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# HERPETOLOGICA

## CALL TRAIT VARIATION IN MORELETT'S TREE FROG, *AGALYCHNIS MORELETII*, OF BELIZE

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ABSTRACT: Calling behavior and the properties of a male's call directly affect mate choice and mating success in frogs. In this study, I investigated the difference in call properties within and among males of *Agalychnis moreletii* at a breeding population in Belize. As a first step toward understanding female preference for specific male advertisement calls, I examined the variation of call traits from 575 calls of 30 individuals. I described and quantified call properties both within and among males and examined the relationship between mating success and body size. All of the call traits that I examined exhibited significantly higher among-male variation than within-male variation. Static call properties such as dominant frequency and call amplitude had the lowest variation within and among males. Dominant frequency was negatively correlated with body size, supporting a body-size constraint for this call trait. Call properties such as call rates, mean pulses per call, and call durations displayed greater variability among males. Such variability in these dynamic call traits suggests energy constraints because calling longer and calling more frequently are energetically costly. As a result, dynamic properties may be indicators of male quality and play a greater role in mate choice. Indeed, males found in amplexus produced a greater number of calls and those calls were of longer durations and tended to have a shorter intercall interval. Here, I characterize call trait variation and document call properties as indicators of mating success in the process of sexual selection in anuran communication.

*Key words:* Acoustic communication; Advertisement calls; Anurans; Leaf frogs; Vocalizations

SEXUAL selection directly affects courtship and communication used in mate recognition and requires that signal transfer from sender to receiver be effective to enable successful mating. In anurans, acoustic signaling is an important mode of communication and males of many species produce advertisement calls that serve both to attract females and to repel competing males (Halliday and Tejedo, 1995; Ryan, 1980). In mating systems that are driven more by female choice than by male–male competition, male mating fitness has the potential to be affected by female preference

for acoustic characteristics and may influence male calling behavior (Andersson, 1994).

Females that discriminate between different calls may prefer energy-consuming call traits that transmit mate-quality information (Klump and Gerhardt, 1987), because calls require a high energetic investment (Wells and Taigen, 1986) and may be the single most expensive activity in which male frogs engage (Grafe, 1996; Pough et al., 1992). The intensity and structure of a call depends on a male's body condition, and the information encoded therein may be a signal of genetic quality to females. In frogs, a larger body size is negatively correlated with the dominant frequency and fundamental frequency of calls, which are better predictors of male size than other call properties (Bee, 2002; Ryan, 2001) because the shape and mass of the laryngeal

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apparatus determines the call frequency and scales with overall body size (Martin, 1972). Female mating preferences have been shown to be influenced by call properties such as call rate, duration, pulse rate, and dominant frequency (Gerhardt et al., 2000; Ryan, 1980; Ryan and Keddy-Hector, 1992). If a female preference exists for calls of lower dominant frequency, as a function of body size, then mated males are expected to be larger than unmated males. Indeed, among several anuran species, there is evidence for a large-male mating advantage resulting from female choice (reviewed in Sullivan et al., 1995).

Call characteristics can show substantial variation within a single population (Sullivan and Wagner, 1988) but also within a single individual (Gerhardt, 1991). As a result, traits can be classified as static (low within-male variation) or dynamic (high within-male variation) call properties, and the variability found in dynamic properties may account for their importance in mate choice (Gerhardt, 1991, 1994). Static call traits include dominant frequency, and this is not expected to change greatly because it is a function of body size (Gerhardt, 1991). Dynamic call properties include call rate and call duration and are typically the products of both abiotic and biotic factors (Gerhardt, 1991; Ryan and Keddy-Hector, 1992). In more recent studies, analyses have incorporated both the variability of several male traits, i.e., morphometrics, alongside acoustic traits to determine their roles in the mate selection process (reviewed in Sullivan and Kwiatkowski, 2007).

*Agalychnis moreletii* is a good study model to compare call-trait variation both within and among males because they exhibit stereotyped calling behavior used in intra- and inter-sexual interactions. Males descend from the forest canopy and congregate in choruses shortly after sunset and call from vegetation surrounding bodies of water (Lee, 1996). Advertisement "zworp" calls function to attract females and aggressive "chuckling" calls are used during intrasexual encounters (Duellman, 1970; Lee, 1996). To date, call trait descriptions have been made (Ryan, 2001; Savage, 2002), but there has been no quantitative assessment of call properties in relation to male mating success.

In this project, I documented the reproductive activity of natural aggregations of *A. moreletii* and recorded the calls of individual males found at these aggregations in order to achieve the following goals: to examine the potential for within- and among-male variation in call properties, to determine whether individual males differed in their calling behavior, to compare call traits between males, to investigate the presence of size-related call traits, and finally to determine whether call properties influence mating success in *A. moreletii*. In particular, I test the hypotheses that there is greater variability in calls among males than within the calls produced by a single male (Gerhardt, 1991; Tárano, 2001) and that the calls of an individual male can be differentiated from those of a competing male based on call traits (Bee et al., 2001; Tárano 2001). Previous work has documented seasonal fluctuations of a size-related mating advantage in *A. moreletii*, in which larger males were found to be disproportionately mated (Briggs, 2008). Hence, I also investigate whether body-size information is encoded in advertisement calls and test the hypotheses that larger males are preferred by females, ultimately experience enhanced mating success, and are found in amplexus more often than smaller-sized males (Ryan, 1985; Sullivan et al., 1995). Finally, I test the hypothesis that acoustic traits that reflect larger body size or greater energetic capability affect female preference, and as a consequence influence male mating success (Gerhardt et al., 2000; Ryan, 1980; Ryan and Keddy-Hector, 1992).

## MATERIALS AND METHODS

Research was conducted at the Las Cuevas Research Station (16° 43′ N, 88° 59′ W), Cayo District, Belize. I collected amplectant pairs and calling nonamplectant males of *A. moreletii* at breeding aggregations between 2200 and 0300 h on 26 nights between 8 June and 25 August 2005. Males began calling at dusk and females arrived at the pond between 2100 and 2200 h. Nonamplectant males were collected after amplectant pairs had been located, and thus amplectant males are expected to have advertisement call traits that are more attractive to females relative to
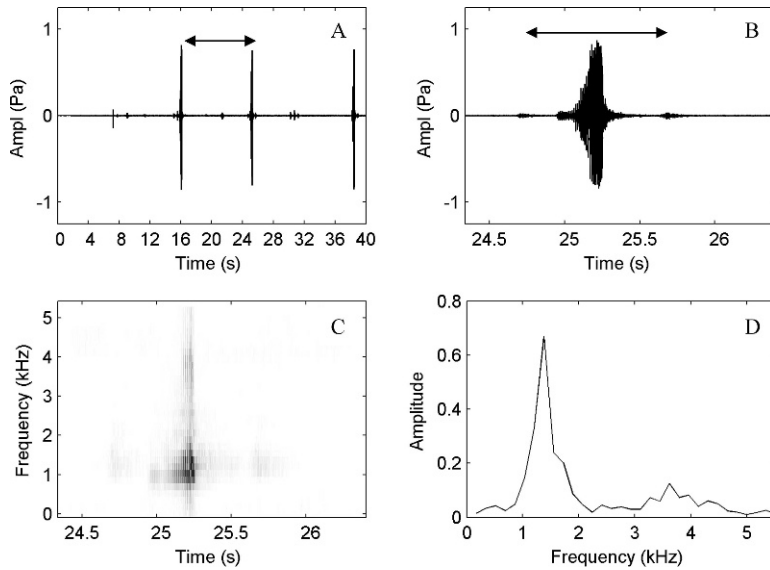
FIG. 1.—Advertisement call of *Agalychnis moreletii* as (A) an oscillogram of a sequence of calls separated by intercall intervals (denoted), (B) an expanded view of a single call illustrating the pulsed structure per call and the duration of the call (denoted), (C) spectrogram and (D) a power spectrum that shows the energy distribution across the call.

males not found in amplexus (Briggs, 2008; Lee, 2001).

### Recording and Acoustic Analysis

Calls were recorded during active chorusing with a SONY TC-D5M tape-recorder equipped with a Sennheiser K3 directional microphone. Advertisement calls, "zworps" were produced as single calls dispersed over time and not as clusters within a call bout. I recorded the calls of 30 males (24 amplectant males and six nonamplectant males) in an open-air laboratory. Amplectant males were separated from their mate and calls were recorded before being returned to the original female. Males called from perch sites near the top of a mesh-covered 5-gal. bucket and were recorded for a 10-min period. The microphone was placed immediately above the target male at the top of each housing chamber at 30 cm and at a 45° angle from the horizontal. The recording level was adjusted and kept constant and I used a calibrated RadioShack digital sound pressure level meter to measure call amplitude (dB, flat weighting, flat response) that was kept at the same distance from the microphone, and thus I assumed that the relative amplitudes of fundamental and dominant frequencies were

not affected by frequency-dependent attenuation with distance (Gerhardt, 1976). The amplitude of each call, or calling intensity, measured as "loudness" was recorded and minimum (MinAmp) and maximum (MaxAmp) amplitude per male ($N = 18$) were documented. Temperature fluctuated between 22.5 and 23 °C for the open-air laboratory during the study. On the morning following capture, I measured each individual for snout–vent length (SVL) with the use of dial calipers read to the nearest 0.5 mm, and mass using an Ohaus Scout Pro fine scale balance read to 0.001 g. I uniquely toe-clipped each individual and released individuals at site of capture.

Sound files were digitized with the use of Audacity version 1.2.6 (Mazzonni, 2006) and analyzed with SoundRuler version 0.9.6.0 (Gridi-Papp, 2007). A call is defined as a complete sequence of pulses separated from the next call by an intercall interval (Fig. 1A). Call attributes that were measured included total number of calls produced within the recording session, from which call rate was calculated, total number of pulses produced within the recording session, mean number of pulses per call, mean call duration (length of time from the beginning to the end of a single

TABLE 1.—Variation of call traits of male advertisement calls of *Agalychnis moreletii*. Mean, standard deviation (SD), range and between-male and within-male variability (CV = coefficient of variation) of call traits. *N* = total number of recorded males followed by total number of calls analyzed, duration = mean length of call, DF = call dominant frequency and call intensity as MinAmp = minimum call amplitude per call, and MaxAmp = maximum call amplitude per call.

| Call trait | Grand mean ± SD (N = 30 [575]) | Range | Mean within-male CV$_w$% | Range of within-male CV% | Mean between-male CV$_b$% | Ratio CV$_b$/CV$_w$ |
|---|---|---|---|---|---|---|
| Total calls | 19.2 ± 14.4 | 4–68 | – | – | 75.0 | – |
| Call rate (no./s) | 0.03 ± 0.02 | 0.004–0.1 | – | – | 66.7 | – |
| Duration (ms) | 39.3 ± 18.8 | 21.5–87.8 | 29.6 | 12.0–122.2 | 47.8 | 1.6 |
| MinAmp (dB) | 54.2 ± 3.4* | 50–62 | 3.2 | 0.9–7.6 | 6.3 | 2.0 |
| MaxAmp (dB) | 60.6 ± 5.0* | 53–68 | 3.5 | 1.5–5.9 | 8.2 | 2.3 |
| Intercall interval (s) | 44.6 ± 25.0 | 9.3–118.4 | 32.1 | 7.3–105.1 | 56.1 | 1.7 |
| Total pulses | 78.3 ± 97.7 | 4–436 | 33.1 | 15.9–62.6 | 124.8 | 3.8 |
| Pulses/call | 4.1 ± 4.9 | 1.0–26.0 | 39.7 | 16.5–71.1 | 119.5 | 3.0 |
| DF (Hz) | 1233 ± 98 | 1046–1396 | 8.3 | 2.7–14.7 | 7.9 | 1.0 |

* *N* = 18.

call; Fig. 1B), and mean intercall interval (time between calls as a function of both individual call duration and total calls, Fig. 1A). I also measured mean dominant frequency (the frequency that carries the most energy; Fig. 1C,D), minimum and maximum dominant frequency, and minimum and maximum amplitude (Fig. 1D) of each male's call.

## Statistical Analysis of Acoustic Traits

Variations in call traits within and among males were expressed as coefficients of variations (CVs) based on mean values for each male (CVs = [SD/mean] × 100%; Gerhardt, 1991). For each call trait, I calculated the grand mean and standard deviation based on the mean for each male (Table 1). Within-male coefficients of variation (CV$_w$) were calculated from the calls produced in a recording session for each individual male. The between-male coefficients of variation (CV$_b$) were based on the grand mean and standard deviation. I calculated the ratio of between-male to within-male coefficients of variation (CV$_b$/CV$_w$) to determine the variability of call traits. If CV$_b$/CV$_w$ > 1.0 for a call trait then there is more variability among males and this may have behavioral consequences for individual recognition (Bee et al., 2001).

I conducted Pearson's product-moment correlation analyses to determine the relationship among call traits. To reduce the number of variables describing advertisement calls, a subset of the most salient call traits that did not carry redundant call trait data were then used in a logistic regression with mating status as the dependent variable and call traits and male body size traits as independent variables. Subsequently, I conducted pair-wise comparisons between amplectant and nonamplectant males for call traits using two-tailed two-sample *t*-tests with equal variances not assumed to locate origins of differences that may not have emerged in the overall logistic regression model and also did this for size-related call traits among males of different body size. Statistical comparisons were done with SPSS version 17.0.

## RESULTS

The visual representation of the advertisement call of *A. moreletii* (Fig. 1) illustrates the structure of the call and the energy and frequency distribution within a call. Descriptive statistics and variability for all call traits are listed in Table 1 illustrating differences in call traits amongst males. Following Gerhardt (1991), call traits with CVs above 12% were classified as dynamic properties and those below were classified as static properties. Calling sound intensity measured as minimum and maximum amplitudes and dominant frequency had the lowest coefficients of variation, and are thus classified as static properties. They were the least likely to vary both within a male and among males (Table 1). The other traits, including call rate, call duration, total calls, and intercall interval varied within a male by 30–40%, but had greater variability among males (48–75%) and

as such were classified as dynamic properties (Table 1). There was a wide range of total calls produced by males because some males produced several calls within the recording session, whereas other males called intermittently, and as such, intercall interval was also highly variable (Table 1). The most variable of call traits involved the number of pulses produced per call, where some males produced a single pulse per call and another produced up to 26 pulses within a call (Table 1). The calculated ratio of all call traits varied in excess of 1.0, demonstrating that call trait variability was more pronounced among males than within males and indicating that individual males produce differences in call traits (Table 1).

I obtained recordings from 30 males, including 24 amplectant males and six non-amplectant males. SVL ranged from 54.9 to 63.7 mm, and mass ranged from 6.8 to 9.4 g. Mass and SVL were positively correlated, and several call traits were significantly correlated with each other (Table 2). Call rate was correlated with intercall interval and call duration, as well as total pulses produced and maximum call amplitude (Table 2). None of the measured call traits was correlated with body size measured as SVL, but dominant frequency and mean number of pulses per call were negatively correlated with male body mass (Table 2). As body mass increased, males produced calls with a lower dominant frequency ($r = -0.55$, $n = 30$, $P = 0.002$). Mating status was negatively correlated with minimum amplitude, but positively correlated with mean number of pulses per call. There were only two nonamplectant males for which calling sound intensity was measured, and thus they are not included in this comparison. There was no significant difference in body size between amplectant males (SVL: $58.68 \pm 0.44$, mass: $7.97 \pm 0.13$, $n = 24$) and nonamplectant males (SVL: $59.03 \pm 0.86$, mass: $8.52 \pm 0.64$, $n = 6$; $t$-test $t_{SVL} = 1.34$, df = 28, $P = 0.19$; $t_{mass} = 0.35$, df = 28, $P = 0.73$), but this may be due to a small sample size.

Results of a logistic regression model did not reveal overall detectable effects of the series of call traits or male body size on male mating status. The mean number of pulses per call ($z = 1.87$, $P = 0.06$) was the only trait that tended to

TABLE 2.—Pearson's product moment correlation ($r$) of mean values among call traits, and in relation to mating status and body size traits of males of *Agalychnis moreletii*.

| Call trait | Total calls | Call rate | Duration | MinAmp | MaxAmp | Intercall interval | Total pulses | Pulses per call | DF | Mating status | SVL | Mass |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total calls | — | | | | | | | | | | | |
| Call rate | 0.916** | — | | | | | | | | | | |
| Duration | 0.601** | 0.631** | — | | | | | | | | | |
| MinAmp | 0.081 | 0.187 | 0.285 | — | | | | | | | | |
| MaxAmp | 0.491 | 0.582* | 0.637 | 0.717** | — | | | | | | | |
| Intercall interval | -0.738** | -0.708** | -0.518** | -0.384 | -0.704** | — | | | | | | |
| Total pulses | 0.894** | 0.876** | 0.790** | 0.176 | 0.544* | -0.636** | — | | | | | |
| Pulses/call | 0.587** | 0.601** | 0.880** | 0.300 | 0.642** | -0.556** | 0.819** | — | | | | |
| DF | 0.286 | 0.386 | 0.546** | 0.098 | 0.318 | -0.416* | 0.356 | 0.446* | — | | | |
| Mating status | 0.283 | 0.229 | 0.310 | -0.568* | -0.248 | -0.300 | 0.281 | 0.375* | 0.304 | — | | |
| SVL | 0.176 | 0.073 | -0.084 | -0.052 | -0.128 | 0.048 | 0.036 | -0.208 | -0.338 | -0.067 | — | |
| Mass | -0.168 | -0.181 | -0.318 | -0.154 | -0.354 | 0.211 | -0.211 | -0.373* | -0.551** | -0.245 | 0.644** | — |

* $P < 0.05$.
** $P < 0.01$.

TABLE 3.—Results of two-tailed two-sample *t*-tests of call traits between amplectant and nonamplectant males of *Agalychnis moreletii*. Values represent mean ±1 SD for each measure.

| Call trait | Amplectant (24) | Nonamplectant (6) | t | P |
|---|---|---|---|---|
| Total calls | 21.17 ± 15.20 | 11.17 ± 6.49 | −2.451 | 0.024* |
| Call rate (no./s) | 0.03 ± 0.02 | 0.02 ± 0.01 | −1.242 | 0.112 |
| Duration (ms) | 41.95 ± 19.75 | 28.52 ± 9.41 | −1.723 | 0.048* |
| Intercall interval (s) | 40.89 ± 22.09 | 59.31 ± 32.27 | 1.666 | 0.053 |
| Total pulses | 91.75 ± 104.74 | 24.33 ± 22.21 | −1.548 | 0.066 |
| Pulses/call | 4.70 ± 5.30 | 1.90 ± 0.90 | −2.138 | 0.021* |
| Mean DF (Hz) | 1248 ± 93 | 1174 ± 104 | −1.690 | 0.051 |

* $P < 0.05$

have an influence on mating status, but all other variables did not show statistically detectable effects (all $P > 0.05$). However, pairwise comparisons of call traits between amplectant and nonamplectant males show that amplectant males produced a greater number of calls per recording session and these were of longer call durations relative to nonamplectant males (Table 3). There was also a trend for amplectant males to call with shorter intercall intervals with more pulses encoded per call (Table 3). Nonamplectant males tended to produce calls that were of a slightly lower dominant frequency (Table 3).

## DISCUSSION

All of the advertisement call traits examined in this study for *A. moreletii* demonstrated greater variability among males than within males, supporting the hypothesis that individual males differ in their calling behavior and can be individually distinguished. These findings are consistent with the results of other species (Bee et al., 2001; Gerhardt et al., 1996; Pröhl, 2003). Differences in calling behavior have potential consequences for mating success and here I demonstrate that males found in amplexus produced a greater number of calls with longer call duration with less time in between calls relative to nonamplectant males, which supports the hypothesis that acoustic traits influence mating success (Ryan, 1980). This difference in call properties may have been attractive to females and resulted in males possessing these increased trait levels gaining increased mating opportunities (reviewed by Halliday and Tejedo, 1995; Sullivan and Kwiatkowski, 2007). In addition, the results of this study support the hypothesis that heavier males of

*A. moreletii* produced calls with lower dominant frequencies, corroborating the often-seen inverse relationship between dominant frequency and male body size where it may benefit females to mate with males of a particular size class (reviewed by Gerhardt and Huber, 2002; Sullivan and Kwiatkowski, 2007).

Gerhardt's (1991, 1994) static call properties were the least variable traits among males and tend to be under stabilizing selection, with strong morphological and/or physiological constraints (Castellano and Giacoma, 1998). Results of this study show that dominant frequency and calling sound intensity had the lowest coefficients of variation and are static call properties reflecting body size constraints. Dominant and fundamental frequencies depend on the resonance frequency of the vocal cords, and thus on length, mass, and tension of the cords (Gerhardt and Huber, 2002). Larger males tend to have more massive laryngeal structures and call at lower frequencies relative to smaller males. Clearly in this species, dominant frequency is constrained by a male's body size (reviewed by Ryan, 2001) and would indicate an honest signal to females for body size and support previous findings for a large-male mating advantage in *A. moreletii* (Briggs, 2008). In this study, nonamplectant males produced calls that were somewhat lower in dominant frequency relative to amplectant males, which does not provide support for the hypothesis that amplectant males produce calls with a lower dominant frequency (Murphy, 1999; Robertson, 1990; Ryan, 1983), but a larger sample size of nonamplectant males may not show this trend. Call traits such as call duration and call rate are indicators of

energetic expenditure and may vary significantly more so than call traits that are constrained by body size (Gerhardt, 1991; Sullivan and Kwiatkowski, 2007; Tárano and Herrera, 2003). Thus, though dominant frequency approached a statistical difference between males in this study, there was no statistical difference amongst amplectant and nonamplectant males for body size, in either SVL or mass. This lack of difference according to mating status may be attributed to the very small sample size of nonamplectant males collected in this study and the need for a larger sample size to represent the population where body size is concerned. Nonetheless, I present data illustrating that the costly call traits of amplectant males exceed those produced by nonamplectant males and may have been sufficiently different in call character to attract a female and procure amplexus, thereby increasing mating success. An increased sample size of nonamplectant males may not change these results.

Dynamic properties are typically under directional selection and are mostly under energetic constraints (Gerhardt et al., 1996). As a result, dynamic properties may serve as an honest indicator of male condition and explain more variation in mating success from one male to another (Gerhardt, 1991; Pröhl, 2003; Tárano, 2001). Here, call rate and call duration were among the more highly variable temporal call traits (Gerhardt, 1991, 1994), and thus may be influenced by physical conditions and transmit mate-quality information (reviewed Bee et al., 2001; Castellano et al., 2002; Howard and Young, 1998). Additionally, several of the call traits measured in this study were correlated. Call rate was negatively correlated with intercall interval, and one would predict that greater intercall intervals would affect the number of calls being produced. On the contrary, one would not expect a strong positive association between call rate and call duration; however, males that are capable of calling at a faster rate may also have an advantage to producing calls of longer durations in order to attract females.

In several anuran species, females prefer faster calls (Lopez and Narins, 1991; Tárano and Herrera, 2003), more complex calls (Ryan, 1980), calls of longer duration (Gerhardt et al., 2000; Tárano and Herrera, 2003), calls of lower dominant frequency (Howard and Young, 1998; Ryan, 1983), or a combination of call parameters (e.g., Murphy and Gerhardt, 2000; Sullivan, 1992; Sullivan and Hinshaw, 1992; Welch et al., 1998; Witte et al., 2001). Calling rate, including the number of days present and calling at a breeding pond, has been shown to be the most important determinant of male mating success in several species of frogs (e.g., Ryan, 1983; Sullivan and Hinshaw, 1992). Males that were found in amplexus in this study produced a greater number of calls and called for a longer duration when compared to nonamplectant males. Reduced intercall intervals may translate into a faster call rate and longer call durations because there is less time between calls and the opportunity for more calls to be produced. In natural choruses, these traits may provide females with information regarding motivation, availability, and energy levels, i.e., male quality (Dyson et al., 1998).

This is the first study to characterize the variation in call properties of this species of red-eyed tree frog and it is one of a handful of studies to document call properties as potential determinants of mating success. Herein I present evidence for individual call discrimination amongst males and illustrate body-size correlates as well as call traits that may indicate male quality via mating success. This study highlights the need to sample several individuals from breeding aggregates to reflect the variation within a population accurately before incorporating other populations. I demonstrate that multiple call traits ought to be considered when accounting for mate preferences, as some may be better indicator traits, whereas others may carry redundant acoustic information. It is necessary to investigate individual variation in call production and female preference for that range of variation in order to understand fully the nature of acoustic properties and their role in social interactions, including mating behavior.

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