

1 COMMENTARY

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3 **Chimpanzees' responses to the dead body of a nine-year old group**
4 **member**

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15 Short title: Chimpanzee group's response to death

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23 ABSTRACT

24 The social behavior of chimpanzees has been extensively studied, yet not much is
25 known about how they behave in response to the death of a group member. Here we
26 provide a detailed report of the reactions of a group of chimpanzees to finding the dead
27 body of a nine-year-old male group member. The behavior of the group was
28 characterized by quiet attendance and close inspections punctuated by rare displays.
29 Moreover, the body was continuously attended and closely inspected by several adults
30 and juveniles, including an adult male who formed a close social bond with the
31 deceased individual after the deceased individual's mother died four years earlier. When
32 considered with observations of how chimpanzees respond to dead infants and adults in
33 this group and in others, these observations suggest that chimpanzees' responses to
34 death may be mediated by social bonds with the deceased individual. The results are
35 discussed in light of recent reports on chimpanzees' reactions to dead community
36 members and more general primate thanatology.

37

38 Keywords: social relationships, response to death, thanatology, *Pan troglodytes*, group
39 processes

40

41 INTRODUCTION

42

43 There is growing interest in documenting and understanding how many primate species
44 respond to death (prosimians, New World Monkeys, Old World Monkeys and apes
45 reviewed in [Anderson 2011; see also Fashing et al. 2011; Li et al. 2012; Buhl et al.
46 2012; Bezerra et al. 2014]). Primates' behavioral responses toward deceased infants
47 have predominated (e.g. [Biro et al. 2010; Cronin et al. 2011; Hosaka et al. 2000;
48 Kooriyama 2009; Matsuzawa 1997; Sugiyama et al. 2009; Watson et al. 2015]). In
49 conjunction, these reports indicate that primate mothers often remain attached to the
50 body of their deceased offspring in form of carrying around the body and protecting it
51 from interactions with other group members. One study reported the repeated
52 interactions of a chimpanzee mother with her deceased 16-month-old daughter in the
53 transitional phase between constant care and separation [Cronin et al. 2011]. Among
54 chimpanzees specifically, mothers seem to gradually allow conspecifics to approach the
55 corpse and even condone manipulation of and playful interactions with the body (see
56 [Biro et al. 2010; Hosaka et al. 2000]).

57 Chimpanzees are highly social animals. They live in social groups, spend a
58 substantial amount of their time grooming and playing with each other and have the
59 tendency to re-establish relationships after they have been compromised by aggression
60 (e.g. [de Waal 1998; Nishida et al. 1999; van Lawick-Goodall 1968]). A paucity in our
61 understanding of chimpanzees' sociality, however, exists with regard to their tendency
62 to respond to the loss of group members. Where chimpanzees establish and actively
63 maintain social bonds throughout life (e.g. [Langergraber et al. 2009; Mitani 2009]), we
64 know little about how these bonds might translate to behavior when confronted with
65 death.

66 While these observations provide valuable insights for our understanding of how
67 chimpanzee mothers cope with the abrupt ending of the life of their closest kin, we
68 know little about how the broader chimpanzee community responds to death, and
69 specifically to the loss of a group member who is not an infant but rather has established
70 social relationships with multiple others (hereafter “socially integrated” or “socially
71 active”). Stewart and colleagues [2012] observed that the responses of the Gombe
72 chimpanzees to the dead body of an adult female community member ranged from
73 “curious observation and passive investigation (e.g. smelling and grooming) to the
74 shaking, dragging, and frustrated beating of the body” [Stewart et al. 2012, p 1]. More
75 specifically, based on their observations, they proposed that the age of the “griever”
76 should be incorporated in the quest to better understand what chimpanzees experience
77 in response to death. They also noted that there is substantial individual and group-level
78 variation in chimpanzees’ death responses, as this report differed substantially from an
79 earlier account of different Gombe chimpanzees who refrained from touching a dead
80 body [Teleki 1973]. Anderson and colleagues [2010] reported a case of a group
81 response to ‘the peaceful demise of an elderly female’ (p 349), a process characterized
82 by ‘several behaviors that recall human responses to the death of a close relative’ (p
83 349). Only by aggregating careful descriptions of primates’ behavioral responses when
84 confronted with naturally occurring deaths will we ultimately move toward an
85 understanding of how nonhuman primates process death and uniquely advance our
86 understanding of primate sociality [Anderson 2011; Cronin et al. 2011].

87 Following is a detailed report of the reactions of a group of chimpanzees to
88 finding the dead body of one of the group’s socially active members: a nine-year-old
89 adolescent male (“Thomas”). The observations start when the dead body is encountered
90 by the chimpanzee caretakers and presumably also by the other chimpanzees. The
91 behaviors of the chimpanzees in the area where the body was found are reported and

92 subsequently compared to their behaviors toward two chimpanzee infants that had died
93 previously in the same community and compared with reports from other communities
94 in order to shed light on group responses toward the death of an active social member of
95 a chimpanzee group.

96

97 METHODS

98

99 Study Site and Subjects

100

101 Observations were conducted at Chimfunshi Wildlife Orphanage Trust (Chimfunshi), a
102 chimpanzee sanctuary accredited by the Pan African Sanctuary Alliance (PASA) in the
103 Copperbelt region of Northwestern Zambia located approximately 60 km west of
104 Chingola on the southern bank of the Kafue River. Many of the chimpanzees at
105 Chimfunshi were rescued from illegal trade in Zambia between 1983 and 2004 and
106 brought to Chimfunshi for rehabilitation and socialization. This report focuses on
107 “Group 2”, a group comprised of 43 individuals (3 adult males, 17 adult females, 7
108 juvenile males, 10 juvenile females, 6 infants). In Group 2 specifically, 65% of the
109 population was born in the group (35% thus being wild-born), and the group had been
110 closed to the introduction of newly rescued individuals for over ten years prior to the
111 event (for additional demographic details see [Cronin et al. 2014]).

112 Group 2 lives outdoors in densely vegetated Miombo forest suitable for
113 chimpanzees [Ron & McGrew, 1988]. All enclosures have indoor holding areas used
114 for mid-day feeding and visual health inspections, solar-powered electric fencing
115 around the perimeter, and one observation deck. Group 2 inhabits a 0.65 km² (160 acre)
116 enclosure. Chimpanzees are provisioned in or near the indoor holding area from 11:30
117 AM until 1:30 PM; the whole group is in their forested enclosures at all other times of

118 the day and overnight. Given the large size of the enclosure, it is not uncommon for the
119 chimpanzees to be out of sight for researchers located at the fence or observation deck.

120 The deceased individual, Thomas (male), was born at the sanctuary on the 15th
121 of February 2001 to TamTam, a wild-born chimpanzee who entered the sanctuary in
122 July 1994 at approximately 7 years of age after confiscation from an Egyptian Circus.
123 TamTam died in late 2006 when Thomas was 5 years old. In general, Thomas was
124 characterized as a highly social individual, which was reflected in his tendency to
125 frequently roam between sub-parties in the enclosure and remain near the entrance of
126 the feeding building, where he, together with Pan (adult male), would vocalize or
127 physically engage (greeting, playing, provoking) with passing conspecifics, mostly the
128 adult females (Staff reports, pers.comm. 2007-2010).

129 Thomas was noted as missing from the mid-day feeding on May 16, 2010. Post-
130 mortem inspection revealed that Thomas probably died from the combination of a viral
131 and bacterial infection, causing severe impairments in breathing. The veterinarian was
132 unable to determine how recently the death had occurred but the body was rigid upon
133 removal from the enclosure. No injuries were found on his body.

134

135 Data Collection and Coding

136

137 On May 18, 2010, after two days of absence during mid-day feeding, Thomas' dead
138 body was found by one of the chimpanzee caretakers (JK) approximately 3 meters from
139 the fence line (see Figure 1 for orientation of body). The body had not been present in
140 this location in the preceding hours thus it appeared that one of the chimpanzees had
141 recently dragged the body to this visible location. Upon immediate signaling of JK,
142 researcher EJC rushed to the location, arriving approximately 30 seconds after JK.

143 Upon arrival, EJC started video recording the scene immediately (Suppl. Video 1).
144 KAC (Suppl. Video 2) arrived 3 minutes later.

145 The scene was subsequently recorded uninterrupted for 20 minutes (Suppl.
146 Video 1). EJC recorded with a Canon miniDV camera, approximately 1.5 meters from
147 KAC, who recorded with a Sony HD Handycam. Data collection adhered with PASA
148 guidelines as well as the American Society of Primatologists Principles for the Ethical
149 Treatment of Non Human Primates.

150 Videos were synchronized for simultaneous dual views using ELAN 3.9
151 [Chebotko et al. 2004]. Behavior was coded using the ethogram in Table 1. Thomas'
152 dead body was treated as a passive focal subject, where proximity to the body and
153 behaviors toward the body were coded for all chimpanzees within a radius of 3 meters
154 (reliable view) using scan sampling every 30 seconds [Martin and Bateson 2007]. For
155 behavioral coding, we did not include physical contact with the body other than
156 "inspection" and "hit", for in many instances this would have been difficult to code
157 reliably due to the obstructed view from several individuals surrounding the body.
158 Proximity data were coded conservatively with 0.5 meter increments (range 0.5 to 3.0
159 from the body; distances less than 0.5 were coded as 0.5). In addition, all displays
160 involving the body and one extended grooming event (teeth cleaning) are reported in
161 detail.

162

163 RESULTS

164

165 Presence and Proximity of Group Members to Thomas' Body

166

167 At the start of the data collection, two chimpanzees (Pippa: adult female, and Vis:
168 juvenile male) were present near Thomas' body. The proportional presence of the group

169 around Thomas' body throughout the observation window is presented in Figure 2.
170 Given the large size of the enclosure of Group 2 (0.65 km²) and the natural tendency of
171 chimpanzees to organize themselves in fission-fusion communities [Stanford 1998], we
172 do not know to what extent all group members were aware of the death and location of
173 Thomas at the time of video recording. Therefore, all the presented data are relative to
174 the total number of individuals that were observed (and hence assumed to be
175 knowledgeable of the location of the body) at least once within a radius of 3 meters of
176 the body (N=28, 65% of the group) throughout the entire observation window (thus
177 likely making for a conservative estimate of the proportion of individuals present at
178 Thomas' body). The average percent of the knowledgeable group present at the location
179 of the body over the 20-minute period was 42.8% (SD=23.1). Just prior to minute 3.5
180 and 17, a display by Pan and Violet (the alpha female), respectively, scattered the group
181 from the body (see below for detailed descriptions). After minute 17, the chimpanzee
182 caretakers started their attempt to lure the chimpanzees away from the body (minute 17
183 seconds 21, Suppl. Video 1), in order to be able to safely remove the body from the
184 enclosure. Excluding the data of minute 3.5 and minutes 17.5 – 20, the average
185 percentage of the knowledgeable group present at the location of the body was 48.5%
186 (SD=20.7).

187 The average proximity of the chimpanzees to the body throughout the
188 observation window was 0.92 meters (SD=0.57). Since space is limited within the 1
189 meter diameter around the body, we also report the median and IQR for proximity to the
190 body (both 0.5 meters). Excluding the data of minute 3.5 and minutes 17.5 – 20, the
191 proximity measures representing chimpanzees' closeness to the body remained exactly
192 the same ($X \pm SD = 0.92 \pm 0.57$ meters, Median & IQR=0.5 meters). Notably, immediately
193 following the two displays described below, the average proximity of the chimpanzees

194 differed by more than two standard deviations from the overall average proximity (both
195 1.3 meters), indicating that the displays temporarily distanced others from the body.

196

197 Behaviors of the Group Members in Proximity to Thomas' Body

198

199 The behaviors of the group members who were present at Thomas' body (within 3
200 meters) are presented together with frequencies in Figure 3. We observed individuals
201 peering (watching the body closely from within 35 cm, see ethogram), inspecting, and
202 hitting the body, yet most frequently, the group members sat quietly around the body
203 (resting: 72.6% of scored behaviors; see Figure 4a), while occasionally one or more
204 individuals would physically inspect the body (5.1% of scored behaviors; see Figure 4b).
205 In total, at least nine individuals physically interacted with the body at least once, while
206 at least 22 individuals peered at the body at least once (see Figure 3). Videos in the
207 supplementary data show the full time course of events (Suppl. Video 1 & 2).

208

209 Displays

210

211 During the observation period, two individuals displayed over Thomas' body: Pan
212 (adult male) and Violet (adult female).

213

214 *Pan displays over Thomas' body*

215

216 At 2m09, two adult females and their offspring (Masya and Diana) were being followed
217 on their way to the body, where at least four individuals had gathered already (2m13).
218 An unknown individual started vocalizing, and several individuals subsequently joined.
219 Between 2m12-2m20, at least two adult females (Violet and Diana) touched the body,

220 then Pan (2m20) and Zsabu (2m24; alpha male) arrived. Between 2m25-2m28, Pan
221 displaced an adult female (presumably Pippa) who appeared to touch Thomas' body.
222 Over the next 20 seconds, several adult females peered at the body, as did Pan and
223 Zsabu. Zsabu and Pan left the scene a few seconds before Noel touched the body
224 between 2m58-3m09 and subsequently brought her hand to her lips. Pan returned at
225 3m17, when he approached Noel, approximately 3m from body. Together with Violet,
226 Pan peered at Noel, where he held his face close (within 10cm) to Noel's face for 1
227 second. Subsequently, Pan departed Noel bipedally in the direction of the body, where
228 at least 12 individuals had gathered within 3 meters of the body. Immediately following,
229 Pan grabbed a branch and lunged with high speed over the body. In response to Pan's
230 lunge, the gathered individuals scattered, and at least 4 individuals screamed. At 3m20-
231 3m22, Pan lunged past the left side of the body, piloerect, with both arms raised, then
232 hits an unidentified female or the ground near her. The respective female immediately
233 started chasing Pan, during which they both disappear from the scene.

234 After his display, Pan forced access to the body by pushing through others on
235 three separate occasions, then peered closely and inspected the body (at 6m21-6m51,
236 9m57-10m54, and 16m46-17m18). Moreover, between 18m35-18m40, Pan arrived at
237 Thomas' body running and mildly displaying again (pulling branches twice, shortly
238 chasing a female once), after which he left the scene again at 18m42 (still running).
239 While not being counted present within a 3-meter radius of the body, Pan was captured
240 on video approximately 6 meters southwest of the body three more times during
241 infrequent video scans that occurred at 11m20, 12m53 and 13m19 (see Suppl. Video 2).

242

243 *Violet displays over Thomas' body*

244

245 At 17m0, Violet sat down 1 meter north of the body, while holding on to a branch with
246 her left arm. From 17m0-17m10, she watched the body, while at least 16 individuals
247 were present within a radius of 3 meters. At 17m11, Violet, together with Trixie (adult
248 female) and Nikkie (adolescent female), started looking west toward the food building
249 located approximately 30 meters away where chimpanzee caretakers had gathered to
250 start luring the chimpanzees away from the body. At 17m18, Pan left the scene; Violet
251 watched him leave. At 17m20, one of the females began to pant hoot. At 17m21, the
252 chimpanzee caretakers started calling the chimpanzees toward the food building, which
253 coincided with at least four individuals at the body vocalizing with increasing intensity
254 (17m21 – 17m30). Between 17m24 and 17m30, Violet built up her scream while
255 standing bipedally and holding on to the same branch as before with her left arm.
256 During this display, Violet swayed back and forth while intensifying her scream and
257 slowly getting closer to the body. At 17m30, Violet released the branch and hit the body
258 hard with her right arm. After hitting the body, Violet immediately lunged away from
259 the body, leaving the scene running northwest, where she halted approximately 3.5
260 meters from the body at 17m33. From 17m33 – 17m39, Violet stood quadrupedally
261 with her back toward the body, after which she started moving further northwest until
262 she was out of sight at 17m42.

263

264 Teeth Cleaning

265

266 We describe in some detail one additional behavior directed to Thomas' body, given the
267 persistence with which the female performed it.

268 Following the display by Violet, who hit Thomas' body at 17m30 (see above),
269 several individuals returned to the body to within 0.5 meters at 17m35-17m37 (adult
270 females: Coco, Dora and Noel; juveniles: Darwin, on the back of Dora, and Taylor).

271 Nikkie and Trixie had remained in proximity to Thomas' body throughout Violet's
272 display. At 18m01, Noel started inspecting Thomas' face with her mouth and hands.
273 She paused briefly while caretakers were calling the chimpanzees toward the feeding
274 building, but at 18m29 Noel resumed inspecting Thomas' face. At 19m17, Noel picked
275 a piece of grass, put it in her mouth, and started to inspect Thomas' face with her hands.
276 At 19m21, Noel took the grass from her mouth and used it to clean Thomas' teeth. At
277 19m47, Noel raised her hands, touched the end of the grass stem with her free hand, put
278 the hand that touched the grass stem in her mouth and did the same with the grass stem.
279 Between 19m59-20m08, Noel resumed cleaning Thomas' teeth with her grass stem,
280 regularly putting the grass stem in her own mouth as well. Nina (Noel's daughter) was
281 the only other chimpanzee present. When the recording ended at 20m08, Noel and Nina
282 were still within 0.5 meters of Thomas body while Noel cleaned Thomas' teeth with a
283 grass stem and Nina watched (see Figure 5).

284

285 DISCUSSION

286

287 Reported here are the behavioral responses of a group of chimpanzees after finding the
288 dead body of an active social group member, a 9-year-old male. The observations
289 occurred during a unique window where most chimpanzees presumably arrived at the
290 body for the first time and could behave freely in their natural environment for
291 approximately 20 minutes, after which the chimpanzee caretakers started the process of
292 removing the body from the enclosure. While reports on the behavioral responses of
293 primate mothers toward their deceased offspring have accumulated over time allowing
294 for an interesting insight into the strength of primate mother-infant bonds and flexible
295 nature of their response, little is known about how chimpanzees respond to the death of
296 older, presumably more integrated members of the social group.

297 Our observations show that more than half of all group members approached
298 Thomas' body at least once and that close to half of the group members remained in
299 close proximity to his body for the full observation period. These behavioral responses
300 are strikingly different from the group responses to the death of a chimpanzee infant in
301 the same group, where only one adult female (Noel) other than the mother (Masya)
302 spent time in close proximity to the dead body, and only 3 juveniles and 4 adults (3
303 females) briefly interacted with the body (see [Cronin et al. 2011]). When another
304 chimpanzee infant from the same group died one year later, the behavioral responses of
305 the group were even less pronounced, as the mother let other individuals (primarily two
306 juveniles) play with the dying infant before the moment of death. Similar to the first
307 case of infant death, there was no prolonged group attendance in close proximity to the
308 body (while there was ample opportunity for it), nor any close inspections by group
309 members other than the mother [Cronin et al. unpublished data]. These opportunistically
310 observed group processes indicate that chimpanzees' responses to the death of group
311 members may be mediated by age, and the social integration or social history of the
312 deceased. Interestingly, anthropological accounts of early human societies similarly
313 indicate that while the death of an infant remains largely insignificant, the death of an
314 active, adult group member triggers the society into an elaborate state of grievance and
315 rituals [Hertz, 1960]. While more observations are obviously needed, these findings
316 indicate that social animals may share the tendency to respond to the death of socially
317 active group members collectively, while socially less active group members may be
318 only attended to by close relatives (see [Anderson et al. 2010; Cronin et al. 2011; Hertz,
319 1960]).

320 It is difficult to assess the impact of the chimpanzees' captive environment on
321 their responses to finding a dead group member. While wild chimpanzees may have
322 more space to roam, the chimpanzees of this particular group in Chimfunshi have

323 sufficient space available to disperse in sub-groups typical of their fission-fusion form
324 of subsistence [Ron & McGrew 1988; Stanford 1998]. However, it is plausible that
325 because these chimpanzees are provided supplementary food every day in a set location
326 that brings the group into proximity, members of the group may have discovered the
327 body sooner than they would have if they were more dispersed in the wild. The specific
328 behavioral patterns described in this report – the resting party around the body, the adult
329 male’s behavior, the teeth cleaning – are not easily interpreted by referring to the
330 chimpanzees’ captive environment. Lastly, to consider differences between
331 chimpanzees’ responses to the death of infants versus integrated members of the society,
332 the report compares the focal observations to the chimpanzees’ behavior during another
333 death encounter in the same group [Cronin et al. 2011], thereby “controlling” for any
334 kind of behavioral artifact induced by the captive environment.

335 The behavior of Pan supports the hypothesis that social bonds may influence
336 chimpanzee responses to the death of group mates. Staff reports from 2007-2010
337 indicate that after TamTam died, Thomas continuously stayed close to Pan while
338 foraging and sleeping, both outdoors and inside the holding building (where space is
339 limited), and received support from Pan during agonistic encounters. Pan was one of
340 only two individuals to display near the body and, unlike Violet, he refrained from
341 physically contacting the body during his displays. The observation that Pan visited and
342 inspected Thomas’ body more than any other adult male may reflect the strong social
343 connection they shared in life. The fact that chimpanzee males adopt and take care of
344 (unrelated) infants and juveniles in the wild (see [Boesch et al. 2010]) and form long-
345 term social bonds [Mitani 2009], at least allows for this interpretation to be considered.
346 Alternatively, the display behaviors could be interpreted more in line with the potential
347 function of the chimpanzees’ physical inspections of the body: learning about their
348 close surroundings, in this case ‘death’ [Cronin et al. 2011; Hosaka et al. 2000]. By

349 engaging in behaviors that would normally elicit clear behavioral responses, both Pan
350 and Violet could have acquired reliable information on the status of Thomas' body (see
351 also the increased investigatory reactions of the other chimpanzees after Violet's
352 display). Clearly, an interaction between these two alternatives would also be possible,
353 where the individuals that were socially most connected with Thomas throughout life
354 could be most motivated to gather information about the body.

355 We additionally report that the adult female, Noel, inspected and cleaned
356 Thomas' teeth with extensive care (Suppl. Videos; also see Figure 5). Thomas appeared
357 to have shared a close relationship with Noel. Staff reports indicate that the relationship
358 between Thomas and Noel was established prior to TamTam's (Thomas' mother) death,
359 as Noel and her offspring (Nina and Nikkie) spent a substantial amount of time in close
360 proximity to TamTam and Thomas, including while feeding. Noel, Nikkie and Nina
361 engaged in grooming and playing behavior with Thomas regularly (Staff reports, pers.
362 comm. 2010). Cleaning and inspecting another's teeth has been reported between live
363 chimpanzees (see [McGrew and Tutin 1973]). This was the most prolonged and detailed
364 behavior directed toward the body, and the fact that it was performed by an individual
365 who shared a close social relationship with Thomas further supports the hypothesis that
366 chimpanzees may respond differently to the death of group members based on their
367 previous social relationships. Moreover, teeth cleaning of a recently deceased individual
368 could arguably be seen as a "compassionate" behavior, adding to the previous
369 description of captive chimpanzees' responses to the death of a group member
370 [Anderson et al. 2010] and supporting the claim that within the non-human primate
371 order perhaps chimpanzees respond to the death of group members with relatively
372 marked empathetic care (also see [Fashing et al. 2011], but see [Bezerra et al. 2014]).
373 Clearly, however, more systematic observations are needed to verify this claim.

374 The frequency of “resting,” or quiet, calm sitting in close proximity to one
375 another was striking considering the high level of excitement often shown by
376 chimpanzees when large groups are attracted to interesting or novel “commodities.”
377 Interestingly, similar quiet attendance was reported for the Tai forest chimpanzees in
378 response to the death of a 10-year-old juvenile [Pettitt 2011], and for the Gombe
379 National Park chimpanzees (Kasekela community) in response to the death of a 20-
380 year-old (estimated) female [Stewart et al. 2012], and has been designated as one of the
381 main characteristics of (early) human mourning responses [Davies & Rumble, 2012].

382 Teleki [1973] proposed that the Gombe chimpanzees might have responded
383 differently to the death of a group member based on their social relationship with the
384 deceased, and that does seem to explain the group response in the current report. While
385 we lack the systematic data collection prior to Thomas’ death that would allow us to
386 statistically determine whether those with close social bonds were more likely than
387 others to attend to and interact with the body, the extensive keeper reports and our own
388 observations of the chimpanzee relationships prior to Thomas’ death suggest that the
389 interest in the body was not random but related to prior social relationships. These
390 observations suggest that in non-human primates as in humans, close relationships
391 mitigate individual differences in behavioral responses to death.

392

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401

402 REFERENCES

403

404 Anderson JR. 2011. A Primatological Perspective on Death. *American Journal of*
405 *Primatology* 73(5):410-414.

406 Anderson JR, Gillies A, Lock LC. 2010. Pan thanatology. *Current Biology* 20(8):R349-
407 R351.

408 Bezerra, B. M., Keasey, M. P., Schiel, N., & da Silva Souto, A. (2014). Responses
409 towards a dying adult group member in a wild New World monkey. *Primates*,
410 55(2), 185–188.

411 Biro D, Humle T, Koops K, Souse C, Hayashi M, Matsuzawa T. 2010. Chimpanzee
412 mothers at Bossou, Guinea carry the mummified remains of their dead infants.
413 *Current Biology* 20(8):R351-R352.

414 Boesch C, Bole C, Eckhardt N, Boesch H. 2010. Altruism in Forest Chimpanzees: The
415 Case of Adoption. *Plos One* 5(1).

416 Buhl, J. S., Aure, B., Ruiz-Lambides, A., Gonzalez-Martinez, J., Platt, M. L., & Brent,
417 L. J. (2012). Response of rhesus macaques (*Macaca mulatta*) to the body of a
418 group member that died from a fatal attack. *International Journal of*
419 *Primatology*, 33(4), 860–871.

420 Chebotko A, Yu D, Lu S, Fotouhi F, Aristar A, Brugman H, Klassmann A, Sloetjes H,
421 Russel A, Wittenburg P. 2004. OntoELAN: an ontology-based linguistic
422 multimedia annotator. Proceedings. IEEE Sixth International Symposium on
423 Multimedia Software.

424 Cronin KA, van Leeuwen EJC, Mulenga IC, Bodamer MD. 2011. Behavioral Response
425 of a Chimpanzee Mother Toward her Dead Infant. *American Journal of*
426 *Primatology* 73(5):415-421.

- 427 Cronin KA, van Leeuwen EJC, Vreeman V, Haun DBM. 2014. Population-level
428 variability in the social climates of four chimpanzee societies. *Evolution and*
429 *Human Behavior* 35:389–396.
- 430 Davies, D. & Rumble, H. 2012. *Natural Burial: Traditional-Secular Spiritualities and*
431 *Funeral Innovation*. London: Continuum.
- 432 de Waal F. 1998. *Chimpanzee politics: power and sex among apes*. Revised edition.
433 Baltimore, Maryland: The Johns Hopkins University Press.
- 434 Fashing PJ, Nguyen N, Barry TS, Goodale CB, Burke RJ, Jones SCZ, Kerby JT, Lee
435 LM, Nurmi NO, Venkataraman VV. 2011. Death among geladas (*Theropithecus*
436 *gelada*): a broader perspective on mummified infants and primate thanatology.
437 *American Journal of Primatology* 73:405–409.
- 438 Hertz, R. 1960. *A Contribution to the Study of the Collective Representation of Death*.
439 In: Needham R & Needham C, editors. *Death and the Right Hand*. New York:
440 Free Press. p 27-86.
- 441 Hosaka K, Matsumoto-Oda A, Huffman MA, Kawanaka K. 2000. Reactions to dead
442 bodies of conspecifics by wild chimpanzees in the Mahale Mountains, Tanzania.
443 *Primate Research* 16(1):1-15.
- 444 Kooriyama T. 2009. The death of a newborn chimpanzee at Mahale: reactions of its
445 mother and other individuals to the body. *Pan Africa News* 16(2):19-21.
- 446 Langergraber K, Mitani J, Vigilant L. 2009. Kinship and Social Bonds in Female
447 Chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 71(10):840-
448 851.
- 449 Li, T., Ren, B., Li, D., Zhang, Y., & Li, M. (2012). Maternal responses to dead infants
450 in Yunnan snub-nosed monkey (*Rhinopithecus bieti*) in the Baimaxueshan
451 Nature Reserve, Yunnan, China. *Primates*, 53(2), 127–132.

- 452 Martin P, Bateson P. 2007. *Measuring Behaviour: An Introductory Guide*. Cambridge:
453 Cambridge University Press.
- 454 Matsuzawa T. 1997. The death of an infant chimpanzee at Bossou, Guinea. *Pan Africa*
455 *News* 4:4-6.
- 456 McGrew WC, Tutin CEG. 1973. Chimpanzee Tool Use in Dental Grooming. *Nature*
457 241(5390):477-478.
- 458 Mitani JC. 2009. Male chimpanzees form enduring and equitable social bonds.
459 *American Journal of Physical Anthropology*:192-192.
- 460 Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M. 1999. Ethogram and
461 ethnography of Mahale chimpanzees. *Anthropological Science* 107(2):141-188.
- 462 Pettitt P. 2011. *The Palaeolithic Origins of Human Burial*. London: Routledge.
- 463 Ron T, McGrew WC. 1988. Ecological assessment for a chimpanzee rehabilitation project in
464 Northern Zambia. *Primate Conservation*, 9, 37–41.
- 465 Stanford CB. 1998. The social behavior of chimpanzees and bonobos - empirical
466 evidence and shifting assumptions. *Current Anthropology* 39(4):399-420.
- 467 Stewart FA, Piel AK, O'Malley RC. 2012. Responses of chimpanzees to a recently dead
468 community member at Gombe National Park, Tanzania. *American Journal of*
469 *Primatology* 74(1):1-7.
- 470 Sugiyama, Y., Kurita, H., Matsui, T., Kimoto, S., & Shimomura, T. (2009). Carrying of
471 dead infants by Japanese macaque (*Macaca fuscata*) mothers. *Anthropological*
472 *Science*, 117, 113–119. <http://doi.org/10.1537/ase.080919>
- 473 Teleki G. 1973. Group Response to Accidental Death of a Chimpanzee in Gombe-
474 National-Park, Tanzania. *Folia Primatologica* 20(2-3):81-94.
- 475 van Lawick-Goodall J. 1968. The behaviour of free-living chimpanzees in the Gombe
476 Stream Reserve. *Animal Behaviour Monographs* 1(3):161-311.

477 Watson, C., Hashimoto, N., Takayoshi, N., Okamoto, M., & Matsuzawa, T. (2015).
478 Two cases of dead-infant carrying followed by mother-infant cannibalism in
479 captive socially housed Japanese macaques. *Folia Primatologica*, 86(4), 378-
480 379.
481

482 FIGURE LEGENDS

483

484 **Figure 1.** Body lies approximately 3 meters from the fence line from where the
485 observations were made.

486

487 **Figure 2.** Proportional presence of group members at Thomas' body. Indicated with
488 photos and arrows are the two displays that occurred close to the body, the first by Pan
489 (adult male) and the second by Violet (adult female).

490

491 **Figure 3.** Number of 30-sec intervals in which individuals were observed to engage in
492 moving around, resting, peering, inspecting, and hitting the body. Data shown for all
493 individuals who were present within 3 meters of the body at some point during the
494 observation period. "Present – nv" indicates that individuals were present but obscured
495 to an extent that the exact behavior was impossible to score. In total, 41 scans were
496 made; during the last 6 scans, the chimpanzee caretakers worked on luring the
497 chimpanzees away from Thomas' body in order to be able to remove the body from the
498 enclosure.

499

500 **Figure 4.** Example behavioral responses at the location of Thomas' dead body, where
501 (a) adult females gather around the body, and (b) adult females and juveniles inspect the
502 body.

503

504 **Figure 5.** One of the adult females (Noel) (a) selects a grass stem, (b) holds the grass in
505 her mouth while inspecting Thomas' mouth with her hands, and (c) subsequently uses
506 the grass stem to pick at Thomas' teeth.

507

508 TABLES

509

510 **Table 1.** Ethogram of the behaviors scored during the observations around Thomas'

511 body.

512

Behavior	Description
Rest	Individual is sleeping, standing or sitting but not actively playing, grooming or engaging in any social behavior. Eyes may be open or closed. Not vocalizing.
Peer	Individual moves within a distance of less than half of the length of one chimpanzee arm (~35 centimeters) and orients their head toward the dead body without physically engaging.
Inspect	Manual or other physical inspection of any region of the dead body (does include grooming, with and without objects).
Move	Individual changes location by at least one body length by walking, running, crawling or climbing.
Hit	Making physical contact with the body by means of a rapid movement with one or two arms.

513

514