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Parental reactions to a dying marmoset infant: conditional investment by the mother, but not the father

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Summary

The reproductive costs of cooperatively breeding callitrichid mothers are remarkable. They rely on fathers and other group members to raise their offspring. Consequently, maternal responsiveness to and investment in infants tends to be conditional, and especially sensitive to infant cues and signals of vigour. Since fathers don't bear the same excessive reproductive costs, their threshold to invest in a dying immature may be lower than in mothers. We present an anecdotal report of reactions of a first-time breeding pair of captive common marmosets (*Callithrix jacchus*) to their dying infant. We found a male bias in all interactions with the dying infant that did not show typical cues of infant vigour. These results show that the dying infant elicited more investment by the father than the mother. Because of this conditional maternal investment, infants of cooperatively breeding primates may be under selection to advertise their viability, in particular to their mothers.

Keywords: common marmosets, platyrrhine primates, conditional investment, reactions to dying infants, cooperative breeding

Introduction

All primate mothers bear large energetic costs associated with producing and caring for their offspring (Altmann & Samuels, 1992; Key & Ross, 1999). However, these costs are especially high in the cooperatively breeding *Callitrichidae*, consisting of marmosets and tamarins whose new-borns (normally born as dizygotic twins) weigh up to 20 % of the mother's body weight (Leutenegger, 1973, 1979) and are almost exclusively carried during the first 5–6 weeks of their lives (Savage et al., 1996; Snowdon, 1996; Santos, French, & Otta, 1997). Not only are callitrichid infants exceptionally large; mothers experience post-partum oestrus (2–4 weeks after birth) instead of the usual lactational suppression of ovulation (Beehner & Lu, 2013) and thus can conceive another set of offspring while still nursing and carrying their current litter (Lunn & McNeilly, 1982; Heistermann & Hodges, 1995; Tardif et al., 2003; reviewed in French et al., 2002). This high energetic investment is only possible because mothers receive substantial help in raising the offspring from her group members (Erb & Porter, 2017).

Because of the trade-off between individual survival and the survival of (current and future) offspring, mothers' investment in the current offspring can depend on the probability to successfully raise it. In cooperative breeders, these decisions not only depend on maternal physical condition and environmental factors, but also on the perceived availability of help (Hrdy, 2016). For instance, marmoset mothers who conceived another set of offspring during the period of critical dependence of the previous immatures reduced their caregiving effort significantly (Fite et al., 2005). Even more strikingly, in some species of callitrichids infants are frequently rejected by mothers who experience signals that indicate a lack of available help by alloparents (Bardi, Petto, & Lee-Parritz, 2001; reviewed in Hrdy, 2016; but see Bardi & Petto, 2002).

53

54 Fathers (as well as helpers) have long been known to play an important role in cooperative
55 infant rearing in callitrichids. They provide assistance in four main domains: infant carrying
56 (e.g. Goldizen, 1987; Garber, 1997; Zahed, Kurian, & Snowdon, 2010; Erb & Porter, 2020),
57 food sharing (Price & Feistner, 2001; Roush & Snowdon, 2001; Guerreiro Martins et al., 2019;
58 reviewed in Brown, Almond, & van Bergen, 2004; but see Brown, Almond, & Bates, 2005; Erb
59 & Porter, 2020), shared vigilance, and group defence (Goldizen, 1989; Savage et al., 1996;
60 Koenig, 1998; Gosselin-Ildari & Koenig, 2012; but see Barros, Alencar, & Tomaz, 2004; Smith,
61 Kelez, & Buchanan-Smith, 2004). Moreover, some evidence suggests that fathers have stronger
62 social bonds with immatures than mothers (Storey & Ziegler, 2016) and can even be primary
63 attachment figures for immatures. Fathers have for instance been shown to be approached
64 preferentially in fearful situations (Kostan & Snowdon, 2002).

65

66 Since fathers don't bear the same excessive reproductive costs, their threshold to invest in a
67 dying immature that doesn't provide strong signs and signals of vigour (e.g. clinging on firmly
68 to the carrier, protest vocalisations when not carried) may be lower than in mothers. In addition,
69 they might have stronger social bonds with immatures that could manifest in a higher reluctance
70 to abandon dying infants. This is consistent with recent reports of a male bias in responses to
71 dead or dying infants in callitrichids (Thompson et al., 2020). Here we add to the sparse
72 literature on cooperatively breeding callitrichid reactions to dying infants with a case report in
73 captive common marmosets (*Callithrix jacchus*). We provide detailed descriptions of the
74 behaviours directed towards the dying infant with a focus on the different patterns for the
75 breeding male and female. We additionally quantify the time spent in proximity with the dying
76 infant to compare between the parents, controlling for whether they were at the same time
77 carrying the healthy infants of the triplet, as well as the specific behaviours directed towards
78 the dying infant. Similar to Thompson et al. 2020, we have access to video recordings and

photographs of the event and can quantitatively analyse the reactions of both parents (following Watson & Matsuzawa, 2018; Sándor & Miklósi, 2020).

Methods

2.1 Individuals and housing

We observed a pair of primiparous captive-born common marmosets (Jam, breeding male, birthdate: 2016/07/01; Nutella, breeding female, birthdate: 2015/04/15) three days after the birth of their first triplets. We subsequently refer to the dying infant as DI (male, sex was determined after his death) and to his two (healthy) female siblings as SI(s). The dying infant was characterized by low muscle tonus, very rare movements, the inability to cling to the parents and only occasional, very faint vocalizations even though not being carried (healthy marmoset infants typically vocalize loudly when not carried). They live in a heated indoor enclosure (4 m³) equipped with ample climbing materials, a sleeping box, and a heated resting platform. The floor is covered in bark mulch. In the front of the enclosure a small, green metal box was permanently installed, used to separate animals for husbandry reasons but normally freely available for the animals to enter or sit on.

2.2 Ethics statement

All observations and animal husbandry were in accordance with the Swiss legislation and licensed by the Kantonales Veterinäramt Zurich (license number ZH223/16, degree of severity 0).

Figure 1. Graphical representation of the data collection period with the daytime when photos or videos were collected, starting at 10:08 am and ending at 12:36 am. Periods where data was collected either as photos or videos are marked in blue (photos) or green (videos). Periods where data is available, but animals could not be identified are marked in red. The first line on top of the timeline indicates the duration of the videos (s) or the number of photos (#) that were taken within the period. The first line below the timeline indicates the behavioral sequence (1–33, see Methods).

2.3 Data collection and coding

All photo and video material was collected ad libitum on November 21, 2019 by JMB from 10:08 until 12:37 when the infant no longer showed any signs of life and resulted in 16 videos (totalling 45.25 minutes) and 170 photos (for more details about the data available, see Figure 1). During the observation period they received their daily fruit meal between 11:15 and 11:30. The video and photo material was analysed by RKB. Since photos were often taken in quick succession, we organized them into “behavioural sequences”. Photos were included within one behavioural sequence when they were taken in succession (meaning multiple photos within the same minute and in consecutive minutes) and clearly depicting the same situation. If the photos were taken more than 1 minute apart a new behavioural sequence was started. Each video would automatically count as a new behavioural sequence. We identified 33 behavioural sequences during the data collection period (Figure 1). The individuals in the photos were identified either by the marking of the tail (the female had a segment of hair shaved off at the bottom of the tail),

the sex of the animal (genital region), or a small black point at the corner of the left eye of the male (see Figure S1). When that was not possible, we used the following very conservative rule to infer the identity of the animal: 1) the photo had to be taken within the same behavioural sequence, and consequently, the animal was in the same position as the last photo where direct identification was possible, and 2) the photo was taken a maximum of 1 minute after or before the last photo with direct identification. For each photo we additionally recorded the behaviours operationalized in Table 1 to measure how much time either of the parents spent with the dying infant, and who was carrying the healthy infants. For all videos we used continuous recording via INTERACT (Mangold GmbH, version 18.6.9.1) of the behaviours defined in Table 1.

The analysis of the coded material is twofold: First we provide a detailed description summarizing the interactions of the parents with the dying infant. Second, we quantify the proportions of total time or number of photos taken that each parent alone, both parents or none of the parents spent in close proximity to the dying infant. We define close proximity as being at least within arm's length of the dying infant (behaviours "within arm's length" and "body contact", see Table 1). When individuals were in body contact, we further specified if they were grooming, licking, or trying to pick up the dying infant. These additional descriptions of the type of body contact are non-exhaustive, individuals could be in body contact without doing any of the additional behaviours but maybe be vigilant or self-groom etc. and/or carry SIs. We did not code for these other behaviours that did not include the dying infant and only summarized them as "not infant directed" contact. Finally, we calculated the proportions of total time or percentage of photos when the parents were in close proximity (as defined above) to the dying infant while carrying at least one of the healthy infants as well as while not carrying any of the healthy infants.

Behaviour	Definition
Within arm's length	<p><i>For photos:</i></p> <p>Individual is located within one arm's length of the immature (excluding body contact). If the immature is not visible on the photo, the behaviour is coded as NA (only 2 photos)</p> <p><i>For videos:</i></p> <p>Continuous recording of individual(s) within arm's length of immature (excluding body contact)</p>
Body contact	<p><i>For photos and videos:</i></p> <p>Individual is touching the infant with any body part, often covering the infant with the whole body, as is usually done to facilitate climbing on the adult's back</p>
Grooming <i>(implies body contact)</i>	<p><i>For videos only (not unambiguously identifiable on a still image, thus not coded):</i></p> <p>Individual is parting or picking the fur on face or body of immature using hand or mouth</p>
Licking <i>(implies body contact)</i>	<p><i>For photos and videos:</i></p> <p>Brushing the fur, eyes, mouth of the infant with the tongue</p>
Trying to pick up <i>(implies body contact)</i>	<p><i>For photos and videos:</i></p> <p>Individual is standing on top of the infant, holding the infant with one or both hands ventrally, pulling it close to their body. Often involves lifting head up close to own head or to the stomach region</p>
Carrying	<p><i>For photos and videos:</i></p> <p>Healthy infants are clinging onto body of either parent</p>

Results

3.1 Overview of events

Behavioural Sequence 1–2: Neither parent could be identified. The observation started with one parent touching the dying infant (DI) that was lying on top of the green box in the front of the enclosure. The second parent approached within the same minute and both of them were in body contact with the DI. One of the parents inspected the DI with the hands for a very brief moment and then left again. The parent came back shortly after to hang at the side of the green box close to where the other parent and the immature were still sitting.

Behavioural Sequences 3: The father held the DI continuously close to his body ventrally and was trying to pick up the infant to continue to carry him (Figure 2 A, supplementary video S1). His head was mostly close to the DI's head (Figure 2 B) and he occasionally licked him (supplementary video S1). After two minutes the mother approached the father, sat down on the other end of the green box, but did not initiate any body contact with the DI.

Behavioural Sequence 4: Neither of the parents were within arm's length of the DI and the infant was lying alone on the green box. For the first time, it was visible that the other two healthy babies (SI) were being carried by the mother.

Behavioural Sequence 5: At the beginning one of the SIs was carried by the father as the other one was being picked up from a branch by the mother in the back of the cage. The father was standing further away from the DI (on a wooden beam closer to the mother) but he quickly approached the DI and positioned himself on top of the infant, covering him with his whole body (Figure 2 C). He then shortly touched the DI's head with his face.

168

169 Behavioural Sequence 6–9: During the next behavioural sequence (6) both parents were on top
170 of the green box and the father was carrying both SIs whereas the mother was covering the DI
171 with her body. She was not paying a lot of attention to the infant and was grooming herself
172 rather than interacting with the DI. After ca. 40 seconds of the behavioural sequence (7), the
173 father stood up and sat down again, further away on a wooden beam to the right of the green
174 box (no longer within arm's length). The mother continued to cover the DI with her body and
175 shortly groomed herself again before she changed her position to start grooming the DI,
176 including licking the anal region. After about 30 seconds of grooming, she left the DI and the
177 father approached immediately after her departure (at around 10:43). He carried both SIs and
178 continued to groom (supplementary video S1) and lick the DI who was still lying on the green
179 box while mostly covering him with his body and being in almost constant body contact for the
180 rest of behavioural sequences (7)–(9).

181

182 Behavioural Sequence 10: Both parents were within arm's length of the DI and the infant was
183 in body contact with the father. The mother inspected the anal region again, then drew the DI
184 towards herself in a pretty rough way continuing to turn the DI's body around, grooming and
185 licking it. 30 seconds later she walked away while the DI was still holding on to her foot and
186 consequently got dragged to the end of the green box. The mother noticed and continued to try
187 to pick up the DI and licked its face very shortly. After 50 seconds of body contact, she left the
188 DI on the green box and moved away to the back of the enclosure. The father was still sitting
189 on the left side of the green box carrying the SIs and as soon as the mother left, he approached
190 the DI and immediately started being in body contact. 15 seconds later the mother approached
191 again and groomed the SIs on the father's back and tried to transfer them onto her own back
192 which was unsuccessful. She gave up after 1:20 minutes and walked away to the back of the
193 enclosure. The father continued to lie on top of the DI keeping constant body contact.

Figure 2. Examples for typical interactions of the parents with the dying infant: (A) The father (Jam) is trying to pick up the DI. (B) The father (Jam) is moving his head close to the immature's head. (C) The father (Jam) is covering the DI with his body. (D) The father (Jam) is in body contact with the DI while the mother (Nutella) is lying on a wooden board under the red light carrying the SIs.

Behavioural Sequence 11–12: The mother returned to the small green box and was in body contact with the DI, but she was predominantly occupied with trying to move one of the SIs onto her back. When the father tried to touch the DI and started to grab the infant to move him towards his body, she immediately pushed him away with the back of her hand (see supplementary video S1), but he continued to reach for the DI and tried to move him towards his body. He managed to pull the infant towards his stomach area so that the DI was lying on his back and he continued to touch him with his hand keeping body contact.

209 Behavioural Sequence 13: Both the father and the mother had moved away from the DI. The
210 mother was sitting on a wooden shelf under the red light picking up one SI that was crawling
211 around. The father was standing on a wooden beam to the right of the green box a bit closer to
212 the DI.

213

214 Behavioural Sequence 14–15: The father returned to the DI on the green box and kept body
215 contact with the infant but was mostly occupied with licking his own hand. The fruit feeding
216 most likely happened shortly before behavioural sequence 14, which could explain the fathers
217 licking of his own hand.

218

219 Behavioural Sequence 16–22: Once more the mother was standing on top of the DI but only
220 for a few seconds. Next the DI was alone for 40 seconds before the father approached again
221 (carrying both SIs). He resumed touching the DI shortly with his hand but continued to sit in
222 close contact without interacting. After about 1 minute he started touching the DI with his hand,
223 trying to turn him over. Then the mother approached and tried to pick up the DI by repeatedly
224 picking up the head of the infant and lifting him up to her stomach. After being unsuccessful
225 she ceased body contact with the infant and sat down on the wooden beam to the right of the
226 green box (after about 70 s). The father continued to try to pick up and groom the DI. He put
227 his head close to the head of the DI and kept body contact, covering the immature with his
228 body. During behavioural sequence (18) the mother moved further away (no longer within
229 arm's length) but the father sustained contact, covering the DI with his body. At the beginning
230 of behavioural sequence (19) the mother had returned to the green box and both parents sat side
231 by side on the green box while the father was still covering the DI with his body. Throughout
232 the behavioural sequence (20) body position changed only slightly; both parents sat to the left
233 of the immature (within a few centimetres of the immature's body). The mother kept body
234 contact for about 2:40 min and also shortly tried to pick up the DI. The father did not initiate

235 any body contact. For the next behavioural sequences (21) and (22), the situation remained the
236 same. Both parents sat in very close proximity to the DI while neither was initiating any body
237 contact with the exception of a few seconds during both sequences when the father touched the
238 DI with his hand.

239

240 Behavioural Sequence 23–24: After roughly 20 minutes of both parents sitting in close
241 proximity, the mother moved away while the father started interacting with the DI and touched
242 its head with his hand once more.

243

244 Behavioural Sequence 25: The mother moved to the shelf under the red light carrying both SIs
245 while the father ate a piece of food further away to the left of the green box.

246

247 Behavioural Sequence 26–29: After about 1 minute the father approached the DI very carefully
248 and continued to focus on the DI for an extended period of time (behavioural sequences 26–29,
249 ca. 20 minutes). Compared to previous interactions, he was not only sitting close to the DI but
250 was also interacting with the infant almost continuously. He licked and groomed the DI very
251 thoroughly with little interruptions for more than 4:00 minutes of the video recordings
252 (behavioural sequences 26 and 28). He would even lift up the DI's head (since the infant was
253 too weak to carry itself) and lick his face and mouth. Mostly he covered the infant's body with
254 his own body and held his head close to the infant's head. On multiple occasions he attempted
255 to pick up the DI. The mother continued to sit on the shelf under the red light carrying the SIs
256 (Figure 2 D). At the end of behavioural sequence 29 (at 12:28) the father started moving away
257 from the DI.

258

259 Behavioural sequence 30: The individuals could not be identified during this behavioural
260 sequence, but the DI was first still lying alone on the green box. Then one of the parents

approached, initiated body contact, and covered the DI with the body while being in close contact with his head.

Behavioural sequence 31–33: Both parents sat under the red light on the shelf and after about 1 minute, the father approached the DI and came close to the infants' head and body for a short moment and subsequently left the DI lying on the green box. Finally, the mother approached the DI and was touching the infant with her hand, bringing her head close to the head of the DI, and licking him.

The infant was removed from the home enclosure at 13:25 after not having shown any signs of vitality for at least half an hour. The infant was dead and the temperature of the corpse already cold when he was removed.

3.2 Quantitative analysis

The quantitative analysis of the video and photo material (Figure 3) revealed that the breeding male (Jam) spent 57.2 % of the total video recorded time and 71 % of all photos taken in close proximity to the dying infant. This was clearly higher compared to both the time the mother spent in proximity or both of the parents together. Most of this time in close proximity was spent in body contact (53.7 % of the total video recorded time and on 61.2 % of all photos taken). The breeding female (Nutella) on the other hand only spent 6.1 % of the total video time and 6.6 % of the photos taken either within arm's length or in body contact with the dying infant (again most of the time was occupied with body contact and only a very minor amounts within arm length). From the video material 33.9 % of the time was spent with both parents either within arm length or in body contact with the dying infant. When both parents were in proximity to the DI, the largest percentage namely 14.3 % consisted of the mother being in body contact

with the infant while the father was still close by within arm's length. It was very rare that both parents were at the same time in body contact with the DI. In only 14.5 % of the photos taken both parents were in close proximity to the DI, either both parents were within arm's length (9.2 %) or Jam was in body contact and Nutella still within arm's length (5.3 %). For the video material only 2.8 % of time the infant was left alone, for the photos this percentage was a bit higher, namely 7.9 %. When analysing the different behaviours that involved the infant during body contact, we found that both parents would engage in grooming, licking as well as trying to pick up the infant, markedly with different preferences for certain behaviours. For both parents most of the time in body contact was spent not directly interacting with the DI, but rather being vigilant themselves, resting or self-grooming, while it was possible that the parents were also carrying the SIs (for a detailed analysis of being in proximity to the DI when carrying the SIs vs not, see Table 2). Considering the video data only, when the father was in body contact with the infant and indeed was interacting with him, he spent most of his time licking the infant. The mother on the other hand was predominantly grooming the DI. On the photos available the mother was only seen licking the infant but not trying to pick him up whereas the father was mostly trying to pick up the DI.

For both parents we calculated the conditional probability of interacting with the DI while either carrying at least one SI or none of the SIs. Both parents were slightly more likely to interact with the DI when not carrying one of the healthy infants for both the video and photo data (for exact percentages, see Table 2).

Table 2 Time (as a percentage of total time for the videos or percentage of total number of photos) spent in proximity (at least within arm's length, includes within body contact) with the dying infant while carrying at least one healthy sibling or none of the healthy siblings (SI).

		% time/#of photos in proximity with DI when carrying at least 1 SI	% time/# of photos in proximity with DI when not carrying a SI
Videos	Father	79.3 %	97 %
	Mother	21.5 %	33.6 %
Photos	Father	85.7 %	93.3 %
	Mother	12.5 % (only based on 7 pictures)	NA

The photo data is based on 42% for the father and 35% for the mother of all pictures taken, since for many of the pictures it was not visible who was carrying the SIs.

Figure 3. Time spent in proximity to the dying infant (as a percentage of total time for the videos or percentage of total number of photos) split up by individual as well as type of contact. A & C are based on the videos, B & D are based on the photos. The plots on top (A & B) show the time none of the parents, both together or either parent alone, spent within arm's length including body contact. The bottom two plots (C & D) show the proportions of different types of body contacts that were coded, namely grooming, licking or trying to pick up. These percentages are relative to the percentage either parent spent in body contact. (bc = body contact; wal = within arm's length).

Discussion

We provide a detailed report and quantitative analysis of the interactions between first time parents and their dying infant in captive common marmosets. We found that the breeding male spent the majority of the time with the dying infant, without the breeding female being in close proximity. We thus report a strong male bias in all infant-directed behaviours despite the fact that for both parents, the same amount of help was available (no additional helpers, because they were first time parents), and the mother was in good physical shape and cared well for the two healthy siblings of the dying infant. It therefore appears that the faint cues of vigour of the dying infant (throughout the videos, the infant never screamed but only occasionally produced very faint vocalisations; he had low body tonus and was too weak to cling to the fur of the parents) elicited more care from the father than the mother. We additionally found that both parents were interacting less with the DI when carrying on or both SIs. This could indicate that rather than a male bias in persistent efforts to interact with the infant, the father was merely more engaged with it because he may have been carrying the SI's less overall, and therefore interacted more with the DI. This alternative explanation, however, is incompatible with observations in a similar situation in a different marmoset pair when only one infant was born, and still mostly the male interacted with it when it's vital signals became weaker and weaker (no vocalizations, not able to cling to the parents' fur; pers. obs. May 14, 2021, JMB). Our report is thus consistent with the idea that mothers in cooperative breeders are particularly sensitive to such cues of infant vigour, and the low threshold of mothers to stop investing in the infant may well put them under particular selection pressure to advertise their vigour (Hrdy & Burkart, 2020).

346 Our observations are in stark contrast to most reports of reactions to dead or dying infants in
347 the primate literature where mothers are the main individuals interacting with dead or dying
348 infants (reviewed in Watson & Matsuzawa, 2018; Gonçalves & Carvalho, 2019; Bercovitch,
349 2020), mostly by carrying their dead offspring over extended periods of time (e.g. Hosaka et
350 al., 2000; Warren & Williamson, 2004; recent case reports e.g. Georgiev et al., 2019; Andrade,
351 Freire-Filho, & Bezerra, 2020; Botting & van de Waal, 2020; Carter et al., 2020; De Marco,
352 Cozzolino, & Thierry, 2020; Takeshita et al., 2020; Trapanese et al., 2020; Watts, 2020). There
353 are many potential proximate explanations for behavioural responses to dead/dying infants (for
354 an overview see Table 2, Watson & Matsuzawa, 2018). When applying them to callitrichids,
355 three main differences in the social system need to be taken into account which can explain the
356 male bias that we found in the marmosets: (1) Mothers particularly have high energetic
357 demands due to post-partum oestrus (Beehner & Lu, 2013) and large neonatal body-size of
358 offspring (Leutenegger, 1973, 1979); (2) mothers are unable to raise the infants alone and
359 fathers are the main care-givers, playing an important role in carrying, food sharing and
360 vigilance behaviour and their care-giving efforts are hormonally regulated (Saltzman & Ziegler,
361 2014; Erb & Porter, 2017); (3) father-infant bonds are particularly strong (Storey & Ziegler,
362 2016). Our reported case of prolonged contact by the father with the dying infant could thus
363 likely be explained by a combination of a strong paternal bond (vs. maternal bond strength in
364 most other primates; Biro, Carvalho, & Matsuzawa, 2010) mediated by hormonal changes that
365 influence care-giving behaviours in the father (vs. post parturition hormones; Warren &
366 Williamson, 2004; Finkenwirth et al., 2016). Additionally, in this reported case the dying infant
367 is part of the first set of offspring of this breeding pair. A strategy that is based on “wait and
368 see”, in particular when the infant is not yet dead, would be highly beneficial for the parent that
369 is investing more into infant care (Hrdy, 1999; Appleby, Smith, & Jones, 2013) and can thus
370 explain the relative reluctance of the mother to engage with the dying infant. Accordingly, it is
371 well possible that in multiparous parents with older, but still dependent offspring, the wait and

see strategy would be given up faster, thus weak or dying infants would be abandoned relatively earlier to invest resources in the older dependent offspring in which they already invested more. Finally, the proximate function of the prolonged contact could be to gather more information about the animacy of the infant (Cronin et al., 2011). We observed a strong interest in the facial region and close head-to-head contact especially by the father as well as inspections of the anal region by both parents. Whether these behaviours predominantly represent information seeking or are simply intense affiliative behaviours (eye-to-eye contact) cannot be established from our observations. Yet, overall, when taking the social system of the marmosets into account, they are fully in line with the proximate explanations of the way parents interact with their dying infants proposed for primates in general.

Our results correspond to one of the few reports of reactions of marmosets to a dead or dying infant (Thompson et al., 2020). This case report from the wild revealed a similar pattern of mostly male biased and sustained contact with the dead infant. The authors reported that even after the rest of his group travelled away (around 1 hour after the presumed death of the infant) this particular male stayed for almost 2 additional hours very close to the infant's body on branches 1–2 m above the place where the infant had fallen to the ground. In the same publication the available literature on callitrichid responses to dead/dying infants is reviewed and results revealed that within the few published cases of interactions with dead infants, males would interact in 100 % of cases where the cause of death was accidental ($N = 6$ of 6), whereas females interacted significantly less, in only 60 % of the cases ($N = 3$ of 5).

With the case report presented here we thus add to the sparse literature on interactions with the dead/dying in platyrrhine and callitrichids in particular and moreover provide a rare report of reactions to a dying infant where we directly compare the amount and type of behaviour directed to the infant by both parents. We acknowledge that the parents' reactions could be

influenced by the housing situation, since animals (especially ones that prefer not to sustain contact with the dead/dying individual) are not able to travel away from the infant, as is the case for reports available from free-ranging populations (e.g. Digby, 1995; Roda & Pontes, 1998; Culot et al., 2011; Thompson et al., 2020). Nevertheless, our finding of similar and clearly male biased interactions with the dying infant as reported in the wild, indicates that this pattern seems to be rather stable within callitrichids. Clearly though, the small numbers of accidental deaths reported in the published literature does call for cautious interpretation of the found male bias. Despite the male bias in our data, the mother was not indifferent to the dying infant. 33.9 % of the total recorded time and the 14.5 % of all photos both parents were in close proximity to the immature. This may be a consequence of the captive conditions, and these proportions might have been smaller (and the male bias thus stronger) in a wild setting, where the parent with lower interest in the dying immature could have moved away.

With this anecdotal report we add to the evidence for a male biased pattern of interactions with dying infants in callitrichids, most likely driven by a conditional investment of mothers, and mediated by the strong social bond between fathers and their offspring. Sadly, there are only very few case reports of reactions towards dead or dying infants in cooperatively breeding species outside the primate order. A short report on free ranging dingos details four occasions of carrying of the deceased pup by the presumed mother (Appleby, Smith, & Jones, 2013). Corvids have been most systematically studied in their responses towards dead conspecifics, since carcasses are smaller and more easily obtainable (Swift & Marzluff, 2015). Even though research on corvids has repeatedly shown animals to gather in large, mobbing groups around deceased conspecifics, influences of social relationships of the living with the dead individuals has not been a focus in most studies within this group (reviewed in Gonçalves & Biro, 2018; case reports: Marzluff & Angell, 2013; Pierotti & Annett, 2014). More studies would thus clearly be desirable, and they would benefit from including more fine-grained analysis of the

motivational underpinnings of parental interactions with dying infants. Specifically, by coding infant behaviours such as vocalizations or movement as well as parental vocal behaviour during approaches of infants, to better understand which factors facilitate parental interest towards dying infants.

Importantly, we can exclude low level explanations for the male bias, such as differing environmental conditions (standardized captive environment), availability of helpers in the group (no helpers were present in this group) or parity between the parents (both parents were primiparous), further strengthening the argument that reproductive cost might be a critical factor to determining the investment into dying offspring. We found no indications that the mother was in anyway unfit to care for her offspring in general since she was observed carrying and nursing the SIs over long stretches of time and both infants survived to adulthood. Given this pressure of the conditional investment by the mother, immatures of cooperative breeders might be under strong selection to advertise their vigour. Immature babbling vocalizations are likely to fulfil this function by advertising the neediness to caregivers, especially the mother (Hrdy, 2016; Burkart et al., 2018). Future studies on callitrichid responses to dead and dying infants could benefit from including information on both parents' reactions to the surviving infants. This additional perspective would highlight the differences in caregiving effort and investment depending on signals of vigour by the immatures.

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