1   Why do some primate mothers carry their infant's corpse? A cross-species

2   comparative study

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12

Abstract

Non-human primates respond to the death of a conspecific in diverse ways, some which may present phylogenetic continuity with human thanatological responses. Of these responses, infant corpse carrying by mothers (ICC) is the most-frequently reported. Despite its prevalence, quantitative analyses of this behaviour are scarce and inconclusive. We compiled a database of 409 published cases across 50 different primate species of mothers' responses to their infants' deaths and used Bayesian phylogenetic regressions with an information-theoretic approach to test hypotheses proposed to explain between- and within-species variation in ICC. We found that ICC was more likely when the infant's death was non-traumatic (e.g. illness) *versus* traumatic (e.g. infanticide), and when the mother was younger. These results support the death detection hypothesis, which hypothesises that ICC occurs when there are fewer contextual or sensory cues indicating death. Such an interpretation suggests that primates are able to attain an awareness of death. In addition, when carried, infant age affected ICC duration, with longer ICC observed for younger infants. This result suggests that ICC is a by-product of strong selection on maternal behaviour. The findings are discussed in the context of the evolution of emotion, and implications for evolutionary thanatology are proposed.

Introduction

Non-human animals direct a diverse range of behaviours towards their dead [1,2], from burial behaviour observed in termites (*Reticulitermes fukienensis*) [3] to necrophagia or feeding on corpses observed in Taiwanese macaques (*Macaca cyclopis*) [4]. 'Comparative thanatology' aims to investigate non-human animals' (hereafter 'animals') responses to dead conspecifics and heterospecifics [2]. It addresses questions such as: why do animals respond to death in the ways they do; what do animals understand of death; and, do animals grieve?

Despite a recent surge of interest in comparative thanatology [1], the majority of the work to date has been descriptive, theoretical and/or anecdotal [5,6], with two hypothesis-testing exceptions in primates. These exceptions (detailed below) have focused on the most commonly-reported thanatological behaviour: infant corpse carrying by mothers (ICC) (figure S1) [5,7]. ICC occurs across several mammalian taxa (e.g. cetaceans [8], proboscids [2], canids [9], and felids [10]), and is highly variable both between- and within-species. Such behaviour ranges from immediate abandonment after death to mothers carrying corpses past decomposition and mummification [2,5,7]. ICC is *prima facie* a non-adaptive or maladaptive behaviour, as it provides no obvious fitness benefit, yet incurs presumed energetic costs and hinders locomotion, foraging and predator evasive behaviour [5,7,11].

Multiple, non-mutually exclusive hypotheses have been proposed to explain the proximate and ultimate causes of within- and between-species variation in ICC. These hypotheses also explain extrinsic constraints on its expression, which may also account for variation between populations (for those tested in this study, see table 1) [reviewed in 5]. Ultimate explanations of ICC have generally focused on selection on maternal behaviour [5], suggesting that it arises due to carry-over or generalization of maternal behaviour from live to dead infants. This predicts greater ICC (more frequent and/or longer) in mothers with highly

56   dependent or strongly-bonded infants [12–16], greater experience with previous infants [13,17],

57   and in species with high maternal investment [18,19]. In addition, ICC could help develop

58   maternal skills, being more common in nulliparous and primiparous females [20]. Proximate

59   hypotheses suggest that females' natal attraction [21,22] elicits ICC, predicting greater ICC for

60   corpses with more infantile cues (i.e. younger at death) [23,24]. The death detection hypothesis

61   suggests that mothers are better able to determine their infant's death when there are reliable

62   external contextual and sensory cues, such as traumatic injuries, and thus are less likely to

63   perform ICC in these cases compared to infants who suffered 'peaceful,' non-traumatic deaths,

64   e.g. from illness [2,7,25]. Extrinsic constraints are thought to involve presumed costs of ICC,

65   predicting greater ICC when it is energetically or physically less costly due to high rank [5],

66   terrestrial locomotion [25,26] and/or shorter daily travel distances [6]. We further test whether

67   ICC is more common in species with greater body size relative to the infant. Finally, ICC is

68   predicted to be greater in cold or dry climates with slower corpse putrefaction, allowing the

69   corpse to be carried for longer [12,27].

70   Two attempts have been made to quantitatively study ICC using a hypothesis-testing

71   framework [19,28]. In the first case, Das *et al.* [28] collated 43 records of ICC from 18 species

72   of anthropoid primates and found no significant effect of infant sex or age at death on the length

73   of ICC, and no support for the death detection, parity and climate hypotheses (see Table 1 for

74   definitions). However, their data suggested that the mother's age, the infant's cause of death,

75   arboreality, and the living condition (e.g. captivity) affected ICC duration [28]. In the second

76   case, Lonsdorf *et al.* [19] analysed 22 records of ICC from the Gombe chimpanzees but found

77   no support for any of the hypotheses they tested, specifically the hormonal, mother-infant bond

78   strength, death awareness (predictors: maternal age and cause of death), and climate

79   hypotheses. Although both studies establish a framework for testing hypotheses suggested to

80   explain ICC, the results are inconclusive due to the low sample size and Das *et al.*'s [28]

81   comparative study was not systematic. There is thus a need for a more rigorous and

82   comprehensive comparative study. Identifying the factors that influence ICC variation is crucial

83   for understanding both the selective pressures that may favour responses to death and

84   underlying mechanisms of these responses [29] in primates, humans, and other animals.

85   To test hypotheses that explain between- and within-species variation in ICC, we

86   created the largest database of primate mothers' responses to their infants' death. Our database

87   includes available data on associated intrinsic and extrinsic factors, some of which have not yet

88   been tested. Using a comparative approach, we (1) tested a subset of the ICC hypotheses for

89   which there are available data to explain variation in (1a) the occurrence of ICC and (1b) the

90   duration of ICC across primates. We also (2) determined the phylogenetic continuity of ICC

91   across the primate order.

92

Materials and methods

94   *Database creation*

95   We searched the scientific literature for cases of primate mothers responding to the

96   corpse of their dead infant. Cases were cross-referenced using three published reviews [5,7,28].

97   We included only events in which there was enough opportunity for the mother to carry the

98   corpse [5]. Specifically, we recorded a case of 'corpse not carried' if the mother was in the

99   vicinity of the infant when the death occurred and the corpse was not consumed or monopolised

100   by other individuals or removed by observers after the death, but the mother did not carry it.

101   Additionally, we classified attempted but unsuccessful lifting [e.g. 30,31] as 'corpse not

102   carried' to avoid interpretation of underlying motivation. Our definition thus does not

103 differentiate between mothers who are unable or unwilling to carry their young. For each case,

104 we recorded 10 variables where possible: (1) the species; (2) the site where the case was

105 reported; (3) whether the corpse was carried or not; and, if carried, (4) the carry duration (in

106 days); the mother's (5) parity; (6) age; and (7) rank; (8) the infant's age; (9) the cause of the

107 death; and (10) the living condition (wild, provisioned, laboratory or captive). In cases where

108 the exact duration was not known, we used the minimum (where $> N$) or maximum (when $<$

109 N) confirmed carrying days or the mid-point of a stated range. We also included the minimum

110 carry duration in cases where the corpse was removed after the mother had carried. We

111 classified maternal age in two categories (young *versus* old) to make them consistent across

112 studies. In the few cases in which infant age was not reported precisely, we took the mid-point

113 of a range, or $N + 1$ or $N - 1$ if it was reported as $> N$ or $< N$ days, respectively. Infant ages

114 were divided by the species weaning age to make them comparable across species. We also

115 compiled data on additional variables to test further hypotheses. These additional variables

116 included information about the species or the site. Specifically, we recorded the: (1) daily travel

117 distance for the species at the site; species' (2) degree of terrestriality; (3) body mass; and (4)

118 level of maternal investment; and the site's (5) maximum temperature; and (6) climate type.

119 See Electronic Supplementary Material (ESM §2.1) for details of how these variables were

120 measured and of resources from which they were obtained.

121

122   *Statistical analyses*

123   Species for which no data on mothers' responses to their dead infants were available

124 were excluded from all the analyses. Because of the risk of over-parameterisation with the

125 number of explanatory variables and the relative scarcity of data for some of the variables, our

126 analyses proceeded in two steps. First, we performed a set of exploratory models to identify

127 single predictors that were associated with the response variables: (a) ICC occurrence

128 (presence/absence) and (b) ICC duration (in days). Our second step tested for support for

129 additive effects on ICC occurrence and duration using an information theoretic approach with

130 the variables identified in step 1 as being associated with the response variables (see tables S1

131 and S2 for sample sizes for the exploratory and information theoretic analyses, respectively).

132   For all models in both steps 1 and 2, we performed Bayesian phylogenetic generalised

133 linear mixed models using the package 'MCMCglmm' in R version 4.0.2 (2020-06-22) [32,33].

134 Binary occurrence data (a) were analysed using threshold models; we log-transformed ICC

135 duration (b) and used a Gaussian distribution. To control for relatedness amongst species, we

136 included a random effect for primate phylogeny. The variance/covariance matrix was derived

137 from the branch lengths of Version 3 of the 10kTrees Primates consensus tree (in the

138 chronogram form) [34]. See the ESM §2.2 for details. Because our database had multiple ICC

139 records from single sites, site was included as a random effect. Pseudoreplication at the species

140 level was controlled for by the matrix to control for phylogeny. Because living conditions

141 determine the energy available to individuals and we *a priori* predicted it to be important for

142 ICC, we included condition as a fixed effect as a control in all the models.

143   To identify predictors in step 1, we compared models with each variable of interest to a

144 null model using the Deviance Information Criterion (DIC) [35]. The null model used the same

145 subset of the data as the model with the variable of interest and contained only the control

146 variables: living condition (fixed), site and phylogeny (random). We retained for step 2

147 variables that, when compared to the null, improved the model fit by > 4 DIC (ΔDIC_{null}). To

148 perform model selection in step 2, we tested all combinations of the retained variables using

149 the 'dredge' function of the R package 'MuMIn' [36], including in the model set the same null

150   model as in step 1. Competing models were considered those with a ΔDIC < 4 compared to the

151   best model (ΔDIC$_{best}$) and a high weight (w).

152   Both sets of analyses were repeated excluding 157 cases from the Takasakiyama

153   Japanese macaques (*Macaca mulatta*) [11] to determine whether those over-represented cases

154   biased the results.

155   Although our predictions are in line with published hypotheses (Table 1), we deviate in

156   one instance: the mother-infant bond strength hypothesis has suggested that the mother-infant

157   bond strengthens linearly with infant age [15,19]. However, this prediction does not take into

158   account the nuances of maternal behaviour during bond establishment and approaching

159   weaning. The mother-infant bond is weak in primates until a few days after birth [37], and it

160   starts to weaken again near weaning [38–40]. Consequently, we make a different prediction for

161   this hypothesis: that the mother-infant bond shows a quadratic relationship with infant age,

162   being strongest at intermediate ages.

163   Finally, we estimated the phylogenetic signal present in ICC to determine whether

164   closely-related species are more similar in ICC than distant species. The phylogenetic distance

165   between species was derived from the branch lengths of Version 3 of the 10kTrees Primates

166   consensus tree (in the chronogram form) [34]. To estimate the phylogenetic signal of ICC

167   occurrence, we calculated the D value–a measure of phylogenetic signal in binary traits [41]–

168   using the 'phylo.d' function of the R package 'caper' [42]. D values closer to or lower than 0

169   indicate a phylogenetically conserved trait, i.e. Brownian phylogenetic structure; values closer

170   to or above 1 indicate a labile trait that has evolved independently of phylogeny. We defined

171   species as non-carriers when only cases of ICC absence were reported for that species. We

172   calculated Blomberg's K to estimate the phylogenetic signal of ICC duration using the

173   'phylosig' function of the R package 'phytools' [43]. In contrast to the D value, Blomberg's K

174 closer to 0 indicates a labile trait with no phylogenetic signal; values closer to 1 indicate a highly

175 phylogenetically conserved trait. To provide a single value per species, we used the median

176 ICC duration and accounted for within-species variability by including the species' interquartile

177 ranges as an error term.

178

Results

180   We identified 409 reports of mothers' responses to their infants' deaths in 50 primate

181 species across 126 different studies (median number of reports/species: 3; range: 1-161, see

182 table S1 for details). These species belonged to 9 different primate families: Atelidae,

183 Callitrichidae, Cebidae, Cercopithecidae, Galagidae, Hominidae, Hylobatidae, Indriidae and

184 Lemuridae. Of the primate species for which records existed, 40 (80%) had been observed to

185 perform ICC and 10 (20%) had been observed only *not* to perform this behaviour. Of those

186 families that had records, presence of ICC was not observed in any species of the Callitrichidae,

187 Galagidae, Indriidae and Lemuridae families (Figure 1A). The longest ICC durations were

188 reported in the families Hominidae (the great apes) and Cercopithecidae (Old World monkeys)

189 (Figure 1B).

A

B

190
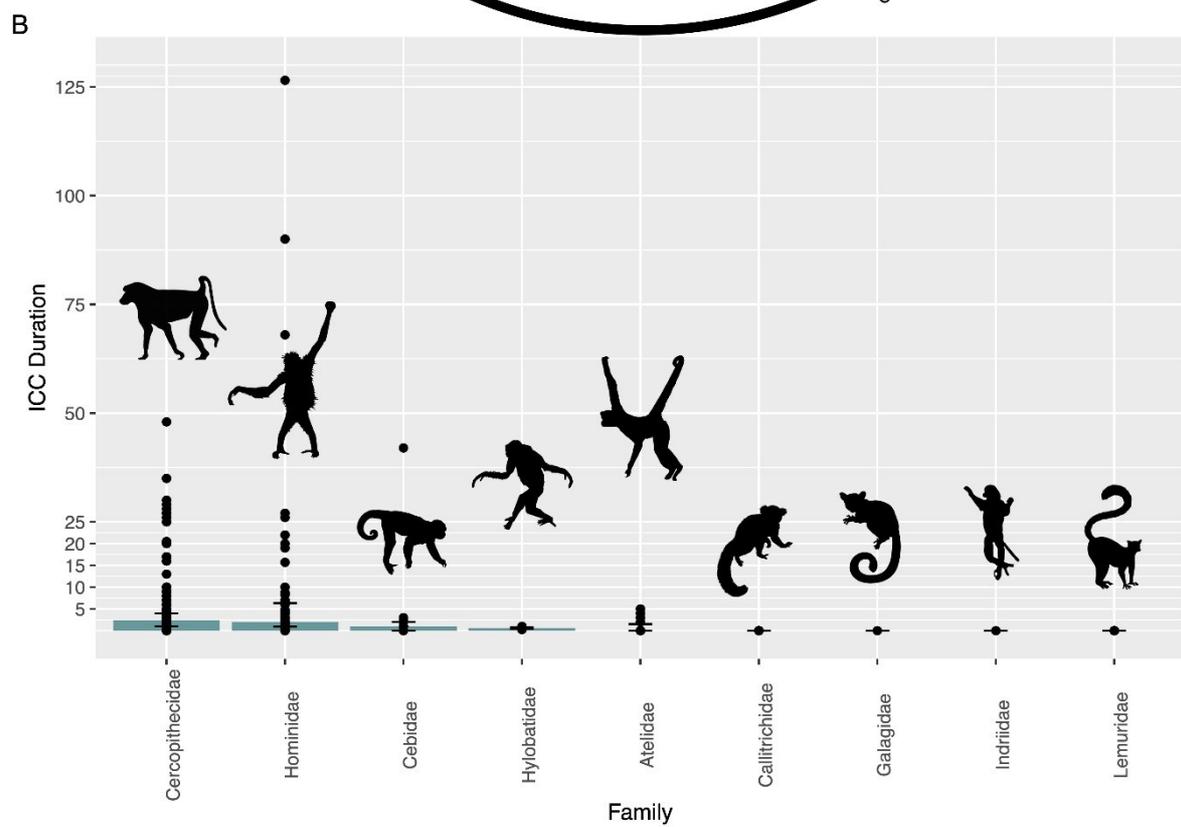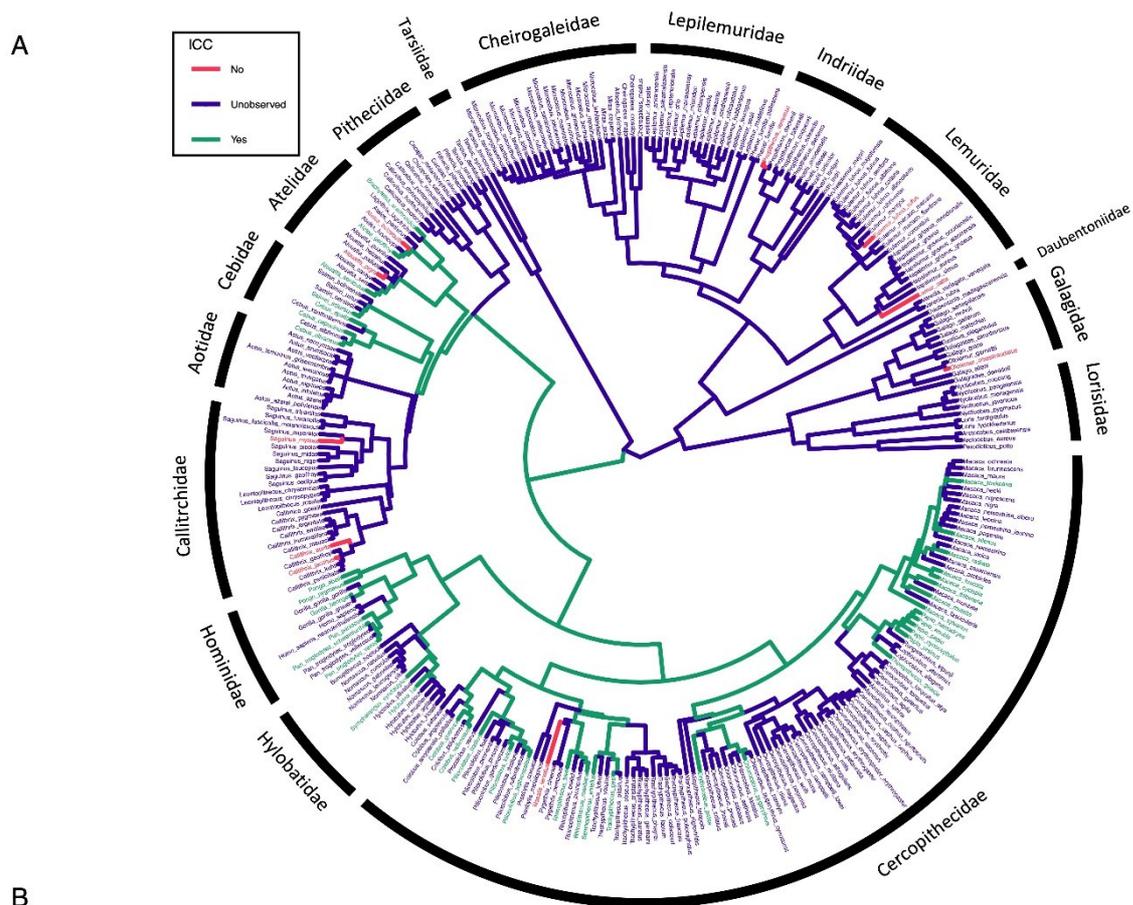
191   Figure 1.

192   The (a) distribution of ICC and (b) average durations of ICC across the primate order. (a) Shown

193   is a primate phylogenetic tree indicating in which species ICC has been observed or not (Yes

194   or No, respectively), and those for which no data exists (Unobserved). (b) A bar chart showing

195   the median durations of ICC in primate families for which data exist. The blue bars indicate

196   median ICC duration (days), and the black arrows indicate the first and third quartiles. Black

197   points show the distribution of observations of ICC duration. See ESM §3.1 for details (primate

198   silhouettes were obtained from phylopic.org).

199

200   *Variation in ICC*

201   From the exploratory analyses of single predictors in step 1, only one variable showed

202   explanatory power for ICC occurrence in the full dataset: cause of death (ΔDIC_{null} = 15.72;

203   table S3). In the reduced dataset without the Takasakiyama cases, both cause of death (ΔDIC_{null}

204   = 18.61; table S4) and mother's age class (ΔDIC_{null} = 4.27; table S4) explained variation in ICC

205   occurrence. Thus, we retained both variables in step 2 for the reduced dataset, resulting in three

206   models to compare against the null. For ICC duration, one hypothesis had explanatory power

207   in the full dataset: the mother-infant bond strength hypothesis, which included infant age and

208   the quadratic of infant age as predictors (ΔDIC_{null} = 24.84; table S5). With the reduced dataset,

209   in addition to the mother-infant bond strength hypothesis with the quadratic of infant age

210   (ΔDIC_{null} = 10.24; table S6), there was some support for the infant dependency / infantile cues

211   hypothesis, with infant age as a linear predictor (ΔDIC_{null} = 5.85; table S6). Both models were

212   compared in step 2 from the reduced dataset.

213   Step 2 aimed to determine the additive combinations of predictors that best explained

214   variation in ICC using an information-theoretic hypothesis-testing approach. As multiple

215   predictors were supported only when using the reduced dataset, we present only these results

216   here. Whilst all three models tested for ICC occurrence were supported (table 2; see table S7

217   for parameter estimates), the death detection hypothesis alone ($\Delta DIC_{best} = 0$; $w = 0.56$) and in

218   combination with maternal experience ($\Delta DIC_{best} = 1.31$; $w = 0.29$) could be considered best,

219   given their weights. The estimates for the death detection hypothesis were in the predicted

220   direction, with lower probabilities of ICC occurrence in traumatic deaths i.e. those imposed by

221   an external, observable event (Figure 2A). However, in contrast to our prediction, older mothers

222   were less likely to carry corpses than younger mothers (Figure 2B). For ICC duration, the

223   quadratic infant age model was best supported, having a high weight ($w = 0.89$) compared to

224   the linear model ($\Delta DIC_{best} = 4.19$; $w = 0.11$; table 2; S8), as was the case for the full dataset.

225   Infants were carried for longer when they died at younger ages, with a sharp decline when

226   infants reached approximately half the weaning age (Figure 2C).

227

13
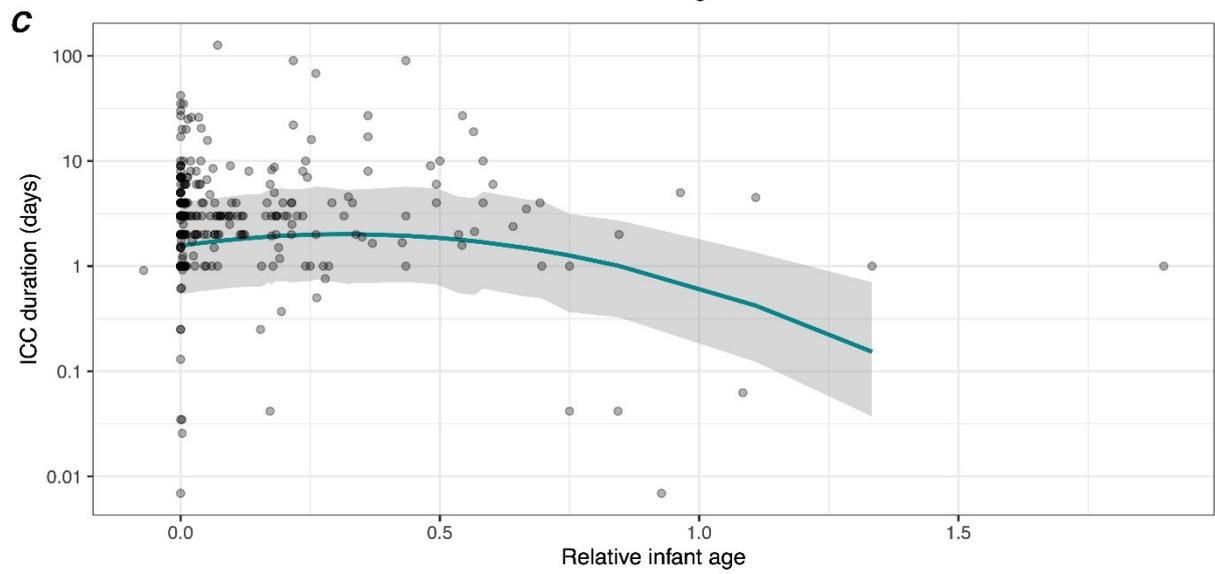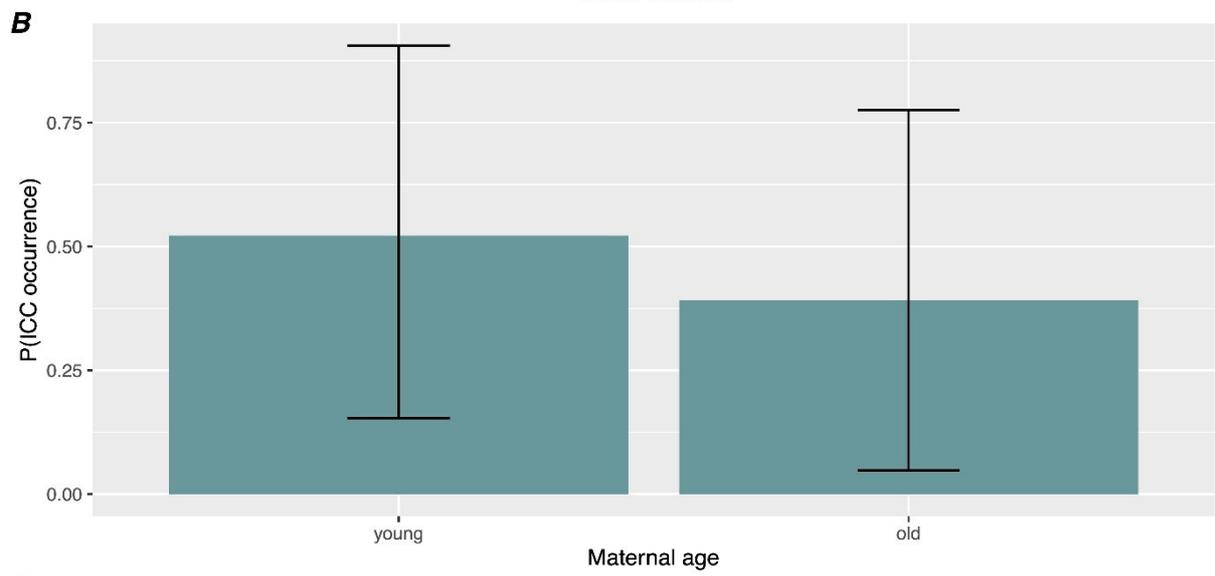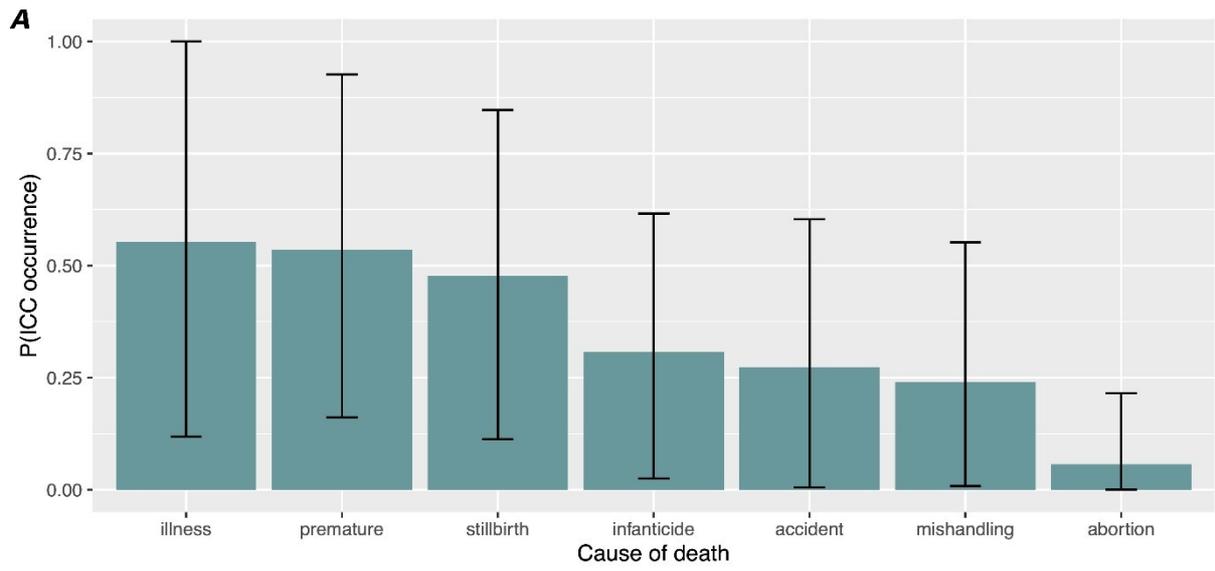
228   Figure 2.

229   Plots presenting the predicted effects for the best models for ICC occurrence (A, B) and

230   duration (C) for wild-living primates. (A, B) Bar plots showing the predicted probability of ICC

231   occurrence depending on (A) the cause of death and (B) the age of the mother using the reduced

232   dataset. (C) Scatter plot showing the relationship between relative infant age at death (Infant

233   age at death/Species weaning age) and ICC duration in days using the full dataset. Shown are:

234   the predicted relationship (blue line); 95% CI (dashed lines); and the observations (shaded

235   points).

236

237   *Phylogenetic signal*

238   The estimated D value for ICC occurrence was -0.310 ($P_{random} = 0$; $P_{Brownian} = 0.761$),

239   indicating that ICC occurrence is a highly phylogenetically conserved trait. The estimated

240   Blomberg's K for ICC duration was 0.143 ($p = 0.191$) based on 1000 randomizations, indicating

241   that there was no strong phylogenetic signal in the trait.

242

243   **Discussion**

244   Primate mothers' infant corpse carrying is the most frequently reported thanatological

245   behaviour [5,7]. As new reports of this behaviour accumulate, quantitative assessment of

246   hypotheses that explain ICC becomes possible. Here, we performed the largest quantitative

247   study of the variation in ICC across different primate species. We show that: (a) the probability

248   of ICC occurring is highest for infants that died from non-traumatic causes and for younger

249   mothers; and (b) younger infants are carried for longer than older infants. We further show that

250   ICC is widely distributed across the primate order but is most frequent in great apes and Old

251   World monkeys. Below, we discuss these findings before considering the possible implications

252   that our results have for the field of evolutionary thanatology.

253   ICC occurrence had a strong phylogenetic signal [41]; it was more commonly reported

254   in Old World monkeys and great apes, and reported absent in strepsirrhines. According to the

255   currently-available data, ICC seems to have evolved once in the haplorrhines after they split

256   from the strepsirrhines, and it may have been lost in the callitrichids and some atelids (see ESM

257   for a discussion of ICC loss in proboscis monkeys *Nasalis larvatus*). This pattern could in part

258   be explained by whether species carry or park their young while foraging, which also seems to

259   present a phylogenetic signal [44,45]. In general, Old World monkey, New World monkey and

260   ape mothers carry their young during large periods of their daily activities, while some

261   strepsirrhines leave their young parked in nests, tree-holes, or clinging to a branch [44].

262   However, our data do not support this hypothesis: the majority of species in which there was

263   an absence of ICC carry their live young, except brown greater galagos (*Otolemur*

264   *crassicaudatus*) that park their infants. Relatedly, ICC may be more common in taxa that

265   actively cradle or support their ventrally-carried infants *c.f.* 'passively' carrying clinging infants

266   [7]; for example, callitrichid infants cling dorsally to the caregiver immediately after birth and

267   are never 'actively' cradled. Another trait that may be responsible for this pattern is polytocy—

268   a mother may not carry a deceased infant if a live infant is present. Litters are relatively

269   common, i.e. >1 in 10 births, in the strepsirrhine (except *Propithecus verreauxi*) and callitrichid

270   species [46] in which ICC is absent. In the same way that monotocy has been suggested as a

271   preadaptation for carrying live offspring [44,45], it may be a prerequisite for ICC in primates.

272   In addition, callitrichids and ring-tailed lemurs (*Lemur catta*) have high levels of allomaternal

273   care [47–49]; this trait may further impede ICC occurrence in these taxa.

274   We do not suggest that mothers are indifferent to their dead infants in taxa with only

275   records of absence of ICC, but that carrying is not usual for those mothers. Strepsirrhine and

276   some callitrichid mothers give mother-infant contact, cohesion and lost calls, and usually stay

277 next to the corpse, attempt to lift, groom and/or keep coming back to it for some hours after the

278 death [7,30,31,50,51]. Alternatively, this result could have arisen due to research and

279 publication biases, as strepsirrhines and some New World monkeys are historically less well-

280 studied [52]. It is likely that some of the species with reported absence of ICC or without records

281 perform ICC but it has not yet been reported. Additionally, many of these taxa are nocturnal

282 or/and arboreal, which could further hinder the observation of ICC. The fact that the

283 phylogenetic signal of ICC duration is low may be due in part to the high within-species

284 variability in ICC duration; high evolutionary and environmental variation are responsible for

285 the low phylogenetic signal observed in many behavioural traits [53].

286   We found support for one hypothesis predicting variation in ICC occurrence: the death

287 detection hypothesis. This hypothesis suggests that mothers are better able to determine their

288 infant's death when there are reliable external contextual and sensory cues such as traumatic

289 injuries, and thus are less likely to perform ICC in these cases [2,7]. Although we found that

290 the mother's age predicted variation in ICC occurrence, this finding did not support the maternal

291 experience hypothesis, as younger mothers were more likely to perform ICC than older

292 mothers. This may provide further support for the death detection hypothesis: older mothers

293 could be more experienced in detecting death [reviewed in 5], and thus less likely to carry a

294 dead infant. If correct, this interpretation could provide evidence that primates have, or are able

295 to attain, an awareness of death and the causality subcomponent of death [2]. However, this

296 interpretation assumes that, at least in part, mothers carry offspring only when they are unaware

297 or uncertain that their infant is dead. Alternatively, the circumstances surrounding traumatic

298 deaths could be acutely stressful to the mother, resulting in a lower probability of ICC if the

299 mother is motivated to leave the area of the death rapidly and unencumbered.

300   Our results suggest that ICC duration is predicted by the age of the infant at death, with

301   the longest durations occurring before infants reach half the weaning age. This is in contrast to

302   the findings of Das *et al.* [28], which may be due to their lower sample size and power. This

303   result may support at least three related hypotheses that predict an overall negative function of

304   infant age at death on ICC: the mother-infant bond strength, infant dependency, and infantile

305   cues hypotheses. These hypotheses are not mutually exclusive, and it is possible that all

306   contribute to how long an infant's corpse is carried. We suggest that the duration of ICC may

307   have evolved as a by-product of strong selection on maternal behaviour. An alternative or

308   additional explanation could be that older infants are heavier and, presumably, more costly to

309   carry. Our other results—that wild-living primates carry, on average, for shorter durations (see

310   ESM tables S7 and S8)—support that ICC is energetically costly, assuming that wild-living

311   primates have the least available energy to spare. On balance, the non-linear relationship with

312   infant age indicates a role of the carry-over of maternal behaviour rather than an effect of infant

313   weight increase with age, but we acknowledge that more data are necessary to confirm this

314   hypothesis.

315   Our findings may have implications for understanding primate emotion i.e. internal

316   states of the central nervous system triggered by specific stimuli that produce externally

317   observable behaviours and cognitive, somatic and physiological responses [54]. Although

318   speculative, emotions seem to be involved in primates' responses to the deaths of others. For

319   example, primates who have lost a close associate show increased glucocorticoid levels and

320   self-directed behaviours indicative of stress [55–58]. Moreover, after the removal or accidental

321   loss of infants' corpses, capuchin (*Cebus capucinus*), snub-nosed monkey (*Rhinopithecus*

322   *bieti*), and chacma baboon (*Papio ursinus*) mothers emit alarm calls—an indicator of stress [59]

323   —and search for the corpse [6,15,60]. In light of our findings, we suggest that emotional

324 mechanisms that regulate maternal behaviour and the mother-infant bond may underlie the

325 latter observations. Consequently, a proximate mechanism for ICC could be the maternal

326 anxiety triggered by separation from an infant [54]: mothers may carry corpses to avoid this

327 'separation anxiety' [61].

328   In agreement with previous studies [19,28], we found that climate, specifically

329 temperature and climate type, did not influence ICC duration. We suggest that the climate

330 hypothesis, which suggests that slow putrefaction in dry and cold climates enables extended

331 ICC [27], can be rejected at this stage. Instead, we propose that extended ICC occurs in mothers

332 who have a particularly strong bond with their infant at death (see above).

333   Finally, we turn to the 'bigger' evolutionary and comparative thanatology question

334 about the implications of these findings for our understanding of the evolution of responses to

335 death. Broadly, primates' responses to dead conspecifics seem to be promoted by social bonds

336 [7]. As the mother-infant bond is the most significant bond among primates, prolonged ICC

337 may represent the most extreme manifestation of that bond. Attentive thanatological behaviours

338 have also been observed in other social vertebrates, particularly in proboscids, cetaceans and,

339 possibly, corvids [2,62]. These taxa live in hierarchical, complex societies in which individuals

340 recognize each other and base their behaviour on previous social interactions [63–67]. The

341 mammalian taxa have prosocial tendencies and a slow life history strategy with low birth rates,

342 strong mother-infant bonds, and extended maternal investment [2,68]. Attentive thanatological

343 behaviours may thus have evolved in different social animals as a by-product of strong social

344 bonds through parallel evolution and/or phylogenetic continuity [69]. If so, it is possible that

345 early human mortuary practices arose as an extension of primates' attentive thanatological

346 behaviour [70].

347   Although our results indicate some evidence for predictors of ICC occurrence and

348   duration, we acknowledge that the interpretation of these results is complicated by the range of

349   possible explanations suggested by competing hypotheses. We are also aware, despite creating

350   and using the largest database of ICC to date, that our interpretations are particularly limited

351   for understudied primate species [52] for which neither absence nor presence of thanatological

352   behaviours have been recorded. Our study highlights that the unsystematic recording of ICC is

353   an important limitation for comparative thanatology. Thus, we encourage long-term sites to

354   systematically record ICC and to make data publicly available through publication or data

355   sharing projects such as 'ThanatoBase' (http://thanatobase.mystrikingly.com/).

356

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556

557   Table 1.

558   Hypotheses and predictions proposed to explain infant corpse carrying (ICC) tested in the paper. Shown are: the hypotheses; followed by a brief

559   description; the predictors and direction of the predicted relationship; the level of explanation (within-species (WS), between-population (BP)

560   and/or between-species (BS)); whether the predictor had any support for each response (occurrence or duration) and the direction of the relationship;

561   and the references for the hypotheses (see ESM §1.1 for a full list).

562

563

Hypothesis	Description	<u>Predictor</u> and relationship	Level	Support?
Maternal behaviour	Strong selection on maternal investment and care of offspring can carry over post-mortem.	*Infant dependency*: <u>Infant age</u>: ↑ICC for younger infants	WS	Duration: as predicted
		Mother-infant bond strength: <u>Infant age</u>: ↑ICC for infants of intermediate ages (see text for details)	WS	Duration: as predicted
		Learning to mother: <u>Parity</u>: ↑ICC for nulliparous and primiparous mothers	WS	No
		Maternal investment: <u>Inter-birth interval (IBI)</u>: ↑ICC in species with relatively longer IBIs	BS	No
		Maternal experience: <u>Parity</u>: ↑ICC in multiparous mothers	WS	No
		Maternal experience: <u>Maternal age</u>: ↑ICC in older mothers	WS	Occurrence: ↑ICC in *younger* mothers
Infantile cues	Infantile characteristics are attractive to primates, eliciting caring behaviour	<u>Infant age</u>: ↑ICC for younger infants (but aborted foetuses will not be carried)	WS	Duration: as predicted

Death detection	Death is easier to detect in corpses with cues of trauma	Cause of death: ↑ICC for non-traumatic (e.g. illness) vs traumatic deaths	WS	Occurrence: as predicted
Putrefaction rate	Corpses are carried only as long as they resemble an infant i.e. until putrefaction	Climate type and temperature: ↑ICC in dryer climates and/or colder habitats where putrefaction is slower	BP, BS	No
Energetic costs	Because ICC is costly, it is more prevalent when conditions are favourable	Terrestriality: ↑ICC in terrestrial species	BS	No
		Travel distance: ↑ICC in species or populations with shorter daily travel distances	BP, BS	No
		Maternal rank: ↑ICC in high ranking mothers	WS	No
		Body mass: ↑ICC in species with greater relative body mass	BS	No

27

564   Table 2.

565   Summary of the information theoretic approach determining the predictors of ICC occurrence

566   and duration (see text for details). Reported are: the intercept (β_0); the presence of particular

567   predictors in each model (+); the deviance information criterion (DIC); the difference in DIC

568   between the given model and the best model (ΔDIC); and the weight (w) of each model.

Response	Corresponding hypothesis	β_0	Predictor			DIC	ΔDIC	w
Occurrence			Maternal age	Cause of death	Living condition			
	Death detection	5.208		+	+	43.4	0.00	0.562
	Maternal experience + Death detection	5.237	+	+	+	44.7	1.31	0.292
	Maternal experience	4.402	+		+	47.0	3.64	0.091
	Null	4.492			+	48.1	4.69	0.054
Duration			Infant age	Infant age^2	Living condition			
	Mother-infant bond strength	2.329	+	+	+	565.2	0.00	0.886
	Infant-dependency	2.322	+		+	569.4	4.19	0.109
	Null	2.241			+	575.7	10.53	0.005

569