



# Callitrichid responses to dead and dying infants: the effects of paternal bonding and cause of death

Cynthia L. Thompson<sup>1</sup> · Rebecca Hrit<sup>1</sup> · Leonardo C. O. Melo<sup>2</sup> · Christopher J. Vinyard<sup>3</sup> · Kimberly N. Bottenberg<sup>1</sup> · Maria A. B. de Oliveira<sup>2</sup>

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## Abstract

Many primates show responses to dead infants, yet testing explanations for these behaviors has been difficult. Callitrichids present a unique opportunity to delineate between hypotheses, since unlike most species, male caretakers form closer social bonds with infants than mothers. Callitrichids are also known to commit infanticide, leaving obvious wounds that may enable them to more readily recognize death. We present: (1) a case study of a wild common marmoset (*Callithrix jacchus*) group responding to an infant's natural death, and (2) a review of published infant deaths across callitrichids ( $N=16$ ), testing for trends in the sex of reacting individuals and cause of death. In our case study, several group members frequently interacted with the dead infant, attempting to carry it. However, the strongest response was from a male that remained with the corpse for ~3 h, despite his group leaving the area. Across callitrichid species, corpse interactions were significantly sex-biased: 100% ( $N=6$ ) of accidental deaths involved corpse interaction by males ( $p=0.007$ ), compared to 60% ( $N=3$  of 5) by females ( $p=0.095$ ). Cause of death also played a significant role, with individuals attempting to carry dead infants in 100% ( $N=6$ ) of accidental deaths, but only 11.1% ( $N=1$  of 9) of infanticides ( $p=0.001$ ). Although the available literature is small and potentially subject to publication biases, these data support the idea that visually obvious wounds may influence callitrichids' perception of dead conspecifics. Additionally, male-biased patterns of corpse interaction in callitrichids indicate that social bonds likely shape reactions to the dead, in addition to kinship. While published data on primate thanatology are limited, this study demonstrates quantitative approaches that can provide empirical insights into primates' responses to dead conspecifics.

**Keywords** Thanatology · Marmoset · Death · Infanticide · Animacy detection · Dead-infant carrying · Quantitative methods

## Introduction

Primates show striking responses to the death of infants. Evolutionary thanatology has recently flourished, with advancements in theory, a movement toward empirical

testing, and reviews for several mammalian taxa (Anderson et al. 2018; Reggente et al. 2018; Watson and Matsuzawa 2018; Gonçalves and Carvalho 2019; Bercovitch 2020). Yet challenges remain in explaining these observations in primates. The majority of reports remain largely descriptive and/or limited to brief anecdotes (Watson and Matsuzawa 2018). Published accounts also show taxonomic biases, with far fewer cases from New World than Old World monkeys [15.7% ( $N=20$ ) vs. 47.2% ( $N=40$ ) of all primate reports ( $N=127$ )], despite similar number of species known to display such reactions (Gonçalves and Carvalho 2019). Additionally, reported case studies often focus on only the most overt behaviors, such as extended carrying of dead infants and infanticide. Beyond these potential report biases, the myriad contexts of death (infanticide, sickness, falls, etc.) may also underlie variation in group members' response to dead infants. The currently sporadic (although quickly

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✉ Cynthia L. Thompson  
thompscy@gvsu.edu

<sup>1</sup> Department of Biomedical Sciences, Grand Valley State University, Allendale, MI, USA

<sup>2</sup> Departamento de Morfologia e Fisiologia Animal, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

<sup>3</sup> Department of Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, OH, USA

growing) data on primate thanatology includes few empirical tests of explanations for why primates interact with dead infants.

There are multiple hypotheses for why corpse interactions occur (Watson and Matsuzawa 2018). From an evolutionary perspective, the death of an infant represents a significant loss of reproductive success for parents. This is particularly true for primate mothers that invest heavily in gestation and lactation. Continued interest in deceased infants may be an adaptation to avoid the costs of abandoning sick or temporarily incapacitated infants that may survive, to safeguard reproductive success (i.e., the ‘wait and see’ strategy: Watson and Matsuzawa 2018). This suggests that kinship should be a strong determinant of responses to dead or dying infants (because the moment of death is rarely identified, we consider these jointly; see the Methods section). However, the maternal bonding hypothesis suggests a more nuanced explanation, that interactions with corpses may result from the extensive social bonding, and associated neuroendocrine regulation, between mothers and infants. This social bonding is reinforced by hormonal responses mediated through oxytocin, vasopressin, and prolactin (Lieberwirth and Wang 2014; Gangestad and Grebe 2017). While death presents a sudden change in this social bond, prolonged hormone levels may manifest as a reluctance to abandon dead infants. In most primate species, mothers and infants are both the most closely related dyad (with higher certainty of kinship) and have the strongest social bonds, making it difficult to tease apart the effects of decreased reproductive success vs. severing of social bonds when assessing reactions to dead infants.

Callitrichids are one of the few primates that display cooperative paternal care, related to their high levels of polyandrous, polygynous, and polygynandrous mating (Digby et al. 2011). Dominant females display hormonal suppression of subordinate females’ reproduction, but this suppression is frequently incomplete (Digby and Saltzman 2009). Females give birth and nurse infants, while males (most often two) routinely carry them. Callitrichid male caretakers form stronger social bonds with infants than mothers (Storey and Ziegler 2016). Hence, mothers and sires may be equally related to offspring (noting that real and perceived relatedness may be convoluted in callitrichids due to chimerism: Ross et al. 2007) and both invest heavily in offspring, albeit in different ways (Achenbach and Snowdon 2002; Fite et al. 2005). However, females have higher certainty of kinship with infants, but weaker social bonds, while males have less certain kinship with infants, but stronger social bonds. Thus, the death of an infant represents a known loss of reproductive success and substantial investment for mothers, but comparatively less loss of an existing social bond. Conversely, an infant’s death represents a substantial loss of social bond for males, with the loss in reproductive success being either equal to or lower than females, depending on

the individual male. Loss of reproductive success and investment would be similar for male sires and mothers (although sires have less certainty of their paternity). Non-sire male caretakers would not lose any reproductive success (or if a relative, would lose some inclusive fitness, but less than mothers), and indeed would no longer be investing energy in an unrelated infant. Thus, this taxon can provide a valuable test of kinship and loss of reproductive success versus social bonding in reactions to dead infants. If the effect of lost reproductive success drives reactions to infant corpses, then marmoset mothers should display a reaction that is either equal to, or stronger than males. However, if interactions with corpses are influenced by social bonds (and the associated neuroendocrine response), then male caretakers should display a stronger response to the infant’s death.

The context of death may also influence responses to dead infants. Previous work has suggested that interactions with corpses may result from an “animacy detection malfunction” (Gonçalves and Biro 2018). Under this idea, conspecific corpses resemble an animate being (i.e., the former group member), yet are unresponsive, akin to an inanimate object. Interactions with corpses may allow individuals to gather information that enables recategorization of a formerly live, animate conspecific into the inanimate corpse. It has been hypothesized that the context of death and appearance of obvious wounds may facilitate this switch without direct investigation of the corpse (Gonçalves and Biro 2018). In callitrichids female-perpetrated infanticide occurs, resulting in obvious wounds to the corpse (e.g., missing body parts, large gashes, etc.). This provides the opportunity to assess the effect of cause of death on interactions with the corpse.

The aims of this paper are twofold. First, we report observations of the death of a wild infant common marmoset monkey (*Callithrix jacchus*) and the subsequent behavioral reaction of group members. Unlike previous marmoset observations, most of this incident was video recorded (following Watson and Matsuzawa 2018), allowing detailed quantitative analysis of the event. To date, this case report provides the most thorough description of marmoset reactions to the death of an infant (but see Bezerra et al. 2014 for an adult marmoset), and is the first to provide quantitative assessments. Second, to place this case report in a broader empirical context, we reviewed the available literature on infant death across callitrichid species. We use these assembled metadata to test for trends in callitrichid responses to dead infants based on sex of the reacting individuals, attempts to carry dead infants, and cause of death. If social bonding has a larger impact on interactions with corpses than kinship, then we expect male callitrichids to display more corpse interactions than females, and vice versa. If animacy detection malfunctions play a role in corpse interactions, then we expect to see fewer corpse interactions when infants have obvious wounds that indicate death.

## Methods

### Case study

#### Study site and animals

Data were collected at Tapacurá Ecological Field Station, Pernambuco, Brazil (08°03S, 35°12W) in July 2017. Tapacurá is within the Atlantic coastal forest and hosts predominantly semideciduous, secondary growth broad-leaf perennials (Moura et al. 2012; Thompson et al. 2013; Moura 2019). The incident occurred near an exudate feeding site regularly visited by three marmoset groups and monitored by observers; to the best of our knowledge the location did not impact data collection of this event. While we were unable to determine which group was involved, the composition of groups visiting the site ranged from 5–11 adults, some with 1–2 juveniles present. Marmosets at Tapacurá are habituated to seeing humans, due to intermittent studies over the long term (e.g., Hubrecht 1984; Scanlon et al. 1988; Melo 2001; Faulkes et al. 2003; Vinyard et al. 2009; Moura et al. 2012; Moura 2019).

#### Data collection and analysis

The initial behavioral reaction of the group was seen from three different vantage points by observers (MABO & LCOM, CJV, CLT); the events reported below are combined across observers. After initial observations, we began video recording the incident with a tablet (Xperia X, Sony). Recording started 16 min after the presumed death (described below) and we recorded 2 h 30 min of video across the 2 h 48 min event. All videos were scored by RH to avoid interobserver error. We used recordings to score the total number of visits by group members to the infant's corpse, which was summed with the observed visits prior to the video recording. To collect proximity of individuals to the corpse, we used natural landmarks on the tree (i.e., tree hollow, trunk bend/knob) nearest the corpse that were consistently visible in videos and measured in the field (Fig. 1a). Although this resulted in unequal distance categories, it enabled systematic video analysis and represents divisions of the area used by marmosets. Using instantaneous sampling at 10-s intervals we recorded the number of individuals at the following proximity levels: on the ground with the infant, within 0.84 m, within 0.84–1.29 m, > 1.29 m away but still in the tree nearest the infant, and in a nearby tree. From these tallies we also determined the total number of individuals known to be in the vicinity. To characterize the group's activity level, we quantified the number of 10-s intervals with

movement by individuals between distance categories. This is a novel approach we developed to measure group activity, which may be useful for quantifying changes in interest around acute events that generate 'excitement' and frequent movements of individuals around a point of interest (e.g., corpses, predator mobbing, novel objects, etc.).

To present changes in the group's reaction over time, we grouped behaviors in hour increments after presumed death of the infant (following De Marco et al. 2020). It should be noted that video data were slightly unequal across hours (Hour 1: 44 min; 2: 53 min, 3: 47 min) due to a lag in beginning video recording, gaps when beginning a new video file, and the last marmoset leaving the area prior to the end of the third full hour. To characterize changes in the group's response to the corpse over time, we compared behavioral data across these three intervals. A  $\chi^2$  goodness of fit test was used to assess differences in the number of visits to the corpse among the hours after presumed death. A one-way ANOVA was used to test for differences in duration of visits to the corpse between hours. Changes in proximity over hours were tested via Friedman's test, using the percent of samples in which any marmoset was on the ground, within 0.84 m, and 0.84–1.29 m of the corpse. Changes in the activity of individuals present were evaluated by comparing the proportion of samples with movement between proximity categories over hours, using Cochran's *Q* test, with McNemar post hoc tests with a Bonferroni correction for multiple comparisons.

The infant's body was retrieved 33 min after the last observed marmoset left the area. Morphological measurements were taken (following Glander et al. 1991) and the body was frozen and transported to the Universidade Federal Rural de Pernambuco (UFRPE) for a necropsy. Brazilian guidelines at the time recommended submitting dead monkeys for yellow fever testing, preventing us from leaving the corpse in situ. Nonetheless, to assess any long-term revisitations, observers remained at the site for the remainder of the day. The following morning (05:33) we placed a camera trap (M-990i, Moultrie) on the site which remained there for 48 h.

#### Review of callitrichid responses to dead infants

We surveyed the literature to find cases of responses to infant death by callitrichid species. We included any cases that provided enough detail to determine whether or not interaction with the corpse occurred. Biases in the literature notwithstanding, including cases both with and without reactions allows a more empirical comparison of factors leading to corpse interactions (e.g., Watson and Matsuzawa 2018). Only cases from free-ranging populations were included to avoid potential unnaturalistic effects of captivity, such as forced proximity to the corpses and failed social



**Fig. 1** Dead male common marmoset infant. **a** Site of death and tree shown in video recordings. Infant corpse is circled in red. Black lines show proximity categories used for data collection. **b** Close up of infant corpse, in situ at site of death. Upper numbers are inches, lower numbers are cm. **c** Retrieved corpse of infant showing no wounds; grid is 6.35 × 6.35 mm. **d** Head and chest of corpse, showing dental eruption and parasites



introductions. We treated each reported infant death within a publication as a separate case. From reports, we collected (1) the cause of death, classified as either accidental (i.e., falls, attacks by a predator, natural illnesses) or infanticide (defined as an observed attack by an adult marmoset); (2) whether or not any group members interacted with the dead/dying infant (defined as approaching, close proximity, or touching of the infant); (3) sex of individual that interacted (as reported in the publication); and (4) whether group members attempted to carry the infant (defined as reports of “attempts” or “tries” to “pick up,” “recover,” collect,” or “retrieve” dead/dying infants from the ground). For two reports (Herrera et al. 2000; Bezerra et al. 2007), infants were severely injured (and appeared to be dying) due to

accidents, and after an initial reaction by the group, infanticide occurred. For these cases, behaviors of the group after the injury (but prior to infanticide), and those after infanticide, were scored separately. Although not ideal, splitting these cases prevents misrepresenting the series of events, while also fully utilizing the available literature on this topic. In both cases, scoring these cases together would create datapoints in which group members attempted to carry dead infants with infanticide as the final cause of death, despite that no carrying attempts occurred after infanticidal attacks, without prior injury. Unfortunately, scoring cases by whether infants were dead or dying was impractical as the moment of death is generally unfeasible to determine for observational field studies. For this literature review,  $N = 11$

of 14 accounts do not specify when death occurred. It is also unknown whether human determinations of death would be relevant cues for callitrichids, or whether callitrichids (and other primates) are aware of death at all (Watson and Matsuzawa 2018). As such, we considered reports of infants that are dying, known to be dead, or for which death is unknown together in this analysis.

We conducted Fisher's exact tests, appropriate for smaller sample sizes, to assess the relationship between cause of death (accidental vs. infanticide) and (1) whether any interaction with dead infants occurred, and (2) whether attempts to carry dead infants occurred. To evaluate sex differences in responses to dead infants, we conducted Fisher's exact tests of whether a corpse interaction occurred and cause of death separately for males and females. Since in one case the infant's presumed mother died prior to the infant, this case was excluded from the Fisher's exact test for female responses, but not males.

## Results

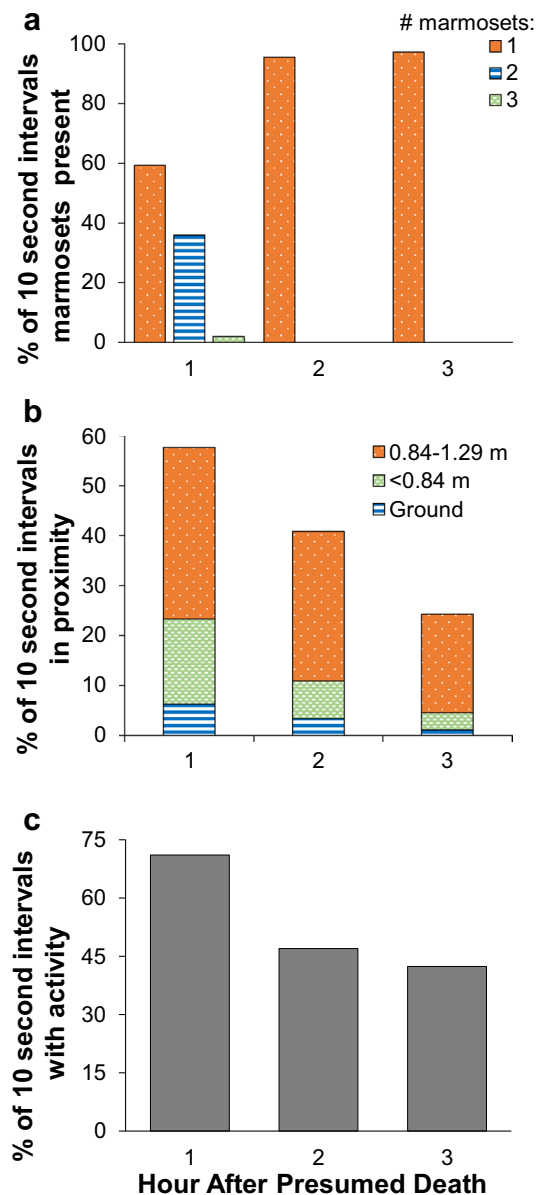
### Case study

#### Group reaction to marmoset infant's death

At the start of the event on 7/23/17, the group was somewhat dispersed (group diameter ~20 m) while feeding on exudates. The infant was first observed at 08:50, seen falling through the air, and its body became caught on a branch. The observer noted that the infant appeared 'lifeless' but was uncertain whether the body had snagged on the branch or if the infant had grasped it. From this position, the infant then fell an additional ~2 m to the ground. Hereafter, we refer to this as the 'presumed time of death' although we cannot verify whether the infant died before or after this event. Once the infant was on the ground, we observed two adults (based on size and pelage), one male and one female, attempt to pick up the infant. In both cases the adults approached the fallen infant, picked it up using their forelimbs, and placed it on their ventrum. The infant stayed on the adult for <5 s, first sliding to the genital and tail region, and eventually falling to the ground when the adult started locomoting. The infant fell ~1 m to the ground in both cases as it appeared unable to grasp onto either adult.

After these observed attempts to pick up the infant, at least five marmosets congregated on a low branch (1–2 m above ground) in the area the infant had last fallen. At the start of this activity, there were frequent vocalizations, including 'chirp' and 'tsik' calls. Several marmosets went down to the ground to inspect the infant. The observers reported that group members visited the site of the infant's body on the ground (Fig. 1b) five times before video

recording started. At the start of video recording, several marmosets remained low in the tree near the infant, frequently visiting the infant on the ground. Several individuals stayed for ~1 h (see below), but by 10:27 (1 h 37 min after presumed death), there was only one adult male left at the site (Fig. 2a), and distant long calls ('loud shrill') were



**Fig. 2** Quantitative response of marmoset group to dead infant, grouped by hour after presumed death. **a** The total number of marmosets visible in area during group response to infant's death, measured at 10-s intervals. **b** Proximity of group members to infant corpse at 10-s intervals. For the first hour, 1.2% of samples between 0.84 and 1.29 m contained two marmosets in that proximity category. All other samples represent one marmoset in the proximity category. **c** Activity of group members, defined as the percent of 10-s intervals with movement between proximity categories, during response to infant's death

heard from the direction in which the remainder of the group had moved. From 10:27–11:46, the male left the tree nearest the infant's location eight times, but each time returned to nearby the infant. For seven of these leave events, the male only moved to a nearby tree (~2–5 m), however in one event he traveled ~10 m away from the infant and gave long calls ('loud shrill'). Besides these long calls, this male did not vocalize after his group mates had moved away.

The male left the area viewable by video recordings at 11:38 (2 h 48 min after presumed death), and was seen quietly traveling away from the general area (>25 m away) at 11:46. The infant body was documented and collected at 12:19 (Fig. 1a–c). No marmosets were seen revisiting the site of the corpse later that day. Our camera trap did not document any revisits by marmosets or other animals within the next 48 h.

### Quantitative analyses of group response

Over the course of the 2 h 48 min reaction, interest in the infant corpse was highest during the first hour after the presumed death, and gradually decreased through hours two and three (Table 1; Fig. 2a). Marmosets visited the corpse on the ground significantly more frequently in the first hour than the second or third ( $\chi^2$  goodness of fit test:  $\chi^2_2 = 30.33$ ,  $p < 0.001$ ) (Table 1). The duration of ground visits did not significantly differ across hours (one-way ANOVA  $F_{2,35} = 2.10$ ,  $p = 0.138$ ; Table 1). There were significant differences in proximity to the corpse across hours (Friedman's test:  $\chi^2_2 = 6.00$ ,  $p = 0.050$ ), with high proximity during the first hour, and the percent of samples with marmosets on the ground or within 0.84 m decreasing by roughly half each hour (Fig. 2b). However, at least one marmoset remained present in the area for >95% of samples across all hours (Fig. 2a), indicating a shift toward further proximity from the infant during later hours. Group members' activity,

measured as movement between distance categories, significantly changed across the hours (Cochran's Test  $Q = 38.21$ ,  $p < 0.001$ ), with the greatest activity during the first hour, and a significant decrease into the second hour (McNemar test:  $\chi^2 = 26.88$ ,  $p = 0.001$ ). No change in activity was found between hours two and three (McNemar test:  $\chi^2 = 0.77$ ,  $p = 0.380$ ) (Fig. 2c).

### Marmoset infant corpse

The infant was male. Based on dental eruption patterns, it was <1 month old, and potentially only a few weeks old, as its deciduous first and second incisors were just starting to erupt on both upper and lower dentition (no other teeth were erupted) (Fig. 1d) (Goss 1984; Smith et al. 1994). Morphological measurements are included as Supplementary Material. Upon collection, the corpse had superficial ectoparasites on its head, dorsum, ano-genital region, and in its mouth (Fig. 1d). No wounds were found on the body. Necropsy results indicated pneumonia was the cause of death.

### Review of callitrichid responses to dead infants

Our meta-analysis showed clear trends in how callitrichids responded to dead infants (Table 2). Of the 16 published accounts, 35.3% ( $N = 6$ ) of dead or dying infants were a result of accidents, 56.3% ( $N = 9$ ) were infanticides (noting that  $N = 2$  cases of accidental injury later had infanticidal attacks: see methods), and one partial observation had an unknown cause of death. Interactions by (any) group members with the dead/dying infant occurred in 100% ( $N = 6$ ) of accidental deaths, compared to only 22.2% ( $N = 2$ ) of infanticides, demonstrating a significant association between cause of death and propensity to interact with the corpse (Fisher's exact test  $p = 0.007$ ). Likewise, marmosets attempted to carry dead/dying infants in all accidental deaths, compared to only 11.1% ( $N = 1$ ) of infanticides, also demonstrating a significant relationship between cause of death and response to the corpse (Fisher's exact test  $p = 0.001$ ). Attempts to carry were unsuccessful in 100% ( $N = 7$ ) of cases, as infants were reported to fall from the carrier. Authors used remarkably consistent wording to describe this behavior (see methods) suggesting that observers witnessed similar actions. Cannibalism occurred in 66.7% ( $N = 6$ ) of infanticidal deaths, but did not occur in any cases of accidental death. All instances of cannibalism included consumption of the infant's head. In one of these cases, the infant was noted as still alive when cannibalism occurred (Bezerra et al. 2007).

Response to the death of callitrichid infants differed between the sexes (Table 3). There was a significant relationship between interaction with corpses and cause of death for males (Fisher's exact test  $p = 0.007$ ); adult males interacted with dead infants in 100% ( $N = 6$ ) of accidental

**Table 1** Visits by group members to corpse of infant common marmoset on the ground

Variable	Hour 1	Hour 2	Hour 3
Total visits ( $N$ )	31 <sup>a</sup>	9	3
Mean visit duration ( $\pm$ SD)	5.91 ( $\pm$ 3.45)	8.91 ( $\pm$ 5.83)	4.52 ( $\pm$ 4.41)
Maximum visit duration (s)	16.63	18.58	9.22
Minimum visit duration (s)	1.75	1.62	0.47

<sup>a</sup> $N = 5$  of these visits were observed prior to video recording; data on duration are not available

Movements of small mammals are generally fast; for a biological scale of duration values, the time for a full chewing cycle by marmosets is 0.26 s (Gerstner and Gerstein 2008) and they quadrupedally locomote on average 0.62 m/s (Schmitt 2003)



**Table 2** Published accounts of dead and dying infants in callitrichids

Cause of death	Species	Cannibalism?	Interactions with dead infant? <sup>a</sup>	Sexes that interacted	Attempt to carry (sex)? <sup>b</sup>	Interaction by adult female? <sup>a,b</sup>	Interaction by adult male? <sup>a,b</sup>	Reference
Accidental	<i>Callithrix jacchus</i>	N	Y	M	Y (M)	N	Y (3)	Roda and Pontes (1998) <sup>c</sup>
Accidental	<i>C. jacchus</i>	N	Y	M <sup>d</sup>	Y (M) <sup>d</sup>	N <sup>d</sup>	Y	Lazaro-Perea (2000) <sup>e</sup>
Accidental	<i>C. jacchus</i>	N	Y	M, F	Y (M, F)	Y (2 <sup>f</sup> )	Y	Bezerra et al. (2007) <sup>g</sup>
Accidental	<i>C. jacchus</i>	N	Y	M, F	Y (M, F)	Y	Y	This study
Accidental	<i>Saguinus mystax</i>	N	Y	M	Y (M-3)	N	Y (3)	Culot et al. (2011)
Accidental	<i>S. fuscicollis</i>	N	Y	M, F	Y (M)	Y (2 <sup>f</sup> )	Y (2)	Herrera et al. (2000) <sup>g</sup>
Infanticide	<i>C. flaviceps</i>	N	Y	M, F	N	Y	Y	Hilário and Ferrari (2009) <sup>h</sup>
Infanticide	<i>C. flaviceps</i>	Y	N	–	N	N	N	Hilário and Ferrari (2009)
Infanticide	<i>C. jacchus</i>	N	Y	M	Y (M)	N	Y	Digby (1995)
Infanticide	<i>C. jacchus</i>	N	N	–	N	N	N	Roda and Pontes (1998)
Infanticide	<i>C. jacchus</i>	Y	N	–	N	N	N	Lazaro-Perea (2000)
Infanticide	<i>C. jacchus</i>	Y	N	–	N	N	N	Melo et al. (2003) <sup>i</sup>
Infanticide	<i>C. jacchus</i>	Y	N	–	N	N	N	Bezerra et al. (2007) <sup>g,j</sup>
Infanticide	<i>S. fuscicollis</i>	Y	N	–	N	N	N	Herrera et al. (2000) <sup>g</sup>
Infanticide	<i>S. mystax</i>	Y	N	–	N	N	N	Culot et al. (2011)
Unknown	<i>S. mystax</i>	N	Y	F	N	Y	N	Culot et al. (2011) <sup>k</sup>

<sup>a</sup>Excluding cannibalism, including approaches, touching, or other contact

<sup>b</sup>Numbers in parentheses indicate when more than one individual of specified sex was involved in interactions with the corpse

<sup>c</sup>Male interactions with the infant occurred before and after the reported moment of death; attempts to carry only occurred prior

<sup>d</sup>Infant's mother died hours before the infant

<sup>e</sup>Attempts to carry appear to have occurred prior to death

<sup>f</sup>One of these two females later killed and cannibalized infant

<sup>g</sup>Infant was initially severely wounded, then later died by infanticide. Behavioral responses for each incident are reported separately

<sup>h</sup>Infant was alive for all reported behaviors

<sup>i</sup>Infant was attacked and taken during a between-group encounter. Recorded reaction was not by infant's natal group

<sup>j</sup>Infant was alive at the time cannibalism began

<sup>k</sup>Partial observation. Initial circumstances of death (and potentially any early interactions) were not observed

cases, with half of these cases ( $N=3$ ) including responses by multiple males within the group. By contrast, females did not show a significant relationship between interaction with dead infants and cause of death (Fisher's exact test  $p=0.095$ ). Only 60% ( $N=3$  of 5) of accidental deaths included responses by females (excluding the case in

which the mother died prior to the infant; no other female group members interacted with this corpse: Table 2) and two of these three responses involved females that later killed and cannibalized the wounded/dying infant. Interactions with the dead infants were infrequent for both sexes for infanticides (Table 3).

**Table 3** Frequencies of response to dead callitrichid infants by sex of the individual interacting with the corpse and cause of death

Sex that Interacted	Cause of death	
	Accidental	Infanticide
Male	100% ( <i>N</i> = 6 of 6)	22.2% ( <i>N</i> = 2 of 9)
Female	60% ( <i>N</i> = 3 of 5) <sup>a</sup>	11.1% ( <i>N</i> = 1 of 9)

Case details are in Table 2

<sup>a</sup>In one accidental death, the mother died prior to the infant and no other female group members reacted to the infant; this case was excluded from the female-specific analysis

## Discussion

In our case study, we observed a strong reaction to the infant marmoset's death. This response involved a significant number of group members, with the most pronounced reaction displayed by an adult male. This contrasts with the majority of primates, where behavioral reactions to infant deaths are most often by mothers (but see Gonçalves and Carvalho 2019). For marmosets, this may indicate that the social bonds between an adult male caregiver and an infant play a stronger role than the (more certain) genetic relationship between a mother and offspring. While case reports only offer limited insight, this idea is also supported by our review across callitrichids with male caretaking. While only a limited number of cases have been published, our meta-analysis similarly suggests that males are the most likely to respond to dead infants. In this way, callitrichids may be considered 'an exception that proves the rule:' their infant bonding patterns are the reverse of most primates (and other mammals), and they in turn show the reverse pattern of sex-specific reactions to dead infants. As an intriguing alternative, it has also been proposed that mothers may carry dead infants to signal their maternal diligence to potential mates (Watson and Matsuzawa 2018). As female marmosets can influence likely paternity through copulation timing (Digby 1999), male responsiveness to dead infants could serve a similar signaling function. However, in the current case study, the long period of time spent by the male near the infant in the absence of other marmosets, does not support this conclusion. We do not have comparative data on marmoset interindividual distances, but callitrichid groups are generally described as cohesive (Digby et al. 2011), and we did not observe other instances of group members alone for such an extended period of time. Other callitrichid cases report similar solo vigils after deaths (Culot et al. 2011), although more detailed accounts are needed to further evaluate a signaling hypothesis. Unfortunately, there are not published reports of infant death responses from other primate species with high paternal care, such as titi or owl monkeys, to provide a comparison (Gonçalves and Carvalho 2019).

Our review of callitrichids also strongly indicates that individuals display different responses to infant corpses based on the cause of death, although the small sample size warrants caution in interpreting these results. Still, individuals rarely interacted with corpses after infanticidal events, while all accidental deaths included responses from at least one group member. This supports the idea that corpse interactions may result from an "animacy detection malfunction." In our review, the majority of infanticide victims lacked heads due to cannibalism. This salient cue may have facilitated the cognitive switch from animacy to inanimate, decreasing interactions with corpses or attempts to carry them. However, we must also consider that this finding could be an artifact of bias in the literature. Published case reports focusing on reactions to dead conspecifics are unlikely to report negative findings, whereas reports of infanticide are likely to be published regardless of the group's response to the corpse. Similarly, common marmosets are far better represented in the literature review than other callitrichid species (Table 2), which may influence our findings. Given these potential biases and low sample size, these interpretations should be considered preliminary.

Previous work on primate thanatology has tended to emphasize carrying behavior, in which mothers carry dead infants for extended periods—often days to weeks. While this behavior is certainly striking, some research has suggested that carrying may be influenced by environmental and ecological variables, rather than the motivation of individuals to interact with the corpse (Fashing et al. 2011; Gonçalves and Carvalho 2019). For callitrichids, group members attempted to carry infants in all cases of accidental death, and were always unsuccessful, with the infant falling from the carrier shortly after it began locomoting. This motivation to carry, but lack of success, may indicate that callitrichids are less able to carry dead infants relative to other primates. Indeed, marmoset infants are relatively large for primates, with a single newborn infant representing ~ 8.5% of adult body mass (Schradin and Anzenberger 2001). Coupled with the strong responses to infants with accidental deaths, this provides a cautionary note about overemphasizing conspicuous behaviors. Dead-infant carrying behaviors may reflect a difference in callitrichids' capacity to display a long-term response, rather than differences in motivation or degree of individuals' 'grief' (sensu Watson and Matsuzawa 2018).

This case study and review of callitrichid responses to infant death contribute to our knowledge of primate thanatology by adding information from an underrepresented taxon. While reports of callitrichid infant deaths are scant and likely subject to publication bias, our review revealed important preliminary trends. For these paternally bonding callitrichid species, males more frequently responded to dead infants than females, supporting the idea that social bonds play a key role in corpse interactions beyond any effects of kinship.



We were likewise able to identify the strong role that cause of death plays in predicting interactions with corpses. While this study demonstrates how empiricism can be used in primate thanatology even with limited reports, greater detail is needed to overcome the current biases in the literature. Future investigations would benefit from more complete documentation of all death responses, across all types of death and regardless of whether group members react to corpses.

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## Compliance with ethical standards

**Conflict of interest** The authors have no conflicts of interest to declare.

**Ethical approval** Permission to conduct research was provided by the Brazilian Science and Technology Ministry (Portaria MCTIC N° 7.423/2017), Brazilian Ministry of the Environment (License SISBIO No 58967–2 ICMBio/MMA) and Ethical Committee (License No 49/2017 CEUA/UFRPE).

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