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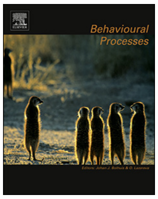

# Mockingbirds imitate frogs and toads across North America

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A R T I C L E I N F O

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A B S T R A C T

Vocal mimicry is taxonomically widespread among birds, but little is known about mimicry of non-avian models. Prior studies show preferential imitation of avian models whose sounds are acoustically similar to the non-imitative songs of the vocal mimic. Based on these studies and anecdotes about frog imitations by northern mockingbirds (*Mimus polyglottos*), we hypothesized which anuran models would be most likely to get imitated by mockingbirds across their geographic range. We tested our hypothesis using > 40 h of archived mockingbird recordings. Our results showed that mockingbirds imitated at least 12 anuran species, and calls were disproportionately mimicked when they contained dominant frequencies within the vocal range of the mockingbird (750–7000 Hz). Mockingbirds also frequently modified model anuran sounds by leaving out formants and/or truncating call duration. Our results represent the most comprehensive survey for any mimicking species of the imitation of anurans.

## 1. Introduction

Avian vocal mimicry has long captured the attention of naturalists and researchers (Pliny the Elder X. Circ. AD 77, 2019; Marshall, 1950), yet we remain mostly ignorant about the patterns and processes associated with mimicry (Baylis, 1982; Kelley et al., 2008; Dalziell et al., 2015). Approximately 11–15% of species within the oscine passerine lineage imitate the sounds of heterospecifics, and vocal mimicry has evolved independently at least 237 times within this lineage (Goller and Shizuka, 2018).

When songbirds imitate, the vast majority of model species are other songbirds (Dowsett-Lemaire, 1979; Chu, 2001; Gammon, 2013; Dalziell and Welbergen, 2016; Riegert and Jůzlová, 2018), but occasionally birds will mimic non-avian taxa. For example, fork-tailed drongos (*Dicrurus adsimilis*) in South Africa occasionally imitate the alarm calls of mammals such as the meerkat (*Suricata suricatta*, Flower, 2011), European tits (Paridae) produce a hissing call similar to the sounds of a snake (Sibley, 1955; Zub et al., 2017), and superb lyrebirds can even imitate camera shutters and chainsaws (Tapper, 2006). Nevertheless, studies that focus on mimicry of non-avian taxa such as frogs and insects remain exceedingly rare.

Mimicry of non-avian taxa is interesting for a variety of reasons. From the perspective of natural history, it would be interesting to create libraries of which model species do and do not get mimicked. From a functional perspective it would be interesting to know the ecological relationships between mimics and their non-avian models (e.g., Flower, 2011; Flower et al., 2014). On a proximate level it would be interesting to understand why non-avian taxa get accepted as suitable models, and to know the physiological limits of what vocal mimics can imitate. Although mimics use similar physiological mechanisms of sound production as their bird models (Zollinger and Suthers, 2004), a mimicking bird clearly cannot inflate a throat sac like a frog (Ryan and Guerra, 2014) or stridulate like an insect (Bennet-Clark, 1975).

In this paper we focus on the rules for model selection used by a prominent North American mimic when it imitates anurans. Our focal species is the northern mockingbird, which is famous for its ability to “mock” the sounds of dozens of species across North America (Farnsworth et al., 2011). Long mockingbird song sequences feature immediate variety and contain hundreds or even thousands of songs (Derrickson, 1987). Approximately half of the songs are mimetic (Gammon, 2014). Both mimetic and non-mimetic songs are repetitive (Wildenthal, 1965; Gammon, 2013), and mockingbirds cannot sing pitches lower than 750 Hz or higher than 7000 Hz (Zollinger and Suthers, 2004).

Gammon (2013) tested several hypotheses for model selection by mockingbirds, and only the ‘acoustic similarity’ hypothesis was supported. According to this hypothesis, vocal mimics preferentially imitate models whose sounds are already acoustically similar to the mimic’s non-mimetic songs. Theoretically, mockingbirds could imitate any heterospecific sound by excluding or transposing notes with pitches outside of their vocal range (see examples from lab-raised mockingbirds in Zollinger and Suthers, 2004). Nevertheless, mockingbirds were more

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likely to copy heterospecific sounds that were already acoustically similar to mockingbird-specific songs (Gammon, 2013).

Several years ago, one of us (DEG) was surprised to observe mockingbirds occasionally imitating the Cope's gray treefrog (*Hyla chrysoscelis*, *unpublished data*), which led him to consider whether his study on model selection (Gammon, 2013) might apply to the dozens of anuran species living across North America. For our study we hypothesized that anurans would get disproportionately imitated by mockingbirds when their calls were repetitive and used acoustic frequencies between 750 and 7000 Hz (Zollinger and Suthers, 2004; Gammon, 2013). We tested this hypothesis using a continental survey of mockingbird song collected from personal and archived recordings. Our results represent the most comprehensive list ever made for non-avian models that get imitated by a bird species.

## 2. Materials and methods

Our first task was to sample mockingbird song from across their geographic range. Going into this project we knew most mimetic types are produced rarely (Gammon and Altizer, 2011; Gammon, 2013, 2014). For example, Gammon (2013) sampled 2200 mimetic events from 22 individuals, but only 8 of these 2200 events were imitations of the Cope's gray treefrog (0.36%, *unpublished data*). Because each minute of mockingbird song normally contains 10 or fewer mimetic events (*unpublished data*), we sampled as much mockingbird song as we could get from as many locations as possible. DEG had already recorded large samples of mockingbird song from North Carolina and Texas, but we also sampled mockingbird song through our personal connections and from sound archives such as Xeno-canto.org and Macaulay Library (Table 1).

Before collecting data from our recordings of mockingbird song, we assumed that northern mockingbirds would imitate only model species that are locally present; this assumption has been met in past studies with mockingbirds (Baylis, 1982; Gammon, 2013). We also needed lists of all possible anuran models for each county from which we had a mockingbird recording so we could know which species to listen for in each bird's song. To form these lists, we used the biogeographic maps for each species on the IUCN red list website (IUCN, 2019). We knew the IUCN list probably had errors, given that geographic ranges are shifting due to land use changes, climate change, etc. (Parmesan and Yohe, 2003; Jetz et al., 2007). We therefore contacted local herpetologists at museums to adjust our lists. These communications led to the following adjustments: we added the recent invasive Cuban tree frog (*Osteopilus septentrionalis*) to a county in South Florida, we removed the locally-extirpated Sierra Nevada yellow-legged frog (*Rana sierrae*) from a county in California, and we excluded two frogs that do not produce calls on land, the African clawed frog (*Xenopus laevis*) and the coastal tailed frog (*Ascaphus truei*).

**Table 1**
Summary of the sampling of mockingbird song.

| State | # counties | # birds recorded | Amt of song (min) | Sources* | # of anuran mimetic events |
|---|---|---|---|---|---|
| North Carolina | 8 | 31 | 500.9 | ML,XC,DEG | 4 |
| Florida | 15 | 54 | 416.2 | ML,XC,P | 5 |
| Louisiana | 5 | 58 | 370.0 | ML,XC,P | 3 |
| California | 16 | 42 | 261.4 | ML,XC,P | 3 |
| New York | 4 | 27 | 244.6 | ML,XC,P | 0 |
| Texas | 11 | 40 | 180.0 | ML,XC,DEG | 0 |
| Arizona | 3 | 34 | 136.5 | ML,XC | 3 |
| Pennsylvania | 4 | 13 | 129.3 | ML,P | 3 |
| Maryland | 2 | 10 | 36.1 | ML,P | 0 |
| New Mexico | 3 | 10 | 31.6 | ML,XC | 0 |
| Connecticut | 2 | 5 | 28.2 | ML,XC | 0 |
| Colorado | 6 | 12 | 21.3 | ML,XC | 2 |
| Massachusetts | 1 | 2 | 16.9 | P | 0 |
| Georgia | 6 | 6 | 14.7 | ML,XC | 0 |
| South Carolina | 2 | 4 | 11.5 | ML,XC | 0 |
| Baja California | 7** | 10 | 11.2 | ML,XC | 1 |
| New Jersey | 3 | 3 | 7.3 | ML,XC | 0 |
| Virginia | 3 | 3 | 3.7 | XC | 0 |
| Utah | 1 | 2 | 1.7 | P | 0 |
| Oregon | 2 | 2 | 1.6 | eB | 0 |
| Washington, DC | 1 | 1 | 1.3 | ML | 0 |
| Delaware | 1 | 1 | 0.6 | XC | 0 |
| **Total:** | 106 | 370 | 2426.2 | | 24 |

* ML = Macaulay Library, XC = xeno-canto.org, eB = eBird.org, DEG = Gammon, P = personal network.

** Baja California, a state in Mexico, is not divided into counties, but we sampled seven distinct locations.

Our final set of county lists contained a total of 71 anuran species. To familiarize ourselves with the calls of these species, we assembled an acoustic library using Macaulay Library, various herpetological websites, and online videos. After assembling an acoustic library, we needed to make predictions for which of the anuran species could potentially be imitated by mockingbirds. We based these predictions primarily on the acoustic frequencies observed in the calls of each species.

From our library we chose for each anuran species one call that stood out as an accurate representative of the species and that possessed a high amplitude signal with minimal background noise (Supplementary Table). About half of these representative calls came from the Macaulay Library (N = 34 species), and the others came from various natural history websites and online videos (N = 37 species, Supplementary Table). Given that all recordings were made by citizen scientists who vary in their herpetological training, technical expertise, equipment, etc., it is possible one or more of our audio files contained inaccurate acoustic frequencies, but we suspect this problem was minimal, given that we referenced multiple sources before choosing a representative call. Any call with an acoustic frequency or call pattern significantly different than the species' average would have therefore been excluded. Spectrograms, power spectrums, and acoustic measurements of all frog calls were prepared using Audacity software (Audacity Team, 2014). We filtered each call using Audacity's 'noise reduction' feature, and we amplified calls to maximize peak amplitude.

We followed the recommendations of Zollinger et al. (2012) when measuring acoustic frequency. Anuran calls normally consist of repeated pulses, each of which contains a "stack" of formants. These formants occupy different frequencies and possess different amounts of energy (Fig. 1). For each call we used cursors in the Audacity software to highlight several pulses from a representative portion of the call, from which we produced a power spectrum (Fig. 1). On each power spectrum, we identified the formant with the highest amplitude and measured the minimum and maximum frequency values for that formant at a level 22 dB below peak amplitude (Fig. 1). Our predictions were based on the resulting frequency bandwidth and other species-related considerations, as explained below.

We predicted that the anuran calls most likely to be imitated would be those with frequency bandwidths entirely within 750–7000 Hz (Zollinger and Suthers, 2004), whereas calls with bandwidths that strayed outside either these limits would be less likely to get imitated (Supplementary Table). We also predicted species with any of the following traits would be less likely to get imitated: 1) anurans listed as "threatened" with extinction (IUCN, 2019; N = 6 species), 2) spadefoot toads (Family Scaphiopodidae, N = 7 species), given that they burrow underground the vast majority of the year and vocalize only during an explosive breeding season that lasts just a few days out of the year (Greenberg and Tanner, 2005), and 3) any anuran species that uses inconsistent call rhythms (N = 6 species), given that normal mockingbird song consists of repetitive and stereotyped rhythms (Wildenthal, 1965; Gammon, 2013).

To test whether these predictions were met, AMC listened to mockingbird recordings to assess which frog species were imitated. Prior to data collection, AMC became an expert in the identification of

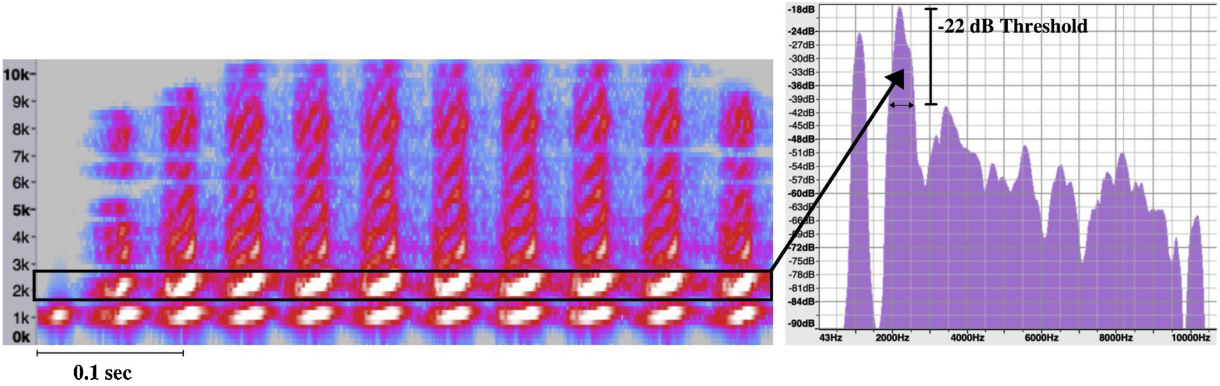

**Fig. 1.** = spectrogram and power spectrum of a gray tree frog call that highlights the dominant formant and how acoustic frequency measurements were made 22 dB below the peak amplitude. (Note: please print using color).

the calls of all 71 frog species. DEG quizzed her over several weeks using frog sounds from our acoustic library and online quizzes (e.g., https://www.pwrc.usgs.gov/frogquiz/) until she regularly identified close to 100%. At that point we determined she was ready to start. AMC then listened to the recordings of mockingbird song, pausing anytime she heard a song that sounded similar to a frog call from that county's list. To verify whether it truly represented mimicry, AMC often replayed the sound multiple times and compared a spectrogram of the sound to spectrograms from our acoustic library of frog calls. AMC also sent unlabeled audio files of all putative mimics to DEG, so he could independently classify which frog species, if any, was imitated. The two of us then met to assess inter-observer reliability and to discuss differences.

## 3. Results

We sampled a total of 2426.2 min (~40.5 h) of mockingbird song from 370 individuals in 106 counties within 22 states (Table 1). As expected, mimicry of any anuran was rare. Based on a prior study (Gammon, 2014), we estimated our entire sample contained 10,000–25,000 mimetic events, but we measured only a few dozen possible events of anuran mimicry. AMC's initial assessment included 33 mimetic events – 26 that convinced her completely and 7 likely mimetic events. DEG independently identified these 33 audio files, and his assessment matched AMC's assessment 28 times (inter-observer reliability = 84.8%). Our discussions of the five disagreements led to AMC changing her mind twice and DEG changing his mind three times. We further decided to eliminate the 7 mimetic events that were initially labeled as likely, due to uncertainty over whether they represented legitimate mimicry. Our final list consisted of 24 instances of anuran mimicry from 12 species (Fig. 2, Supplementary Table).

We had predicted 39 of the 71 anuran species might get imitated because the dominant formant of their calls used a frequency bandwidth nested within the 750–7000 Hz window. Of the anuran species actually imitated, 11 of the 12 came from this list of 39 species, which significantly exceeded chance expectations (*G test*, G = 7.89, df = 1, p = 0.005, Fig. 3). The remaining species imitated was the gopher frog (*Lithobates capito*). This species normally uses a dominant frequency below 750 Hz, but mockingbirds imitated them by excluding the call's dominant frequency and instead reproducing an upper formant in the call (Fig. 2C). As shown by several side-by-side comparisons of model vs. mimic, leaving out formants was a common strategy when imitating anurans (Fig. 2). Another common acoustic alteration was to truncate the call, especially when imitating long-duration toad calls (Fig. 2D-F).

## 4. Discussion

Although vocal mimics imitate predominantly other bird species, our study demonstrates that northern mockingbirds also imitate at least a dozen anuran species across their geographic range. Other vocal mimics have also been observed to imitate non-avian models (e.g., Tapper, 2006; Flower, 2011), but most basic questions regarding mimicry of non-avian models remain unanswered. For example, we cannot make inferences about how, or whether, mockingbirds interact behaviorally with the model anurans, given that our study relied exclusively on archived audio recordings. Previous research with avian models, however, suggests behavioral interactions with model species are unlikely (Gammon, 2013).

With regard to their auditory production capabilities, the mockingbird has been described as a "jack of all trades and master of none" (Zollinger and Suthers, 2004). Accordingly, the full acoustic diversity of anuran calls is not reflected in the mockingbird's mimetic repertoire. To begin with, mockingbirds selected predominantly anuran models with call frequencies already within the 750–7000 Hz limits of mockingbird vocalizations (Zollinger and Suthers, 2004; Gammon, 2013). Furthermore, mockingbirds often modified calls by leaving out formants and/or truncating call duration. Other prominent mimics use similar simplifying strategies. For example, several mimicking species select models with acoustic features that already match those used by the mimic, e.g., marsh warbler (*Acrocephalus palustris,* Dowsett-Lemaire, 1979), European starling (*Sturnus vulgaris*, Hindmarsh, 1984), and icterine warbler, *Hippolais icterina*, Riegert and Jůzlová, 2018). Furthermore, when superb lyrebirds (*Menura novaehollandiae*) imitate the 'whip' element of the eastern whipbird (*Psophodes alivaceus*), they produce only a subset of the model's impressively-large frequency bandwidth (Zann and Dunstan, 2008). It would be interesting to test the physiological production limits of mockingbirds (and other mimics) by tutoring them with model sounds already known to have an unsuitable acoustic structure, such as the low-pitched call of the American bullfrog (*Lithobates catesbeianus*).

To understand fully the mechanisms behind model selection, advances in neuroscience are needed. Vocal mimics are fundamentally distinguished from typical songbirds in that they learn from a broader suite of models rather than just adult conspecifics. Most scientists believe developing songbirds possess an innate auditory template for what constitutes an appropriate song model (Mooney, 2009). Although the sensory basis for this model is supposedly grounded in neuroscience, the available supporting evidence is purely behavioral, focusing on how naïve juveniles call more in response to hearing a suitable model (e.g., Nelson and Marler, 1993; Wright-Nelson, 2016). Prather et al. (2008) showed in adult swamp sparrows (*Melospiza georgiana*) that specific neurons in the HVC (Higher Vocal Center) of the brain fire when the birds either produce or hear an existing song type, but a similar study has never been performed in naïve juveniles. If the neuroscientific basis behind the template model could be established, then it would be particularly fascinating to compare the activity of sensory neurons in

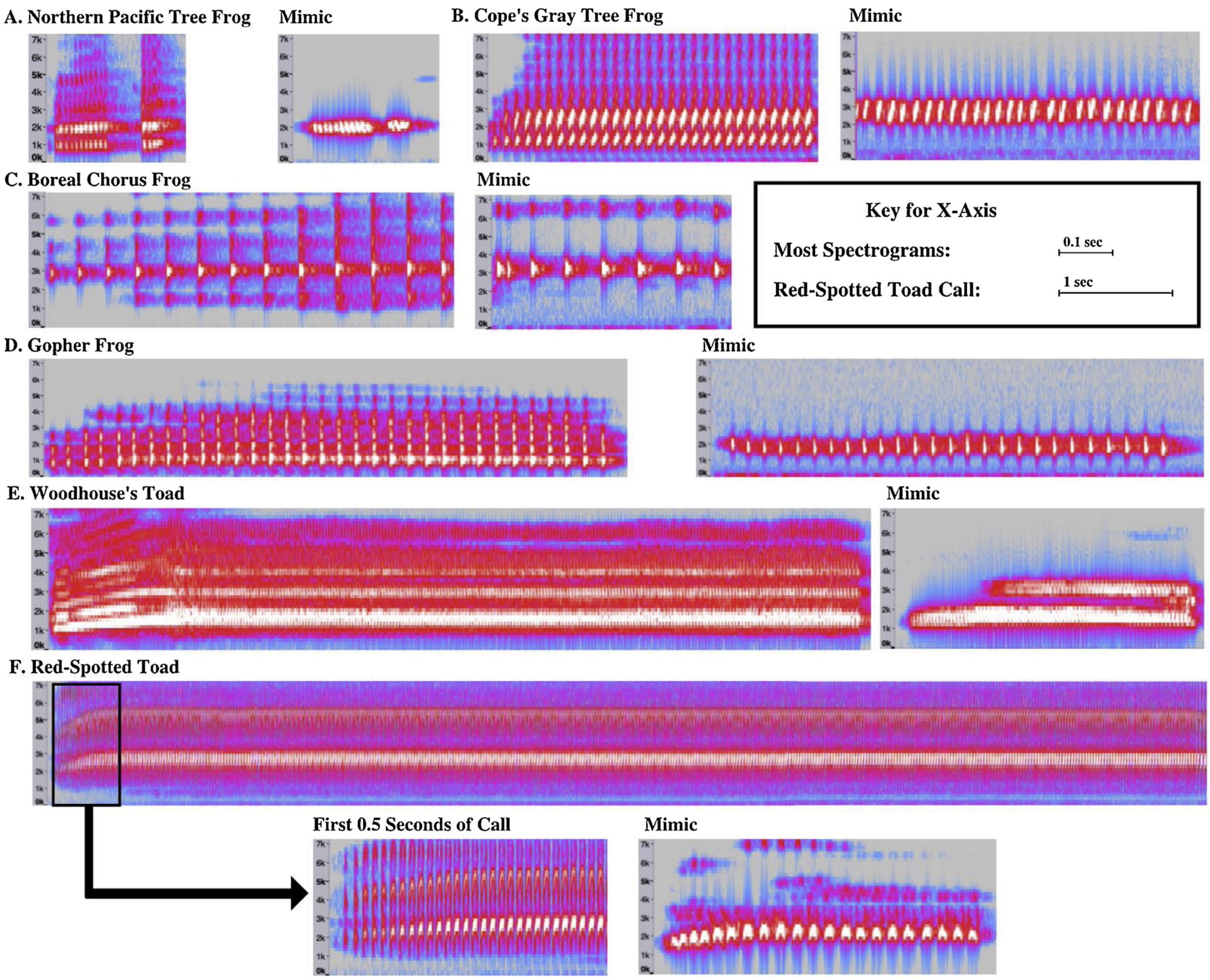

**Fig. 2.** Side-by-side comparisons of the spectrograms of model vs. mimic for the calls of the following anurans: A) northern Pacific tree frog (Pseudacris regilla), B) Cope's gray tree frog (Hyla chrysoscelis), C) boreal chorus frog (Pseudacris maculate), D) gopher frog (Lithobates capito), E) Woodhouse's toad (Anaxyrus woodhousii), and F) red-spotted toad (Anaxyrus punctatus). Six additional anuran species were imitated, but are not shown: gray tree frog (Hyla versicolor), Cajun chorus frog (Pseudacris fouquettei), upland chorus frog (Pseudacris feriarum), American toad (Anaxyrus americanus), southern toad (Anaxyrus terrestris), western narrow-mouthed toad (Gastrophryne olivacea. As illustrated, it was common for mockingbirds to reduce the overall frequency bandwidth by leaving out formants, and to shorten long toad calls. (Note: please print using color).

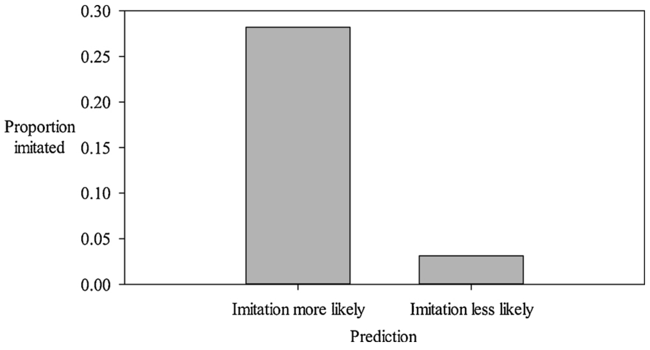

**Fig. 3.** Anurans were much more likely to get imitated if their calls use acoustic frequencies similar to frequencies already used by mockingbirds. Of the 39 anuran species for which the dominant format of their calls used a frequency bandwidth nested within the 750–7000 Hz window, eleven were imitated (28.2%). Of the remaining 32 anuran species, only one was imitated (3.1%). (Note: please print using black-and-white).

the brains of mimicking vs. non-mimicking songbirds when hearing possible models. Comparisons like this would represent a major step forward in our understanding of the proximate and ultimate basis for vocal mimicry.

Declarations of interest: none

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.103982.

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