1). They also shortened the descending cascade portion of their songs and appended more harsh cheet notes in response to playback (Table 1).

Territory-holding wrens sang seven song types during the course of the experiment, with five common types recorded more than 100 times each during the full 2 h period. Canyon wrens altered song type delivery patterns following simulated conspecific intrusion. We found a significant difference in the proportion of songs of each type sung prior to and during the 20 min following playback (Cochran–Mantel–Haenszel test:  $\chi^2_1 = 5.97, P = 0.0146$ ). This change was driven by a decrease in song type 3 and an increase in song type 5 (Table 2). Seven of 11 canyon wrens that used song type 3 during the experiment decreased its use following playback. Five of 10 canyon wrens that used song type 5 increased its use following playback, and when they did so, they increased its use by a larger amount than they did for other song types. We found no strong evidence for song matching in response to playback: only one of eight wrens that could have matched the playback song type did so.

Linear mixed models for each of the five song types sung more than 10 times during the course of the experiment indicated that changes to song types 3 and 5 were the strongest drivers of the overall pattern of lowered low frequency and increased number of cheet notes following playback (Fig. 3). Individuals significantly decreased the low frequencies of song type 3 (LMM:  $F_{1, 97.7} = 6.65, P = 0.011$ ) and song type 5 ( $F_{1, 164.8} = 25.5, P < 0.001$ ). Song types 1 and 4 also showed lowered low song frequencies, but when each song type was analysed alone, these changes were not significant (Fig. 3). Song types 1 (LMM:  $F_{1, 124} = 9.31, P = 0.0028$ ), 3 ( $F_{1, 88.1} = 6.79, P = 0.011$ ) and 5 ( $F_{1, 90.17} = 9.95, P = 0.0022$ ) showed significant increases in the number of cheet notes appended following playback. Song type 2 did not show the predicted changes to song low frequency and number of cheet notes.

## DISCUSSION

Canyon wrens presented with simulated conspecific intrusions altered their singing behaviour in multiple ways. Our subjects sang shorter song cascades in response to playback, but increased the number cheet notes and the number of songs delivered. Reduction in song length is a good indicator of aggressive intent in some species, but is not consistent in male–male contests across all species (Nelson & Poessel 2011). In our study, the decreases in cascade length and cascade syllable number were offset by increases in number of cheet notes, so it is not clear that song length was facultatively modified by our subjects. We did observe

**Table 1**  
Observed song parameters for all song types combined ( $N = 690$ ), and results of linear mixed models testing the effects of conspecific playback on the song features of territory-holding canyon wrens

	Preplayback average	Postplayback average	$\beta \pm SE$	$df$	$F$	$P$
High frequency (Hz)	5893.44	5909.71	$8.13 \pm 18.37$	1,670.7	0.1959	0.66
Low frequency (Hz)	2132.04	1972.90	$-79.57 \pm 15.034$	1,669	28.01	<0.0001*
Frequency range (Hz)	3735.75	3910.62	$87.44 \pm 24.57$	1,664.9	12.66	0.0004*
Frequency with maximum power (Hz)	3814.56	3749.48	$-32.54 \pm 23.42$	1,574.5	1.93	0.17
Cascade duration (s)	2.69	2.57	$-0.058 \pm 0.024$	1,664.3	5.68	0.017*
No. cascade syllables	11.30	10.47	$-0.41 \pm 0.10$	1,637.7	15.91	<0.0001*
No. cheet notes	0.43	0.75	$0.16 \pm 0.031$	1,639.6	26.84	<0.0001*

\* Indicates a significant difference between pre- and postplayback song features.

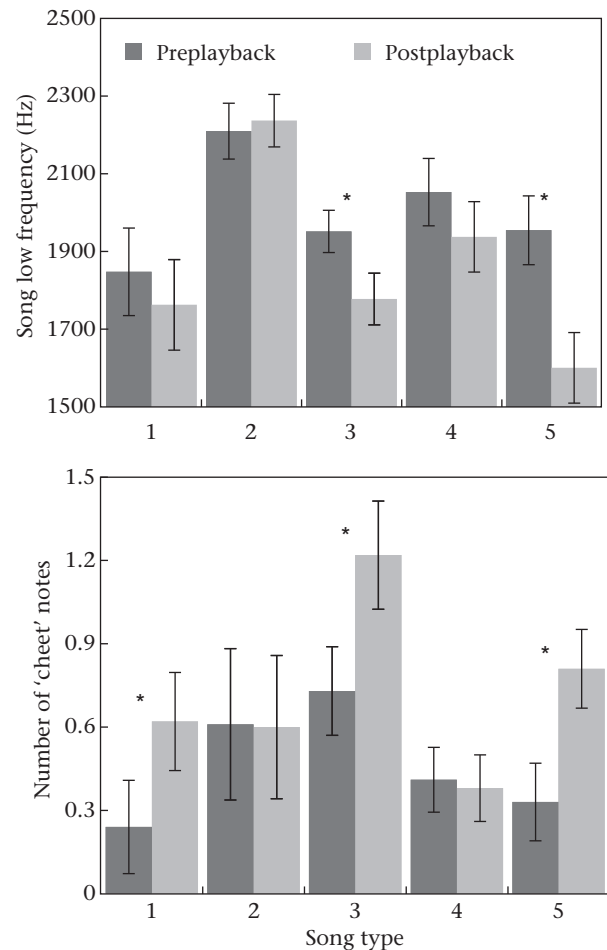
significant increases in song number following playbacks, which is perhaps a more expected aggressive response to conspecific song. Higher song rates require increased energy or time investment, and most likely incur costs that must be offset by benefits related to successful territory defence (Eberhardt 1994).

Canyon wrens in our study adjusted song sound frequency parameters following predictions of the motivation-structural hypothesis (Morton 1977). Our subjects lowered the low frequencies of their songs when challenged. In some avian species, vocalization frequencies are correlated with body size, making low-frequency songs potentially honest indicators of fighting ability. Such correlations have been found in nonpasserines, including scops owls, *Otus scops*, and black swans, *Cygnus atratus*, and in oscine songbirds, including barn swallows, *Hirundo rustica*, and zebra finches, *Taeniopygia guttata* (Galeotti et al. 1997; Hardouin et al. 2007; Forstmeier et al. 2009; Patel et al. 2010). This correlation, however, is not universal and remains to be definitively established for canyon wrens (i.e. Cardoso et al. 2008). Potential for individual variation does exist: published reports show a wide range of body sizes within this species. Jones & Dieni (1995) examined live and museum specimens of adult male canyon wrens (subspecies *consersus*) and found that males varied in mass from 9.9 to 14.8 g (mean  $\pm$  SD =  $11.44 \pm 1.05$  g) and in tarsus length from 11.6 to 22.4 mm (mean  $\pm$  SD =  $18.09 \pm 1.98$  mm).

Birds with repertoires that include multiple song types may adjust song delivery in multiple ways to signal aggressive intent (Searcy & Beecher 2009). Some species adjust song type delivery patterns, but deliver each song type with consistent timing and frequency parameters (Trillo & Vehrencamp 2006). Alternatively, individuals may facultatively alter the timing or frequency parameters of the song types they sing (Price et al. 2006; DuBois et al. 2009). We observed that canyon wrens significantly altered song type delivery patterns and simultaneously lowered the lowest song frequencies of multiple song types. Song type 2 (the common song type sung least often during the preplayback period) was not significantly adjusted following our predictions, but the other four common song types showed the predicted changes to song low frequency, with the strongest changes appearing in song types 3 and 5. Song type 5 increased in usage following playbacks and had an individual average low frequency that dropped by 354 Hz, giving

it the lowest postplayback average low frequency. Three other song types showed decreased low frequencies following playback, but they all dropped by fewer than 175 Hz, less than half as much as song type 5. The frequent use of song type 5 following playback maximized the number of songs delivered that included the lowest recorded frequencies.

Our results also support the prediction of the motivation-structural hypothesis that animals use harsh-sounding notes in aggressive contests (Morton 1977). Following simulated territorial intrusion, male canyon wrens appended significantly more cheet notes to the ends of their songs. This change was driven by significant changes to song types 1, 3 and 5. Results match the pattern first noted by Morton (1977), who enumerated more than



**Figure 3.** Individual mean  $\pm$  SE song low frequency and number of cheet notes pre- and postplayback for each of the five most common canyon wren song types. Asterisks indicate a significant difference between pre- and postplayback song features as determined from linear mixed models.

**Table 2**  
Population-wide song type usage in canyon wrens prior to and following playback

Song type	Preplayback		Postplayback	
	Number of songs	Percentage	Number of songs	Percentage
1	66	20	64	19
2	50	15	53	15
3	70	21	40	12
4	63	19	71	21
5	74	22	108	31
Other	7	2	9	3
Total	330	100	345	100

50 mammal and bird species that use harsh sounds in aggressive contests. Other researchers have noted similar sounds used by avian species and postulated that they may be effective aggressive signals because of their broadband structure (Jarvi et al. 1980; Trillo & Vehrencamp 2006). Broadband, harsh, nonlinear sounds are regularly used as animal alarm calls and are especially effective at grabbing the attention of receivers (Catchpole & Slater 2008; Blumstein & Récapet 2009). By appending cheet notes to their songs in aggressive contests, canyon wrens may better hold the attention of their perceived territorial rival.

Birds use a range of behaviours when responding aggressively to conspecific rivals (Searcy & Beecher 2009). Many studies have found that song frequencies relate to individual quality or aggressive intent, but few have documented the flexible facultative adjustments in song output that we observed during simulated aggressive contests in canyon wrens (Cardoso 2012). Canyon wrens respond to simulated rivals by altering song type output, by altering the frequency parameters of individual song types and by appending broadband notes to the ends of their songs. Furthermore, they adjusted different song types in different ways. These adjustments, taken together, provide support for multiple hypotheses regarding aggressive signalling (Morton 1977; Ryan & Brenowitz 1985; Fitch et al. 2002). Future work correlating song features with body size, fighting ability and attack rates will better help us to understand the function and operation of the facultative song alterations that we observed (Searcy & Beecher 2009).

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