

1 **Is Wounding Aggression in Zoo-housed Chimpanzees and Ring-tailed**
2 **Lemurs related to Zoo Visitor Numbers?**

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22Abstract

23Chimpanzees in laboratory colonies experience more wounds on weekdays than on weekends, which
24has been attributed to the increased number of people present during the week; thus the presence of
25more people was interpreted as stressful. If this were also true for primates in zoos, where high
26human presence is a regular feature, this would clearly be of concern. Here we examine wounding
27rates in two primate species (chimpanzees *Pan troglodytes* and ring-tailed lemurs *Lemur catta*) at
28three different zoos, to determine whether they correlate with mean number of visitors to the zoo.
29Wounding data were obtained from a zoo electronic record keeping system (ZIMS™). The pattern of
30wounds did not correlate with mean gate numbers for those days for either species in any group. We
31conclude that there is no evidence that high visitor numbers result in increased woundings in these
32two species when housed in zoos.

33Keywords: aggression, captivity, visitor effect, animal welfare.

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37Introduction

38Intra-group aggression is an ordinary and everyday part of primate societies, as it is the most obvious
39manifestation of within-group competition [Honest and Marin, 2006; Huchard and Cowlshaw 2011;
40Isbell, 1991; Walters and Seyfarth, 1987]. Indeed, aggression is sufficiently common in most primate
41societies that they have evolved behaviours such as reconciliation and consolation to help repair the
42damage to social relationships that can potentially be caused by conflict [de Waal, 2000]. Much of the
43aggression observed in primate groups is of low intensity and does not result in physical damage, but
44higher intensity violence does occur, often resulting in wounding and occasionally the death of the

45victim, both in haplorhines [eg Arlet et al., 2009; Chapman and Legge, 2009] and strepsirhines [Jolly
46et al., 2000; Vick and Pereira, 1989].

47Chimpanzees *Pan troglodytes* in the wild are particularly aggressive [Wrangham et al., 2006], with
48both male [Newton-Fisher, 2006] and female chimpanzees [Pusey et al., 2008] showing high levels of
49violent aggression. In the Kaskela community at Gombe, Tanzania, for example, intraspecific
50aggression was the cause of death in 20% of cases where the cause of death was known [Williams et
51al., 2008]. Given these high levels of violent aggression in wild chimpanzee populations, we might
52expect wounding and perhaps even killing to occur in captive populations as well. Thus, violent
53aggression in captive chimpanzees (indeed in any species of captive primate which shows this
54behaviour in the wild) should not surprise us, but may have implications for animal welfare and
55captive management of the species, as violent aggression may be deemed an undesirable behaviour in
56captive animals, even if it is normal for the species [Hill, 2004].

57There is limited evidence to suggest that crowds of zoo visitors can increase intra-group aggression in
58chimpanzees in zoos [Perret et al., 1995], but it should be noted that anthropogenic influences have
59been discounted as a cause of increased attacks among wild-living chimpanzees [Wilson et al., 2014].
60However, studies in two different laboratories have shown that wounding rates among chimpanzees
61are higher during the working week than on weekends [Lambeth et al., 1997; Williams et al., 2010],
62and have attributed that finding to the presence of more people during the working week, who are
63probably carrying out different procedures, such as testing, than those present on weekends.
64Laboratories and zoos are quite different [Hosey, 2005], and weekday/weekend differences in staff
65and procedures are less likely to be important in zoos. Nevertheless, it would be of concern if this
66effect of people was a general consequence of captivity, and therefore occurred in zoo chimpanzee
67groups as well, as responsible zoos aim to provide conditions conducive with good welfare [Hill and Broom,
682009].

69It would also be a concern if it were found to be a consequence of captivity in other primate species.
70Ring-tailed lemurs *Lemur catta* are a commonly-held species in zoos, and also show evidence of

71wounding in both wild and captive populations [Pereira and Weiss, 1991; Hood and Jolly, 1995],
72although there appear to be no data for the frequencies of agonistic wounding. Frequencies of
73agonistic attacks in ring-tailed lemurs are generally quite low, but rise during the breeding season in
74both males and females; for example intergroup conflicts range from 0-4.67 conflicts per day at
75Berenty in Madagascar, while intragroup agonism ranges from 0-5.3 acts per hour depending on
76season [Pride, 2005a]. These rates are for all categories of agonistic act, so wounding rates should be
77considerably lower. Since glucocorticoid levels predict individual mortality in wild ring-tailed lemurs
78[Pride, 2005b], and the postulated “weekend effect” in captivity is suggested to be a consequence of
79stress, then ring-tailed lemurs are also a suitable species to investigate whether wounding in captive
80animals is related to visitor pressure in zoos.

81Here we test the hypothesis that wounding rates in zoo-held chimpanzees and ring-tailed lemurs are
82correlated with numbers of human visitors in the zoo.

83**Methods**

84***Subjects***

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

93***Taronga chimpanzees***

94Between the years 1999 and 2012 the Taronga Zoo chimpanzee colony comprised of between 16 and
9519 animals (mean \pm SE per year: females 10.9 ± 0.1 , males 6.9 ± 0.1) ranging from neonates to 58

96years old (mean $20.4 \pm SE 3.89$). During this time the animals were housed under three different
97conditions. From 1980 until 2009, the population lived together in a large outdoor enclosure (1176.5
98 m^2) with grass, rocks and 14 tree trunks and two large off-exhibit night dens ($290 m^2$) connected by an
99elevated causeway. The group was separated from the main viewing area by a moat; the distance
100between the animals and visitors was 6 m including the moat width. Due to refurbishment of the
101chimpanzees' enclosure the population was moved in 2009. The temporary housing between 11/2009
102and 09/2011 consisted of an outdoor enclosure with bark and soil substrates ($120 m^2$), an indoor
103enclosure ($35 m^2$) and adjacent off-exhibit night dens ($135 m^2$). Outdoor and indoor enclosures were
104furnished with climbing structures, platforms, ropes and cargo nets. In both enclosures the animals
105were separated from the main viewing area by a glass window. In 2011 the group moved back into the
106newly refurbished chimpanzee enclosure (dimensions as above) with seven of the original tree trunks
107as 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
109their night dens. All dens featured solid cement floors, with resting boards and hammocks (in some of
110them). All chimpanzees were fed five meals a day, consisting mainly of fruits and vegetables. Water
111was available ad lib both in the night cages and in the exhibition yard. During the study period five
112animals were born and five animals died.

113

114*Chester chimpanzees*

115Between the years 1999 and 2012 the Chester Zoo chimpanzee colony comprised of between 22 and
11630 animals (mean $\pm SE$ per year: females 18.6 ± 0.6 , males 7.0 ± 0.3), ranging from neonates to
117animals over 50 years old (mean $18.5 \pm SE 0.25$). The chimpanzee enclosure at Chester Zoo was
118originally built in 1948, and has undergone several major improvements since then [Wehnelt et al.,
1192006]. In 1989, its three small outdoor islands were joined to make one large, grass-covered island of
1202000 m^2 , separated from the public by a water moat. The renovated island includes an outdoor refuge
121area for chimpanzees and, in the spring of 2000, a major re-planting of the island was undertaken.
122This included provision of hammocks, platforms, poles and ropes, making the island more complex

123and naturalistic; any poles that became rotten have been replaced since then. The indoor on-show area
124comprises a circular building (to prevent animals being cornered in a fight) 13 m diameter and 12 m
125high. There is a shallow water moat in front of the viewing windows, to keep chimpanzees away from
126the glass. Off-show bed areas are linked to the indoor enclosure.

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

135*South Lakes ring-tailed lemurs*

136Between 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
138from newly born infants (the unknowns were animals that died at or soon after birth) to adults of 12
139years of age. In December 2008 there was a fire in one of the lemur houses which killed fourteen
140animals. Subsequently lemurs were brought in from three other zoos, resulting in both introductions
141and removals during 2009.

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

149The typical husbandry routine was that the lemurs were counted and visually checked for any health
150concerns at approximately 0810 h daily. The indoor enclosure would then be cleaned without the
151need for the lemurs to be locked outside. Lemurs were scattered twice daily within the indoor
152enclosure but also had access to berries and leaves growing wild around the park.

153*Data and Analysis*

154We defined a wound as any laceration which required veterinary treatment or was perceived by the
155keepers as potentially needing veterinary treatment. We collected incidences of wounding from zoo
156records, together with the date of the record and the animal's identity. These were medical notes and
157medical observations extracted from ZIMS™ records (Zoo Information Management Software, ISIS
1582014). It is likely that there are between-zoo differences in decisions about which events are recorded,
159and for this reason we cannot use these data to draw any meaningful biological conclusions about
160differences in wounding rates between zoos. These data were available for the period 1999-2012 for
161the two chimpanzee groups and 2008-2012 for the lemur group. We calculated mean daily gate
162numbers from daily attendance records kept by the zoos for those years for which data were available
163and within the time frame of the wounding data. By this we mean that we calculated a mean for all
164Mondays, another mean for all Tuesdays, and so on for the entire period for which we had gate
165numbers. We used gate numbers rather than number of people at the enclosure because these are
166historical data for which enclosure visitor numbers do not exist, but also because the papers which
167inspired this study [Lambeth et al., 1997; Williams et al., 2010] used people in the facility as a
168measure of anthropogenic pressure, rather than number of people in actual contact with the animals.
169Furthermore, in both Chester and Taronga the chimpanzee enclosures are in prominent, well-visited
170positions, while the lemurs at South Lakes are free-range, so we are confident that gate numbers are a
171valid measure of visitor pressure.

172Pearson correlation coefficients were used to test associations between total daily wounds and mean
173daily gate numbers for each zoo, to determine if there were daily effects of visitor number.

174**Results**

175 Total numbers of wounding events and mean daily gate numbers for the three primate groups and
176 three zoos are shown in Table 1. There were significant differences in mean daily gate number
177 between days for all three zoos, primarily because of high Saturday and Sunday attendance (Chester
178 $\chi^2 = 1088.07$, $df = 6$, $P < 0.001$; Taronga $\chi^2 = 1283.69$, $df = 6$, $P < 0.001$; South Lakes $\chi^2 = 27.75$, $df =$
1796, $P < 0.001$).

180

[Table 1]

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

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

185 Discussion

186 *Chimpanzee woundings*

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

200observation hours per male and 911 per female for wild chimpanzees at Gombe-Kasakela and Kibale-
201Kanyawara. A comparable figure of 3213 attacks per individual per 100,000 hours was found in the
202captive group at Arnhem Zoo [Noë et al., 1980]. If we assume that our “observation hours” are the
203total available time during which wounding could occur (ie 14 years, or 122,640 hours per zoo), then
204our figures show median rates of 0.81 woundings per 100,000 hours for the males and 3.26 for
205females at Taronga, and 2.4 for males and 2.85 for females at Chester. This may reflect a real
206difference, but is mostly due to our variable “woundings” being different from “attacks” used by those
207authors. In any case, these figures do not support the suggestion that zoo groups of chimpanzees have
208higher rates of violent aggression than wild ones.

209Why do our two chimpanzee zoo groups show no visitor-related increases in wounding when the
210laboratory groups do? One plausible explanation is that the chimpanzees in the laboratory groups are
211more sensitive to human presence. Neither laboratory study [Lambeth et al., 1997; Williams et al.,
2122010] says what numbers of human visitors their chimpanzees are exposed to, but they are not likely
213to be anywhere near the daily numbers faced by the Taronga and Chester animals. There is some
214evidence that animals in zoos may habituate to the large numbers of people they come into contact
215with [Hosey, 2013], in which case what appears to be an indifference to human crowds (at least as
216measured by numbers of woundings) may represent habituation to chronic human presence.
217Furthermore, zoo chimpanzees have more opportunities than those in laboratories to avoid or conceal
218themselves from human visitors [Wagner and Ross, 2008]. It is also possible that chimpanzees in
219laboratories perceive more threat from people than their zoo counterparts. For the laboratory
220chimpanzee the arrival of people on weekdays perhaps signals the likelihood of experimental
221procedures taking place, so the animals respond to this threat rather than numbers of people *per se*.

222***Lemur woundings***

223Our data from the South Lakes ring-tailed lemur group do not support the hypothesis that wounding
224rates are correlated with visitor number. Studies in zoos on the relationship between visitor presence
225and ring-tailed lemur aggression give ambiguous results. There was a visitor-related increase in

226aggression in one group housed in a glass-fronted indoor enclosure [Chamove et al., 1988], but a
227study of a group in a walk-through exhibit showed no significant effect of human presence on the
228ring-tailed lemurs [Perry, 2011]. Our study shows similar findings relating to wounding in that even
229though the visitors were walking amongst the lemurs through their enclosure, it had no effect on the
230number of woundings between members of the ring-tailed lemur group. We have been unable to find
231any published data on wounding rates of wild ring-tailed lemurs, or indeed other captive groups. Our
232conclusion for these lemurs is the same as for the two chimpanzee groups, that there is no evidence
233that increased visitor presence is responsible for increased rates of woundings in these animals in
234captivity.

235Interestingly, human presence has also been implicated in altering the timing of births in some
236laboratory primates [Alford et al., 1992], but this effect appears not to occur in zoo-housed
237chimpanzees [Wagner and Ross, 2008] or gorillas [Kurtycz and Ross, 2015]. We can only agree with
238the latter authors that the effects of zoo visitors on captive animals may be less profound than
239previous studies suggested.

240**Conclusion**

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

250

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

322

323

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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325