



Wild Baboons Groom Objects with Fur: Implications for Infant Corpse Carrying in Primates?

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Abstract – Nonhuman primates demonstrate great behavioral diversity in their responses to death, yet the most prevalent of these—infant corpse carrying—remains poorly understood. While mothers are the most frequent carriers, corpse carrying can be performed by non-mothers, and heterospecifics' corpses are also carried. We propose a new hypothesis to explain, in part, non-maternal corpse carrying, the 'mammalian cues hypothesis,' and experimentally test it in a population of wild baboons. The mammalian-cues hypothesis argues that evolutionary pressures on maternal responsiveness have created a generalized attraction towards mammalian-typical traits in mammals of both sexes. This attraction may drive interest in inanimate objects (including corpses) that display mammalian cues. To test this, we presented objects that varied in mammalian traits to wild chacma baboons (*Papio ursinus*) and recorded their behavioral responses. Contrary to our hypothesis, baboons handled all objects (i.e., with or without mammalian traits) for similar lengths of time. However, in partial support of our hypothesis, baboons groomed the objects with fur—even those without any other mammalian traits—and explored them in a less destructive manner. We caution that infant corpse grooming by non-mothers in primates may be indicative of the visual and tactile stimuli the corpse presents rather than an interest in death or a reflection of social bonds.

Keywords – Cognitive bias, Core knowledge systems, Corpse-carrying, Primate, Thanatology

Comparative thanatology aims to understand the psychological underpinnings of animals' responses to death (Anderson, 2016; Anderson et al., 2018). Understanding animals' responses to death can provide important insights into species' cognitive abilities and complex emotion (de Waal, 2011; Panksepp & Watt, 2011). Primates represent some of the best-studied taxa in this field and individuals display astonishing variation in their responses to the dead, ranging from aggressive (e.g., chimpanzees throwing rocks and sticks at a corpse: Pruett et al., 2017), to more affiliative and protective behaviors (e.g., langurs protecting the corpse from perceived threats: Gupta, 2000). However, systematically studying primates' responses to death has been difficult because deaths, although inevitable, are unpredictable and rarely observed, meaning that data collection needs to occur opportunistically (but see: Anderson et al., 2021; Gonçalves et al., 2022).

The most commonly reported response to death across mammals is the continued carrying of an infant's corpse (infant corpse carrying, ICC), usually by its mother. This behavior has been observed most frequently in cetaceans (Bearzi et al., 2017), proboscideans (Pokharel et al., 2022), and across most primate taxa (Fernández-Fueyo et al., 2021). Primate mothers, for example, have been observed carrying corpses for less than 1 h to over 125 days, and a large part of the variation in the occurrence and duration of ICC

remains unexplained, including within populations (reviewed in: Fernández-Fueyo et al., 2021; Gonçalves & Carvalho, 2019). Corpses are not only carried, but other behaviors are frequently observed. For example, grooming is a particularly common behavior to occur during ICC in primates, but can differ from the grooming of live infants, with manipulation of the eyes, mouth, or genitals that is not observed in live infants (chacma baboons (*Papio ursinus*), Carter et al., 2020). Corpses can also be cannibalized, which can occur alongside grooming and continued carriage (Tonkean macaque (*Macaca tonkeana*), De Marco et al., 2018), but aggression towards infants' corpses has never been observed. This is in contrast to responses towards non-infant corpses, which are sometimes attacked by conspecifics (Gonçalves & Carvalho, 2019). Although infrequent, infant corpse-directed behaviors are not performed exclusively by mothers: others may carry a corpse before it is eventually discarded, and engage in grooming, guarding or other interactions with the corpse (Carter et al., 2020; Merz, 1978).

ICC is difficult to explain adaptively, because corpse carrying is presumably energetically costly and exposes the carrier to pathogens (Conly & Johnston, 2005; Gonçalves & Biro, 2018; Morgan, 2004). ICC thus presents an 'evolutionary puzzle' and many non-mutually exclusive hypotheses have been proposed to explain this behavior (Watson & Matsuzawa, 2018). The hypotheses cover both ultimate and proximate explanations, within- and between-species variation, and can take either cognitively reductionist or complex viewpoints (reviewed in Brosnan & Vonk, 2019; Gonçalves & Carvalho, 2019; Watson & Matsuzawa, 2018). For example, the hormonal hypothesis proposes that hormones that promote mother-infant bonding are a proximal explanation for ICC (Watson & Matsuzawa, 2018), promoting infant corpse care until the mother's endocrine system 'catches up' with the death of her infant (Brosnan & Vonk, 2019). An ultimate explanation for non-maternal ICC is the 'learning-to-mother' hypothesis, which suggests that inexperienced females carry corpses to gain experience to care for offspring. Whilst the hypotheses to explain ICC have accumulated (Watson & Matsuzawa, 2018), evidence to support them has not. Additionally, most hypotheses either explicitly or implicitly center on maternal ICC, despite non-maternal ICC being relatively common in primates.

Non-maternal corpse carrying has been reported across numerous social primate species including mountain gorillas (*Gorilla beringei beringei*) (Warren & Williamson, 2004), Barbary macaques (*Macaca sylvanus*) (Merz, 1978), geladas (*Theropithecus gelada*) (Fashing et al., 2011) and chacma baboons (Carter et al., 2020). Such corpse carrying is not restricted to females either: male bonobos (*Pan paniscus*), rhesus macaques (*M. mulatta*), Barbary macaques and chacma baboons have been reported carrying and grooming infant corpses (Carter et al., 2020; Kanō, 1992; Merz, 1978; Taylor et al., 1978). Many of the above instances involve infants being carried by entirely unrelated individuals, including newly immigrated group members (Warren & Williamson, 2004). Furthermore, ICC does not need to occur between familiar individuals. For example, two female geladas groomed and carried the corpse of an infant that belonged to another group (Fashing et al., 2011). Although anecdotal, these cases indicate that additional mechanisms or causes may be involved in maintaining this behavior beyond the mother-infant dyad.

Psychological research may provide testable hypotheses to explain, in part, primates' motivations for ICC. Primates, including humans, are attracted to others' infants, which evidence suggests is a carryover of strong selection on maternal responsiveness to infants (Silk, 1999). The infantile cues hypothesis suggests that physical cues that make infants attractive to mothers and others whilst alive, particularly visual cues in the form of infant natal coloration (Alley, 1980; Jay, 1962; Silk, 1999), continue after death and thus garner attention and interest from group mates. While we do not agree with the methods used to obtain these data (see critique here: Badihi & Hobaiter, 2022), recent observations have highlighted the importance of *non-visual*, tactile cues in eliciting care in primate mothers: rhesus macaque (*M. mulatta*) mothers were attracted to and carried furred soft toys after their infants' death or removal, but not hard, non-furred objects; in one case, a mother carried a soft toy for several months (Livingstone, 2022).

The infantile cues hypothesis draws a parallel with Lorenz's (1943) 'baby schema' hypothesis, a human phenomenon in which individuals are sensitive to visual cues derived from infants such as a big eyes, chubby cheeks, small nose and mouth, and plump body shape. Human's attraction to these characteristics translates to behavioral responses, particularly caretaking (Glocker et al., 2009; Langlois et al., 1995). Importantly, humans have a preference for individuals scoring highly on the baby schema across

species (Sanefuji et al., 2007), as well as for objects with these traits (Miesler et al., 2011). As in humans, primates' attraction to infants extends beyond their own species. For example, visual attention tasks demonstrate that primates show a preference for heterospecific infants' images over heterospecific adults' images (Sato et al., 2012). In addition, there are cases of cross-species affiliative play (McGrew, 2013; Morrogh-Bernard et al., 2014; Rose et al., 2003) and even 'adoption' of other primate species (Izar et al., 2006). Primates also perform ICC-like and care-giving behaviors to other mammalian taxa (coatis: De Resende et al., 2004; rabbits: Turckheim and Merz, 1984 in Gonçalves & Carvalho, 2019; rats: Hausfater, 1976; hyraxes: Hirata et al., 2001; van Lawick-Goodall, 1968) and inanimate furred object: for example, in informal experiments, stump-tailed macaques (*M. arctoides*) groomed, among other objects, animal skins, fur slippers, and furry toys (Bertrand, 1969). From these case reports of primates' interactions with other mammals and objects, we can generalize two patterns. First, although primates typically carry (novel) objects only for brief periods of time (Bergman & Kitchen, 2009; Blaszczyk, 2017; Carter et al., 2012), the duration of carrying other mammalian species can extend for as long as conspecific ICC (Toda et al., 2017). Secondly, infant-sized non-conspecifics elicit similar reactions to infant conspecifics (Gonçalves & Carvalho, 2019), with caretaking and carrying behaviors directed towards some species that are often prey animals. Taken together, this body of research suggests that primates' attraction to species-specific cues that elicit care can become generalized to objects that present similar cues.

We propose the 'mammalian cues hypothesis' to explain, in part, ICC in primates. We argue that strong selection for infant attraction in primates has created a receptivity to certain visual and tactile stimuli such as size, fur, and facial or body proportions that extends beyond species boundaries to include heterospecifics (including adults) and objects (including corpses) that display these traits. These stimuli provoke caretaking responses in primates. These features may include: the mammalian bauplan (i.e., four limbs and optionally a tail), large eyes or facial features, and, particularly, fur (Bertrand, 1969).

The aim of this study was to test the mammalian-cues hypothesis by exploring experimentally whether (Q1) primates show a greater attraction to mammalian-like objects and (Q2) which cues or combination of cues are vital in eliciting behavioral responses, in particular caregiving. Our aim was not to represent a corpse-like object, but to provide general mammalian stimuli to determine a primate's attraction to these objects (independent of cues of death). Because female humans and primates show heightened interest and responsiveness to others' infants (Cárdenas et al., 2013; Silk, 1999) and juvenile primates show more interest in novel objects (Carter et al., 2012), we also examined whether (Q3) there were age or sex differences in individuals' responses to particular objects. In line with our hypothesis and our three research questions, we predicted that, if primates are attracted to mammalian features, they would (P1) spend more time with objects that present more mammalian cues, and (P2) direct more caretaking and fewer aggressive behaviors towards these objects. We further predicted that (P3) females would perform caretaking behaviors more frequently than males, and, in line with previous research presenting objects as stimuli (Carter et al., 2012) (Bergman & Kitchen, 2009) populations of baboons, we predicted that juveniles would interact with the objects more than adults. We performed our experiments using wild chacma baboons as a model species, for several reasons: (1) chacma baboons, including unrelated males, perform ICC (Carter et al., 2020); (2) experiments with novel objects can be performed *in situ* (e.g., Carter et al., 2012, 2014); and (3) studies in the wild have high ecological validity.

Method

Permits and Ethical Approval

Research permits were granted by the Namibian National Commission on Research Science and Technology (NCRST permit no. RPIV00392018) and ethical approval was granted through the UCL Animal Welfare and Ethical Review Body.

Study Site

Data were collected from July to September 2021, from two fully habituated troops of wild chacma baboons at Tsaobis Nature Park (15° 45'E, 22° 23'S), at the edge of the Namib Desert, Namibia. Chacma baboons live in multi-male, multi-female groups, where females form a stable core of matriline (adult females and their offspring), and males immigrate, typically on reaching adulthood (Fischer et al., 2019). ICC is reported across multiple species of baboon (Fernández-Fueyo et al., 2021) and chacma baboons in this population carry infants' corpses for up to 10 days, including non-mothers (for up to half a day) (Carter et al., 2020). The troops consisted of 55 (J troop) and 65 (L troop) baboons that were individually recognizable. Age (in years) was calculated based either on known dates of birth or estimated from either infant coloration (Dezeure et al., 2021), or tooth eruption and wear during troop captures (Huchard et al., 2009). Individuals were categorized into binary age classes (juvenile or adult), where females were considered adults at menarche and males after canine eruption at approximately 8 years of age. Social dominance ranks are calculated annually based on agonistic and approach-avoid interactions collected *ad libitum* over the course of that field season (for further details, see: Huchard et al., 2009). The baboon troops are habituated to researchers following them on foot at close range (5-10 m) and are typically followed daily from dawn until dusk during 2-8 month-long field seasons (typically 6 months every year). They have previously been the subjects of non-invasive experiments (e.g., Carter et al., 2014, 2016), including novel object presentations (Carter et al., 2012).

Objects

To investigate whether certain mammalian features provoked prolonged interest or caretaking behaviors in primates, three traits were chosen as potentially important. These traits were: facial features (i.e., eyes and mouth), a mammalian bauplan and the presence of fur. Facial features, particularly the eyes and mouth, were chosen because primates recognize representations of faces (Parr, 2011) and also show preferences for images with a facial configuration (Myowa-Yamakoshi & Tomonaga, 2001). Additionally, baboons show particular interest in images of eyes (Kyes & Candland, 1987), mirroring accounts of primates showing interest in, and manipulating, the eyes of corpses (Cronin et al., 2011; Fashing et al., 2011). A mammalian bauplan was of interest as it is a pivotal way of representing the overall form of mammals. Finally, fur was chosen due to the crucial role it played for macaque infants in Harlow and Zimmerman's (1958) experiments and Zuckerman's (1932) assertion that orphaned baboons showed an indiscriminate reaction to fur. We chose objects with different combinations of these traits to assess which were critical in eliciting different responses. However, we note that it was not possible to procure commercially available objects with only a mammalian bauplan or facial features: all objects with one trait also had the other trait. For this reason, with our design, we cannot tease apart the relative importance of facial features and a mammalian bauplan to the baboons' responses. All objects were pet- or child-safe to minimize risk of injury.

Four objects were originally chosen for the presentations (Table 1, Figure 1). The first object was a control that did not display any of the mammalian traits (a ball on a rope: 'ball'). We also provided an object with both facial features and a mammalian bauplan but no fur ('cow'); fur but no other mammalian features ('furball'); and finally, a combination of all the mammalian features, including a tail ('monkey'). The cow object originally contained a thin plastic sheet inside to make noise when it was handled, which was removed before presentations. The objects were similarly sized, apart from the 'furball' object, which was considerably larger (approx. 20 cm in height *c.f.* approx. 10 cm for the other objects). Objects were presented in a random order. Any object that was damaged (see 'Qualitative analyses' below) was disposed of and replaced with a new object. During the initial experiments, it became clear that presentations with the furball object had a longer duration than presentations with the other objects. Thus, to determine whether this was due to the object's size or the trait being presented (fur), three additional objects were obtained that were analogous to the original objects but differed in size. Specifically, we supplied a large ball with

no fur ('rugby'); a small-furred ball ('pompom'); and a large-furred mammal ('rabbit'). The presentation order of these additional objects was also randomized.

Table 1

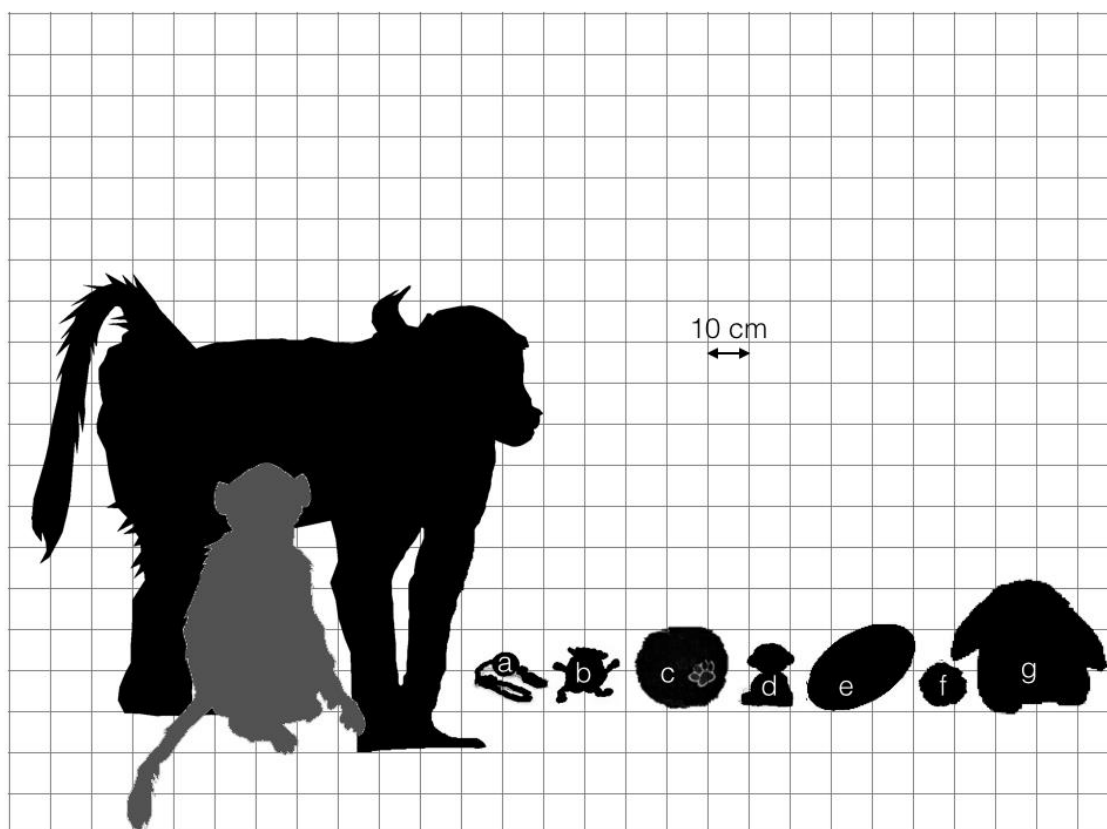
Description of the Objects Presented to the Baboons

Object name	Traits	Length (cm)	Size category	Color
Ball	None	43 (rope length; ball 5)	Small	Blue, green, white
Cow	Bauplan	Approx. 12	Small	White, with black, pink, yellow
Furball	Fur	20	Large	Blue
Monkey	Bauplan + fur	10	Small	Brown
Rugby	None	28	White, with green and blue	
Pompom	Fur	11	Small	Grey
Rabbit	Bauplan + fur	36	Large	Beige

Note. Presented are the names for the objects, the traits that each object showed, the length of the objects (cm), the size category of the objects compared to each other (large or small) and the dominant colors of the objects.

Figure 1

Diagram Depicting the Scale of the Objects Given to the Baboons



Note. Shown are an adult female (black silhouette) and 2-3-year-old juvenile (grey silhouette) and the objects (names consistent with text): (a) ball, (b) cow, (c) furball, (d) monkey, (e) rugby, (f) pompom, and (g) rabbit.

Presentations

Presentations were made by JD and HR. Because there was little temporal overlap on the site between JD and HR, and the baboons can become nervous when being followed by multiple observers (which can both impact the baboons' responses to the objects and the safety of the observers), we did not complete any formal inter-rater reliability of observations, which we acknowledge is a limitation of this study. Presentations were made to small subgroups of baboons (up to 15) in a troop, generally whilst the troop was stationary within an area. This was to increase the visibility of the object both to the baboons and to the researcher. Initially, objects were presented within the troop semi-randomly, based on visibility. However, as the experiments progressed it became clear that females and adults interacted least with the objects. In later experiments, we thus targeted these age/sex classes (females and adults) to create as balanced a design as possible by presenting objects to individuals or groups with adults or juvenile females (following Bergman & Kitchen, 2009).

It was important that the baboons did not learn to associate the researchers with providing objects, as we did not want them to learn to 'take' objects from us. To this end, we made efforts to present objects without the baboons seeing the researcher do so (Bergman & Kitchen, 2009). To initiate an experiment, a single object was discreetly deployed near the targeted subgroup by placing the object behind the researcher's backpack while they were crouching near the ground (as is typical when getting other objects, such as water, from our backpacks), then leaving the immediate vicinity of the object. On leaving the object, a focal observation of the object was started. Data were recorded on handheld computers (Samsung Galaxy S4, Samsung Electronics Co., Ltd, South Korea) in the program Cybertracker (cybertracker.org). We recorded the identities of all interactants and all behaviors directed towards the object during the presentation (see Table 2 for an ethogram). The object focal observation continued until the object was not interacted with for five continuous minutes, after which the object was retrieved.

As the research was conducted during the COVID-19 pandemic, specific mitigation measures were implemented to avoid transmitting viruses to the baboons or between troops. All objects were placed outside for 48 hr prior to being presented, where they were exposed to sunlight during daylight hours. This is because UV exposure can inactivate the COVID-19 virus, with 90% of infectious virus becoming inactive for every 6.8 minutes of UVB exposure (Ratnesar-Shumate et al., 2020). Multiple objects of each type were procured so that there was no mixing of objects between troops. Objects for different troops were stored separately to avoid contamination. Additionally, researchers underwent a 10-day quarantine upon arrival at the field site, and frequent lateral flow testing throughout the field season. Whilst in the field with baboons, observers wore a facemask covering the mouth and nose, and the researchers sanitized their hands both before and after handling any of the objects.

Statistical Analyses

We had two main research questions, and one additional research question. Our main questions were: Q1: Are individuals more attracted to mammalian-like than non-mammalian-like objects? And Q2: Which cues are vital in eliciting particular responses, including care-giving? Our additional question was: Q3: Are there age or sex differences in individuals' responses to particular objects?

To address Q1, we calculated the total duration each individual handled an object during each presentation, assuming that individuals interact with objects that they are attracted to. This proxy for attraction was used as it mirrors how attraction towards infants is measured (Silk, 1999; Silk et al., 2003). Objects were classified according to the mammalian cues present: none (ball, rugby), bauplan (cow), fur (furball, pompom), and bauplan with fur (monkey, rabbit). We did not consider any time where the object was out of sight or the individual was not in physical contact with the object.

Table 2*Ethogram of Behaviors Recorded During Object Presentations*

Behavior	State/Event	Definition
Alone	State	The object has been presented to baboons, but there are currently no individuals within arm's reach (< 60 cm) of the object.
Approach	Event	An individual walks directly/purposefully towards the object, coded when the individual is < 2 m from the object.
Bite	Event	A baboon places its mouth around part of the object and presses down with its mandibles.
Break	State	A prolonged attempt by a baboon to destroy the object or explore the object in a fashion that resulted in its destruction. Often consisted of simultaneous pulling and biting or picking parts of the object apart.
Chase	Event	Context for some of the travelling behavior: the individual with the object is engaged in play with other baboons and is being chased.
Explore	State	An individual is touching the object in an exploratory fashion: turning it over, holding it up or other non-agonistic manipulations.
Groom	State	An individual is passing fingers through / along the surface of the object, in like manner to grooming bouts with other baboons. This activity may also include the individual lowering their mouth the surface of the object, as they do when picking things out of other baboons' fur.
Handle roughly	State	Any incidents of manipulation of the object that are more rough than normal exploratory behaviors but don't escalate to destructive behaviors. Often this behavior was an individual violently swinging the object from side to side, either in their hand or mouth.
Held	State	The object has been picked up or is in clear 'ownership' (e.g., an individual has a foot on it).
Leave	Event	An individual that previously approached and/or interacted with the object travels > 5 m away from the object. NB: this means that the object can be coded as 'alone' if an individual that previously held it moves > 60 cm away but that individual has not 'left' the object until they have moved several meters away.
Pass by	Event	Any individual that passes near (< 5 m) the object but doesn't directly walk towards it, or pause to watch it.
Pull	Event	A baboon takes one part of the object and firmly pulls it away from the rest of the object.
Rest	State	The individual that has taken the object is resting in contact with it. They may be doing other things at the same time, such as grooming or chewing but they remain in the same place with the object in their possession.
Retrieve	Event	The individual that was already in possession of the object immediately picks it back up after it falls—the object is not left for more than 10 s.
Sniff	Event	An individual places their nose close to the object in a deliberate manner, or holds the object to their nose.
Steal	Event	An individual takes the focal object from the baboon that is currently in possession of it.
Travel	State	The individual that has the object carries it with them as they move.
Watch	Event	An individual directs their gaze towards the object from a close distance, either observing the object itself or what another baboon is doing to the object.

Note. Shown is the name of the behavior; whether it was considered an activity state or an event behavior; and the definition used for each behavior. Only behaviors directed towards the object were recorded, along with the identity of the actor.

To address Q2, we created two variables: (1) grooming as a proxy of caregiving and (2) aggressive behaviors directed towards an object. To measure (1) grooming behavior, we calculated the duration (s) that each individual groomed the objects for each presentation i.e., touching and exploring the surface of an object with their hands or digits in a manner reminiscent of grooming (see 10.5281/zenodo.10630925 for a video of object grooming). To measure (2) aggressive behaviors, we summed the number of seconds each baboon spent breaking the object (recorded as a behavioral state) and added 3 s each for all instances of biting or pulling the object (which were recorded as events). The duration of 3 s was chosen as exploration of the raw data showed successive instances of biting occurred in approximately 3 s intervals. Both variables (grooming and aggression) were converted to a proportion of the total time each individual spent handling that object during a presentation. The models used to answer Qs 1 and 2 were also used to address Q3.

To address our research questions, we built three statistical models using R v3.3.3. In all models, we included the baboons' sex and age class as fixed effects, along with the size of the object (as a categorical variable: small or large). Age class was chosen — rather than a continuous variable of age — for comparability to other studies examining object exploration (Bergman & Kitchen, 2009) and because male and female baboons reach adulthood at markedly different ages. Rank was not included as a fixed effect because it co-varied with sex (t-test: $t = -5.91$, $df = 178.08$, $p < .001$) and we were explicitly interested in the effect of sex on handling, grooming and breaking times. To control for repeated measures on individuals, we used a mixed models approach with a random intercept for individual identity. We considered an effect to be significant when the p -value was $<.05$, or the t value $> |1.94|$. We ran model checks and tested for collinearity amongst the fixed effects; all variance inflation factors were < 2 .

To investigate Q1, we built a Linear Mixed-effects Model (LMM) using the lme4 package for R (Bates et al., 2015) using the duration (s) an individual handled an object during a presentation as the response variable and the objects' cues as the predictor of interest (Model 1, M1). Handling time was log transformed to satisfy assumptions of normality (Shapiro-Wilks test, $p = .069$). Because the 'cues' variable is multinomial (with four categories: none, bauplan, fur, bauplan and fur), we performed an ANOVA (package: car (Fox et al., 2012)) to calculate each fixed effect's overall predictive power using χ^2 .

Two models were created to answer Q2, one for each response variable: time spent grooming (M2) and time spent aggressively interacting (M3) with the objects. We used Generalized Linear Mixed Models (GLMMs) using the raw counts of seconds for durations of grooming or breaking as the response with a Poisson family, with the total handling time for each individual with each object included as an offset.

To answer Q3 about the effects of age and sex on responses to the objects, we interpreted the outputs of models 1-3, where age and sex were included as control variables. Finally, several behaviors occurred at low frequencies, which we address in a qualitative analysis.

Results

Quantitative Analysis

In total, we recorded 199 baboon-object interactions across 26 object presentations and 77 individual baboons (62.6% of the studied population of two troops). We presented each object between 2-5 times (ball = 5, rugby = 2, cow = 4, pompom = 3, furball = 4, monkey = 5, rabbit = 3). The objects were handled for a median length of 154 s (inter-quartile range (IQR) = 48-416 s, range = 3-3024 s), groomed for a median of 0 s (IQR = 0-5 s, range = 0-750 s; of those that handled an object, the proportion of juveniles that groomed at least once = 54%; adults = 6%), and aggressively interacted for a median of 0 s (IQR = 0-20 s, range = 0-362 s; proportion of juveniles that groomed an object at least once = 63%; adults = 11%). Overall, 38 females (52.7%) and 39 males (81.3%) interacted with the objects, consisting in 18 adults (33.3%) and 59 juveniles (89.4%) that interacted with the objects on average (median) 2 times (range = 1-10).

Q1: Are Individuals More Attracted to Mammalian-Like Than Non-Mammalian-Like Objects?

We first investigated whether baboons were more attracted to particular cues (Q1). Contrary to our prediction, the cue type did not significantly influence handling duration (model with and without the 'cues' predictor: $\chi^2 = 5.266$, $p = .153$, table 2, figure 2a). All objects were handled for similar amounts of time.

Q2: Which Cues are Vital in Eliciting Particular Responses, i.e., Grooming and Aggression?

We next ran two models to address Q2, which factors affected the time (1) grooming and time (2) being aggressive towards objects. In both cases, object cues significantly predicted the proportion of time baboons directed grooming (model with and without the 'cues' predictor: $\chi^2 = 2497.3$, $df = 3$, $p = < .001$) and aggressive behaviors ($\chi^2 = 1242.8$, $df = 3$, $p = < .001$) at the objects. Specifically, both the objects with fur (fur, bauplan with fur) garnered more grooming than the remaining objects (Table 3, Figure 2b).

Conversely, aggression was directed towards the objects with no mammalian cues the most frequently (Table 3, Figure 2c).

Q3: Are There Age or Sex Differences in Individuals' Responses to Particular Objects?

We used our three models (Ms 1-3) to address Q3 about sex and age class differences in behavior towards the objects, while controlling for the object type and size. Both sex and age class predicted overall handling time (Table 3). Males handled objects for significantly longer than females, and juveniles handled objects longer than adults (Figure 3). Age class but not sex predicted the time spent grooming, with juveniles spending proportionally more time grooming the objects (Figure 3). Similarly, the time spent interacting aggressively with objects was predicted by age class but not sex, with juveniles spending more time behaving aggressively towards objects (Table 3).

Table 3

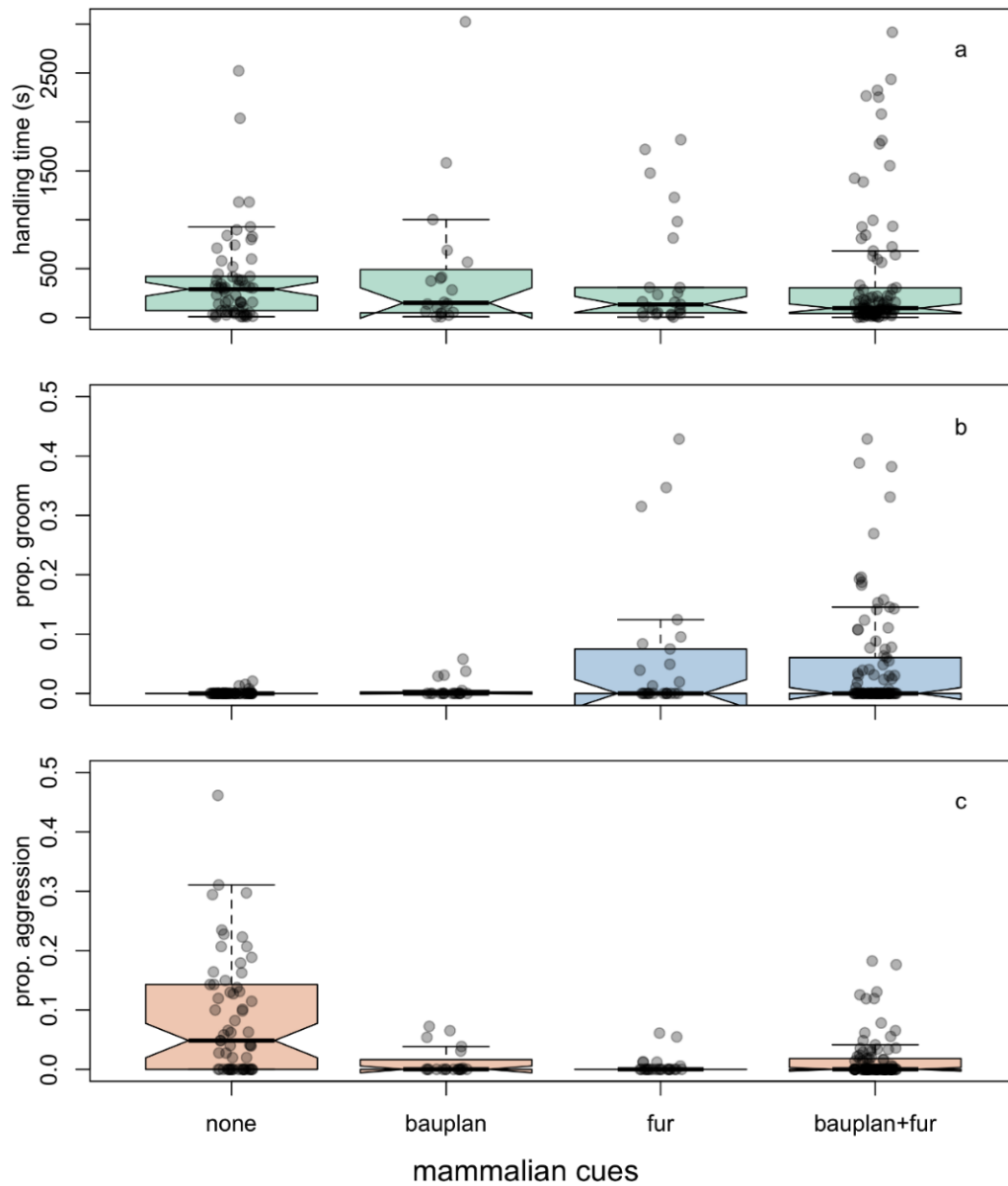
Effect of Sex, Age, Object Cues, And Object Size on Handling, Grooming, and Aggressive Interaction Time on Presented Objects

Model, response	Predictor	β	CI		χ^2	p value
			lower	upper		
1, Handling time (s)	Sex: male ¹	0.541	-0.001	1.086	3.704	0.054
	Age class: juvenile²	1.030	0.33	1.727	8.131	0.004
	Object size: small ³	-0.270	-0.717	0.159	1.499	0.221
	Cues: bauplan ⁴	0.071	-0.642	0.792		
	Cues: fur ⁴	-0.260	-0.887	0.369	5.168	0.160
	Cues: bauplan + fur ⁴	-0.490	-0.943	-0.035		
2, Grooming time (s)	Sex: male ¹	-0.072	-1.574	1.447	0.009	0.923
	Age class: juvenile²	4.257	1.991	7.184	11.471	<0.001
	Object size: small³	0.758	0.670	0.848	278.782	<0.001
	Cues: bauplan⁴	2.525	2.095	2.981		
	Cues: fur⁴	4.523	4.154	4.930	740.018	<0.001
	Cues: bauplan + fur⁴	4.455	4.088	4.861		
3, Aggressive interaction time (s)	Sex: male ¹	0.514	-0.597	1.714	0.818	0.366
	Age class: juvenile²	2.528	0.856	4.499	7.920	0.005
	Object size: small³	-0.364	-0.467	-0.262	48.148	<0.001
	Cues: bauplan⁴	-1.830	-2.051	-1.612		
	Cues: fur⁴	-2.231	-2.387	-2.078	1084.168	<0.001
	Cues: bauplan + fur⁴	-1.156	-1.256	-1.057		

Note. Shown are the models (Models 1-3) and the corresponding response variables; the predictor variables, the estimated effect size (β), confidence interval for each level of fixed effects (CI), and for each fixed effect, the χ^2 and p values. ¹Reference category: female. ²Reference category: adult. ³Reference category: large. ⁴Reference category: none

Figure 2

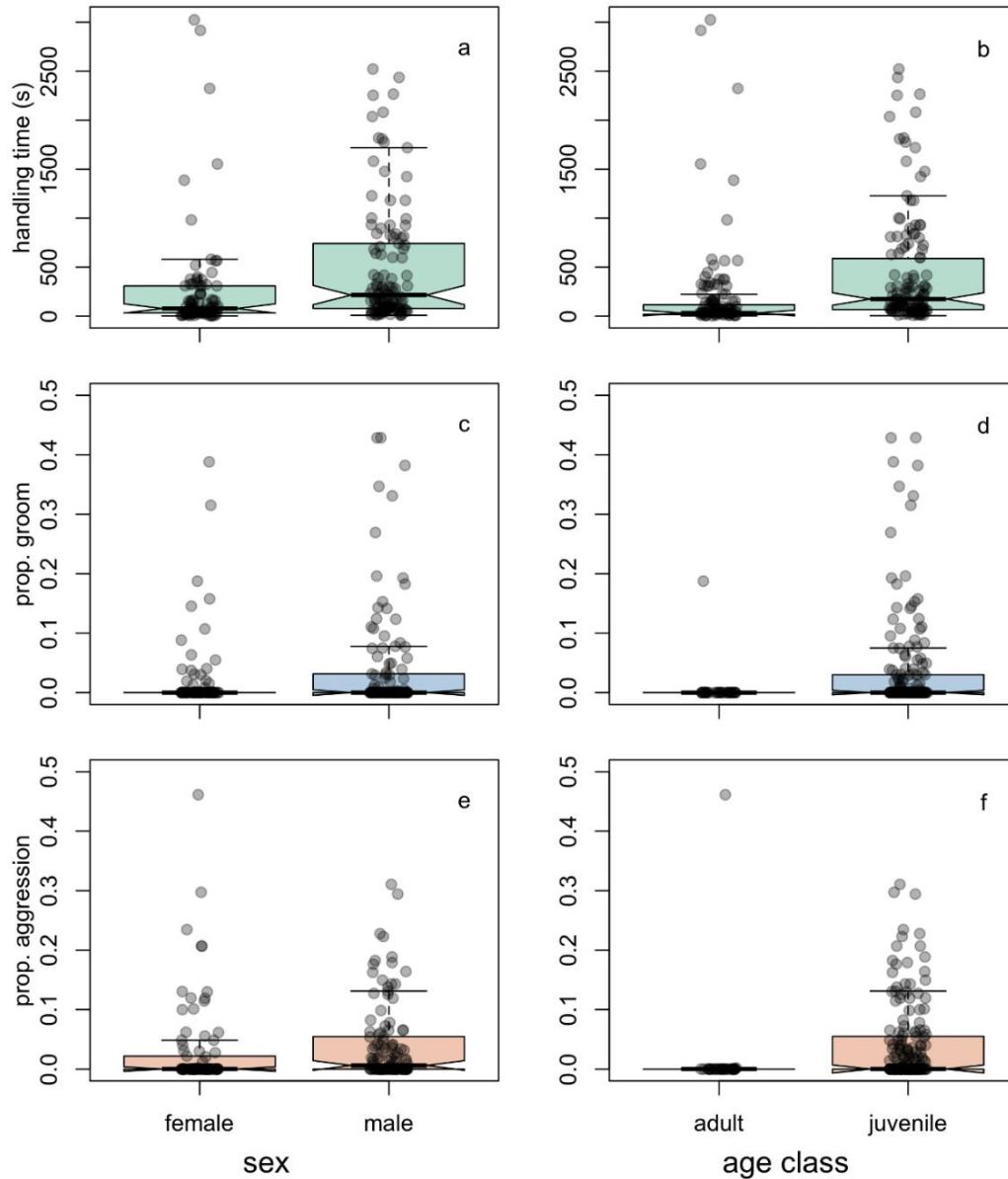
Boxplots Showing the Time Baboons Spent Interacting with, and the Proportions of Time Baboons Spent Grooming and Aggressing Objects Presenting Different Cues



Note. Shown are the boxplots of the raw data with all observations overlaid in transparent black points for the total time (s) baboons spent (a) handling (green boxes) and proportions of time baboons spent (b) grooming (blue boxes) and (c) aggressively interacting with (orange boxes) objects with different cues. NB: data in (b) and (c) are shown as proportions for ease of interpretation, but were analyzed with a Poisson GLMM with the total interaction time as an offset.

Figure 3

Boxplots Showing the Time Baboons Spent Interacting with Objects According to Sex and Age Class



Note. Shown are the boxplots of the raw data with all observations overlaid in transparent black points for the total time (s) baboons spent handling (a,b; green boxes) and proportions of time baboons spent grooming (c,d; blue boxes) and (e,f) aggressively interacting with (orange boxes) objects according to their sex (a,c,e) and age class (b,d,f). Colors are conserved from Figure 2. NB: data in (c-f) are shown as proportions for ease of interpretation, but were analyzed with a Poisson GLMM with the total interaction time as an offset.

Qualitative Analysis

Certain data collected during the object presentations is of interest to our research questions but could not be statistically analyzed. These observations are detailed here. Firstly, although we quantitatively found a difference in the proportions of time individuals spent directing aggressive behaviors towards the objects, there was also a qualitative difference in this behavior reflected in the intensity of the damage they caused to these objects. The objects with no mammalian cues ('ball' and 'rugby') were almost always

completely destroyed by the time they were abandoned, with the object broken into multiple parts on every presentation. No other objects were consistently destroyed. The objects ‘rugby’, ‘cow’, and, on one occasion, ‘rabbit’ (see below) were all broken at least once but ‘pom-pom’, ‘furball’ and ‘monkey’ were never broken or even noticeably damaged.

Second, the baboons directed considerable interest and attention towards the eyes in objects that had them (i.e., cow, monkey and rabbit). The attention to the eyes was both affiliative (gentle touches) and aggressive (biting, pulling). Individuals paid particular attention to the eyes in the ‘rabbit’ objects, possibly because they were three-dimensional (buttons), rather than the two-dimensional eyes (appliqué) on both the ‘cow’ and ‘monkey’ objects. In the case of the ‘rabbit’ objects, the majority of aggressive behavior was directed towards the eyes, as individuals bit and pulled them. Furthermore, the only instance of the ‘rabbit’ object being broken was due to an eye being pulled off. This is in contrast to other patterned aspects of the objects, such as the sewn-on mouth of several objects or paw-print pattern on the object ‘furball,’ that did not garner similar interest.

Baboons also transported all the objects in manners similar to dead-infant carrying. Most frequently, baboons carried an object in one hand whilst walking tripodally or in the mouth. Mouth carrying occurred when most necessary: whilst running or climbing a tree. However, in addition to these more-frequent forms of carrying, which would be expected for carrying any object, one juvenile female lifted the ‘monkey’ object in one hand and held it against her side in a manner reminiscent of the dorsal transport of infants (Figure 4). This juvenile female transported the ‘monkey’ object in this manner multiple times during one presentation but never carried any other objects in the same way.

Figure 4

A Juvenile Female Dorsally Transports the Object ‘Monkey’, with Both Fur and Mammalian Bauplan



Note. Four images of a juvenile female baboon (Cai) lifting the ‘monkey’ object and holding it against her rear leg and back, in a manner reminiscent of the dorsal transport of infants. Images are stills from a video recording of the object presentation, taken by HR.

The objects also facilitated interactions between individuals. Many of the objects were used by juveniles in games of ‘tag’, in which the individual with the object was chased by others to gain possession of the object. The baboons frequently play such games with clods of earth or debris. However, other games of tag generally last only a few minutes, whereas chases for the experimental objects sometimes lasted over half an hour. This could be because these objects are more attractive or desirable to interact with, or because

they are more robust and do not fall apart when carried roughly and rapidly. Additionally, the individual in possession of the object sometimes received considerable attention from conspecifics. Others would gather around the individual holding an object to watch and occasionally interact with the actor. This primarily consisted of grooming the actor, often near where the object was being held, but could also more rarely consist of females presenting their swellings towards and/or copulating with male actors.

Finally, three focal follows were terminated before the object was dropped. In all three cases, the object had been taken onto a sleeping cliff in the evening by a juvenile male (J troop $N = 1$, L $N = 2$) and was not dropped before the light faded. In one case the object was ‘furball’ and in the other two the object was ‘rabbit’. On all these occasions, the object had been dropped by the morning and was found near the base of the sleeping cliff.

Discussion

Primates, including baboons, show a conspicuous and quantifiable interest in live infants (Silk, 1999), images of infants (Sato et al., 2012), corpses of infants (Gonçalves & Carvalho, 2019), even when the infant is unrelated (Carter et al., 2020) or a heterospecific (Sato et al., 2012). We hypothesized that these responses may partly originate from the same evolutionary adaptation for maternal responsiveness, creating a predisposition towards certain mammalian cues. This hypothesis could explain, in part, cases of infant corpse carrying (ICC) by individuals other than the mother. We tested this hypothesis experimentally, presenting wild baboons with a series of objects that varied in mammalian cues, and recorded their responses. We found that individuals handled all objects for similar lengths of time but interacted with mammalian objects with more grooming and less aggression than control objects. Males handled objects for longer but also more aggressively than females. Below, we discuss these findings in relation to our predictions before exploring their implications for understanding ICC.

Contrary to our prediction (P1) that baboons would show more interest in mammalian objects, we found that individuals handled all objects for comparable lengths of time. This may be because the handling time reflects a general interest in novel objects rather than interest in the particular traits those objects display. Primates, including humans, show a pronounced interest in handling novel objects (Ogasawara et al., 2022). To test this, a follow up study could present objects until they become familiar, and subsequently quantify variation in handling times of familiar objects. Alternatively, as different traits elicited different responses (see discussion below), the responses may have driven similar handling times (e.g., a baboon’s interest in aggressively exploring the control objects until destroyed).

We found some support for P2, that baboons would direct more caretaking behavior towards mammalian-like objects: baboons groomed more and aggressed less objects with fur than without. The qualitative data also support this finding, as the objects with no mammalian cues suffered markedly more damage than the furred objects. While it is unsurprising that objects with an appropriate substrate for grooming were groomed more, what was surprising was the highest grooming time was given to the ‘furball’ object that had no additional mammalian traits, such as eyes and limbs (data not shown). Such a finding could suggest that grooming as a caretaking behavior directed to infants’ corpses could be part of a ubiquitous response to furred ‘objects’ and not necessarily demonstrative of a ‘bond’ between the groomer and the deceased individual when alive. This is supported by observations of unrelated and unbonded individuals’ interest in and grooming of infants’ corpses observed in chacma baboons (Carter et al., 2020) and Barbary macaques (Merz, 1978). Furthermore, while we do not agree with the methods used to obtain these data (see also Badihi & Hobaiter, 2022), Livingstone (2022) made similar observations documenting rhesus macaque mothers’ attachment to furred over non-furred toys after the death of their infant.

In partial support of P3, age class, but not sex, predicted baboons’ interactions with the objects: juveniles handled objects for longer, and interacted with them both affiliatively and aggressively more than adults. This finding supports other research showing that juvenile primates engage in more exploration and show greater neophilia (Bergman & Kitchen, 2009; Kendal et al., 2005). While our findings are driven in large part by juveniles’ interactions with the experimental stimuli, we believe that they still provide insight into understanding baboons’ motivations to interact with objects with different stimuli and should be

generalizable. For example, species differences in exploration of novel objects in chacma baboons (higher exploration) and geladas (*Theropithecus gelada*) (lower exploration) were evident in adults and juveniles, despite juveniles of both species interacting with novel objects more than the adults (Bergman & Kitchen, 2009). It is possible that adults demonstrate similar underlying attraction to particular objects, but do not ‘act on’ that attraction because of energetic constraints.

Our findings have implications for understanding ICC and primate thanatology more generally. Although specific infantile cues possibly increase the attractiveness of a corpse, our findings suggest that a non-infantile mammalian cue—fur—may suffice to elicit the carrying and caretaking typical of ICC. Fur elicited grooming even in objects that did not display natal coat coloration, infant size, or shape. Similar observations support the importance of tactile stimuli for eliciting caring responses in primates: some macaque mothers found the provision of a fluffy toy to hold ‘calming’ in the absence of their own infant (Livingstone, 2022). Furred objects also received less aggressive exploration, which may also mirror the lack of aggression infants corpses’ tend to receive (Gonçalves & Carvalho, 2019). In addition, baboons explored the eyes, but not other features, of the objects that had them. Specifically, baboons explored objects’ eyes intensely, both affiliatively (i.e., grooming around them) or aggressively (biting and pulling them off). Primates’ interest in eyes could correspond with primates’ interest in the eyes of corpses (De Marco et al., 2022) and images of eyes (Emery, 2000) and thus may be evolutionarily conserved as a source of information about an individual. Taken together, our findings suggest that behaviors performed by non-maternal individuals that are frequently cited as demonstrative of a bond with the deceased or an awareness of death (De Marco et al., 2022; van Leeuwen et al., 2016) could be indicative of a generalized response to some features of an object (like fur or the presence of eyes), and not evidence of ‘complex’ cognition or mental processing of the death event or bereavement. We are not suggesting that surviving individuals do not grieve the death of familiar infants. We do, however, caution researchers to be more careful when interpreting behaviors as indicative of grief that we demonstrate is a ubiquitous response to objects with particular features.

Our findings might also provide insights into how baboons categorize and respond to objects versus agents. Research into cognitive development has isolated the ‘Core System of Objects’ (CSO) and ‘Core System of Agents’ (CSA) that allow primates to categorize entities as either objects or agents (Spelke & Kinzler, 2007). Objects require outside force to move them, whilst agents can move themselves. The CSO and CSA are not infallible, and both humans and other primates occasionally miscategorize entities (Kamewari et al., 2005; Kupferberg et al., 2013). The objects used in this research did not realistically imitate mammals, nor did the objects display self-propelled movement. Nevertheless, baboons directed agent-specific behaviors (i.e., grooming) towards these objects. Such a response could support Gonçalves’ and Biro’s (Gonçalves & Biro, 2018) ‘animacy detection malfunction’ hypothesis, which suggests that both the CSO and CSA are activated by a corpse, resulting in a violation of expectation and conflicting responses from the observer. Our observations suggest that entities may be primarily categorized as objects, but if appropriate cues exist (in this case, fur) then agent-specific behaviors (grooming) are not inhibited. Accordingly, the ubiquitous response of grooming to furred objects, including corpses, does not necessitate them being viewed as either ‘agents’ or ‘alive’.

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References

- Alley, T. R. (1980). Infantile colouration as an elicitor of caretaking behaviour in Old World primates. *Primates*, 21(3), 416–429.
- Anderson, J. R. (2016). Comparative thanatology. *Current Biology*, 26(13), R553–R556.
- Anderson, J. R., Biro, D., & Pettitt, P. (2018). Evolutionary thanatology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373.
- Anderson, J. R., Yeow, H., & Hirata, S. (2021). Putrescine—a chemical cue of death—is aversive to chimpanzees. *Behavioural Processes*, 193, 104538.
- Badihi, G., & Hobaiter, C. (2022). *Triggers for better science: There is no place for maternal deprivation in ethical scientific practice*. Zenodo. <https://doi.org/10.5281/zenodo.7347808>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bearzi, G., Eddy, L., Piwetz, S., Reggente, M. A., & Cozzi, B. (2017). Cetacean behavior toward the dead and dying. In J. Vonk & TK Shackelford (Eds.) *Encyclopedia of Animal Cognition and Behavior*, (pp. 1–30), Springer, Cham.
- Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Animal Cognition*, 12(1), 63–73.
- Bertrand, M. (1969). *The behavioral repertoire of the stumptail macaque*. Karger Publishers.
- Błaszczuk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal Behaviour*, 123, 91–100.
- Brosnan, S. F., & Vonk, J. (2019). Nonhuman primate responses to death. In T. K. Shackelford & V. Zeigler-Hill (Eds.) *Evolutionary perspectives on death* (pp. 77–107). Springer Nature Switzerland.
- Cárdenas, R. A., Harris, L. J., & Becker, M. W. (2013). Sex differences in visual attention toward infant faces. *Evolution and Human Behavior*, 34(4), 280–287.
- Carter, A. J., Baniel, A., Cowlshaw, G., & Huchard, E. (2020). Baboon thanatology: Responses of filial and non-filial group members to infants' corpses. *Royal Society Open Science*, 7(3), 192206.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, 84(3), 603–609.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, 2, e283.
- Carter, A. J., Torrents Ticó, M., & Cowlshaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *ELife*, 5, e13125.
- Conly, J., & Johnston, B. (2005). Natural disasters, corpses and the risk of infectious diseases. *Canadian Journal of Infectious Diseases and Medical Microbiology*, 16(5), 269–270.
- Cronin, K. A., Van Leeuwen, E. J., 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.
- De Marco, A., Cozzolino, R., & Thierry, B. (2018). Prolonged transport and cannibalism of mummified infant remains by a Tonkean macaque mother. *Primates*, 59(1), 55–59.
- De Marco, A., Cozzolino, R., & Thierry, B. (2022). Coping with mortality: Responses of monkeys and great apes to collapsed, inanimate and dead conspecifics. *Ethology Ecology & Evolution*, 34(1), 1–50.
- De Resende, B. D., Mannu, M., Izar, P., & Ottoni, E. B. (2004). Interaction between capuchins and coatis: Nonagonistic behaviors and lack of predation. *International Journal of Primatology*, 25(6), 1213–1224.
- de Waal, F. B. (2011). What is an animal emotion? *Annals of the New York Academy of Sciences*, 1224(1), 191–206.
- Dezeure, J., Dagorrette, J., Baniel, A., Carter, A. J., Cowlshaw, G., Marshall, H. H., Martina, C., Raby, C. L., & Huchard, E. (2021). Developmental transitions in body color in chacma baboon infants: Implications to estimate age and developmental pace. *American Journal of Physical Anthropology*, 174(1), 89–102.

- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience & Biobehavioral Reviews*, 24(6), 581–604.
- Fashing, P. J., Nguyen, N., Barry, T. S., Goodale, C. B., Burke, R. J., Jones, S. C., Kerby, J. T., Lee, L. M., Nurmi, N. O., & Venkataraman, V. V. (2011). Death among geladas (*Theropithecus gelada*): A broader perspective on mummified infants and primate thanatology. *American Journal of Primatology*, 73(5), 405–409.
- Fernández-Fueyo, E., Sugiyama, Y., Matsui, T., & Carter, A. J. (2021). Why do some primate mothers carry their infant's corpse? A cross-species comparative study. *Proceedings of the Royal Society B: Biological Sciences*, 288.
- Fischer, J., Higham, J. P., Alberts, S. C., Barrett, L., Beehner, J. C., Bergman, T. J., Carter, A. J., Collins, A., Elton, S., Fagot, J., Ferreira da Silva, M. J., Hammerschmidt, K., Henzi, P., Jolly, C. J., Knauf, S., Kopp, G. H., Rogers, J., Roos, C., Ross, C., ... Zinner, D. (2019). The Natural History of Model Organisms: Insights into the evolution of social systems and species from baboon studies. *ELife*, 8, e50989.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., & others. (2012). Package 'car'. *Vienna: R Foundation for Statistical Computing*, 16.
- Glocker, M. L., Langleben, D. D., Ruparel, K., Loughead, J. W., Valdez, J. N., Griffin, M. D., Sachser, N., & Gur, R. C. (2009). Baby schema modulates the brain reward system in nulliparous women. *Proceedings of the National Academy of Sciences*, 106(22), 9115–9119.
- Gonçalves, A., & Biro, D. (2018). Comparative thanatology, an integrative approach: Exploring sensory/cognitive aspects of death recognition in vertebrates and invertebrates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1754), 20170263.
- 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.
- Gonçalves, A., Hattori, Y., & Adachi, I. (2022). Staring death in the face: Chimpanzees' attention towards conspecific skulls and the implications of a face module guiding their behaviour. *Royal Society Open Science*, 9(3), 210349.
- Gupta, A. (2000). Behaviour of Phayre's langur (*Trachypithecus phayrei*) on the death of one adult female. *Mammalia (Paris)*, 64(4), 477–480.
- Harlow, H. F., & Zimmermann, R. R. (1958). The development of affectional responses in infant monkeys. *Proceedings of the American Philosophical Society*, 102(5), 501–509.
- Hausfater, G. (1976). Predatory behavior of yellow baboons. *Behaviour*, 56(1), 44–67.
- Hirata, S., Yamakoshi, G., Fujita, S., Ohashi, G., & Matsuzawa, T. (2001). Capturing and toying with hyraxes (*Dendrohyrax dorsalis*) by wild chimpanzees (*Pan troglodytes*) at Bossou, Guinea. *American Journal of Primatology*, 53(2), 93–97.
- Huchard, E., Courtiol, A., Benavides, J. A., Knapp, L. A., Raymond, M., & Cowlishaw, G. (2009). Can fertility signals lead to quality signals? Insights from the evolution of primate sexual swellings. *Proceedings of the Royal Society B: Biological Sciences*, 276(1663), 1889–1897.
- Izar, P., Verderane, M. P., Visalberghi, E., Ottoni, E. B., Gomes De Oliveira, M., Shirley, J., & Fragaszy, D. (2006). Cross-genus adoption of a marmoset (*Callithrix jacchus*) by wild capuchin monkeys (*Cebus libidinosus*): Case report. *American Journal of Primatology*, 68(7), 692–700.
- Jay, P. C. (1962). Aspects of maternal behavior among langurs. *Annals of the New York Academy of Sciences*, 102(2), 468–476.
- Kamewari, K., Kato, M., Kanda, T., Ishiguro, H., & Hiraki, K. (2005). Six-and-a-half-month-old children positively attribute goals to human action and to humanoid-robot motion. *Cognitive Development*, 20(2), 303–320.
- Kanō, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford: Stanford University Press.
- Kendal, R., Coe, R., & Laland, K. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, 66(2), 167–188.
- Kupferberg, A., Glasauer, S., & Burkart, J. M. (2013). Do robots have goals? How agent cues influence action understanding in non-human primates. *Behavioural Brain Research*, 246, 47–54.
- Kyes, R. C., & Candland, D. K. (1987). Baboon (*Papio hamadryas*) visual preferences for regions of the face. *Journal of Comparative Psychology*, 101(4), 345.
- Langlois, J. H., Ritter, J. M., Casey, R. J., & Sawin, D. B. (1995). Infant attractiveness predicts maternal behaviors and attitudes. *Developmental Psychology*, 31(3), 464.
- Livingstone, M. S. (2022). Triggers for mother love. *Proceedings of the National Academy of Sciences*, 119(39), e2212224119. <https://doi.org/10.1073/pnas.2212224119>
- Lorenz, K. (1943). Die angeborenen formen möglicher erfahrung. *Zeitschrift Für Tierpsychologie*, 5(2), 235–409.

- McGrew, W. C. (2013). Ten Dispatches from the Chimpanzee Culture Wars. In *Animal social complexity* (pp. 419–439). Harvard University Press.
- Merz, E. (1978). Male-male interactions with dead infants in *Macaca sylvanus*. *Primates*, 19(4), 749–754.
- Miesler, L., Leder, H., & Herrmann, A. (2011). Isn't it cute: An evolutionary perspective of baby-schema effects in visual product designs. *International Journal of Design*, 5(3).
- Morgan, O. (2004). Infectious disease risks from dead bodies following natural disasters. *Revista Panamericana de Salud Pública*, 15, 307–312.
- Morrogh-Bernard, H. C., Stitt, J. M., Yeen, Z., Nekaris, K., & Cheyne, S. M. (2014). Interactions between a wild Bornean orang-utan and a Philippine slow loris in a peat-swamp forest. *Primates*, 55(3), 365–368.
- Myowa-Yamakoshi, M., & Tomonaga, M. (2001). Development of face recognition in an infant gibbon (*Hylobates agilis*). *Infant Behavior and Development*, 24(2), 215–227.
- Ogasawara, T., Sogukpinar, F., Zhang, K., Feng, Y.-Y., Pai, J., Jezzini, A., & Monosov, I. E. (2022). A primate temporal cortex–zona incerta pathway for novelty seeking. *Nature Neuroscience*, 25(1), 50–60.
- Panksepp, J., & Watt, D. (2011). What is Basic About Basic Emotions? Lasting Lessons From Affective Neuroscience. *Emotion Review*, 3(4), 1–10.
- Parr, L. A. (2011). The evolution of face processing in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1571), 1764–1777.
- Pokharel, S. S., Sharma, N., & Sukumar, R. (2022). Viewing the rare through public lenses: Insights into dead calf carrying and other thanatological responses in Asian elephants using YouTube videos. *Royal Society Open Science*, 9(5), 211740.x
- Pruetz, J. D., Ontl, K. B., Cleaveland, E., Lindshield, S., Marshack, J., & Wessling, E. G. (2017). Intragroup lethal aggression in West African chimpanzees (*Pan troglodytes verus*): Inferred killing of a former alpha male at Fongoli, Senegal. *International Journal of Primatology*, 38(1), 31–57.
- Ratnesar-Shumate, S., Williams, G., Green, B., Krause, M., Holland, B., Wood, S., Bohannon, J., Boydston, J., Freeburger, D., Hooper, I., & others. (2020). Simulated sunlight rapidly inactivates SARS-CoV-2 on surfaces. *The Journal of Infectious Diseases*, 222(2), 214–222.
- Rose, L. M., Perry, S., Panger, M. A., Jack, K., Manson, J. H., Gros-Louis, J., Mackinnon, K. C., & Vogel, E. (2003). Interspecific interactions between *Cebus capucinus* and other species: Data from three Costa Rican sites. *International Journal of Primatology*, 24(4), 759–796.
- Sanefuji, W., Ohgami, H., & Hashiya, K. (2007). Development of preference for baby faces across species in humans (*Homo sapiens*). *Journal of Ethology*, 25(3), 249–254.
- Sato, A., Koda, H., Lemasson, A., Nagumo, S., & Masataka, N. (2012). Visual recognition of age class and preference for infantile features: Implications for species-specific vs universal cognitive traits in primates. *PLoS One*, 7(5), e38387.
- Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57(5), 1021–1032.
- Silk, J. B., Rendall, D., Cheney, D. L., & Seyfarth, R. M. (2003). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology*, 109(8), 627–644.
- Spelke, E. S., & Kinzler, K. D. (2007). Core knowledge. *Developmental Science*, 10(1), 89–96.
- Taylor, H., Teas, J., Richie, T., Southwick, C., & Shrestha, R. (1978). Social interactions between adult male and infant rhesus monkeys in Nepal. *Primates*, 19(2), 343–351.
- Toda, K., Tokuyama, N., & Furuichi, T. (2017). An Old Female Bonobo Carried a Dead Red-Tailed Monkey for over a Month. *Pan Africa News*, 24(2), 19–21.
- van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1(3), 161–311.
- van Leeuwen, E. J., Mulenga, I. C., Bodamer, M. D., & Cronin, K. A. (2016). Chimpanzees' responses to the dead body of a 9-year-old group member. *American Journal of Primatology*, 78(9), 914–922.
- Warren, Y., & Williamson, E. A. (2004). Transport of dead infant mountain gorillas by mothers and unrelated females. *Zoo Biology*, 23(4), 375–378.
- Watson, C. F., & 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.
- Zuckerman, S. (1932). *The Social Life of Monkeys and Apes*. Routledge.