

1 **Behavioral responses to injury and death in wild Barbary macaques (*Macaca sylvanus*)**

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25 **Abstract**

26 The wounding or death of a conspecific has been shown to elicit varied behavioral responses  
27 throughout thanatology. Recently, a number of reports have presented contentious evidence  
28 of epimeletic behavior towards the dying and dead among non-human animals, a behavioral  
29 trait previously considered uniquely human. Here, we report on the behavioral responses of  
30 Barbary macaques, a social, non-human primate, to the deaths of four group members (one  
31 high-ranking adult female, one high-ranking adult male, one juvenile male and one female  
32 infant), all caused by road traffic accidents. Responses appeared to vary based on the nature  
33 of the death (protracted or instant) and the age class of the deceased. Responses included  
34 several behaviors with potential adaptive explanations or consequences. These included  
35 exploration, caretaking (guarding, carrying, and grooming) and proximity to wounded  
36 individuals or corpses, and immediate as well as longer-lasting distress behaviors from other  
37 group members following death, all of which have been reported in other non-human primate  
38 species. These observations add to a growing body of comparative evolutionary analysis of  
39 primate thanatology and help to highlight the multifaceted impacts of human-induced  
40 fatalities on an endangered and socially complex primate.

41 **KEYWORDS:** Thanatology · Barbary macaque · Epimeletic behavior

42

### 43 **Introduction**

44 Responses to dying and dead conspecifics have been documented in several non-  
45 human primates, ranging from cannibalism (orangutans [*Pongo abelii*], Dellatore et al, 2009),  
46 to curiosity and exploration (snub-nosed monkey [*Rhinopithecus bieti*], Li et al, 2012;  
47 chimpanzees [*Pan troglodytes*], Biro et al, 2010), to putative compassion and caretaking (e.g.  
48 chimpanzees, Anderson et al, 2010; Biro et al, 2010, Cronin et al, 2011; common marmosets  
49 [*Callithrix jacchus*], Bezerra et al, 2014), and group distress (chimpanzees, Boesch 1991;  
50 Anderson et al, 2010). Epimeletic behavior, i.e., care or apparent altruism to the dying or

51 dead, is widely considered uniquely human (Counts and Counts, 1991), and certain reports  
52 have contended that it is absent in non-human primate species such as geladas (*Theropithecus*  
53 *gelada*; Fashing et al, 2011), and individual chimpanzee populations (Stewart et al, 2012).  
54 However, reports of apparent epileptic behavior from other taxonomic groups (e.g African  
55 elephants [*Loxodonta africana*], Douglas-Hamilton et al, 2006; river otters [*Pteronura*  
56 *brasiliensis*], Davenport, 2010; long-beaked common dolphins, [*Delphinus capensis*], Park et  
57 al, 2013), in addition to the aforementioned examples in non-human primates, have provoked  
58 calls for developing a comparative evolutionary approach towards animal thanatology and  
59 compassionate behavior in particular (Anderson, 2011; Fashing and Nyugen, 2011).

60         Variation in responses to the dying and dead may be related to inter-species  
61 behavioral differences, inter-individual variation in the experience of observing death, or a  
62 reflection of varying strengths of social ties with the deceased (Appleby et al, 2013;  
63 Bercovitch, 2012; Stewart et al, 2012). Due to intensive infant-rearing in mammals,  
64 especially by females (Hirshfield and Tinkle, 1977), the death of an infant is likely to have  
65 notable physical and psychological impacts (Majolo and McFarland, 2009). Unsurprisingly  
66 then, animal thanatology literature, particularly for non-human primates, is largely dominated  
67 by analyses of conspecific responses to infant death (Sugiyama et al, 2009). The most  
68 frequently reported response to infant death is the continued carrying of the infant corpse,  
69 which has been documented in a range of primate species including Japanese macaques  
70 (*Macaca fuscata*; Sugiyama et al, 2009), chimpanzees (Biro et al, 2010; Cronin et al, 2011),  
71 gorillas (*Gorilla beringei*; Warren and Williamson, 2004) and Barbary macaques (*Macaca*  
72 *sylvanus*). Barbary macaque mothers have been observed to carry their dead infants  
73 (Campbell, pers. obs.), while males have been reported to continue using infant corpses in  
74 “agonistic buffering” with other males (Merz, 1978). Females have also been observed to

75 increase self-suckling following the death of their infants, possibly as a means of stress relief  
76 (Majolo and McFarland, 2009).

77         Less frequently observed and reported, particularly in the wild, are the reactions and  
78 responses of non-human primates to dying or dead conspecifics of other age-classes. Such  
79 information could be particularly informative with respect to how variation in social ties may  
80 reflect variation in responses to death (Buhl et al, 2012). Here, we report on the deaths of four  
81 Barbary macaques of differing sex- and age-classes resulting from impact with road vehicles.  
82 In two cases, the monkeys were mortally wounded and the death protracted, while in the two  
83 other cases, death was instant. Supported by photographic and video evidence, we describe  
84 behavioral responses to these events and highlight differences in response according to the  
85 nature of the death and the age-class of the deceased.

86

## 87 **Methods**

88 Observations were made at a study site located in the oak and cedar forest near the city of  
89 Azrou, Morocco (33° 24'N to 05° 12'W; elevation 1,500-2,000 m above sea level). This area  
90 is located within the Ifrane National Park, in the Middle Atlas Mountains. Barbary macaques  
91 are an endangered species (IUCN, 2012) and this region contains the largest remaining  
92 population of the species (van Lavieren and Wich, 2010). Barbary macaques live in multi-  
93 male, multi-female, female-bonded groups and have been shown to form long-term intra- and  
94 inter-sex relationships with conspecifics (Fooden, 2007; Young et al, 2014). The group of  
95 macaques in this report (the Blue group) has been habituated and studied since January 2013.  
96 All deaths occurred at a tourist picnicking site which the group frequently visits. Prior to the  
97 deaths reported here, the group consisted of approximately 34 individuals: eight adult males,  
98 seven adult females, one sub-adult male, one sub-adult female, approximately thirteen  
99 juveniles (as juveniles have not been individually identified for study, this number is an

100 estimate based on an initial census) and four infants. The four reported deaths occurred  
101 between September 2013 and October 2014. Data from focal samples and *ad libitum* scan  
102 samples (Altmann, 1974) were used to calculate dominance hierarchies prior to the first  
103 reported death (calculated from four months of behavioral data; May-September 2013).  
104 David's score calculations (David, 1987) were used to determine the hierarchies, an approach  
105 which has previously been applied in this species (e.g. Kaburu et al, 2012; see supplementary  
106 materials for details). Observations of responses to deaths were recorded using focal and *ad*  
107 *libitum* sampling of all individuals which approached within 15 m of the injured or dead  
108 individual (Altmann, 1974). Behaviors recorded included all orientation toward, approaches  
109 toward, and any social interactions with the injured or dead individual, as well as anxiety-  
110 related behaviours (scratching, yawning). In addition to these field notes, for two of the  
111 observations, responses to the deaths were video recorded using a Sony Handycam DCR-  
112 SX33. For the other observations, only photographic evidence was collected.

113

## 114 **Results**

### 115 *Dominance hierarchy*

116 A significant linear hierarchy was found in both males ( $r=0.90$ ;  $p<0.00$ ;  $n=9$ ) and females  
117 ( $r=0.97$ ;  $p<0.00$ ;  $n=7$ ).

118

### 119 *Observation 1: Protracted death of high-ranking female*

120 The highest-ranked cycling female of the group, MA, was hit by a bus when crossing a road  
121 at approximately 15:00 on 27/09/2013. Visible injuries included partial detachment of one leg  
122 and a large laceration of her anogenital swelling. MA was able to climb into a tree,  
123 approximately 10 m above the ground. Two adult males (RG and IS) climbed the tree and  
124 approached her, teeth-chattering and lip-smacking; behaviors associated with reassurance and

125 reconciliation. Both monkeys were observed delicately touching and inspecting the wounds.  
126 As the other group members left the tourist site to go into the forest to sleep they made  
127 several “long-calls”, presumably to MA, from approximately 100 m away; such calls are  
128 usually used when an individual is separated from the group or the group is searching for a  
129 separated individual. MA vocalised back but was unable to move to join them. Subsequently,  
130 the group began to make fear screams and grimacing facial displays. The group, now  
131 including IS and RG, then left to sleep approximately 500 m from MA. Approximately one  
132 hour after the group left, RG returned to MA. They teeth-chattered at one another, he touched  
133 her injured leg several times, including prolonged body contact between his hand and her  
134 injured leg (figure 1a), and groomed her (figure 1b). Approximately 30 minutes after the  
135 return of RG, several more males returned from the forest (IS, RO, GU) and sat below the  
136 tree MA was in, with some climbing up sit beside her. As it became dark (c.19:00), all males  
137 eventually left MA to join the rest of the group at their sleeping site. An hour after dark, IS  
138 returned and sat in an adjacent tree to MA, where he remained until the observers left for the  
139 night (c.22:00).

140

141 When observers returned at approximately 05:00, MA’s corpse was discovered unmoved  
142 from the tree in which she was previously observed. IS was found in the same adjacent tree as  
143 he had been seen in the night before. It is assumed IS remained with MA when she died  
144 during the night. At c.06:30, IS crossed the canopy to approach MA’s corpse. He touched her  
145 body twice, before moving back to the tree he had been in before, where he remained for the  
146 following eight hours, until 15:41, when he left the tree to feed for the first time that day. The  
147 rest of the group returned to the vicinity of MA’s corpse at c.09:35. Table 1 in the  
148 supplementary material provides a detailed timeline of group members’ responses to MA’s  
149 corpse. Males showed the strongest behavioral response. Three males (GU, TI and FE)

150 entered the tree she was in, spending an average of 18:09 ( $\pm$ 10:29) minutes in the tree with  
151 her. One male (TI) approached within 1 m of the body, displaying 5 anxiety-related behaviors  
152 (scratching and yawning) and six exploratory/vigilance behaviors (head-bobbing). Two (of  
153 six) adult females (SA and WA) passed the tree without showing any reaction, while two  
154 others (IZ and EL) were not seen near the body. The two remaining females (CO and PE)  
155 spent a short amount of time within 10 m of the body (average 2:28 minutes) during which  
156 they watched the body and exhibited one anxiety-related behavior (scratching) and three  
157 exploratory/vigilance behaviors (glance and head-bobs). One sub-adult female (NI) spent  
158 more than 20 minutes within 1 m of the body, head-bobbing at her four times, grooming  
159 herself for 2:44 minutes, and grooming the body for 14:00 minutes (video 1 in supplementary  
160 material). Three juveniles entered the tree MA's body was in and remained for approximately  
161 one minute, spending the entire time watching her. At approximately 17:00 when the group  
162 had begun to move away from the tourist site, and 19 hours since MA was last seen alive,  
163 local merchants removed the corpse from the tree for burial as it posed a danger to visiting  
164 tourists. When the corpse was removed from the tree, the high-ranking male RG sprinted  
165 back to the corpse, screamed, threatened and charged at the merchants as they took the body  
166 for burial.

167

#### 168 *Observation 2: Immediate death of alpha male*

169 FE, the highest-ranking male in the group, was killed on 31/10/13 at 12:20 following a  
170 collision with a vehicle on a road. He died instantly and there were few signs of external  
171 damage or wounds. When local merchants removed the corpse to avoid conflict between the  
172 monkeys and feral dogs, at least three adults within the group screamed at the merchants,  
173 while at least three juveniles and a sub-adult female (UR) observed the body from trees  
174 above. Due to crowding over the corpse by tourists and the initial vocal reaction of the

175 monkeys, FE was swiftly taken to be buried. UR and approximately three juveniles followed  
176 the sellers to the burial site, an open area the monkeys had never before been observed to use,  
177 and watched silently from a distance as the body was buried. They returned to the group  
178 several minutes after the burial. No adult monkeys were observed near the site during this  
179 burial.

180

181 *Observation 3: Immediate death of juvenile*

182 On 19/05/14 at 14:00, a male juvenile (between 2-3 years old) was struck by a vehicle and  
183 instantly killed (struck in the head, one eye hanging out and jaw dislocated). The body was  
184 moved off the road by local merchants immediately following the collision. The group  
185 screamed and became extremely agitated, causing the merchants to abandon the corpse. One  
186 adult male, CA, took the corpse up a tree (figure 2). CA remained with the juvenile's corpse  
187 for over 30 minutes, before eventually dropping it to the ground. UR (sub-adult female) spent  
188 several minutes with the body on the ground. The body was guarded by group members  
189 (including CA and another adult male, GU) for approximately 80 minutes after the accident,  
190 including threatening and charging a park official who attempted to get close to the body.  
191 After the group moved away from the corpse and left the area, local merchants removed the  
192 corpse for burial. CA and GU followed the merchants and corpse to the burial site (the area  
193 used to bury FE described previously). During the burial, adult male monkeys threatened and  
194 vocalised at the merchants. CA was at the forefront of the group, approaching as close as 5 m  
195 to the merchants and threatening them. One unidentified male, the lowest-ranking female  
196 (PE) and approximately three juveniles joined them at the burial site (figure 3). Many  
197 performed aggressive calls and threats. Due to the clear agitation of the monkeys and the  
198 potential risk of aggression from the group, particularly from CA, the burial was abandoned  
199 and all human observers moved away from the corpse. CA moved immediately to sit near the

200 body and remained in this area with at least one other juvenile for two hours before they  
201 eventually departed and the body could be buried.

202

203 *Observation 4: Protracted death of infant*

204 On 24/10/14 at 12:03, WE, the approximately 4-month-old infant of the female WA, was hit  
205 by an automobile, partially severing one leg. WA immediately carried WE, still alive at this  
206 point, into a tree and began grooming her. A sub-adult male (ME) approached the pair and  
207 teeth-chattered at them. At 12:25, while adjusting position within the tree, WE fell around 3  
208 m to the ground. WA climbed down from the tree and dragged WE approximately 5 m, but  
209 she was displaced from WE by the presence of merchants, tourists and dogs. WE continued  
210 to struggle on the ground, crawling on her arms, but succumbed to her injuries at 12:33.

211 Table 2 in the supplementary material provides a detailed timeline of group members'  
212 responses to WE's corpse. After WE's death, WA climbed down from the tree and inspected  
213 the body, but was disturbed by a local merchant who came close to determine if the infant  
214 had died. WA threatened the merchant and retreated into a tree. When the merchant left, WA  
215 descended, inspected and lifted the corpse before carrying it approximately 10 m to the other  
216 side of the road (see video 2 in supplementary material). She then moved several metres away  
217 to feed on bread distributed by tourists. At 12:47, feral dogs approached the corpse; WA  
218 alarm barked and threatened the dogs, which left after several minutes. Over the next hour,  
219 WA engaged in extensive bouts of self-grooming in a tree above WE's corpse, occasionally  
220 making distress/fear screams (see video 3 in supplementary materials). At 14:30, WA left the  
221 tree and the corpse. At 14:35, after the whole group had moved more than 100 m away from  
222 the corpse and were leaving the tourist site, a local merchant took the corpse for burial. Many  
223 members of the group rushed back to the merchant carrying the corpse and performed several  
224 threatening behaviors (bared teeth, ground slaps, growling etc.). At the forefront of the group

225 were WA, two adult males (GU and IS) and another adult female (IZ). The monkeys reacted  
226 thus for around 30 seconds, until the merchant was out of sight, after which they moved away  
227 from the tourist site. No monkeys followed the merchant to the burial site. For the remainder  
228 of the day, WA was observed intermittently (approximately every 30 minutes) making  
229 distress/fear screams and displaying vigilance/searching behavior. At c.16:00, WA left the  
230 group to return in the direction of the tourist site and stayed 75 m from the tourist site (100 m  
231 from the rest of the group) for approximately 45 minutes, continuing to display  
232 vigilance/searching behavior, before returning to the group. The next day, she sporadically  
233 made distress vocalisations and was often seen away from the group.

234

## 235 **Discussion**

236 This report presents the behavioral responses of conspecific group members to the  
237 mortal wounding and death of four wild Barbary macaques. In these accounts, several  
238 behaviors directed to the dying and dead are reported which are similar to those seen in other  
239 mammals, especially non-human primates; namely exploration (sniffing and touching of  
240 wounds or corpses, Buhl et al, 2012) and caretaking behaviors, including guarding (Boesch  
241 1991), carrying (Fashing et al, 2011), and grooming of corpses (Boesch 1991).

242 Affiliative behaviors resembling epimeletic behavior were shown in both cases where  
243 death was protracted. Prior to death, MA was attended by males which examined her wounds,  
244 displayed mollifying facial displays (lipsmacks and teeth-chattering), and groomed her. When  
245 WE was wounded, her mother carried and groomed her, and both the mother and infant  
246 received affiliative teeth-chattering from a sub-adult male of the group. These behaviors are  
247 similar to those observed in chimpanzees (Anderson et al, 2010) and more recently in  
248 common marmosets (Bezerra et al, 2014), where individuals were attentive and affiliative to  
249 dying conspecifics. In the cases presented here, some affiliative behaviors continued post-

250 mortem. Grooming of corpses has been witnessed in a number of non-human primates,  
251 typically with deceased infants (Boesch 1991; Anderson et al, 2010; Biro et al, 2010; Cronin  
252 et al, 2011; Fashing et al, 2011; Li et al, 2012; Buhl et al, 2012). Explorative or curiosity  
253 behaviors towards the body of the dead conspecifics have been recorded in other non-human  
254 primate species (Biro et al, 2010; Fashing et al, 2011; Cronin et al, 2011) and appears to be a  
255 common reaction in the majority of reported animal thanatology (Bercovitch, 2012). Such  
256 responses have been suggested to reflect a cognitive inability of the animal to “understand”  
257 death. Alternatively, they may reflect an adaptive “wait and see” strategy whereby  
258 conspecifics are unsure of the state of the injured, diseased or deceased, requiring time to  
259 make an accurate assessment of whether to abandon their stricken group member; this  
260 strategy could have long-term advantages if individuals sometimes recover (Hrdy, 1999;  
261 Sugiyama et al, 2009; Li et al, 2012; Appleby et al, 2013). Additionally, these behaviors may  
262 present a learning opportunity, helping individuals to avoid a cause of death or injury if  
263 similar conditions are encountered again (Cronin et al, 2011).

264         In all four cases reported here, other group-members screamed, threatened, and  
265 charged when humans or feral dogs approached or moved the body. They also followed  
266 merchants to the burial site. Guarding of corpses has been reported in, among others,  
267 chimpanzees (Boesch 1991), rhesus macaques (*Macaca mulatta*, Buhl et al, 2012) and  
268 common marmosets (Bezerra et al, 2014). The male IS remained with MA overnight,  
269 recalling the all-night attendance following a female chimpanzee’s death reported by  
270 Anderson et al (2010). Unlike other non-human primate examples of motherly reactions to  
271 infant death (Biro et al, 2010; Fashing et al, 2011; Li et al, 2012), WA carried her deceased  
272 infant only for a short period of time, although this may be a consequence of the highly  
273 disturbed environment at the tourist site (including feral dogs, local merchants, and tourists).  
274 In line with the aforementioned “wait and see” strategy, guarding and/or carrying of corpses

275 could be advantageous if individuals sometimes recover or by preventing predation (Hrdy,  
276 1999; Sugiyama et al, 2009). Violent deaths with graphic injuries may also cause heightened  
277 behavioral and physiological stimulation, leading to increased guarding and aggression (Buhl  
278 et al, 2012). These responses can be maladaptive; for example, when mothers carry dead  
279 infants, the cost is predominantly energetic (Sugiyama et al, 2009). We also observed  
280 instances of individuals separating themselves from the group or placing themselves at risk  
281 by guarding corpses in close proximity to humans and feral dogs.

282         The injury and death of the high-ranking female, MA and the death of the juvenile,  
283 invoked strong, nearly group-wide responses, with males showing particularly strong  
284 reactions in both cases. In contrast, responses to the death of the alpha male FE and the infant  
285 WE were limited to a few individuals. The strength of social ties between the surviving and  
286 deceased has been proposed to explain the variation in the strength of responses to a death  
287 (Appleby et al, 2013; Bercovitch, 2012; Stewart et al, 2012) and possibly to injury as well. In  
288 female-bonded groups, dominance and kinship are expected to predict the strength of female  
289 social bonds (Johnson et al, 2014), while Barbary macaque males are known to invest time  
290 and effort in forming social bonds with infants and juveniles through playing and grooming  
291 (Deag, 1980; Small, 1990) and have recently been shown to form stable social bonds with  
292 other adult males (Young et al, 2014). The protracted nature of MA's injury and death may  
293 have allowed more opportunity for reactions from other group members. Strong social bonds  
294 and paternal care may explain the sustained defense of the juvenile corpse, particularly by  
295 males. It is also possible that the very graphic nature of MA's and the juvenile's injuries  
296 evoked a strong response among group members (Buhl et al, 2012). The comparatively  
297 subdued behavioral response to the alpha male's (FE) death may be a consequence of weak  
298 social ties, or may simply have been due to the relatively quick removal of the corpse and the  
299 proximity of local merchants and tourists. The injury and death of the infant WE produced

300 notable responses only from the mother and a sub-adult male, though the moving of her  
301 corpse elicited strong aggressive responses from several adults in the group, both males and  
302 females. As a 4-month-old infant of a low-ranking female, it is possible that WE had not yet  
303 formed any strong relationship in the group other than with her mother. Concurrently, the  
304 mother's low rank may reduce the likelihood of other group members, particularly females,  
305 investing in the protection of her infant.

306 In all cases, the injury and death of a group member caused observable distress to  
307 other monkeys, including vocalisations, agitation, and anxiety-related behaviors. Similar  
308 responses have been reported in chimpanzees following the death of a group member  
309 (Boesch 1991; Anderson et al, 2010). Aside from these immediate reactions, there were also  
310 obvious longer-lasting effects of these deaths on some individuals, including prolonged  
311 distress behaviors, separation from the group, and behavioral inactivity. In the case of WA,  
312 distress behaviors (vocalisations and searching behaviors) were displayed long after the  
313 burial of her infant, and continued the following day. Our report outlines the complex  
314 behavioral responses of Barbary macaques to dying and deceased conspecifics, adding to our  
315 understanding of both Barbary macaque sociality and more broadly, animal thanatology.

316

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326

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408

## 409 **FIGURES**

410

411 **Figure 1:** RG inspecting the wound of (a) and grooming (b) the mortally wounded MA  
412 (27/09/13).

413

414 **Figure 2:** CA (adult male) takes corpse of juvenile male into tree (centre of picture)  
415 (19/05/14).

416

417 **Figure 3:** Photograph showing group members following the corpse of the dead juvenile  
418 male to an exposed burial site. The monkeys of this group had previously never entered this  
419 exposed area. The blue circle highlights the burial site, the red circles highlight group  
420 members (19/05/14).

421