

ECOLOGY

Tool-assisted rhythmic drumming in palm cockatoos shares key elements of human instrumental music

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All human societies have music with a rhythmic “beat,” typically produced with percussive instruments such as drums. The set of capacities that allows humans to produce and perceive music appears to be deeply rooted in human biology, but an understanding of its evolutionary origins requires cross-taxa comparisons. We show that drumming by palm cockatoos (*Probosciger aterrimus*) shares the key rudiments of human instrumental music, including manufacture of a sound tool, performance in a consistent context, regular beat production, repeated components, and individual styles. Over 131 drumming sequences produced by 18 males, the beats occurred at nonrandom, regular intervals, yet individual males differed significantly in the shape parameters describing the distribution of their beat patterns, indicating individual drumming styles. Autocorrelation analyses of the longest drumming sequences further showed that they were highly regular and predictable like human music. These discoveries provide a rare comparative perspective on the evolution of rhythmicity and instrumental music in our own species, and show that a preference for a regular beat can have other origins before being co-opted into group-based music and dance.

INTRODUCTION

The production of music with a regular pulse or rhythmic “beat” is ubiquitous across human cultures, and in many cases, the beat is produced and amplified with percussive musical instruments such as drums (1–3). Darwin proposed that human rhythmicity reflects ancient aspects of brain function that are likely to be shared across taxa (4). Some species produce communicative displays with precise timing and coordination (5–7), add percussion using body parts to multimodal displays (8), use tools to amplify sounds (9), and even produce a percussive rhythmic beat (10). The ability to perceive and entrain to an external beat (for example, from a metronome) has also been documented in several taxa (11–14). However, there have been no demonstrations that nonhuman species create their own isochronous (regular) percussive beats using sound tools that they have manufactured themselves in analogous fashion to humans (1, 2).

The only reported nonhuman example of drumming using manufactured sound tools occurs in palm cockatoos (*Probosciger aterrimus*). Male palm cockatoos from northern Australia use a modified stick or seedpod to strike a hollow tree limb repeatedly during their vocal and visual display (Fig. 1A, fig. S1, and movies S1 and S2) (15, 16). This behavior is remarkable because tool manufacture among nonhuman species is rare and almost always occurs in the context of solving problems related to foraging (16–18), but palm cockatoos use their tools only to make sounds. Drumming occurs alongside other aspects of display (for example, calling, darkening of red cheek patch or “blushing,” and crest erection) (19, 20) but is also performed for long periods without accompanying vocalizations or visual displays.

RESULTS

Our study of 18 wild male palm cockatoos in northern Australia confirmed that, like human music, drumming occurs in a consistent performative context (21), with most drumming bouts performed by males directed to females. The sequences of taps made by palm cockatoos with their sound tools are strongly nonrandom, creating a regular pulse such as that found in human music. Our analysis of 131 sequences of drumming (each comprising 5 to 92 percussive taps, mean = 10.32 ± 0.91 SE; 2 to 33 sequences per male) revealed that males have a wide range of possible tapping rates (range of intertap intervals = 0.09 to 2.77 s; fig. S2) both within and between individuals and that the mean interval (801 ± 289 ms) between taps often entailed a brief pause. Thus, they do not drum as fast as they are physically capable and do not appear to be constrained to any particular rate when drumming (22). Random sequences of taps should follow a Poisson process, with the intervals between taps distributed according to an exponential distribution (23). However, the intervals between taps were clearly nonrandom ($t_{130} = 22.59$, $P < 0.001$), with all sequences showing significantly less variation, that is, greater consistency in the spacing between taps, than expected from a Poisson distribution (Figs. 1 and 2 and fig. S3).

For further evidence of periodicity and rhythm, we examined, by calculating the sample autocorrelation function, our seven longest drumming sequences ($n = 27$ to 92 beats) for linear dependency between consecutive interbeat intervals (10). We used both a global test for autocorrelation (10 lags) and specific test (1 lag) to reveal strong evidence of temporal dependence within five of these sequences (Table 1). Our tests revealed dependency between one interbeat interval and the next in two sequences and dependency between two, three, and five consecutive interbeat intervals in three further sequences (Table 1 and fig. S4). This analysis demonstrated that the sequences not only were marked by low variance in interbeat intervals (Figs. 1 and 2) but also were highly regular and predictable, a key feature of human music (10, 24).

We found that a disproportionate number of drumming sessions (including sessions observed but not recorded by video, 54 of 80 or 67.5%) were performed by males when a female was present. In a separate sample of 135 palm cockatoo encounters that did not involve drumming, the female was present on only 35 (25.9%) occasions. This

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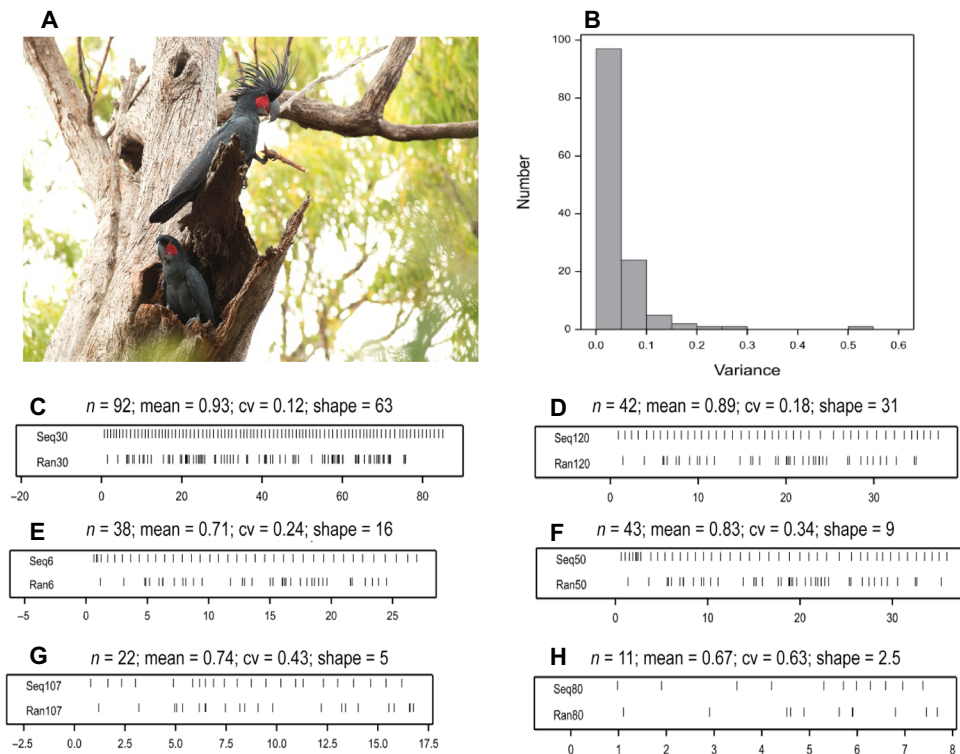


Fig. 1. Palm cockatoos use sound tools to produce a rhythmic beat. (A) Male palm cockatoo drumming on a hollow tree with a manufactured “drumstick.” Photo: C.N.Z. (B) Distribution of variances for intertap intervals (seconds) over 131 sequences of drumming by 18 male palm cockatoos. (C to H) Examples of drumming sequences of varying length showing time on x axis (seconds). Temporal spacing of drumming taps is shown in the top row of each figure and is compared to a randomly generated sequence in the lower row. Sample sizes, mean intertap intervals, coefficients of variation (cv), and shape parameters are given above each sequence.

difference was significant ($\chi^2_1 = 31.7$, $P < 0.001$) and suggests that drumming is predominantly performed in intersexual display.

DISCUSSION

Recent research has focused on whether nonhuman species have the ability to perceive and entrain their movements to a regular beat (for example, as given by a metronome or music), with preliminary evidence suggesting that this ability is most common in, but not limited to, species with vocal learning (2, 12, 25, 26). Our data suggest that, as distinct from entraining to a beat from an external stimulus, palm cockatoos generate their own regular percussive beat when displaying to females. Palm cockatoos would rarely have the chance to entrain to a beat provided by others because their drumming sounds only travel short distances (<100 m), and nests are likely to be too widely spaced for neighbors to hear each other (territory diameter of approximately 170 m) (15, 16, 19). Male palm cockatoos thus appear to be more like solo musical artists or the beat setters of musical ensembles (for example, drummers in western rock bands) who have their own internalized notion of a regular pulse, and then generate the motor pattern that creates the beat. In humans, this beat may, in turn, be entrained to by other individuals (27), but we have no evidence that other palm cockatoos respond in any way to the rhythms produced by males when they perform their drumming display.

Drumming by palm cockatoos is consistent with a further distinguishing feature of human music, in which performances typically entail repertoires of identifiable phrases or components within the performance (3, 21). We found that individual male palm cockatoos have their own consistent drumming patterns (or “signatures”), in

strong analogy to human musicians and composers who show distinct individual styles in the timing of musical notes (28). Males differed significantly from each other in the shape parameters describing the distribution of intertap intervals ($F_{17,113} = 2.55$, $P = 0.002$; Fig. 2A). Some males had slower, highly consistent drumming rates, whereas others had faster drumming rates with higher variance, and some displayed mostly consistent drumming rates with occasional sequences of faster drumming (Fig. 2B and fig. S3). Females were the apparent target audience most of the time, but the shape parameters did not vary significantly in relation to female presence ($F_{1,129} = 2.08$, $P = 0.152$), confirming consistency in individual style regardless of this external stimulus.

Individually recognizable song styles are known to be of adaptive benefit to singing birds, for example, in distinguishing between neighbors and strangers (29). The elaboration of song through the addition of syllables and motifs is also a well-established method for male birds to compete when attempting to attract females (30). The addition of individually recognizable rhythmic signatures in palm cockatoos to their complex vocal displays (20) may have a similar function. It is also possible that drumming displays encode further information about the drummer. For example, humans can produce a regular beat without entrainment from early childhood, but their spontaneous beat rate slows down with age, suggesting a gradual slowing of the referent period (22). The mean beat rate across all palm cockatoos in our study was slower than the spontaneous beat rate of adult humans [mean \pm SD interval between beats of 628 ± 166 ms for humans (22) compared with 801 ± 289 ms for palm cockatoos], but the high variability among male palm cockatoos (Fig. 2) also indicates the possibility of age-related beat rates in this long-lived species (maximum age, >50 years).

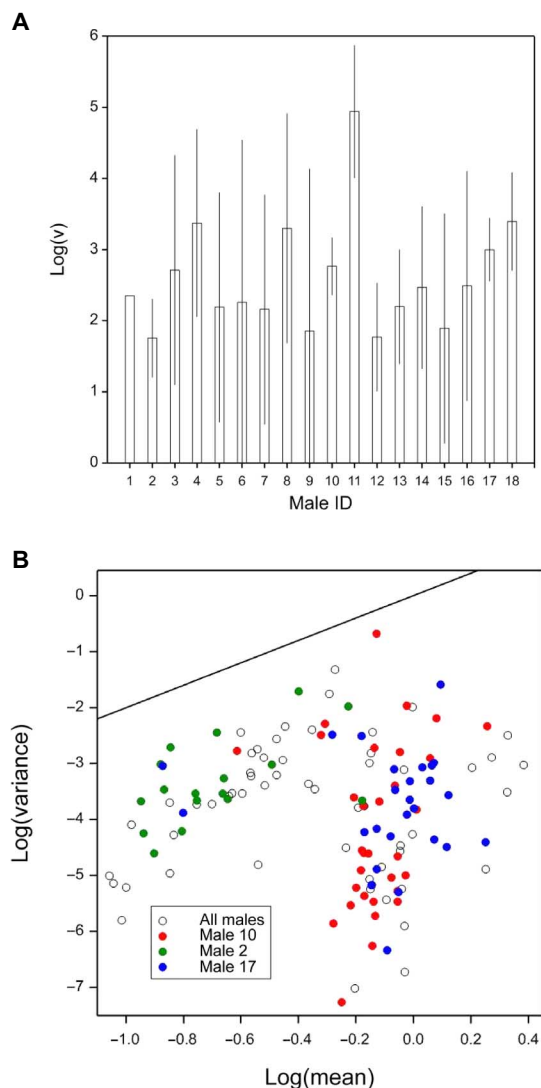


Fig. 2. Individual drumming styles of male palm cockatoos. (A) Log of shape parameter $v \pm SEs$ for the intertap intervals of 18 male palm cockatoos. (B) Log of mean intertap interval versus log variance for 131 sequences across 18 male palm cockatoos. Three males are highlighted: male 2 (green) illustrating a consistently faster drumming rate with higher variance, male 10 (red) showing slower drumming rates, and male 17 (blue) showing mostly slower drumming rates with occasional sequences of faster drumming. The line illustrates expected values from the Poisson process, where the variance and mean are equal.

Our study of tool-assisted drumming in palm cockatoos shows that they use abilities seen separately in other nonhuman species in a combination that has, to our knowledge, been recorded only in humans when performing percussive musical rhythms. A considerable number of species are known to communicate with conspecifics by drumming or percussion using body parts only (for example, hands, feet, or beaks) (1, 31–33), and some of these do so with impressive timing and coordination (8). Similarly, regularity in the structure of vocalizations appears to be relatively common among some animal taxa (34), suggesting that analogs for the rhythmic abilities of humans may not be scarce. However, palm cockatoos appear to provide the closest animal analog to the percussive rhythms favored across human societies; they are the only species known to fashion specific tools to amplify the

sound made by using a limb alone (1), and they then use the tool to drum in a regular rhythm.

Humans share a propensity for drumming with their closest relative, the common chimpanzee (*Pan troglodytes*), which may drum with hands and feet on hollow trees or other resonant objects (28, 29), and bang and throw rocks against trees (9). These behaviors share some similarities with palm cockatoo drumming. Chimpanzees banging with their hands and feet showed individual differences in beat patterns, and one hypothesis to explain stone-throwing behavior is that the stone tool serves as an extension of banging with hands and feet, to enhance sound propagation (9). However, the short sound sequences produced by chimpanzees in these studies differ from palm cockatoo drumming in two important elements: They lack a regular beat, and there is no evidence of tool manufacture. These two elements are key features of human percussive music (1, 2). However, an important study of captive chimpanzees revealed that they may have underlying rhythmic abilities when drumming. An episode of spontaneous drumming by an individual chimpanzee on an upturned bucket showed the structural and contextual properties of human musical drumming, suggesting that humans may share this capacity with their closest relatives (10). It is curious therefore that rhythmic abilities in apes (for example, ability to entrain to a rhythmic beat) have thus far appeared to be limited compared to some other taxa (27) and that they do not fashion their own percussive sound tools, despite advanced toolmaking abilities in the context of foraging (17, 18).

Our demonstration of a nonhuman species using manufactured tools to produce rhythmic sounds has broad implications for understanding the evolution of music. Palm cockatoo drumming conforms to several musical features that are statistically universal among human societies, including the use of percussion, a regular beat, and repeated components (3). However, it differs in a key characteristic. Among humans, a regular beat is significantly associated with dance, group-based activity, and percussion (3). In palm cockatoos, a regular beat is usually the product of a solo activity linked to percussion but not to group-based activity or dance. This difference between humans and palm cockatoos is important because, whereas the present-day tight associations between rhythm, dance, group-based activity, and percussion make the origins of human rhythm difficult to disentangle (3, 27), palm cockatoos indicate that regular percussive rhythm can evolve as part of a solo performance by males to females.

In conclusion, our analysis demonstrates that the tool-assisted drumming displays of palm cockatoos have key hallmarks of human music as distinct from other forms of communication, most notably language (3, 21). These include performance in a consistent display context, regular beat production over long sequences, repeated components, and individual signatures or styles (3, 21, 28). Regular rhythm is widespread among human societies and is strongly linked to dance, group-based activity, and percussion (3), but the origins of our preference for a regular beat remain obscure. The simple, regular drumming displays of palm cockatoos in just one population in northern Australia may provide a much needed comparative clue to help solve this riddle. Palm cockatoos suggest an evolutionary link between regular rhythm and solo-based percussive performances by males to females. This supports Darwin's contention that a regular beat has primeval aesthetic appeal across species, and points to the distinct possibility that the preference for a regular beat in human societies had other origins before being co-opted into group-based music and dance (4).

Table 1. Descriptive data for seven drumming sequences with >25 beats. Sequence number, mean and SD of the interbeat interval, and total number of beats in the sequence are shown. χ^2 statistics and *P* values for a global test of autocorrelation in each sequence (testing for autocorrelation up to 10 lags) and a test of autocorrelation at the first lag, together with the number of beats over which significant autocorrelation was detected, are also given. Sequences were performed by male 17 (30, 49, 50), male 10 (112, 120), male 8 (6), and male 2 (88).

Sequence	Mean interbeat interval (s)	SD	Total number of beats	Global test of autocorrelation (χ^2_{10})	<i>P</i>	Autocorrelation at first lag (χ^2_1)	<i>P</i>	Autocorrelation for next <i>n</i> beats
30	0.92	0.17	92	36.2	<0.001	21.5	<0.001	2
49	0.94	0.18	51	21.3	0.020	7.6	0.006	1
50	0.84	0.29	43	71.3	<0.001	25.6	<0.001	5
120	0.89	0.16	42	21.6	0.020	17.0	<0.001	1
6	0.71	0.18	38	49.8	<0.001	25.5	<0.001	3
88	0.47	0.17	31	2.9	0.98	0	0.93	0
112	0.83	0.10	27	3.4	0.97	0.3	0.58	0

MATERIALS AND METHODS
Study species, site, and tool use

Palm cockatoos (*P. aterrimus*) are restricted to Cape York Peninsula in northern Australia, lowland New Guinea, and some offshore islands (35). In Australia, they are a monogamous, slowly reproducing, nonflocking species that defends breeding territories, incorporating multiple hollows in trees that are used for nesting and displays. Pairs show nest-site fidelity between years, although females only lay a single-egg clutch every 2 years on average (19). Palm cockatoos are highly unusual among nonhuman species because they manufacture sound tools for use during their displays (15, 16). Palm cockatoos manufacture two types of sound tools. They make drumsticks by breaking off a living or dead branch, snipping off the foliage, and trimming it to approximately 20 cm (mean = 20.2 ± 6.9 SD, *n* = 25). Drumstick making appears to occur as part of a broader activity whereby sticks are broken into appropriate lengths before being added to a nesting platform, but only some sticks are used for drumming. The second type of tool used is a hard seedpod from *Grevillea glauca* (bushman's clothes peg), which the birds may adjust in shape (using their beak) before drumming with it (fig. S1). They then grasp the drumstick or seedpod in their foot and beat it against a tree limb or hollow trunk (15, 16) (Fig. 1). To date, this tool use behavior by palm cockatoos has only been recorded from the Australian population on Cape York Peninsula (15, 16, 19). In New Guinea, there are anecdotes of drumming by male palm cockatoos using their clenched foot, but tool use does not appear to have been recorded for this species outside of Australia.

Field observations and video recordings

Recordings of vocal and drumming displays were acquired in Kutini-Payamu (Iron Range) National Park and surrounding aboriginal freehold lands on Cape York Peninsula (12°47'S, 143°18'E) from June to December between 2009 and 2015. The region contains a diverse mosaic of semideciduous mesophyll vine forest interspersed with various types of savannah woodland and grassland (19, 20). Displaying birds were located by their calls and then video-recorded as soon as the bird began to fashion a sound tool. In some instances, when displays were already under way, video recording started partway through the display.

Video and audio data were collected simultaneously using either a Sony HD Handycam video recorder (model HDRXR260V) or a Canon EOS 5D Mark III camera with a 400-mm EF 5.6L image stabilization

ultrasonic motor lens (attached to a Manfrotto tripod) and a directional Rode VideoMic pro external microphone (with a windshield) set to 0-dB gain boost. For further details of methods including sexing and individual identification, see the study of Zdenek *et al.* (20). Sample videos of drumming with a stick and seedpod are provided (movies S1 and S2).

Within recording sessions, “sequences” were defined as continuous drumming with less than 5 s between taps. If drumming resumed after a 5-s (or greater) pause, it was treated as a new sequence. Only sequences of five or more “taps” with the drumstick or seedpod were considered in our analysis. A total of 131 sequences of drumming (each comprising 5 to 92 percussive taps; mean = 10.32 ± 0.91 SE) were recorded from 18 individual males (2 to 33 sequences per male) over an area greater than 70 km².

Statistical analysis
Intertap intervals

Spectrograms of drumming sequences were viewed and analyzed using Raven Pro version 1.4 (36). Each tap by the palm cockatoo using a stick or seedpod was boxed by hand from the beginning of each tapping sound pulse, and both the start time of each tap and the interval between start times of successive taps were extracted for analysis. Figure S2A provides an example of a spectrogram of tapping sounds. The distribution of intertap intervals across all data (0.09 to 2.77 s) is shown in fig. S2B. The wide range of possible tapping intervals combined with the relatively slow mean rate of tapping (801 ± 289 ms) suggests that palm cockatoos are not physically constrained to any particular rate when drumming. In particular, drumming rates do not appear to be determined by mechanical constraints, such as the limb acting as a pendulum. The swing and thump on the tree trunk is not a suspension from above. Instead, the drumming is more like the action observed in a human drummer where the trunk is hit from above or the side. This makes a purely mechanical action unlikely because the bird has to lift and release the stick regularly.

We examined the rhythmic properties of the taps made by drumming palm cockatoos. A sequence of events (in this case, the audible taps) that occur individually at random moments, but which tend to occur at an average rate per unit time when viewed as a group, can be modeled by a Poisson process. Further, the intervals between events will have an exponential distribution, which is known to be a

special case of the gamma distribution with the property that variance = (mean)²/ ν , where ν is the shape parameter of the gamma distribution (23). This implies that the coefficient of variation [$cv = SD/mean = \sqrt{1/\nu}$] is constant. In the case of the exponential distribution, $\nu = 1$, and so, $cv = 1$. If $\nu > 1$, then the distribution is unimodal and tends to be a “low”-variance distribution.

For our data, we estimated ν by fitting a generalized linear model (37) for the variance of intervals between drumming events for each of 131 drumming sequences performed by 18 males. We performed this by specifying the distribution as a gamma distribution and link as the natural logarithm with an offset variable as $2 \cdot \log(\text{mean})$. The constant term from the generated model is then an estimate of $-\log(\nu)$, allowing an estimate of the parameter of interest. If $\log(\nu)$ was significantly different from 0, then we inferred that an exponential distribution for intervals between events (taps) was not tenable and therefore that the process was not random. For our data, $-\log(\nu)$ was -2.48 ($SE = 0.110$, $P < 0.001$), confirming that sequences of taps were not stationary, homogeneous Poisson processes but were instead nonrandom with low variance. Furthermore, by fitting a factor for individual males, we showed that there was significant systematic departure from the mean ν among males ($F_{17,113} = 2.55$, $P = 0.002$), showing that they have consistent but individually different styles of drumming (Fig. 2 and fig. S3). However, the shape parameters did not vary significantly in relation to female presence ($F_{1,129} = 2.08$, $P = 0.152$).

For illustration of the comparison between our realized processes and truly random Poisson point processes, we generated sequences of random timings as follows. By evaluating the known mathematical function for each male [at random values x , between 0 and 1, specifying the exponential distribution $F(x) = 1 - \exp(-\lambda x)$, where λ is the mean rate], we obtained sequences of random times between beats. The cumulative sequences of these intervals provided simulated Poisson processes of given length, with average rates [$\lambda = 1/E(x)$]. Figure 1 illustrates the difference between these simulated sequences of random tap times and the corresponding observed sequences.

Further to the above demonstration of low variance in interbeat intervals, we examined our seven longest drumming sequences (>25 beats; Table 1) for linear dependency between each consecutive interbeat interval (10) by calculating sample autocorrelations. We assessed temporal dependence globally (10 lags) and for 1 lag (Table 1 and fig. S4).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/6/e1602399/DC1>

fig. S1. Typical drumsticks manufactured by palm cockatoos (left) and a modified seedpod (right).

fig. S2. Sound properties and spacing of drumming.

fig. S3. Log of mean intertap interval versus log variance over 131 sequences of drumming by 18 male palm cockatoos.

fig. S4. Correlograms for seven longest drumming sequences.

movie S1. A male palm cockatoo drumming on a nest hollow using a seedpod.

movie S2. A male palm cockatoo drumming on a hollow tree stump using a drumstick fashioned from a tree branch.

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Tool-assisted rhythmic drumming in palm cockatoos shares key elements of human instrumental music

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