

22

23 Abstract

24 Chimpanzees in laboratory colonies experience more wounds on week days than on weekends, which
25 has been attributed to the increased number of people present during the week; thus the presence of
26 more people was interpreted as stressful. If this were also true for primates in zoos, where high
27 human presence is a regular feature, this would clearly be of concern. Here we examine wounding
28 rates in two primate species (chimpanzees *Pan troglodytes* and ring-tailed lemurs *Lemur catta*) at
29 three different zoos, to determine whether they correlate with mean number of visitors to the zoo.
30 Wounding data were obtained from zoo electronic record keeping system (ZIMS™). The pattern of
31 wounds did not correlate with mean gate numbers for those days for either species in any group. We
32 conclude that there is no evidence that high visitor numbers result in increased woundings in these
33 two species when housed in zoos.

34 Keywords: aggression, captivity, visitor effect, animal welfare.

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38 Introduction

39 Intra-group aggression is an ordinary and everyday part of primate societies, as it is the most obvious
40 manifestation of within-group competition [Honeess and Marin, 2006; Huchard and Cowlshaw 2011;
41 Isbell, 1991; Walters and Seyfarth, 1987]. Indeed, aggression is sufficiently common in most primate
42 societies that they have evolved behaviours such as reconciliation and consolation to help repair the
43 damage to social relationships that can potentially be caused by conflict [de Waal, 2000]. Much of the
44 aggression observed in primate groups is of low intensity and does not result in physical damage, but
45 higher intensity violence does occur, often resulting in wounding and occasionally the death of the

46 victim, both in haplorhines [eg Arlet et al., 2009; Chapman and Legge, 2009] and strepsirhines [Jolly
47 et al., 2000; Vick and Pereira, 1989].

48 Chimpanzees *Pan troglodytes* in the wild are particularly aggressive [Wrangham et al., 2006], with
49 both male [Newton-Fisher, 2006] and female chimpanzees [Pusey et al., 2008] showing high levels of
50 violent aggression. In the Kasakela community at Gombe, Tanzania, for example, intraspecific
51 aggression was the cause of death in 20% of cases where the cause of death was known [Williams et
52 al., 2008]. Given these high levels of violent aggression in wild chimpanzee populations, we might
53 expect wounding and perhaps even killing to occur in captive populations as well. Thus, violent
54 aggression in captive chimpanzees (indeed in any species of captive primate which shows this
55 behaviour in the wild) should not surprise us, but may have implications for animal welfare and
56 captive management of the species, as violent aggression may be deemed an undesirable behaviour in
57 captive animals, even if it is normal for the species [Hill, 2004].

58 There is limited evidence to suggest that crowds of zoo visitors can increase intra-group aggression in
59 chimpanzees in zoos [Perret et al., 1995], but it should be noted that anthropogenic influences have
60 been discounted as a cause of increased attacks among wild-living chimpanzees [Wilson et al., 2014].
61 However, studies in two different laboratories have shown that wounding rates among chimpanzees
62 are higher during the working week than on weekends [Lambeth et al., 1997; Williams et al., 2010],
63 and have attributed that finding to the presence of more people during the working week, who are
64 probably carrying out different procedures, such as testing, than those present on weekends.
65 Laboratories and zoos are quite different [Hosey, 2005], and weekday/weekend differences in staff
66 and procedures are less likely to be important in zoos. Nevertheless, it would be of concern if this
67 effect of people was a general consequence of captivity, and therefore occurred in zoo chimpanzee
68 groups as well, as responsible zoos aim to provide conditions conducive with good welfare [Hill and Broom,
69 2009].

70 It would also be a concern if it were found to be a consequence of captivity in other primate species.
71 Ring-tailed lemurs *Lemur catta* are a commonly-held species in zoos, and also show evidence of

72 wounding in both wild and captive populations [Pereira and Weiss, 1991; Hood and Jolly, 1995],
73 although there appear to be no data for the frequencies of agonistic wounding. Frequencies of
74 agonistic attacks in ring-tailed lemurs are generally quite low, but rise during the breeding season in
75 both males and females; for example intergroup conflicts range from 0-4.67 per day at Berenty in
76 Madagascar, while intragroup agonism ranges from 0-5.3 acts per hour depending on season [Pride,
77 2005a]. These rates are for all categories of agonistic act, so wounding rates should be considerably
78 lower. Since glucocorticoid levels predict individual mortality in wild ring-tailed lemurs [Pride,
79 2005b], and the postulated “weekend effect” in captivity is suggested to be a consequence of stress,
80 then ring-tailed lemurs are also a suitable species to investigate whether wounding in captive animals
81 is related to visitor pressure in zoos.

82 Here we test the hypothesis that wounding rates in zoo-held chimpanzees and ring-tailed lemurs are
83 correlated with numbers of human visitors in the zoo. **Methods**

84 *Subjects*

85 We collected data for two chimpanzee groups at two different zoos, Taronga Zoo in Sydney,
86 Australia, and Chester Zoo in the UK; and a ring-tailed lemur group at South Lakes Wild Animal
87 Park, also in the UK. These two species were chosen because chimpanzees were the subjects of the
88 original reports by Lambeth et al [1997] and Williams et al [2010], and ring-tailed lemurs are
89 commonly-held primates in zoos for which we would be able to obtain sufficient data for analysis.
90 Ring-tailed lemurs at Chester Zoo were considered unsuitable for this study as they are housed on an
91 island, with limited public visibility; and Taronga lemurs were too few in number to provide a suitable
92 database.

93 *Taronga chimpanzees*

94 Between the years 1999 and 2012 the Taronga Zoo chimpanzee colony comprised of between 16 and
95 19 animals (mean \pm SE per year: females 10.9 ± 0.1 , males 6.9 ± 0.1) ranging from neonates to 58
96 years old (mean $20.4 \pm$ SE 3.89). During this time the animals were housed under three different
97 conditions. From 1980 until 2009, the population lived together in a large outdoor enclosure (1176.5

98 m²) with grass, rocks and 14 tree trunks and two large off-exhibit night dens (290 m²) connected by an
99 elevated causeway. The group was separated from the main viewing area by a moat; the distance
100 between the animals and visitors was 6 m including the moat width. Due to refurbishment of the
101 chimpanzees' enclosure the population was moved in 2009. The temporary housing between 11/2009
102 and 09/2011 consisted of an outdoor enclosure with bark and soil substrates (120 m²), an indoor
103 enclosure (35 m²) and adjacent off-exhibit night dens (135 m²). Outdoor and indoor enclosures were
104 furnished with climbing structures, platforms, ropes and cargo nets. In both enclosures the animals
105 were separated from the main viewing area by a glass window. In 2011 the group moved back into the
106 newly refurbished chimpanzee enclosure (dimensions as above) with seven of the original tree trunks
107 as well as new climbing structures, platforms, ropes and cargo nets. All animals spent daylight hours
108 (0800–1700) in the outdoor exhibit before being secured for the remainder of the day (1700–0800) in
109 their night dens. All dens featured solid cement floors, with resting boards and hammocks (in some of
110 them). All chimpanzees were fed five meals a day, consisting mainly of fruits and vegetables. Water
111 was available ad lib both in the night cages and in the exhibition yard. During the study period five
112 animals were born and five animals died

113

114 *Chester chimpanzees*

115 Between the years 1999 and 2012 the Chester Zoo chimpanzee colony comprised of between 22 and
116 30 animals (mean \pm SE per year: females 18.6 \pm 0.6, males 7.0 \pm 0.3), ranging from neonates to animals
117 over 50 years old (mean 18.5 \pm SE 0.25). The chimpanzee enclosure at Chester Zoo was originally
118 built in 1948, and has undergone several major improvements since then [Wehnelt et al., 2006]. In
119 1989, its three small outdoor islands were joined to make one large, grass-covered island of 2000 m²,
120 separated from the public by a water moat. The renovated island includes an outdoor refuge area for
121 chimpanzees and, in the spring of 2000, a major re-planting of the island was undertaken. This
122 included provision of hammocks, platforms, poles and ropes, making the island more complex and
123 naturalistic; any poles that became rotten have been replaced since then. The indoor on-show area
124 comprises a circular building (to prevent animals being cornered in a fight) 13 m diameter and 12 m

125 high. There is a shallow water moat in front of the viewing windows, to keep chimpanzees away from
126 the glass. Off-show bed areas are linked to the indoor enclosure.

127 Between 1999 and 2003, the chimpanzees usually had access indoors and outdoors during zoo
128 opening hours (weather permitting, e.g. not if the water moat was likely to freeze), and at night they
129 would usually have access to their indoor enclosure and off-show bed areas. From 2003 onwards, they
130 have indoor and outdoor access approximately 24 hours a day, between about the end of March until
131 October. In winter they have daily access indoors and outdoors during zoo opening hours (weather
132 permitting), and at night they have access to the indoor enclosure and off-show bed areas. The
133 chimpanzees are fed a nutritionally-balanced diet of mostly fruit and vegetables, scattered about three
134 times each day, and occasionally have additional browse on top of this.

135 *South Lakes ring-tailed lemurs*

136 Between 2008 and 2012 there were between 38 and 53 ring-tailed lemurs each year in the group
137 (mean \pm SE animals per year: males 20.2 ± 1.46 , females 20.4 ± 1.36 , unknowns 6.6 ± 1.29), ranging
138 from newly born infants (the unknowns were animals that died at or soon after birth) to adults of 12
139 years of age. In December 2008 there was a fire in one of the lemur houses which killed fourteen
140 animals. Subsequently lemurs were brought in from three other zoos, resulting in both introductions
141 and removals during 2009.

142 The ring-tailed lemurs were housed within a mixed-species walk-through exhibit including black-and-
143 white ruffed *Varecia variegata variegata*, black-and-white belted *Varecia variegata subcincta*, red
144 ruffed *Varecia rubra*, black *Eulemur macaco*, white-fronted brown *Eulemur albifrons*, mongoose
145 *Eulemur mongoz* and gentle *Hapalemur alaotrensis* lemurs. All lemur species shared the indoor
146 enclosures (approximately 100m²) but tended to separate into intra-specific groups at night. The
147 outdoor enclosure that was directly accessible was approximately 1ha; however, the ring-tailed lemurs
148 had access to the entire zoo within the perimeter fence (approx 5ha).

149 The typical husbandry routine was that the lemurs were counted and visually checked for any health
150 concerns at approximately 0810 h daily. The indoor enclosure would then be cleaned without the

151 need for the lemurs to be locked outside. Lemurs were scatter fed twice daily within the indoor
152 enclosure but also had access to berries and leaves growing wild around the park.

153 *Data and Analysis*

154 We defined a wound as any laceration which required veterinary treatment or was perceived by the
155 keepers as potentially needing veterinary treatment. We collected incidences of wounding from zoo
156 records, together with the date of the record and the animal's identity. These were medical notes and
157 medical observations extracted from ZIMS™ records (Zoo Information Management Software, ISIS
158 2014). It is likely that there are between-zoo differences in decisions about which events are recorded,
159 and for this reason we cannot use these data to draw any meaningful biological conclusions about
160 differences in wounding rates between zoos. These data were available for the period 1999-2012 for
161 the two chimpanzee groups and 2008-2012 for the lemur group. We calculated mean daily gate
162 numbers from daily attendance records kept by the zoos for those years for which data were available
163 and within the time frame of the wounding data. By this we mean that we calculated a mean for all
164 Mondays, another mean for all Tuesdays, and so on for the entire period for which we had gate
165 numbers. We used gate numbers rather than number of people at the enclosure because these are
166 historical data for which enclosure visitor numbers do not exist, but also because the papers which
167 inspired this study [Lambeth et al., 1997; Williams et al., 2010] used people in the facility as a
168 measure of anthropogenic pressure, rather than number of people in actual contact with the animals.
169 Furthermore, in both Chester and Taronga the chimpanzee enclosures are in prominent, well-visited
170 positions, while the lemurs at South Lakes are free-range, so we are confident that gate numbers are a
171 valid measure of visitor pressure.

172 Pearson correlation coefficients were used to detect significant correlations of total daily wounds
173 against mean daily gate numbers for each zoo, to determine if there were daily effects of visitor
174 number.

175 **Results**

176 Total numbers of wounding events and mean daily gate numbers for the three primate groups and
177 three zoos are shown in Table 1. There were significant differences in mean daily gate number
178 between days for all three zoos, primarily because of high Saturday and Sunday attendance (Chester
179 $\chi^2 = 1088.07$, $df = 6$, $P < 0.001$; Taronga $\chi^2 = 1283.69$, $df = 6$, $P < 0.001$; South Lakes $\chi^2 = 27.75$, $df =$
180 6 , $P < 0.001$).

181 [Table 1]

182 There was no significant correlation of daily wounds with mean daily gate numbers in the Taronga
183 chimpanzees ($r = 0.261$, $P = 0.572$, ns) or the Chester chimpanzees ($r = -0.427$, $P = 0.339$, ns).

184 There was also no significant correlation of daily wounds with mean daily gate number in the South
185 Lakes lemurs ($r = -0.13$, $P = 0.781$, ns).

186 **Discussion**

187 *Chimpanzee woundings*

188 Our data from the Taronga and Chester chimpanzee groups do not support the hypothesis that
189 wounding rates are correlated with visitor number. In neither group were days with high average gate
190 numbers associated with high rates of wounding. There are at least two possible reasons why no
191 correlations were found: i) there really is no effect of zoo visitor numbers on chimpanzee woundings;
192 or ii) rates of woundings are related to visitor number up to a certain threshold, after which further
193 increases in numbers of visitors are not discerned by the animals or are dealt with in other ways such
194 as by increasing allo-grooming. For the latter to be true, both of our groups would have to already
195 have passed that threshold regardless of what day it was, implying that zoo chimpanzee wounding
196 rates are chronically high already compared with situations which do not experience high visitor
197 numbers. This possibility can be tested by comparing the zoo wounding rates with those found
198 elsewhere. This is not straightforward as group size and composition change over time in both wild
199 and captive groups, and behavioural definitions and sampling methods differ between different
200 studies. Nevertheless, Wrangham et al [2006] report median attack rates of 2,301 attacks per 100,000

201 observation hours per male and 911 per female for wild chimpanzees at Gombe-Kasakela and Kibale-
202 Kanyawara. A comparable figure of 3213 attacks per individual per 100,000 hours was found in the
203 captive group at Arnhem Zoo [Noë et al., 1980]. If we assume that our “observation hours” are the
204 total available time during which wounding could occur (ie 14 years, or 122,640 hours per zoo), then
205 our figures show median rates of 0.81 woundings per 100,000 hours for the males and 3.26 for
206 females at Taronga, and 2.4 for males and 2.85 for females at Chester. This may reflect a real
207 difference, but is mostly due to our variable “woundings” being different from “attacks” used by those
208 authors. In any case, these figures do not support the suggestion that zoo groups of chimpanzees have
209 higher rates of violent aggression than wild ones.

210 Why do our two chimpanzee zoo groups show no visitor-related increases in wounding when the
211 laboratory groups do? One plausible explanation is that the chimpanzees in the laboratory groups are
212 more sensitive to human presence. Neither laboratory study [Lambeth et al., 1997; Williams et al.,
213 2010] says what numbers of human visitors their chimpanzees are exposed to, but they are not likely
214 to be anywhere near the daily numbers faced by the Taronga and Chester animals. There is some
215 evidence that animals in zoos may habituate to the large numbers of people they come into contact
216 with [Hosey, 2013], in which case what appears to be an indifference to human crowds (at least as
217 measured by numbers of woundings) may represent habituation to chronic human presence.
218 Furthermore, zoo chimpanzees have more opportunities than those in laboratories to avoid or conceal
219 themselves from human visitors [Wagner and Ross, 2008]. It is also possible that chimpanzees in
220 laboratories perceive more threat from people than their zoo counterparts. For the laboratory
221 chimpanzee the arrival of people on weekdays perhaps signals the likelihood of experimental
222 procedures taking place, so the animals respond to this threat rather than numbers of people *per se*.

223 *Lemur woundings*

224 Our data from the South Lakes ring-tailed lemur group do not support the hypothesis that wounding
225 rates are correlated with visitor number. Studies in zoos on the relationship between visitor presence
226 and ring-tailed lemur aggression give ambiguous results. There was a visitor-related increase in

227 aggression in one group housed in a glass-fronted indoor enclosure [Chamove et al., 1988], but a
228 study of a group in a walk-through exhibit showed no significant effect of human presence on the
229 ring-tailed lemurs [Perry, 2011]. Our study shows similar findings relating to wounding in that even
230 though the visitors were walking amongst the lemurs through their enclosure, it had no effect on the
231 number of woundings between members of the ring tail lemur group. We have been unable to find
232 any published data on wounding rates of wild ring-tailed lemurs, or indeed other captive groups. Our
233 conclusion for these lemurs is the same as for the two chimpanzee groups, that there is no evidence
234 that increased visitor presence is responsible for increased rates of woundings in these animals in
235 captivity.

236 Interestingly, human presence has also been implicated in altering the timing of births in some
237 laboratory primates [Alford et al., 1992], but this effect appears not to occur in zoo-housed
238 chimpanzees [Wagner and Ross, 2008] or gorillas [Kurtycz and Ross, 2015]. We can only agree with
239 the latter authors that the effects of zoo visitors on captive animals may be less profound than
240 previous studies suggested.

241 **Conclusion**

- 242 1. There is no evidence in our data to support the hypothesis that increases in daily zoo visitor
243 numbers result in more wounding by captive chimpanzees or ring-tailed lemurs.
- 244 2. More observational studies are needed to assess whether there is any relationship between
245 visitor numbers and aggression in other zoo primates, and if so, what the nature of that
246 relationship is. This will contribute to our understanding of the effects of the zoo environment
247 on animal behaviour and welfare, and help enable zoos to implement the necessary additional
248 measures to ensure optimal welfare.

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252 **References**

- 253 Alford PL, Nash LT, Fritz, J., Bowen JA. 1992. Effects of management practices on the timing of
254 captive chimpanzee births. *Zoo Biol* 11: 253-260.
- 255 Arlet ME, Carey JR, Molleman E. 2009. Species, age and sex differences in type and frequencies of
256 injuries and impairments among four arboreal species in Kibale National Park, Uganda. *Primates* 50:
257 65-73.
- 258 Chamove AS, Hosey GR, Schaetzel P. 1988. Visitors excite primates in zoos. *Zoo Biol* 7: 359-369.
- 259 Chapman TJ, Legge SS. 2009. The dangers of multi-male groupings: trauma and healing in
260 cercopithecoid monkeys from Cameroon. *Am J Primatol* 71: 567-573.
- 261 de Waal FBM. 2000. Primates – a natural heritage of conflict resolution. *Science* 289: 586-590.
- 262 Hill SP. 2004. Behavioural and Physiological Investigations of Welfare in Captive Western Lowland
263 Gorillas (*Gorilla gorilla gorilla*). [dissertation]. Cambridge. University of Cambridge.
- 264 Hill SP, Broom DM. 2009. Measuring zoo animal welfare: theory and practice. *Zoo Biol* 28: 531-544.
- 265 Honess PE, Marin CM. 2006. Behavioural and physiological aspects of stress and aggression in
266 nonhuman primates. *Neurosci Biobehav Revs* 30: 390-412.
- 267 Hood LC, Jolly A. 1995. Troop fission in female *Lemur catta* at Berenty reserve, Madagascar. *Int J*
268 *Primatol* 16: 997-1015.
- 269 Hosey GR. 2005. How does the zoo environment affect the behaviour of captive primates? *Appl*
270 *Anim Behav Sci* 90: 107-129.
- 271 Hosey G. 2013. Hediger revisited: how do zoo animals see us? *JAAWS* 16: 338-359.
- 272 Huchard E, Cowlshaw G. 2011. Female-female aggression around mating: an extra cost of sociality
273 in a multimale primate society. *Behav Ecol* 22: 1003-1011.

- 274 Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging
275 behaviour among primates. *Behav Ecol* 2: 143-155.
- 276 Jolly A, Caless S, Cavigelli S, et al. 2000. Infant killing, wounding and predation in *Eulemur* and
277 *Lemur*. *Int J Primatol* 21: 21-40.
- 278 Kurtycz LMB, Ross SR. 2015. Western lowland gorilla (*Gorilla gorilla gorilla*) birth patterns and
279 human presence in zoological settings. *Zoo Biol* 34: 518-521.
- 280 Lambeth SP, Bloomsmith MA, Alford PL. 1997. Effects of human activity on chimpanzee wounding.
281 *Zoo Biol* 16: 327-333.
- 282 Newton-Fisher NE. 2006. Female coalitions against male aggression in wild chimpanzees of the
283 Budongo Forest. *Int J Primatol* 27: 1589-1599.
- 284 Noë R, de Waal FBM, van Hooff JARAM. 1980. Types of dominance in a chimpanzee colony. *Folia*
285 *Primatol* 34: 90-110.
- 286 Pereira ME, Weiss ML. 1991. Female mate choice, male migration, and the threat of infanticide in
287 ringtailed lemurs. *Behav Ecol Sociobiol* 28: 141-152.
- 288 Perret K, Preuschoft H, Preuschoft S. 1995 Einfluss von Zoobesuchen auf das Verhalten von
289 Schimpansen (*Pan troglodytes*). *Der Zool Gart NF* 65: 314-322. Perry A. 2011. Assessment of the
290 effects of visitors on four species of lemur (*Lemur catta*, *Varecia variegata*, *Varecia rubra* and
291 *Eulemur rufifrons*) at the Wingham Wildlife Park. *Canopy* 12 (1): 12-14.
- 292 Pride RE. 2005a. Foraging success, agonism, and predator alarms: behavioural predictors of cortisol
293 in *Lemur catta*. *Int J Primatol* 26: 295-319.
- 294 Pride RE. 2005b. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur*
295 *catta*). *Biol Lett* 1: 60-63

- 296 Pusey A, Murray C, Wallauer W, Wilson M, Wroblewski E, Goodall J. 2008. Severe aggression
297 among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *Int J Primatol* 29:
298 949-973.
- 299 Vick LG, Pereira ME. 1989. Episodic targeting aggression and the histories of *Lemur* social groups.
300 *Behav Ecol Sociobiol* 25: 3-12.
- 301 Wagner KE, Ross SR. 2008. Chimpanzee (*Pan troglodytes*) birth patterns and human presence in
302 zoological settings. *Am J Primatol* 70: 703-706.
- 303 Walters JR, Seyfarth RM. 1987. Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth RM,
304 Wrangham RW, Struhsaker TT, editors. *Primate Societies*. Chicago USA. University of Chicago
305 Press. p 306-317.
- 306 Wehnelt S, Bird S, Lenihan A. 2006. Chimpanzee Forest exhibit at Chester Zoo. *Int Zoo Ybk* 40:
307 313-322.
- 308 Williams JM, Lonsdorf EV, Wilson ML, Schumacher-Stankey J, Goodall J, Pusey AE. 2008. Causes
309 of death in the Kasakela chimpanzees of Gombe National Park, Tanzania. *Am J Primatol* 70: 766-777.
- 310 Williams RC, Nash LT, Scarry CJ, Videan EN, Fritz J. 2010. Factors affecting wounding aggression
311 in a colony of captive chimpanzees (*Pan troglodytes*). *Zoo Biol* 29: 351-364.
- 312 Wilson ML, Boesch C, Fruth B et al. 2014 Lethal aggression in *Pan* is better explained by adaptive
313 strategies than human impacts. *Nature* 513: 414-417.
- 314 Wrangham RW, Wilson ML, Muller MN. 2006. Comparative rates of violence in chimpanzees and
315 humans. *Primates* 47: 14-26.
- 316

317 Table 1. Total number of wounds and mean daily zoo visitor numbers, recorded as gate number for
 318 each day of the week, for the three study groups.

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320

Group	Measure	Day of Week						
		M	T	W	Th	F	Sa	Su
Taronga chimpanzees	Total no. of wounds	15	7	11	8	13	11	8
	Mean gate number	3037	3109	3120	3168	3659	4253	5466
Chester chimpanzees	Total no. of wounds	4	23	17	24	29	3	17
	Mean gate number	2963	2677	2836	2829	2924	4460	4416
South Lakes ring-tailed lemurs	Total no. of wounds	24	20	7	22	19	11	13
	Mean gate number	564	500	493	507	576	602	630

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