



Vocal mimicry in spotted bowerbirds is associated with an alarming context

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Although the presence of vocal mimicry in songbirds is well documented, the function of such impressive copying is poorly understood. One explanation for mimicry in species that predominantly mimic alarm calls and predator vocalisations is that these birds use mimicry to confuse or deter potential threats or intruders, so these vocalisations should therefore be produced when the mimic is alarmed and be uncommon in other contexts. Male bowerbirds construct bowers to display to females and anecdotal reports from the *Ptilonorhynchus* genus suggest that males mimic alarm sounds when disturbed at their bowers. We quantified and compared the rate of mimicry during disturbance to the bower by a human and in naturally occurring social contexts in a population of spotted bowerbirds *Ptilonorhynchus maculatus*. Male bowerbirds produced mimicry more than thirty times more frequently in response to bower disturbance than they did in any other context. Neither conspecifics nor heterospecifics were attracted to the bower area by mimicry. These data are consistent with the hypothesis that the production of mimicry is associated with a response to an alarming situation. Additionally, the predominance of alarm mimicry by spotted bowerbirds raises the possibility that the birds learn these sounds when they experience alarming situations and they reproduce them in subsequent alarming situations.

Approximately 20% of songbirds produce vocal mimicry by copying the vocalisations of other species or abiotic sounds (Baylis 1982). Mimicry may be used to communicate with conspecifics, for example, by augmenting displays to attract females (Howard 1974, Coleman et al. 2007) or it may function in interspecific communication, for example, by increasing foraging success or deterring potential predators (Dobkin 1979, Flower 2010). However, despite its prevalence many aspects of vocal mimicry remain poorly understood: its function has been conclusively demonstrated in only a handful of songbird species and how and when the sounds are acquired is even less clear (Kelley et al. 2008).

The prevalence of heterospecific alarm calls in the mimetic repertoires of many bird species has led to the suggestion that mimicry is used to deter predators by deceiving them as to the identity of their prey, but there is little evidence that mimicry is used in this way (Rechten 1978). To our knowledge, the only documented example of vocalisations being used in this way comes from burrowing owls *Athene cunicularia* that produce vocalisations that resemble rattlesnake *Crotalus viridis* rattles, which are produced to deter mammalian predators (Rowe et al. 1986, Owings et al. 2002).

Mimicry of alarm calls may also be produced in an attempt to recruit assistance from conspecifics or heterospecifics

during a predator attack, but while there are numerous reports of species mimicking in alarming contexts, such as during egg collecting and mist netting, there is little information concerning what species or types of sounds are mimicked (Vernon 1973, Morton 1976, Chu 2001a, b). Several species produce mimetic alarm calls alongside their own alarm vocalisations, which may mean that mimicry is used to recruit assistance from conspecifics or heterospecifics (Chu 2001b, Goodale and Kotagama 2006). For example, although phainopepla *Phainopepla nitens* alarm calls alone were more successful at eliciting aid than was mimicry alone, birds were more likely to mob a predator decoy in response to a combination of mimicry and phainopepla alarm calls rather than in response to a combination of alarm calls and digitally scrambled mimicry (Chu 2001a).

Mimicry may also serve more than one function within a species. For example, greater racket-tailed drongos *Dicrurus paradiseus* produce alarm vocalisations when alarmed and mimicry of non-alarm sounds (songs and contact calls) to attract heterospecifics to form a mixed-species flock. For other species that include alarm calls in their mimicry repertoire, such as the grey bowerbirds (previously *Chlamydera* genus, now *Ptilonorhynchus*), however, we know little about the context in which they use their mimicry (Frith and Frith 2004, Kelley and Healy 2011).

There have been anecdotal reports of males at bowers and females at nests producing mimicry, including alarm calls, when approached (Frith and Frith 2004), but the amount and type of mimicry produced has never been quantified across contexts.

If mimicry is associated with alarming situations, we would expect bowerbirds to increase production of mimicry in an alarming situation and it should be uncommon or absent in other contexts. Situations of alarm may include attacks by predators and, for male bowerbirds, may also include disturbance to their bowers. Male bowerbirds maintain their bowers for at least four months and spend approximately 50% of daylight hours at their bowers during this time. Males may mimic when alarmed to attract mobbing assistance from heterospecifics or conspecifics to drive off predators or intruders. Alternatively, birds may deter conspecifics from a resource by mimicking alarm calls so it appears that predators are present in the area, in which case mimicry should increase specifically in the presence of other bowerbirds.

Here we quantified the mimicry that male spotted bowerbirds *Ptilonorhynchus maculatus* (one of the grey bowerbirds) produce in different contexts. To simulate a mildly alarming event we approached male bowerbirds when at their bowers. Although humans can be an experimental proxy for predators (Frid and Dill 2002, Beale and Monaghan 2004, Tilgar et al. 2010), this was not the intention here. We compared the rate of mimicry birds produced in response to human approach (hereafter referred to as 'alarm' context) with the amount and type of mimicry the birds produced under a range of naturally occurring contexts: alone, in the presence of a conspecific and in the presence of a heterospecific.

Methods

Spotted bowerbirds *Ptilonorhynchus maculatus* are Australian passerines that will mimic up to 15 other bird species and human voices (Kelley and Healy 2010). Bowerbirds do not have a specific alarm call and their species-specific vocal repertoire is mainly composed of broadband hisses, 'advertisement' calls produced from the top of a tall tree near the bower, cat-like sounds and mechanical noises (Frith and Frith 2004). Male spotted bowerbirds construct, decorate and maintain bowers that are the site of female mate choice and male competition (Madden 2003). During the breeding season (June to December), males construct and maintain their bowers (Frith and Frith 2004). Bowes, therefore, represent a significant investment in time and energy, and males actively defend the bower from interference by rival males (Madden 2002).

Fieldwork was conducted at Taunton National Park (23.3°S, 149.1°E), central Queensland, Australia, in 2007 and 2008. Male bower owners in this population were ringed with a unique series of colour bands on both legs. Recordings were carried out by an observer sitting approximately 10–15 m from the bower and took place between 5:00 am and 2:00 pm, using a Sennheiser ME66/K6 microphone onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. We observed and recorded 19 males in

2007 and of these, 14 males retained their bowers and were observed again the following year.

We simulated a mildly alarming context using a human approaching the bower and sitting near the bower touching the walls and decorations for approximately nine minutes ($9 \text{ min} \pm 30 \text{ s}$; mean \pm SE). As bowerbirds in this population are rarely exposed to human disturbance we considered that this simulation was likely to be mildly alarming for the birds. When approached by humans bowerbirds tend to fly off but will generally remain in the vicinity, particularly if the human is near a bower. We have never observed a bowerbird mobbing a human.

Over the course of the study eight different experimenters carried out the disturbances. Thirteen males were tested in total and eight males were tested more than once each year. No male was tested more than four times and there was an average of $28 \pm 8 \text{ d}$ between tests. Males were not subjected to any human disturbance apart from these simulations. We recorded all vocalisations produced by the bower owner for the duration of the disturbance. We also recorded the vocalisations of all bower-owning males in a range of naturally occurring contexts around the bower: alone, in the presence of one or more conspecifics and when a heterospecific was in close proximity. We considered bower owners to be in the presence of a conspecific whenever a bowerbird that was not the bower owner was within sight of the observer or was heard shortly after disappearing from view. A heterospecific was considered to be present when that individual was interacting either physically or vocally with the bower owner or with the bower itself when the bower owner was nearby. Observation sessions lasted between three and seven hours and the average time spent recording at each bower was $16 \pm 1 \text{ h}$ (mean \pm SE) in 2007 and $17 \pm 2 \text{ h}$ in 2008. We recorded vocalisations continually throughout the session and the duration of total time the bower owner spent alone, with a conspecific or with a heterospecific was calculated for each observation session.

All recordings were converted into spectrograms using Raven Pro ver. 1.3 (Charif et al. 2004) using a Hann window and a 512 point fast Fourier transform. We isolated and classified vocalisations into two categories: mimicry and the most common species-specific vocalisation, hissing (Fig. 1). We identified mimicry by listening to recordings and visually inspecting spectrograms (as described in Kelley and Healy 2010). Hisses are typically harsh notes often produced in bouts and were easily identified from the recordings.

We calculated the rate of mimicry and hissing in each context by calculating the total time spent mimicking or hissing as a proportion of time in each context. We included only the time periods during which a bowerbird was observed in each context, so we excluded periods when the bower owner was absent. The durations of vocalisations in the alarming context were expressed as a proportion of the duration of time the observer was at the bower when the bowerbird was present. Most individuals were observed in each context more than once and all observations were included. A total of 37 approaches to simulate alarm were carried out on 13 birds, 18 birds interacted with conspecifics in 67 observation sessions, and 18 birds

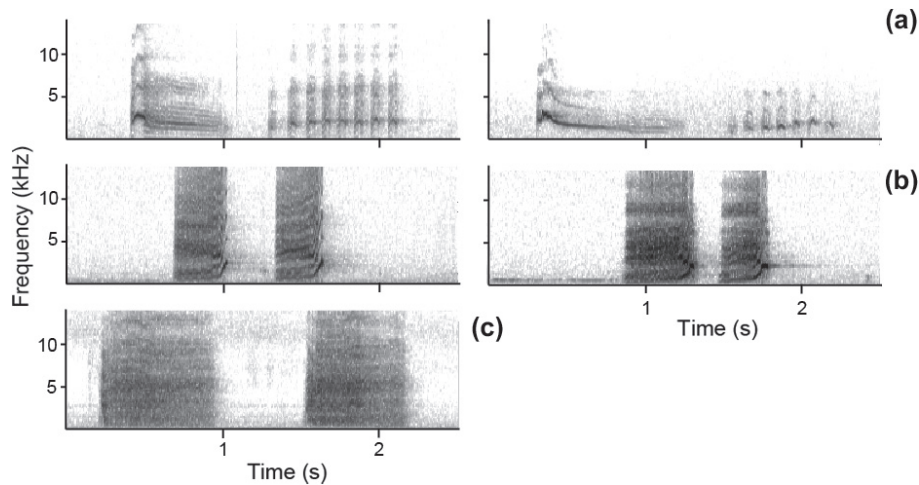


Figure 1. (a) Spectrogram of a whistling kite *Haliastur sphenurus* call (left) and bowerbird mimicry of a kite (right); (b) spectrogram of a pied butcherbird *Cracticus nigrogularis* call (left) and bowerbird mimicry of a butcherbird (right); (c) spectrogram of a bowerbird species-specific hiss.

were observed alone in 75 observation sessions. In response to the 37 approaches, eight males did not mimic (but did hiss) and one male did not vocalise at all.

To examine whether vocalisations occurred or increased in any context we compared the proportion of time spent vocalising in each context. The data were analysed in R (R Development Core Team). Mimicry data could not be transformed to normality so we investigated the likelihood of males mimicking in each context using a binomial linear mixed-effects model. We fitted individual bird as a random factor to control for repeated measures, context as a fixed factor and mimicry/no mimicry as the response variable. We transformed the hiss data to normality and analysed them using a Gaussian linear mixed-effects model

with individual bird fitted as a random factor to control for repeated measures, context as a fixed factor and proportion of time hissing as the response variable to test whether the proportion of time spent hissing differed with context. Post-hoc Tukey tests were used to identify differences among groups (Bretz et al. 2011).

Results

Bower owners were more likely to mimic (and therefore had an overall higher rate of mimicry) when alarmed during simulated predation events when compared to other contexts (Tukey's test: alarm vs alone: $z = 3.65$, $p < 0.001$;

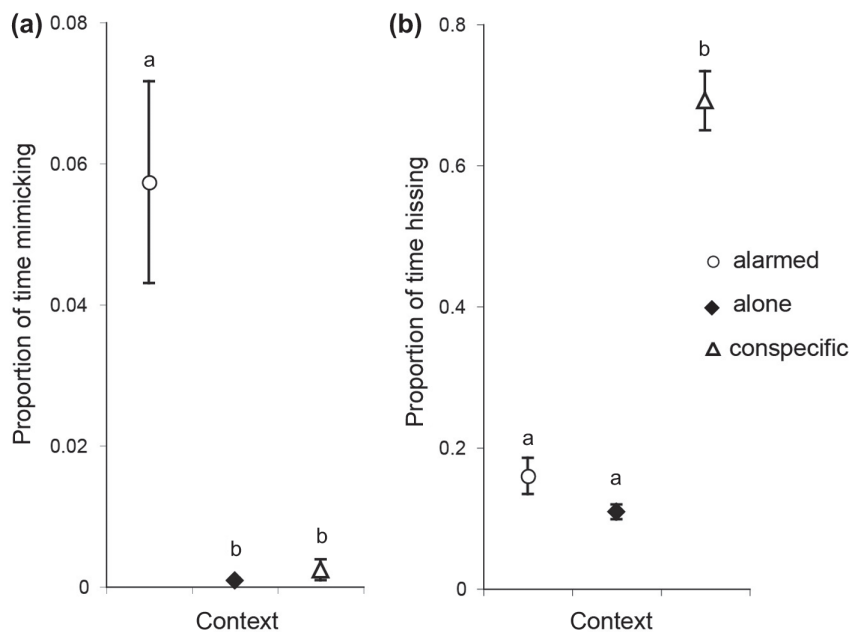


Figure 2. (a) Average proportion of time (\pm SE) bower-owners spent mimicking when alarmed at the bower (white circles), when alone (black diamonds) and when with a conspecific (white triangles); (b) average proportion of time (\pm SE) bower-owners spent hissing when alarmed at the bower (white circles), when alone (black diamonds) and when with a conspecific (white triangles). Alone and with conspecific $n = 18$, alarmed $n = 13$. Note different scales, different letters indicate significance of $p < 0.001$.

alarmed vs with conspecific: $z = 4.40$, $p < 0.001$; alarmed: $n = 13$, conspecific: $n = 18$, alone: $n = 18$; Fig. 2a). When males were approached multiple times within a field season, individuals did not change the proportion of time they spent mimicking in response to repeated approaches (paired t-test: $t = 0.42$, $DF = 7$, $p = 0.69$). The proportion of time spent mimicking when alone did not differ from the proportion of time spent mimicking when in the presence of another bowerbird (Tukey's test: $z = -1.18$, $p = 0.46$, $n = 18$). During simulated predation males spent approximately 7% of time mimicking compared to an average of 0.2% in other contexts.

When alarmed, males predominantly mimicked alarm vocalisations (78.2% of all mimicry). One male never mimicked at all. Males did not mimic a higher proportion

of alarm mimicry when alarmed compared to when they were alone or with a conspecific (Wilcoxon test, $n = 12$, $p = 0.29$; Fig. 3).

A range of vocalisations were included in the mimicry: alarm calls of the pied butcherbird *Cracticus nigrogularis*, white winged chough *Concorax melanorhampbos*, yellow-throated miner *Manorina flavigula*, Australian magpie *Gymnorhina tibicen* were mimicked, calls of raptors such as the whistling kite *Haliastur sphenurus* and wedge-tailed eagle *Aquila audax* as well as the 'babble' vocalisation of the grey crowned babbler *Pomatostomus temporalis* and the 'laugh' vocalisation of the laughing kookaburra *Dacelo novaeguineae*.

There were insufficient data to determine whether the proportion of time spent mimicking was affected by the

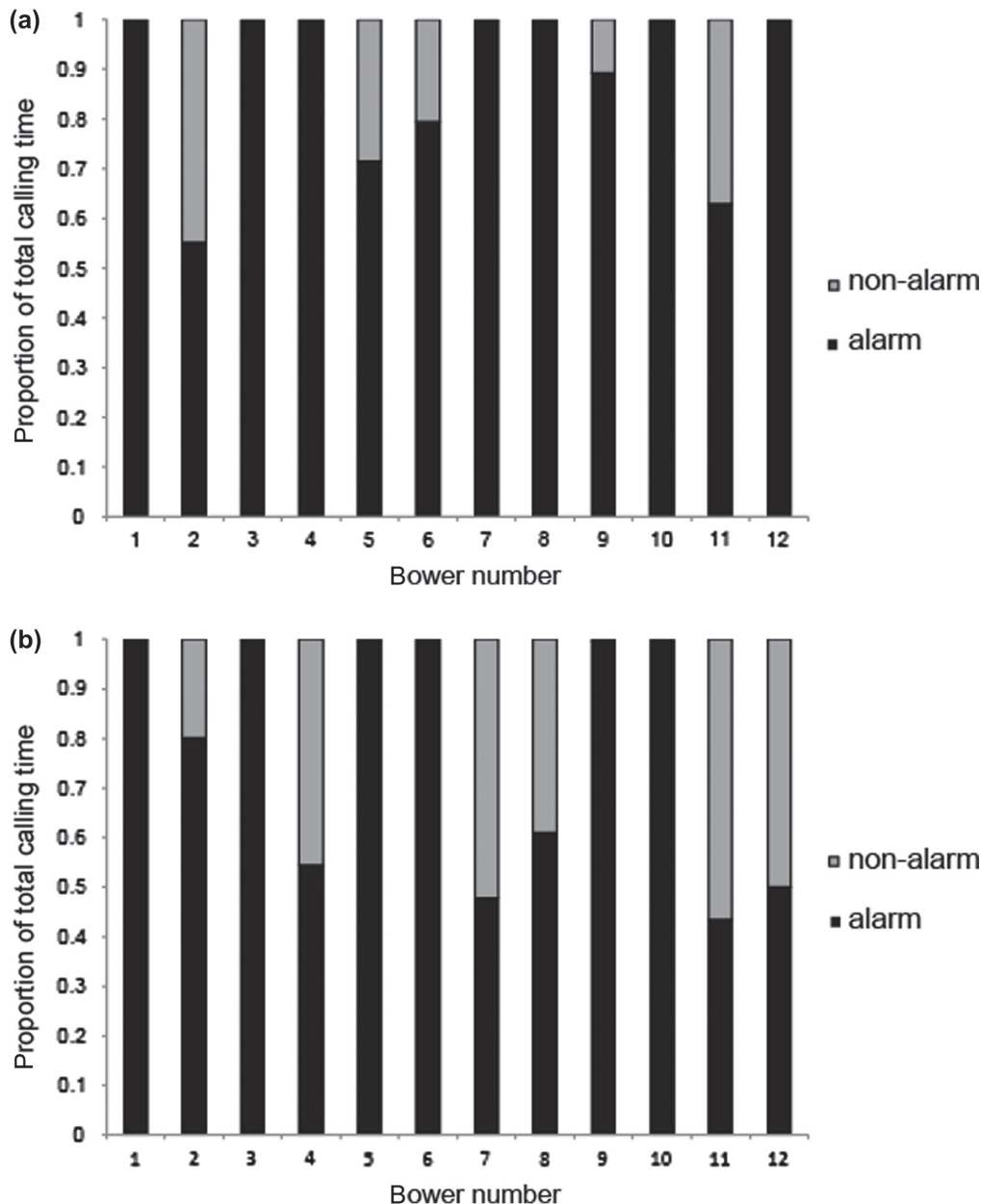


Figure 3. Average total proportion of calling time spent mimicking alarm calls (black bars) or non-alarm calls (grey bars) when (a) alone or with a conspecific; or (b) disturbed at the bower, $n = 12$.

presence of a heterospecific as there were only three cases of heterospecific birds interacting with the bower. In every case these were apostlebirds *Struthidea cinerea*, which are not predatory but bowerbirds mimic their aggressive call. No mimicry was observed during these events and bower owners spent half of the interaction time hissing (proportion of time hissing 0.5 ± 0.1). Mimicry did not appear to act to attract assistance from other birds as the average duration between the production of mimicry and the arrival of a conspecific was 68 ± 13 min and we never observed a heterospecific directly responding to mimicry.

Males spent more time hissing when in the presence of a conspecific than they did when alarmed or when alone (Tukey's test, conspecific vs alone: $t = 17.10$, $p < 0.001$; conspecific vs alarmed: $t = -12.73$, $p < 0.001$; alarmed: $n = 13$, conspecific: $n = 18$, alone: $n = 18$; Fig. 2b). There was no difference in the proportion of time spent hissing when alarmed compared to when males were alone ($t = 1.331$, $p = 0.38$). Of the birds that were approached more than once during the field season, males did not change the proportion of time spent hissing with repeated approaches (paired t-test: $t = -1.42$, $DF = 7$, $p = 0.20$).

Males did not become generally more vocal in response to human approach as the proportion of time hissing did not increase when mimicry increased. This was the case whether or not we analysed each observation or whether we pooled the observations for each individual (pooled Pearson's $r = -0.22$, $DF = 12$, $p = 0.45$; $n = 13$).

Discussion

Males were more likely to mimic when alarmed at their bower by the presence of a human than they were to produce mimicry in other contexts. They did not simply become more vocal as the proportion of time they spent hissing did not increase during those same trials.

These findings are consistent with the prediction that mimicry is produced in response to an alarming situation as mimicry occurred more often and the proportion of time spent mimicking was over thirty times higher in this context. However, the proportion of alarm calls within bouts of mimicry did not change with context. Mimicry did not increase in response to the presence of conspecifics so mimicry in this species is unlikely to be used to deter competitors. There were too few interactions between bowerbirds and heterospecifics (either predators or competitors) to make any specific comment on how males may respond to non-human heterospecifics.

As these bowerbirds appear to have mimicked appropriate sounds when in the 'right' context i.e. when alarmed they mimicked sounds of heterospecifics that are associated with alarm, these findings are consistent with the deterrence hypothesis. Males did not increase the proportion of time they spent producing species-specific vocalisations when mimicry increased, so it is unlikely that mimicry is acting to augment species-specific vocalisations. This contrasts with the use of mimicry in phainopeplas *Phainopepla nitens* and greater racket-tailed drongos *Dicrurus paradiseus*

in which mimicry increases as species-specific alarm calling increases (Chu 2001b, Goodale and Kotagama 2006). Rather more like the bowerbirds, Sri-Lankan magpies *Urocissa ornata* produce alarm mimicry in isolation from species-specific vocalisations when mobbing potential predators (including humans), although it is unclear whether mimicry is used to recruit assistance or to scare off either conspecifics or the potential predator (Ratnayake et al. 2010).

Although the production of alarm calls in an alarming situation is consistent with the predictions of the deterrence hypothesis, this does not mean that birds produced their mimicry in order to deter predatory or non-predatory heterospecifics. Although we know little about the learning of vocal mimicry it seems plausible that sounds heard when experiencing a stressful context may be associated with alarm i.e. predator vocalisations and alarm calls (Joëls et al. 2006). These sounds may then be reproduced when birds are subsequently alarmed, even though this later alarming situation is not necessarily the same as that during which the sound was learned, such as our human approach to the bower manipulation (de Kloet et al. 1999, Kavaliers et al. 2003). Short-term (acute) stress has been shown to enhance learning in a range of taxa, such that a behavioural response is learned faster and retained for longer after a stressful event (Shors 2001, Beylin and Shors 2003, Kavaliers et al. 2003). Particularly striking evidence of this comes from so-called 'flashbulb' memories that humans acquire as a result of highly stressful events (Brown and Kulik 1977, Joëls et al. 2006, Luminet and Curci 2009). This response is mediated by the stress hormones, whereby elevated levels of glucocorticoids are associated with enhanced learning and predator attacks and other stressful events have the potential to induce these hormonal changes (Sandi and Rose 1994, Hubbs et al. 2000, Mateo 2008, Thaker et al. 2010).

The role that stress may play in enhancing the ability to learn vocalisations has been little considered. It is feasible that spotted bowerbirds may learn their mimicry under stressful conditions as they learn their mimicry directly from heterospecifics and many of the heterospecifics they mimic are relatively common species (Kelley and Healy 2010, 2011). Therefore, although our data are consistent with the deterrent hypothesis it may be, in fact, that bowerbirds do not use mimicry as a signal but rather are producing vocalisations in alarm, as many animals do when startled. Support for this hypothesis would come from evidence that birds can learn other sounds in stressful contexts and then reproduce these sounds in later alarming situations. It is also likely that sounds associated with alarm may be learned more readily than other types of sounds as most animal alarm vocalisations have a relatively simple, similar structure (Jurisevic and Sanderson 1994). Enhanced learning ability during stressful situations may also explain why many species of animals have been shown to learn to respond to sounds produced by ecologically relevant heterospecifics that indicate danger (Lea et al. 2008, Magrath et al. 2009). The potential link between acute stress and learning of sounds requires further investigation in both mimetic and non-mimetic species.

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