



# Behavior of Mothers after Infant Loss in Bonnet Macaques (*Macaca radiata*)

Malgorzata E. Arlet<sup>1</sup> · Ashvita Anand<sup>1</sup> · Anushka Saikia<sup>2</sup> · Ants Kaasik<sup>3</sup> ·  
Sindhuja Sirigeri<sup>1</sup> · Lynne A. Isbell<sup>4</sup> · Mewa Singh<sup>5</sup>

Received: 12 April 2023 / Accepted: 17 August 2023  
© The Author(s) 2023

## Abstract

Mother–offspring bonds in primates often last for life and shape the behavior of both mother and offspring. Therefore, the death of an infant may trigger an emotional response from its mother akin to human grief, which is characterized by active distress and passive depression. Our goal was to investigate whether the behavior of female bonnet macaques (*Macaca radiata*) changed after the loss of their infants. In the Thenmala area, southern India, between 2020 and 2022, we observed 18 mothers in two groups who lost, in total, 19 infants and three juveniles aged < 18 months. We compared affiliative, aggressive, and stress-related behavior of females before and after the death of their infants. We also examined individual variation in responses to infant loss. After the death of their infants, females withdrew socially, stayed on the periphery of the group, and had fewer companions. Bereaved females were less involved in grooming and hugging and initiated aggressive behavior more frequently than before they lost their infants. Moreover, females who lost infants showed frequent stress-related behaviors, such as self-scratching and yawning compared with when their infants were alive. Our results suggest that female bonnet macaques react to deaths of their infants in a manner that is consistent with the interpretation of grief in humans and other primates.

---

Handling Editor: Joanna (Jo) M. Setchell

---

✉ Malgorzata E. Arlet  
malarl@amu.edu.pl

<sup>1</sup> Institute of Human Biology and Evolution, Faculty of Biology, Adam Mickiewicz University in Poznań, Poznań, Poland

<sup>2</sup> Zoo Outreach Organization, Coimbatore, India

<sup>3</sup> Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

<sup>4</sup> Department of Anthropology and Animal Behavior Graduate Group, University of California, Davis, CA, USA

<sup>5</sup> Department of Studies in Psychology, University of Mysore, Mysuru, India

**Keywords** Grief · Depression · Stress · Female primates

## Introduction

Grief is characterized by active distress and passive depression in response to the loss (i.e., death) of a parent, mate, or offspring (Archer, 1998; Averill, 1968; Bowlby, 1961; Cowles & Rodgers, 1991; Glass, 2005; Gonçalves & Carvalho, 2019; King, 2013a; Kowalski & Bondmass, 2008). According to King (2013b), grief is suggested when surviving animals show signs of distress or behavior that is different from their normal routine after losing an individual to whom they were emotionally attached. Although not as obvious, expressions of grief also might include behaviors involved in the two-stage process of grief known as protest followed by despair. Protest is marked by increased movement and vocalizations (alarm calls, distress cries, and cohesion-related communication), whereas despair includes withdrawal, reduced activity, and a high frequency of self-directed behaviors (Gonçalves & Carvalho, 2019), such as self-scratching, self-grooming, and yawning.

Anderson (2016) proposed four main components that can be used to ascribe death perception in the human context: (a) inevitability, implying that all individuals will eventually reach the end of life; (b) irreversibility, meaning that those who die cannot come back to life; (c) nonfunctionality, denoting that dead organisms have no perception, thoughts, feelings, or actions; and (d) causality, meaning that death is caused by both external and internal factors. Studies have suggested that irreversibility and nonfunctionality more likely apply to large-brained animals that frequently encounter death in their environment than other mammals (Anderson, 2018). For example, there is evidence that mammals, such as elephants (*Loxodonta africana*) and dolphins (*Tursiops aduncus*), express signs of grief after the death of their conspecifics (Douglas-Hamilton *et al.*, 2006; Dudzinski *et al.*, 2003).

The vast majority of scientific studies of behavioral responses to death involve primates (Bard & Nadler, 1983; Codner & Nadler, 1984; Cronin *et al.*, 2011; Laudenslager *et al.*, 1990; Reite *et al.*, 1989; Seay *et al.*, 1962). Strong indicators of grief-like behaviors in primates include food aversion, passivity, social isolation/withdrawal, and social avoidance (bonnet macaques *Macaca radiata*, lion-tailed macaques *M. silenus*: Das *et al.*, 2019). However, some primates show an increase in seeking social support and affiliation (Engh *et al.*, 2006) rather than withdrawal. Grieving in primates thus has resemblances to human grief. In female chacma baboons (*Papio ursinus*), the death of a close relative resulted in an increase in glucocorticoids showing elevated stress (Engh *et al.*, 2006). Subsequently, they showed an increase in the number of grooming partners, the rate of grooming of other females, and grooming diversity. These results and a commentary by Sapolsky (2016) suggest that increased social support is used as a way to cope with loss. Other responses to dead individuals may include fear and wariness toward corpses (mountain gorilla *Gorilla beringei beringei*, chimpanzee *Pan troglodytes*; Watts, 2020), staring at and resting near the corpse (Eastern gorilla *Gorilla beringei*; Porter *et al.*, 2019), touching and inspecting the wounds of a dead animal (Barbary macaque *Macaca sylvanus*; Campbell *et al.*, 2016; Rhesus macaque *Macaca mulatta*; Buhl

*et al.*, 2012), group distress (chimpanzee; Anderson *et al.*, 2010; Boesch, 1991), and guarding corpses from attackers (*Macaca sylvanus*; Campbell *et al.*, 2016). For instance, Goodall (1986) documented a case in chimpanzees wherein an 8-year-old male stayed close to his mother's corpse and died within a month of losing her.

One might expect grief to be expressed consistently and most obviously when mothers lose their infants. Mothers carry deceased infants (Biro *et al.*, 2010; Das *et al.*, 2019; Watson & Matsuzawa, 2018), providing "intense maternal affection" to the corpse (page 131, Li *et al.*, 2012), and express changes in social behavior, such as increased avoidance and less grooming (Takeshita *et al.*, 2020). A female Barbary macaque who lost her infant self-groomed in multiple bouts during the following hour (Campbell *et al.*, 2016). After the corpse was removed by local merchants for burial, the female was heard giving distress or fear screams and showed vigilance and searching behavior. For the rest of the day, she continued her vigilance and searching behavior, followed by distress calls while staying away from the group.

In another study investigating the response of mothers to dead infants, two of three female Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) carried the corpses of their infants before the corpses were taken away by reserve staff for burial (Li *et al.*, 2012). The first female initially vocalized and showed searching behaviors until the end of the day after the corpse was taken away. She also seemed to avoid interacting with other group members in the days following her loss. The second female was observed to behave normally, except for grabbing another infant and attempting to groom it. The authors hypothesized that the behavioral response of the mother to her dead infant depends on the amount of time she had to bond with it, with the oldest infant being carried the longest and the mother staying the farthest away from the group (Li *et al.*, 2012). Similar observations were made for a blonde capuchin monkey (*Sapajus flavius*; Andrade *et al.*, 2020). As a final example, six bonnet macaque mothers who lost their infants not only carried them but were more passive and fed significantly less than females whose infants remained alive; however, there was some individual variability in the form of less sociality and grooming (Das *et al.*, 2019).

Bonnet macaques occur in southern India and live in multi-male, multi-female groups. Females are philopatric and form stable and matrilineally heritable dominance ranks, whereas males usually disperse when they become adults (Silk *et al.*, 1981; Singh *et al.*, 1984). Most adult female bonnet macaques give birth during the dry season (typically February–May) just before the monsoon season (Rahaman & Parthasarathy, 1969; Sinha, 2001). Mother–infant relationships are strongest from birth to weaning, when the infant is 6 to 10 months old (Nathan & Kaufman, 1972; Rahaman & Parthasarathy, 1969; Simonds, 1965; Singh *et al.*, 1980). Survival of immature individuals was significantly lower in human-made habitats than in more natural, forest habitats (Singh & Rao, 2004).

Due to high infant mortality, we had the opportunity to examine mothers' responses to infant loss in a bonnet macaque population. At the Thenmala study site, many infant deaths were side effects of living in an anthropogenic environment (Arlet *et al.*, 2021). Between 2016 and 2018, 14 infants died (28% mortality; Arlet *et al.*, 2021). In 2020–2022, infant mortality was much higher as 29 infants died (54% mortality in the same groups; unpublished data). While we do not have information

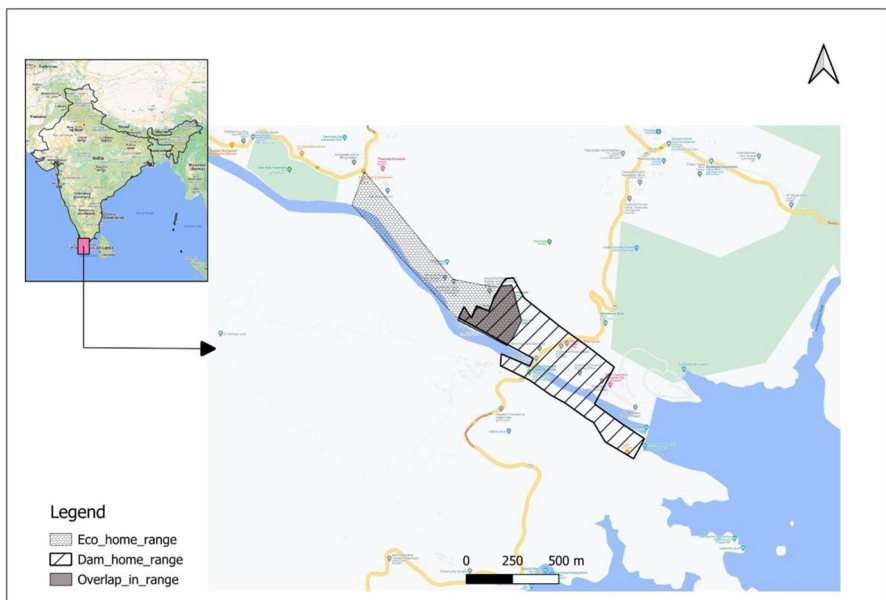
on the cause of each infant's death (due to COVID-19 lockdowns), we know that one infant was stillborn, four died due to electrocution, four due to the death of the mother (probably poisoned), two due to vehicular accidents, and two as a result of conflict with local human residents.

Our goal is to examine whether female bonnet macaque express behavior resembling grief. We compare affiliative (spatial position in the group, number of neighbors within 3 m, grooming, and hugging), agonistic (aggression), and self-regulatory (stress-related behavior, feeding, and vocalizing) behavior of mothers before and after the death of their infants. We also compare the behavior of the bereaved mothers with each other to examine individual variation in responses. Finally, we describe the behavior of the only two mothers who carried their dead infants for some time before relinquishing them.

## Methods

### Study Site and Subjects

We studied two habituated bonnet macaque groups (Dam and Eco) at Thenmala Dam and Ecotourism Recreational Area ( $8^{\circ}57'37''$  N,  $77^{\circ}03'40''$  E) on the outskirts of Thenmala, Kerala, southern India, from January 2020 to February 2022. The home ranges of the study groups include small forest patches, three villages, governmental forest offices, and an ecotourism center (Fig. 1).



**Fig. 1** Thenmala study site in southern India with the home ranges of two study groups of bonnet macaques (January 2020–February 2022).

During our study, the Dam group consisted of 23–43 individuals and the Eco group consisted of 28–53 individuals (Anand *et al.*, 2022). There also were several nonhabituated groups of bonnet macaques in the study area.

Aside from a few times when they disappeared into deep forest, we observed both Dam and Eco groups in most of their home ranges. We classified animals under 12 months of age (all born during the study) as infants, those aged 1–3 years as juveniles, males aged 3–5 years as subadult males, females aged  $\geq 4$  years as adult females, and males aged  $\geq 6$  years as adult males (Simonds, 1965). We studied all 19 mother–infant pairs and three mother–juvenile (< 18 months) pairs in the two groups (Table 1). However, by December 2021, only ten infants remained. Whenever we noticed a new infant in a group, we counted it as a birth. We designated an infant as “dead” when we first noticed that it was either dead or no longer present in a group, because young infants cannot survive long by themselves (Anand *et al.*, 2022).

**Table 1** Characteristics of mothers and infants in bonnet macaque study groups in 2020–2021, in Thenmala, Southern India, 2020–2021

Female (code)	Group	Parity	Rank	Infant	Sex	Birth	Death
Alex (AX)	Eco	P	M	Astin	F	05/2020	25/11/2020
Ashoka (AS)	Dam	P	L	August	M	16/03/2021	29/04/2021
Bella (BE)	Dam	M	H	Bernie	M	1/02/2020	24/11/2020
Blondie (BL)	Dam	M	H	Bono	M	04/2020	24/10/2020
Blondie*	Dam	M	H	-	F	29/04/2021	29/04/2021
Funny Nose (FN)	Dam	P	M	Fion	M	05/2020	26/10/2021
Jane (JN)	Dam	M	H	Jaguar	M	04/2020	26/10/2021
Jane	Dam	M	H	Jude	M	15/05/2021	10/11/2021
Kala (KL)	Dam	M	M	Kulfi	M	06/2020	26/10/2021
Kim (KM)	Dam	M	M	Kaya	F	07/02/2020	04/01/2021
Mar (MR)	Dam	M	L	Mischief	F	05/02/2021	05/07/2021
Maz (MZ)	Dam	M	L	Mowgli	M	05/2020	08/2020
Maz	Dam	M	M	Mimi	F	10/06/2021	01/10/2021
Miley (ML)	Dam	P	L	Morcen	F	11/04/2021	17/06/2021
Norma* (NO)	Eco	P	L	-	-	05/2020	08/2020
Pinduli* (PN)	Eco	P	M	-	-	05/2020	09/2020
Spikey* (SY)	Eco	M	H	Scooby	F	18/02/2020	08/2020
Tess (TS)	Eco	M	L	Truffle	M	09/02/2021	16/08/2021
Trinity (TR)	Eco	M	H	Tin Tin	M	05/2020	17/12/2020
Vivian (VV)	Eco	M	L	Vold	M	05/2021	27/11/2020
Yoda* (YO)	Dam	M	M	Yang	M	07/03/2020	06/2020
Yoda	Dam	M	H	Yuko	F	09/02/2021	17/06/2021

*L* low rank, *M* middle rank, *H* high rank, *M* multiparous, *P* primiparous.

\*Females with insufficient data for comparison because of neonatal death or observer absence due to COVID-19 lockdown.

## Behavioral Observations

As a part of a larger project on bonnet macaque behavior, we have been collecting systematic data on selected behaviors of all adult females and infants, and on group membership in the two study groups. We have collected data on the two groups 5 days per week, from Monday to Friday, since November 2019. All macaques were well habituated to human presence and were individually recognizable by using natural markings, such as face characteristics (color, scars, wrinkles), relative body size, and nipple color and size.

Each observation day, teams of two or three observers (a total of six observers) collected behavioral observations during 15-min focal samples, using *ad libitum* and all occurrences sampling. We sampled in two rounds, once in the morning and again in the afternoon. Each round consisted of one focal sample of each female in one of the two groups until all were sampled. We determined the sampling order in each group based on the first sighting of an adult female that had not yet been sampled during that round, taking care to balance morning and afternoon sampling. Over 23 months, we completed 3,723, 15-min, focal samples (931 h of observations). For the 18 females who lost their infants, we collected 833 h of focal observations, with a mean  $\pm$  SD of  $46.2 \pm 15.7$  h per female. However, for five dead infants, we were unable to collect sufficient behavioral data on the mothers due to COVID-19 lockdowns. During focal sampling, we recorded the following behaviors whenever they occurred: grooming (initiated and received), hugging (initiated and received), aggression (initiated), feeding, the woo-call vocalization (a type of contact call), yawning, and self-scratching (both assumed to be stress-related; Appendix Table 1). We also filmed the behavior of females who carried dead infants.

In addition, we recorded the focal animal's position in the group at the beginning and end of the focal sample as *center* (with majority of group members around the focal animal), *side* (with  $> 50\%$  group members on one side), *periphery* ( $> 20$  m from other group members), *outside with others* (main group not visible but other individuals present), or *alone* (no other group members visible) (Balasubramaniam *et al.*, 2020). We also noted the number of neighbors within 3 m, and their age and sex, before and after every focal sample.

## Adult Female Dominance Ranks

We based dominance ranks of adult females on 750 recorded dyadic agonistic interactions (Dam: 474, Eco: 276). Agonistic interactions included non-physical threats (e.g., facial displays), approach–avoids (moving away from another who is approaching), supplants (taking the place of another), aggressive contacts (e.g., biting, tail-pulling, and pushing), and chases (aggressively pursuing another). From these interactions, we constructed dominance matrices for adult females in each study group following Singh *et al.* (1992, 2003). We classified females as high-, middle-, and low-ranking by using interval scores (for more details of the methodology, see Anand *et al.* (2022)).

## Data Analysis

We analyzed data from when a female had given birth to 180 days later (“baby”) and when the same female had given birth but lost the infant up until 30 days after the day of death (“lost”). The 180 days for mothers and surviving infants are long enough to use most of the data available to establish typical behavior patterns for mothers with infants. The 1-month period for mothers and dead infants was too short to use most of the grieving data, but visualization of the data showed varying patterns across individuals (e.g., some females seemed to show grieving behavior even 3 months after the infant’s death, whereas for others the period appeared to be much shorter; Appendix Fig. 5). We expected that our modeling approach would allow us to detect any initial grieving even if the fixed 1-month step model might not be very realistic, cf. gradually diminishing effect.

We used Generalized Linear Mixed Models using Template Model Builder (package `glmmTMB`; Brooks *et al.*, 2017) in R version 4.3.1 (R core team, 2023). We tested full models against respective null models by using likelihood ratio tests (LRT). We also tested the significance of individual predictors with LRTs by comparing full models against models with the predictor omitted. We calculated and tested estimated marginal means with the `emmeans` package (Lenth, 2023). For spatial position, we used two scan observations per focal sample as correlated data points, including both the female ID and the combination of female ID and Session ID as random effects in the binomial mixed model. We used the same random-effects structure to model the number of neighbors within 3 m and included the zero-inflation parameter in the Poisson mixed-model, as the number of observations per focal sample was roughly equal to the focal sample length in minutes, and the number of zeroes in the data far exceeded the amount expected. For affiliative behaviors (grooming, hugging), female-initiated aggression, stress-related behaviors (self-scratching, yawning), and vocalizations (woo-calls), we calculated the number of events per focal sample as observations and used the logarithm of the focal sample duration as a model offset to account for the difference in effort in a Poisson rate mixed-model with female ID as a random effect. We used status (before and after the loss), rank, parity, and group as fixed effects in all models. We did not include infant age as a factor in models, because we could not specify the shape of the average grieving pattern for a fixed trait correctly due to variation between females. We used visual residual based diagnostics for all models.

## Ethical Note

We collected all data from habituated, wild animals without interfering with their activities. The research complied with the laws of India, and the protocols were approved by the National Biodiversity Authority and Kerala Forest Department at the time the field research was conducted. The authors declare that they have no conflict of interest.

**Data Availability** The data used in this study are available from the first/corresponding author on reasonable request.

## Results

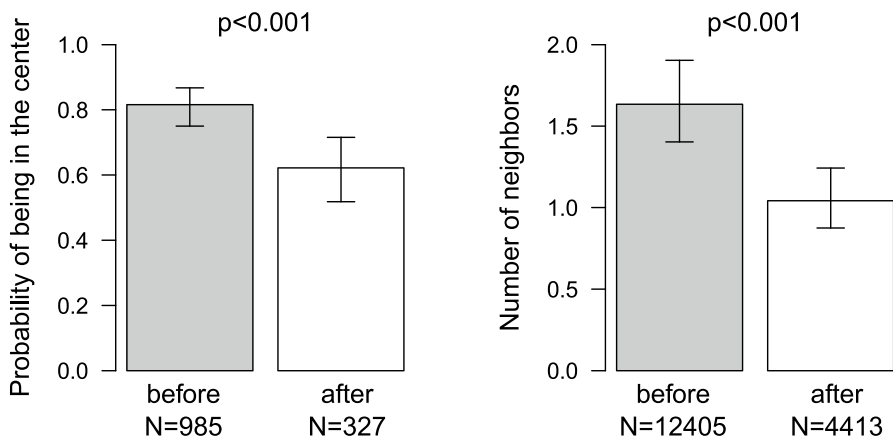
### Spatial Position in the Group and Numbers of Neighbors within 3 m

The full model was significantly different to the null model for both spatial position in the group (LRT:  $\chi^2=26.32$ , degree of freedom [df]=5,  $p<0.001$ ) and number of neighbors with 3 m (LRT:  $\chi^2=52.22$ , df=5,  $p<0.001$ ). Females were significantly more often central when their infants were alive than after they lost their infants (Table II; Fig. 2). Females also had significantly fewer neighbors within 3 m after they lost their infants than when their infants were alive (Table III; Fig. 2). Females also had significantly fewer neighbors within 3 m after infant loss in the Eco group than in the Dam group (Table III). Female dominance ranks were not significantly related to spatial position (Table II).

**Table II** Influence of infant loss and characteristics of mothers on the spatial position of the mothers in two groups of bonnet macaques in Thenmala, Southern India, 2020–2021. Results of LRT based on a Binomial mixed model with individual as the random effect

Term	df	$\chi^2$	<i>p</i>
Infant loss	1	22.51	<b>&lt;0.001</b>
Rank	2	4.37	0.112
Parity	1	0.24	0.625
Group	1	0.76	0.383

Significance is denoted in bold type



**Fig. 2** Probability of being in the center of the group and the number of neighbors within 3 m of female bonnet macaques in Thenmala, Southern India, before and after they lost their infants, 2020–2021. Bars show estimated marginal means of a mixed model. Error bars show asymptotic confidence intervals. *P*-values correspond to the significance test between the means.



**Table III** Influence of infant loss and characteristics of mothers on the number of neighbors within 3 m of the mother in bonnet macaques in Thenmala, Southern India, 2020–2021. Results of LRT based on a zero-inflated Poisson mixed model with individual as the random effect

Term	df	$\chi^2$	<i>p</i>
Infant loss	1	39.24	<b>&lt; 0.001</b>
Rank	2	5.11	0.078
Parity	1	2.11	0.146
Group	1	6.79	<b>0.009</b>

Significance is denoted in bold type

### Affiliative Behaviors

The full model was significantly different to the null model for both receiving grooming (LRT:  $\chi^2=23.59$ ,  $df=5$ ,  $p<0.001$ ) and initiating hugging (LRT:  $\chi^2=22.57$ ,  $df=5$ ,  $p<0.001$ ) but not for initiating grooming and receiving hugging analyses (LRT:  $\chi^2=10.98$ ,  $df=5$ ,  $p=0.052$ ; LRT:  $\chi^2=5.79$ ,  $df=5$ ,  $p=0.327$ ). Females were groomed significantly more and significantly initiated more hugging while their infants were alive than after their infants died (Table IV; Fig. 3). Furthermore, females in Dam group received significantly more grooming and initiated significantly more hugging than females in Eco group.

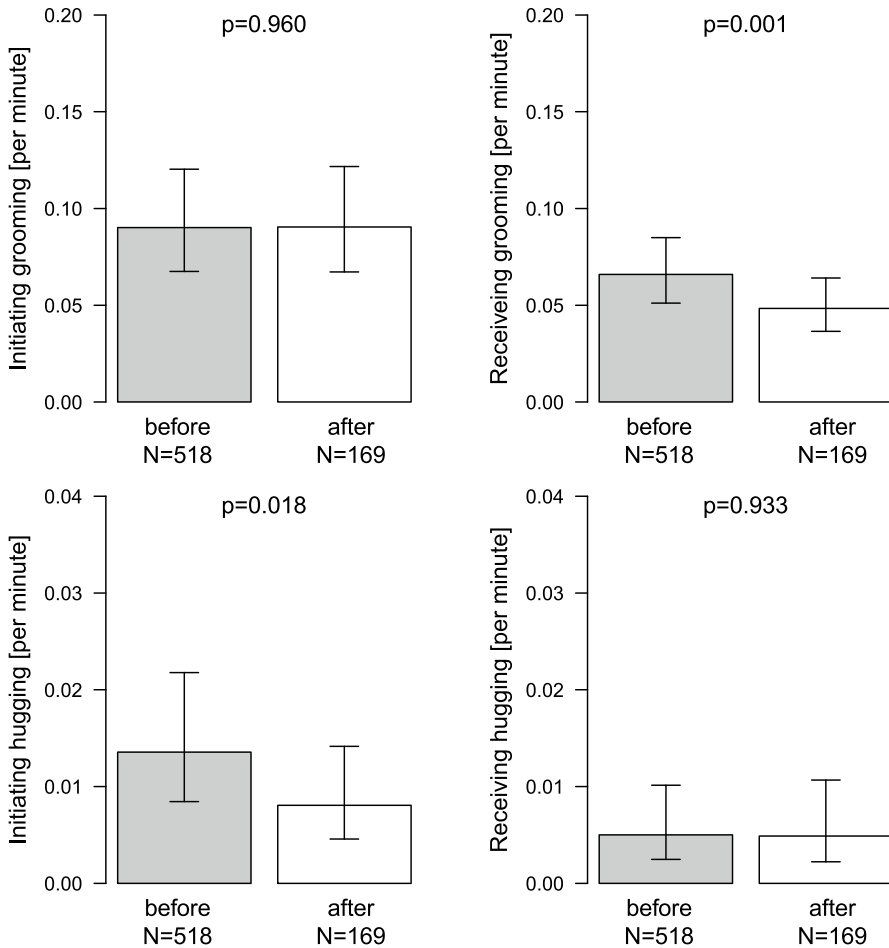
### Feeding Behavior and Aggressive Interactions

The full model was significantly different to the null model for both feeding behavior (LRT:  $\chi^2=54.28$ ,  $df=5$ ,  $p<0.001$ ) and aggressive interactions (LRT:  $\chi^2=30.98$ ,  $df=5$ ,  $p<0.001$ ). We observed significantly higher rates of feeding events and aggression initiation in females after they lost their infants compared with before the loss (Fig. 4). Low-ranking females also spent significantly less time feeding than higher-ranking and middle-ranking females (Fig. 5) and were significantly less frequently involved in aggressive encounters than higher-ranking and middle-ranking females (Table V).

**Table IV** Influence of infant loss and characteristics of the mother on mother's affiliative behavior in bonnet macaques in Thenmala, Southern India, 2020–2021. Results of LRT based on a Poisson rate mixed model with individual as the random effect

Term	df	Receiving grooming		Initiating hugging	
		$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Infant loss	1	10.52	<b>0.001</b>	5.56	<b>0.018</b>
Rank	2	3.64	0.162	4.26	0.119
Parity	1	0.66	0.416	3.13	0.076
Group	1	7.50	<b>0.006</b>	10.49	<b>0.001</b>

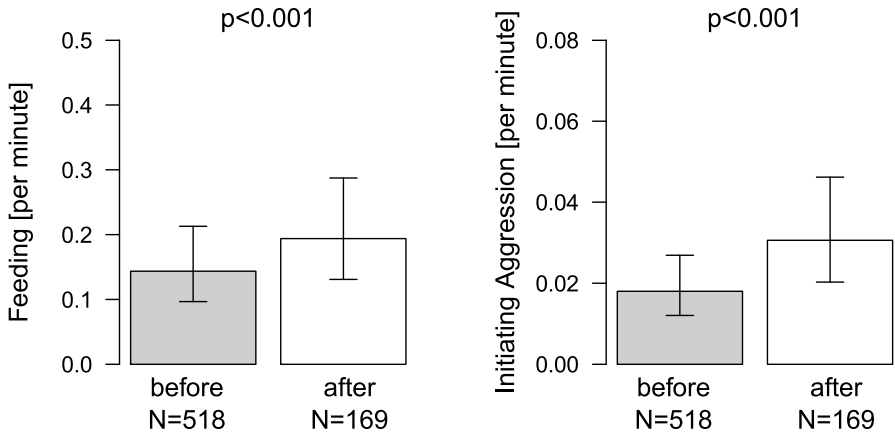
Significance is denoted in bold type



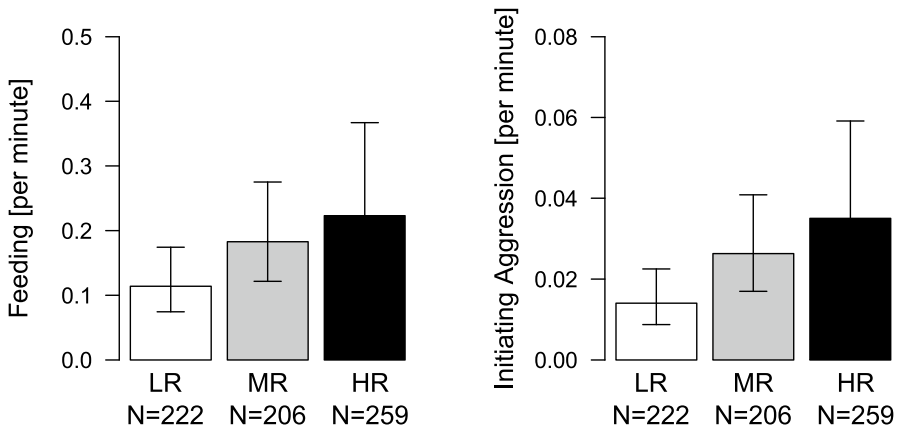
**Fig. 3** Rates of initiating and receiving affiliative behaviors by female bonnet macaques in Thenmala, Southern India before and after infant loss, 2020–2021. Bars show estimated marginal means from a mixed model. Error bars show asymptotic confidence intervals. *P*-values correspond to a significance test between the means.

### Woo-calls and Stress-related Behavior

The full model was significantly different to the null model for both woo-calls (LRT:  $\chi^2 = 14.86$ ,  $df = 5$ ,  $p = 0.01$ ) and stress-related behavior (LRT:  $\chi^2 = 38.01$ ,  $df = 5$ ,  $p < 0.001$ ). We observed significantly higher rates of woo-calls after females lost their infants compared with before. We also observed significantly more frequent scratching and yawning (stress-related behavior) in females after they lost their infants compared to before the loss. Neither of these behaviors showed significant rank effects (Table V; Fig. 6). There were no significant differences in either woo-calls or stress-related behavior by parity or group (Table V).



**Fig. 4** Rates of feeding and initiating aggressive behavior before and after infant loss in female bonnet macaques in Thenmala, Southern India, 2020–2021. Bars show estimated marginal means of from a mixed model. Error bars show asymptotic confidence intervals. *P*-values correspond to the significance test between the means.



**Fig. 5** Rates of feeding and initiating aggressive behavior before and after infant loss in female bonnet macaques in Thenmala, Southern India, 2020–2021. Bars show estimated marginal means of from a mixed model. Error bars show asymptotic confidence intervals. *P*-values correspond to the significance test between the means. For both variables Tukey-adjusted post-hoc tests show significant differences between means of LR and MR categories and LR and HR categories.

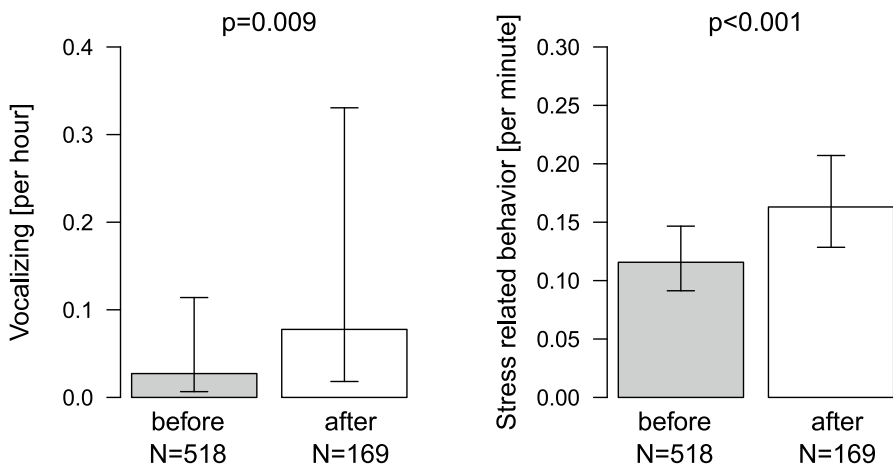
### Individual Differences Among Females

Females varied in the way they responded to infant loss (Supplemental materials: Appendix 1; Appendix Figs. 1–5). For example, whereas the increase in stress-related behavior levels seemed very common for females after infant loss, for some females (e.g., jn, kl, mi), there seemed to be no evidence of the decrease of the levels even 90 days after infant loss (Appendix Fig. 5).

**Table V** Influence of infant loss and characteristics of the mother on feeding, initiating aggressive behavior, vocalizing, and stress-related behavior in bonnet macaques in Thenmala, Southern India, 2020–2021. Results of LRT based on a Poisson rate mixed model with individual as a random effect

Term	df	Feeding events		Initiating aggression		Vocalizing		Stress-related behavior	
		$\chi^2$	P	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Infant loss	1	20.72	<b>&lt;0.001</b>	13.9	<b>&lt;0.001</b>	6.83	<b>0.009</b>	33.54	<b>&lt;0.001</b>
Rank	2	10.48	<b>0.005</b>	10.57	<b>0.005</b>	5.76	0.056	3.81	0.149
Parity	1	3.60	0.058	0.00	0.973	1.87	0.172	1.19	0.274
Group	1	1.02	0.312	0.00	0.978	0.14	0.707	2.12	0.145

Significance is denoted in bold type



**Fig. 6** Vocalization and stress related behavior in female bonnet macaques in Thenmala, Southern India before and after infant loss for the years 2020–2021. Bars show estimated marginal means of the respective mixed model. Error bars show their asymptotic confidence intervals. *P*-values presented correspond to the significance test between the means.

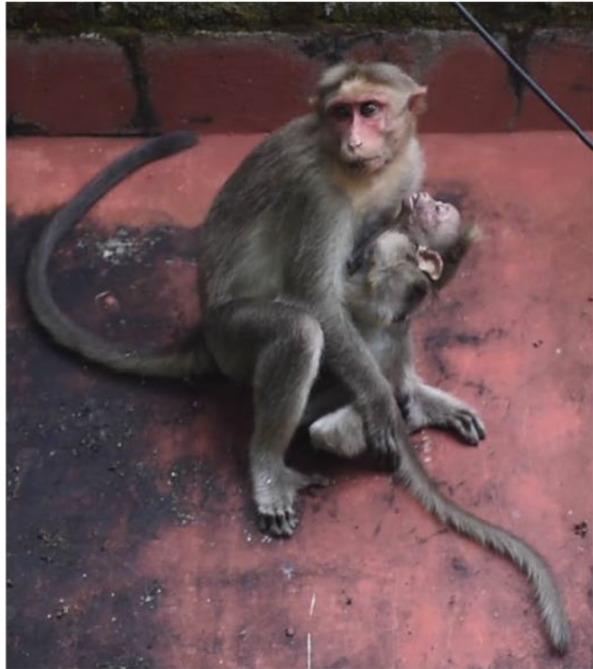
### Cases of Dead Infant Carrying

Of the 18 females, we only observed two carrying their dead infants.

#### Case 1. AX and infant AT

Female AX carried her dead 6-month-old infant, AT, for 1 day. We filmed her for 17 min, 34 s within ~1 h of finding the infant dead on 25 November 2020. During this time, AX spent 7:28 min, or 42.5% of the total filmed time, interacting with AT. The two major interactions were grooming (3:50 min) and holding (2:15 min). AX was not more than 2 m from AT during this period and allowed two juvenile females (OH, SS) and two adult females (BT, SY) to inspect the infant's body. However,

**Photo 1** Female AX with her dead infant AT on 25 November 2021 in Thenmala, Southern India.



she carried AT and avoided two high-ranking adult males (LD, BI), allowing only HN, a low-ranking adult male, to sit next to her. During the filmed period, AX initiated more grooming toward juvenile and adult females (2:05 min) than she received (1:05 min). AX dropped the body of her infant by the end of the same day and did not attempt to retrieve her. It is unclear at what point this occurred and observers located the corpse near the area the group was first sighted at the end of the day (Photo 1).

### **Case 2. BL and Stillborn Infant**

Female, BL carried her stillborn infant (IN) for at least 5 days. We filmed her for a total of 45 min, 49 s on 3 days: the day the infant was born (29 April 2021), 30 April, and 3 May. During this time, BL spent 62.9% (28:49 min) interacting with IN, mainly holding (23:26 min) and carrying it (4:13 min). During the filming time, BL kept IN on her body or within one body length. On all three observation days, BL did not initiate or receive interactions from other individuals except for one instance of grooming by a juvenile female (BV). Additionally, BL vocalized 39 times on the first day and 99 times on the third day. Vocalizations consisted of contact and isolation calls. Only BV and an infant (YU) showed interest in the stillborn infant and inspected it. We were unable to gather further data due to COVID-19 lockdowns at the field site (Photo 2).

**Photo 2** Female bonnet macaque BL with her stillborn infant on 3 May 2021 in Thenmala, Southern India.



## Discussion

We found that females who lost infants exhibited behaviors consistent with the expression of grief, as observed in other primates (Campbell *et al.*, 2016; Li *et al.*, 2012; Sapolsky, 2016; Yang *et al.*, 2022). They were more on the periphery of the group, had fewer neighbors within 3 m, received less grooming, and were less involved in hugging, all of which are indicators of social withdrawal, after they lost their infants than when they had their infants. They also directed aggressive behavior toward other individuals more frequently, gave more contact calls, and scratched and yawned more compared with before the loss of their infants. An increase in self-directed behavior, such as scratching after the loss of an infant, appears to correspond to the despair stage of grieving (Gonçalves & Carvalho, 2019).

Our results are largely consistent with a previous study of bonnet macaques, which found that mothers withdrew socially after the loss of their infants (Das *et al.*, 2019). However, whereas that study found that mothers decreased their feeding, we found that they increased their feeding after infant loss. We also found that high-ranking mothers who lost their infants initiated more aggression and fed more than low-ranking mothers who lost their infants. One limitation of our study is that it is correlational, limiting our ability to rule out explanations other than grief for the behavioral changes that we observed. Given the well-established association between female aggression and competition for food, it is possible that the increases in feeding and aggression after infant loss were not driven by grief but by changes in food availability, because bonnet macaques show birth seasonality. Unfortunately, we cannot examine this, because we do not have data on food availability. Nonetheless, there are enough similarities between the findings of our study and those of other studies to suggest that infant loss is indeed a stressful event for bonnet macaque mothers and that they experience grief

when their infants die. Even if they are unable to understand the concept of death, it is possible for grief to manifest as a result of the absence of the dead individual to whom the “griever” was attached (King, 2013a, b).

Macaque mothers often have been observed to walk on three limbs to facilitate carrying corpses (Anderson, 2017; Sugiyama *et al.*, 2009). We suggest that dead-infant carrying was not widespread among mothers at our study due to their proximity to areas of high human activity, including both vehicular and pedestrian traffic. Moreover, the bonnet macaques often are harassed by residents, shop owners, and street dogs and flee to avoid injury. In such situations, carrying the corpses would make escaping harder.

Individual variation in female responses also was apparent. Reports on chimpanzees (Biro *et al.*, 2010) and semi-free-ranging Japanese macaques (Watson & Matsuzawa, 2018) also suggest that there may be an individual component in mothers’ responses to dead infants. This was perhaps most obviously seen in our study by the fact that only two females carried the corpses of their infants, a behavior that has been documented as a response to infant death in many other primate species (reviewed in Gonçalves & Carvalho, 2019); however, lesser carrying behavior could be the result of living in an anthropogenic landscape. Based on these two cases, we did not find that the duration of dead-infant carrying increased with the age of the infant (i.e., mother–infant bonding time), as found in snub-nosed monkeys (Li *et al.*, 2012). In our study, BL carried her stillborn infant for longer than AX whose infant was ~6 months old at the time of death. Carrying a dead infant poses challenges to foraging and can result in the mother abandoning the infant’s corpse to conserve energy (Sugiyama *et al.*, 2009). It is possible that one of the reasons BL carried her infant longer than AX did was because of the lower energy cost of carrying a smaller infant. Neither female attempted to feed the dead infant.

Previous research has focused on the mother’s response immediately after the loss of her infant or while she carries the dead infant (Das *et al.*, 2019). While infant mortality is common and there appears to be a distinct effect of infant death on the mother’s behavior, the concept of grief behavior in the weeks or months following the loss is relatively understudied. While it would be interesting to compare the behavior of mothers with and without infants of the same age and/or at the same time, we did not have sufficient data points to perform these analyses.

Although we observed two cases of carrying the infant, females did not attempt to feed them, suggesting that females recognize the irreversibility and nonfunctionality of the death of their infants. Moreover, because the females that interacted with their dead infants only carried or groomed them, we suggest that mothers were able to understand the concept of death, and thus, their subsequent behavior reflects their grief.

We also found that grieving is not restricted to the immediate short-term (carrying the dead body) but has long-term effects, sometimes even 3 months after the loss of the infant (Appendix Fig. 5). While females do show signs of grief after the death of their infants, some of these behaviors may be affected by ecological constraints, such as food availability and navigating an anthropogenic landscape. Long-term studies of the behavior of females after losing their infants are necessary to obtain a more complete understanding of grieving behavior in primates.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10764-023-00395-2>.

**Acknowledgements** We thank the National Biodiversity Authority and Kerala Forest Department for permission to work in Thenmala. We are grateful to the Kerala Ecotourism Centre for facilitating our research in the field site. We also thank Snehal Gole, Vinyza Dhanboora, Partha Sarathi Mishra, Nagarathna Balakrishna, Mohammed Ismail Rafi, and Akanksha Pandey for their assistance with data collection. This work was supported by the National Science Centre Harmonia grant (2018/30/M/NZ8/00025) awarded to Dr Małgorzata Arlet. Mewa Singh is supported by Science and Engineering Research Board, Government of India grant under Distinguished Fellowship. We also appreciate the helpful comments from the editor and two reviewers on an earlier version.

**Author Contributions** All authors made substantial contributions to this paper. M.A. conceptualized the paper, M.A., A.A., A.S., and S.S. collected data, M.A., A.A., S.S., and A.S. prepared data for analysis, A.K. analyzed data, M.A., A.A., and A.S. drafted the article, and L.I. and M.S. revised it critically for important intellectual content. All authors gave final approval of the submitted version.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Anand, A., Balakrishna, N., Singh, M., Isbell, L. A., Sirigeri, S., Saikia, A., & Arlet, M. E. (2022). Infant adoptions in wild bonnet macaques (*Macaca radiata*). *Primates*, 63(6), 627–635. <https://doi.org/10.1007/s10329-022-01017-w>
- Anderson, J. R. (2016). Comparative thanatology. *Current Biology*, 26(13), R553–R556. <https://doi.org/10.1016/j.cub.2015.11.010>
- Anderson, J. R. (2017). Comparative Evolutionary Thanatology of Grief, with Special Reference to Non-human Primates. *Japanese Review of Cultural Anthropology*, 18(1), 173–189. [https://doi.org/10.14890/jrca.18.1\\_173](https://doi.org/10.14890/jrca.18.1_173)
- Anderson, J. R. (2018). Chimpanzees and death. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1754), 20170257. <https://doi.org/10.1098/rstb.2017.0257>
- Anderson, J. R., Gillies, A., & Lock, L. C. (2010). Pan thanatology. *Current Biology*, 20(8), R349–R351. <https://doi.org/10.1016/j.cub.2010.02.010>
- Andrade, B. M. T., Freire-Filho, R., & Bezerra, B. (2020). The behaviours of a female blonde capuchin (*Sapajus flavius*) towards her dead infant. *Behaviour*, 157(14–15), 1231–1238. <https://doi.org/10.1163/1568539X-bja10042>
- Archer, J. (1998). *The Nature of Grief: The Evolution and Psychology of Reactions to Loss*. Routledge. <https://doi.org/10.4324/9780203360651>
- Arlet, M. E., Balasubramaniam, K. N., Saha, R., Beisner, B., Marty, P. R., Kaburu, S. S. K., Bliss-Moreau, E., Kaasik, A., Kodandaramaiah, U., & McCowan, B. (2021). Infant survival among free-living bonnet macaques (*Macaca radiata*) in South India. *International Journal of Primatology*, 42(2), 220–236. <https://doi.org/10.1007/s10764-021-00198-3>
- Averill, J. R. (1968). Grief: Its nature and significance. *Psychological Bulletin*, 70, 721–748. <https://doi.org/10.1037/h0026824>



- Balasubramaniam, K. N., Marty, P. R., Samartino, S., Sobrino, A., Gill, T., Ismail, M., Saha, R., Beisner, B. A., Kaburu, S. S. K., Bliss-Moreau, E., Arlet, M. E., Ruppert, N., Ismail, A., Sah, S. A. M., Mohan, L., Rattan, S. K., Kodandaramaiah, U., & McCowan, B. (2020). Impact of individual demographic and social factors on human–wildlife interactions: A comparative study of three macaque species. *Scientific Reports*, *10*(1), Article 1. <https://doi.org/10.1038/s41598-020-78881-3>
- Bard, K. A., & Nadler, R. D. (1983). The effect of peer separation in young chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *5*(1), 25–37. <https://doi.org/10.1002/ajp.1350050104>
- Biro, D., Humle, T., Koops, K., Sousa, C., Hayashi, M., & Matsuzawa, T. (2010). Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants. *Current Biology*, *20*(8), R351–R352. <https://doi.org/10.1016/j.cub.2010.02.031>
- Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, *117*(3–4), 220–241.
- Bowlby, J. (1961). Processes of mourning. *The International Journal of Psycho-Analysis*, *42*, 317–340.
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Buhl, J. S., Aure, B., Ruiz-Lambides, A., Gonzalez-Martinez, J., Platt, M. L., & Brent, L. J. N. (2012). Response of rhesus macaques (*Macaca mulatta*) to the body of a group member that died from a fatal attack. *International Journal of Primatology*, *33*(4), 860–871. <https://doi.org/10.1007/s10764-012-9624-1>
- Campbell, L. A. D., Tkaczynski, P. J., Mouna, M., Qarro, M., Waterman, J., & Majolo, B. (2016). Behavioral responses to injury and death in wild Barbary macaques (*Macaca sylvanus*). *Primates*, *57*(3), 309–315. <https://doi.org/10.1007/s10329-016-0540-4>
- Codner, M. A., & Nadler, R. D. (1984). Mother-infant separation and reunion in the great apes. *Primates*, *25*(2), 204–217. <https://doi.org/10.1007/BF02382392>
- Cowles, K. V., & Rodgers, B. L. (1991). The concept of grief: A foundation for nursing research and practice. *Research in Nursing & Health*, *14*(2), 119–127. <https://doi.org/10.1002/nur.4770140206>
- Cronin, K. A., van Leeuwen, E. J. C., Mulenga, I. C., & Bodamer, M. D. (2011). Behavioral response of a chimpanzee mother toward her dead infant. *American Journal of Primatology*, *73*(5), 415–421. <https://doi.org/10.1002/ajp.20927>
- Das, S., Erinjery, J. J., Desai, N., Mohan, K., Kumara, H. N., & Singh, M. (2019). Deceased-infant carrying in nonhuman anthropoids: Insights from systematic analysis and case studies of bonnet macaques (*Macaca radiata*) and lion-tailed macaques (*Macaca silenus*). *Journal of Comparative Psychology*, *133*, 156–170. <https://doi.org/10.1037/com0000140>
- Douglas-Hamilton, I., Bhalla, S., Wittemyer, G., & Vollrath, F. (2006). Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behaviour Science*, *100*(1), 87–102. <https://doi.org/10.1016/j.applanim.2006.04.014>
- Dudzinski, K., Sakai, M., Masaki, K., Kogi, K., Hishii, T., & Kurimoto, M. (2003). Behavioural observations of bottlenose dolphins towards two dead conspecifics. *Aquatic Mammals*, *29*, 108–116. <https://doi.org/10.1578/016754203101023951>
- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., & Cheney, D. L. (2006). Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 707–712. <https://doi.org/10.1098/rspb.2005.3378>
- Glass, R. M. (2005). Is grief a disease? Sometimes. *JAMA*, *293*(21), 2658–2660. <https://doi.org/10.1001/jama.293.21.2658>
- Gonçalves, A., & Carvalho, S. (2019). Death among primates: A critical review of non-human primate interactions towards their dead and dying. *Biological Reviews*, *94*(4), 1502–1529. <https://doi.org/10.1111/brv.12512>
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Belknap Press.
- King, B. (2013a). When Animals Mourn. *Scientific American*. <https://doi.org/10.1038/scientificamerican0713-62>
- King, B. (2013b). *How Animals Grieve*. University of Chicago Press.
- Kowalski, S. D., & Bondmass, M. D. (2008). Physiological and psychological symptoms of grief in widows. *Research in Nursing & Health*, *31*(1), 23–30. <https://doi.org/10.1002/nur.20228>
- Laudenslager, M. L., Held, P. E., Boccia, M. L., Reite, M. L., & Cohen, J. J. (1990). Behavioral and immunological consequences of brief mother-infant separation: A species comparison. *Developmental Psychobiology*, *23*(3), 247–264. <https://doi.org/10.1002/dev.420230305>

- Lenth, R. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.6. <https://CRAN.R-project.org/package=emmeans>
- Li, T., Ren, B., Li, D., Zhang, Y., & Li, M. (2012). Maternal responses to dead infants in Yunnan snub-nosed monkey (*Rhinopithecus bieti*) in the Baimaxueshan Nature Reserve, Yunnan, China. *Primates*, 53(2), 127–132. <https://doi.org/10.1007/s10329-012-0293-7>
- Nathan, T. S., & Kaufman, I. C. (1972). Perinatal observations of mother-infant behavior in the bonnet macaque. *Israel Annals of Psychiatry & Related Disciplines*, 10, 245–266.
- Porter, A., Eckardt, W., Vecellio, V., Guschanski, K., Niehoff, P. P., Ngobobo-As-Ibungu, U., Pekeyake, R. N., Stoinski, T., & Caillaud, D. (2019). Behavioral responses around conspecific corpses in adult eastern gorillas (*Gorilla beringei* spp.). *PeerJ*, 7, e6655. <https://doi.org/10.7717/peerj.6655>
- R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rahaman, H., & Parthasarathy, M. D. (1969). Studies on the social behaviour of bonnet monkeys. *Primates*, 10(2), 149–162. <https://doi.org/10.1007/BF01730980>
- Reite, M., Kaemingk, K., & Boccia, M. L. (1989). Maternal separation in bonnet monkey infants: Altered attachment and social support. *Child Development*, 60(2), 473–480. <https://doi.org/10.2307/1130991>
- Sapolsky, R. M. (2016). Psychiatric distress in animals versus animal models of psychiatric distress. *Nature Neuroscience*, 19(11), Article 11. <https://doi.org/10.1038/nn.4397> <https://doi.org/10.2460/javma.2003.222.1526>
- Seay, B., Hansen, E., & Harlow, H. F. (1962). Mother-infant separation in monkeys. *Journal of Child Psychology and Psychiatry*, 3(3–4), 123–132. <https://doi.org/10.1111/j.1469-7610.1962.tb02047.x>
- Silk, J. B., Clark-Wheatley, C. B., Rodman, P. S., & Samuels, A. (1981). Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Animal Behaviour*, 29(4), 1106–1120. [https://doi.org/10.1016/S0003-3472\(81\)80063-2](https://doi.org/10.1016/S0003-3472(81)80063-2)
- Simonds, P. (1965). The bonnet macaque in South India. *Primate Behavior: Field Studies of Monkeys and Apes*. <https://cir.nii.ac.jp/crid/1572543025047461632>
- Singh, M., D'Souza, L., & Singh, M. (1992). Hierarchy, kinship and social interaction among Japanese monkeys (*Macaca fuscata*). *Journal of Biosciences*, 17(1), 15–27. <https://doi.org/10.1007/BF02716769>
- Singh, M., Prakash, P., & Pirta, R. S. (1980). Changing patterns of behaviour during the early stages of bonnet monkey *Macaca radiata*. *Proceedings of the Indian Academy of Sciences: Animal Sciences*, 89(2), 101–108. <https://doi.org/10.1007/BF03179149>
- Singh, M., Akram, N., & Pirta R. S. (1984). Evolution of demographic patterns in the bonnet monkey *Macaca radiata*. In: Roonwal ML, Mohnot SM, Rathore NS (eds) Current primate researches. Jodhpur University Press, Jodhur, pp 7–16
- Singh, M., & Rao, N. R. (2004). Population dynamics and conservation of commensal macaques. *International Journal of Primatology*, 25(4), 847–859. <https://doi.org/10.1023/B:IJOP.0000029125.54747.ee>
- Singh, M., Sharma, A. K., & Krishna, B. A. (2003). Methodological considerations in measurement of dominance in primates. *Current Science*, 84(5), 709–713.
- Sinha, A. (2001). The bonnet macaque revisited: Ecology, demography and behavior. *ENVIS Bulletin: Wildlife and Protected Areas*, 1, 30–39.
- Sugiyama, Y., Kurita, H., Matsui, T., Kimoto, S., & Shimomura, T. (2009). Carrying of dead infants by Japanese macaque (*Macaca fuscata*) mothers. *Anthropological Science*, 117(2), 113–119. <https://doi.org/10.1537/ase.080919>
- Takeshita, R. S. C., Huffman, M. A., Kinoshita, K., & Bercovitch, F. B. (2020). Changes in social behavior and fecal glucocorticoids in a Japanese macaque (*Macaca fuscata*) carrying her dead infant. *Primates*, 61(1), 35–40. <https://doi.org/10.1007/s10329-019-00753-w>
- Watson, C. F. I., & Matsuzawa, T. (2018). Behaviour of nonhuman primate mothers toward their dead infants: Uncovering mechanisms. *Philosophical Transactions of the Royal Society b: Biological Sciences*, 373(1754), 20170261. <https://doi.org/10.1098/rstb.2017.0261>
- Watts, D. P. (2020). Responses to dead and dying conspecifics and heterospecifics by wild mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 61(1), 55–68. <https://doi.org/10.1007/s10329-019-00735-y>
- Yang, B., Anderson, J. R., Mao, M., Wang, K., & Li, B. (2022). Maternal caretaking behavior towards a dead juvenile in a wild, multi-level primate society. *Scientific Reports*, 12(1), Article 1. <https://doi.org/10.1038/s41598-022-08660-9>