Why do some primate mothers carry their infant’s corpse? A cross-species comparative study

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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.

Keywords: death detection, emotion, infant corpse carrying, maternal behaviour, primates’ responses to death, thanatology
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
dependent or strongly-bonded infants [12–16], greater experience with previous infants [13,17], and in species with high maternal investment [18,19]. In addition, ICC could help develop maternal skills, being more common in nulliparous and primiparous females [20]. Proximate hypotheses suggest that females’ natal attraction [21,22] elicits ICC, predicting greater ICC for corpses with more infantile cues (i.e. younger at death) [23,24]. The death detection hypothesis suggests that mothers are better able to determine their infant’s death when there are reliable external contextual and sensory cues, such as traumatic injuries, and thus are less likely to perform ICC in these cases compared to infants who suffered ‘peaceful,’ non-traumatic deaths, e.g. from illness [2,7,25]. Extrinsic constraints are thought to involve presumed costs of ICC, predicting greater ICC when it is energetically or physically less costly due to high rank [5], terrestrial locomotion [25,26] and/or shorter daily travel distances [6]. We further test whether ICC is more common in species with greater body size relative to the infant. Finally, ICC is predicted to be greater in cold or dry climates with slower corpse putrefaction, allowing the corpse to be carried for longer [12,27].

Two attempts have been made to quantitatively study ICC using a hypothesis-testing framework [19,28]. In the first case, Das et al. [28] collated 43 records of ICC from 18 species of anthropoid primates and found no significant effect of infant sex or age at death on the length of ICC, and no support for the death detection, parity and climate hypotheses (see Table 1 for definitions). However, their data suggested that the mother’s age, the infant’s cause of death, arboreality, and the living condition (e.g. captivity) affected ICC duration [28]. In the second case, Lonsdorf et al. [19] analysed 22 records of ICC from the Gombe chimpanzees but found no support for any of the hypotheses they tested, specifically the hormonal, mother-infant bond strength, death awareness (predictors: maternal age and cause of death), and climate hypotheses. Although both studies establish a framework for testing hypotheses suggested to
explain ICC, the results are inconclusive due to the low sample size and Das et al.’s [28] comparative study was not systematic. There is thus a need for a more rigorous and comprehensive comparative study. Identifying the factors that influence ICC variation is crucial for understanding both the selective pressures that may favour responses to death and underlying mechanisms of these responses [29] in primates, humans, and other animals.

To test hypotheses that explain between- and within-species variation in ICC, we created the largest database of primate mothers’ responses to their infants’ death. Our database includes available data on associated intrinsic and extrinsic factors, some of which have not yet been tested. Using a comparative approach, we (1) tested a subset of the ICC hypotheses for which there are available data to explain variation in (1a) the occurrence of ICC and (1b) the duration of ICC across primates. We also (2) determined the phylogenetic continuity of ICC across the primate order.

Materials and methods

Database creation

We searched the scientific literature for cases of primate mothers responding to the corpse of their dead infant. Cases were cross-referenced using three published reviews [5,7,28]. We included only events in which there was enough opportunity for the mother to carry the corpse [5]. Specifically, we recorded a case of ‘corpse not carried’ if the mother was in the vicinity of the infant when the death occurred and the corpse was not consumed or monopolised by other individuals or removed by observers after the death, but the mother did not carry it. Additionally, we classified attempted but unsuccessful lifting [e.g. 30,31] as ‘corpse not carried’ to avoid interpretation of underlying motivation. Our definition thus does not
differentiate between mothers who are unable or unwilling to carry their young. For each case, we recorded 10 variables where possible: (1) the species; (2) the site where the case was reported; (3) whether the corpse was carried or not; and, if carried, (4) the carry duration (in days); the mother’s (5) parity; (6) age; and (7) rank; (8) the infant’s age; (9) the cause of the death; and (10) the living condition (wild, provisioned, laboratory or captive). In cases where the exact duration was not known, we used the minimum (where > N) or maximum (when < N) confirmed carrying days or the mid-point of a stated range. We also included the minimum carry duration in cases where the corpse was removed after the mother had carried. We classified maternal age in two categories (young versus old) to make them consistent across studies. In the few cases in which infant age was not reported precisely, we took the mid-point of a range, or N + 1 or N - 1 if it was reported as > N or < N days, respectively. Infant ages were divided by the species weaning age to make them comparable across species. We also compiled data on additional variables to test further hypotheses. These additional variables included information about the species or the site. Specifically, we recorded the: (1) daily travel distance for the species at the site; species’ (2) degree of terrestriality; (3) body mass; and (4) level of maternal investment; and the site’s (5) maximum temperature; and (6) climate type. See Electronic Supplementary Material (ESM §2.1) for details of how these variables were measured and of resources from which they were obtained.

Statistical analyses

Species for which no data on mothers’ responses to their dead infants were available were excluded from all the analyses. Because of the risk of over-parameterisation with the number of explanatory variables and the relative scarcity of data for some of the variables, our analyses proceeded in two steps. First, we performed a set of exploratory models to identify
single predictors that were associated with the response variables: (a) ICC occurrence (presence/absence) and (b) ICC duration (in days). Our second step tested for support for additive effects on ICC occurrence and duration using an information theoretic approach with the variables identified in step 1 as being associated with the response variables (see tables S1 and S2 for sample sizes for the exploratory and information theoretic analyses, respectively).

For all models in both steps 1 and 2, we performed Bayesian phylogenetic generalised linear mixed models using the package ‘MCMCglmm’ in R version 4.0.2 (2020-06-22) [32,33]. Binary occurrence data (a) were analysed using threshold models; we log-transformed ICC duration (b) and used a Gaussian distribution. To control for relatedness amongst species, we included a random effect for primate phylogeny. The variance/covariance matrix was derived from the branch lengths of Version 3 of the 10kTrees Primates consensus tree (in the chronogram form) [34]. See the ESM §2.2 for details. Because our database had multiple ICC records from single sites, site was included as a random effect. Pseudoreplication at the species level was controlled for by the matrix to control for phylogeny. Because living conditions determine the energy available to individuals and we a priori predicted it to be important for ICC, we included condition as a fixed effect as a control in all the models.

To identify predictors in step 1, we compared models with each variable of interest to a null model using the Deviance Information Criterion (DIC) [35]. The null model used the same subset of the data as the model with the variable of interest and contained only the control variables: living condition (fixed), site and phylogeny (random). We retained for step 2 variables that, when compared to the null, improved the model fit by > 4 DIC (ΔDICnull). To perform model selection in step 2, we tested all combinations of the retained variables using the ‘dredge’ function of the R package ‘MuMIn’ [36], including in the model set the same null
model as in step 1. Competing models were considered those with a ΔDIC < 4 compared to the best model (ΔDIC_{best}) and a high weight (w).

Both sets of analyses were repeated excluding 157 cases from the Takasakiyama Japanese macaques (*Macaca mulatta*) [11] to determine whether those over-represented cases biased the results.

Although our predictions are in line with published hypotheses (Table 1), we deviate in one instance: the mother-infant bond strength hypothesis has suggested that the mother-infant bond strengthens linearly with infant age [15,19]. However, this prediction does not take into account the nuances of maternal behaviour during bond establishment and approaching weaning. The mother-infant bond is weak in primates until a few days after birth [37], and it starts to weaken again near weaning [38–40]. Consequently, we make a different prediction for this hypothesis: that the mother-infant bond shows a quadratic relationship with infant age, being strongest at intermediate ages.

Finally, we estimated the phylogenetic signal present in ICC to determine whether closely-related species are more similar in ICC than distant species. The phylogenetic distance between species was derived from the branch lengths of Version 3 of the 10kTrees Primates consensus tree (in the chronogram form) [34]. To estimate the phylogenetic signal of ICC occurrence, we calculated the D value—a measure of phylogenetic signal in binary traits [41]—using the ‘phylo.d’ function of the R package ‘caper’ [42]. D values closer to or lower than 0 indicate a phylogenetically conserved trait, i.e. Brownian phylogenetic structure; values closer to or above 1 indicate a labile trait that has evolved independently of phylogeny. We defined species as non-carriers when only cases of ICC absence were reported for that species. We calculated Blomberg’s K to estimate the phylogenetic signal of ICC duration using the ‘phylosig’ function of the R package ‘phytools’ [43]. In contrast to the D value, Blomberg’s K
closer to 0 indicates a labile trait with no phylogenetic signal; values closer to 1 indicate a highly phylogenetically conserved trait. To provide a single value per species, we used the median ICC duration and accounted for within-species variability by including the species’ interquartile ranges as an error term.

Results

We identified 409 reports of mothers’ responses to their infants’ deaths in 50 primate species across 126 different studies (median number of reports/species: 3; range: 1-161, see table S1 for details). These species belonged to 9 different primate families: Atelidae, Callitrichidae, Cebidae, Cercopithecidae, Galagidae, Hominidae, Hylobatidae, Indriidae and Lemuridae. Of the primate species for which records existed, 40 (80%) had been observed to perform ICC and 10 (20%) had been observed only not to perform this behaviour. Of those families that had records, presence of ICC was not observed in any species of the Callitrichidae, Galagidae, Indriidae and Lemuridae families (Figure 1A). The longest ICC durations were reported in the families Hominidae (the great apes) and Cercopithecidae (Old World monkeys) (Figure 1B).
Figure 1.

The (a) distribution of ICC and (b) average durations of ICC across the primate order. (a) Shown is a primate phylogenetic tree indicating in which species ICC has been observed or not (Yes or No, respectively), and those for which no data exists (Unobserved). (b) A bar chart showing the median durations of ICC in primate families for which data exist. The blue bars indicate median ICC duration (days), and the black arrows indicate the first and third quartiles. Black points show the distribution of observations of ICC duration. See ESM §3.1 for details (primate silhouettes were obtained from phylopic.org).

Variation in ICC

From the exploratory analyses of single predictors in step 1, only one variable showed explanatory power for ICC occurrence in the full dataset: cause of death ($\Delta$DIC$_{null}$ = 15.72; table S3). In the reduced dataset without the Takasakiyama cases, both cause of death ($\Delta$DIC$_{null}$ = 18.61; table S4) and mother’s age class ($\Delta$DIC$_{null}$ = 4.27; table S4) explained variation in ICC occurrence. Thus, we retained both variables in step 2 for the reduced dataset, resulting in three models to compare against the null. For ICC duration, one hypothesis had explanatory power in the full dataset: the mother-infant bond strength hypothesis, which included infant age and the quadratic of infant age as predictors ($\Delta$DIC$_{null}$ = 24.84; table S5). With the reduced dataset, in addition to the mother-infant bond strength hypothesis with the quadratic of infant age ($\Delta$DIC$_{null}$ = 10.24; table S6), there was some support for the infant dependency / infantile cues hypothesis, with infant age as a linear predictor ($\Delta$DIC$_{null}$ = 5.85; table S6). Both models were compared in step 2 from the reduced dataset.

Step 2 aimed to determine the additive combinations of predictors that best explained variation in ICC using an information-theoretic hypothesis-testing approach. As multiple predictors were supported only when using the reduced dataset, we present only these results here. Whilst all three models tested for ICC occurrence were supported (table 2; see table S7
for parameter estimates), the death detection hypothesis alone ($\Delta \text{DIC}_{\text{best}} = 0; w = 0.56$) and in combination with maternal experience ($\Delta \text{DIC}_{\text{best}} = 1.31; w = 0.29$) could be considered best, given their weights. The estimates for the death detection hypothesis were in the predicted direction, with lower probabilities of ICC occurrence in traumatic deaths i.e. those imposed by an external, observable event (Figure 2A). However, in contrast to our prediction, older mothers were less likely to carry corpses than younger mothers (Figure 2B). For ICC duration, the quadratic infant age model was best supported, having a high weight ($w = 0.89$) compared to the linear model ($\Delta \text{DIC}_{\text{best}} = 4.19; w = 0.11$; table 2; S8), as was the case for the full dataset. Infants were carried for longer when they died at younger ages, with a sharp decline when infants reached approximately half the weaning age (Figure 2C).
Figure 2.

Plots presenting the predicted effects for the best models for ICC occurrence (A, B) and duration (C) for wild-living primates. (A, B) Bar plots showing the predicted probability of ICC occurrence depending on (A) the cause of death and (B) the age of the mother using the reduced dataset. (C) Scatter plot showing the relationship between relative infant age at death (Infant age at death/Species weaning age) and ICC duration in days using the full dataset. Shown are: the predicted relationship (blue line); 95% CI (dashed lines); and the observations (shaded points).

Phylogenetic signal

The estimated D value for ICC occurrence was -0.310 ($P_{\text{random}} = 0$; $P_{\text{Brownian}} = 0.761$), indicating that ICC occurrence is a highly phylogenetically conserved trait. The estimated Blomberg’s K for ICC duration was 0.143 ($p = 0.191$) based on 1000 randomizations, indicating that there was no strong phylogenetic signal in the trait.

Discussion

Primate mothers’ infant corpse carrying is the most frequently reported thanatological behaviour [5,7]. As new reports of this behaviour accumulate, quantitative assessment of hypotheses that explain ICC becomes possible. Here, we performed the largest quantitative study of the variation in ICC across different primate species. We show that: (a) the probability of ICC occurring is highest for infants that died from non-traumatic causes and for younger mothers; and (b) younger infants are carried for longer than older infants. We further show that ICC is widely distributed across the primate order but is most frequent in great apes and Old World monkeys. Below, we discuss these findings before considering the possible implications that our results have for the field of evolutionary thanatology.
ICC occurrence had a strong phylogenetic signal [41]; it was more commonly reported in Old World monkeys and great apes, and reported absent in strepsirrhines. According to the currently-available data, ICC seems to have evolved once in the haplorrhines after they split from the strepsirrhines, and it may have been lost in the callitrichids and some atelids (see ESM for a discussion of ICC loss in proboscis monkeys *Nasalis larvatus*). This pattern could in part be explained by whether species carry or park their young while foraging, which also seems to present a phylogenetic signal [44,45]. In general, Old World monkey, New World monkey and ape mothers carry their young during large periods of their daily activities, while some strepsirrhines leave their young parked in nests, tree-holes, or clinging to a branch [44]. However, our data do not support this hypothesis: the majority of species in which there was an absence of ICC carry their live young, except brown greater galagos (*Otolemur crassicaudatus*) that park their infants. Relatedly, ICC may be more common in taxa that actively cradle or support their ventrally-carried infants c.f. ‘passively’ carrying clinging infants [7]; for example, callitrichid infants cling dorsally to the caregiver immediately after birth and are never ‘actively’ cradled. Another trait that may be responsible for this pattern is polytocy—a mother may not carry a deceased infant if a live infant is present. Litters are relatively common, i.e. >1 in 10 births, in the strepsirrhine (except *Propithecus verreauxi*) and callitrichid species [46] in which ICC is absent. In the same way that monotocy has been suggested as a preadaptation for carrying live offspring [44,45], it may be a prerequisite for ICC in primates. In addition, callitrichids and ring-tailed lemurs (*Lemur catta*) have high levels of allomaternal care [47–49]; this trait may further impede ICC occurrence in these taxa.

We do not suggest that mothers are indifferent to their dead infants in taxa with only records of absence of ICC, but that carrying is not usual for those mothers. Strepsirrhine and some callitrichid mothers give mother-infant contact, cohesion and lost calls, and usually stay
next to the corpse, attempt to lift, groom and/or keep coming back to it for some hours after the
death [7,30,31,50,51]. Alternatively, this result could have arisen due to research and
publication biases, as strepsirrhines and some New World monkeys are historically less well-
studied [52]. It is likely that some of the species with reported absence of ICC or without records
perform ICC but it has not yet been reported. Additionally, many of these taxa are nocturnal
or/and arboreal, which could further hinder the observation of ICC. The fact that the
phylogenetic signal of ICC duration is low may be due in part to the high within-species
variability in ICC duration; high evolutionary and environmental variation are responsible for
the low phylogenetic signal observed in many behavioural traits [53].

We found support for one hypothesis predicting variation in ICC occurrence: the death
detection hypothesis. This hypothesis suggests that mothers are better able to determine their
infant’s death when there are reliable external contextual and sensory cues such as traumatic
injuries, and thus are less likely to perform ICC in these cases [2,7]. Although we found that
the mother’s age predicted variation in ICC occurrence, this finding did not support the maternal
experience hypothesis, as younger mothers were more likely to perform ICC than older
mothers. This may provide further support for the death detection hypothesis: older mothers
could be more experienced in detecting death [reviewed in 5], and thus less likely to carry a
dead infant. If correct, this interpretation could provide evidence that primates have, or are able
to attain, an awareness of death and the causality subcomponent of death [2]. However, this
interpretation assumes that, at least in part, mothers carry offspring only when they are unaware
or uncertain that their infant is dead. Alternatively, the circumstances surrounding traumatic
deaths could be acutely stressful to the mother, resulting in a lower probability of ICC if the
mother is motivated to leave the area of the death rapidly and unencumbered.
Our results suggest that ICC duration is predicted by the age of the infant at death, with the longest durations occurring before infants reach half the weaning age. This is in contrast to the findings of Das et al. [28], which may be due to their lower sample size and power. This result may support at least three related hypotheses that predict an overall negative function of infant age at death on ICC: the mother-infant bond strength, infant dependency, and infantile cues hypotheses. These hypotheses are not mutually exclusive, and it is possible that all contribute to how long an infant’s corpse is carried. We suggest that the duration of ICC may have evolved as a by-product of strong selection on maternal behaviour. An alternative or additional explanation could be that older infants are heavier and, presumably, more costly to carry. Our other results—that wild-living primates carry, on average, for shorter durations (see ESM tables S7 and S8)—support that ICC is energetically costly, assuming that wild-living primates have the least available energy to spare. On balance, the non-linear relationship with infant age indicates a role of the carry-over of maternal behaviour rather than an effect of infant weight increase with age, but we acknowledge that more data are necessary to confirm this hypothesis.

Our findings may have implications for understanding primate emotion i.e. internal states of the central nervous system triggered by specific stimuli that produce externally observable behaviours and cognitive, somatic and physiological responses [54]. Although speculative, emotions seem to be involved in primates’ responses to the deaths of others. For example, primates who have lost a close associate show increased glucocorticoid levels and self-directed behaviours indicative of stress [55–58]. Moreover, after the removal or accidental loss of infants’ corpses, capuchin (Cebus capucinus), snub-nosed monkey (Rhinopithecus bieti), and chacma baboon (Papio ursinus) mothers emit alarm calls—an indicator of stress [59]—and search for the corpse [6,15,60]. In light of our findings, we suggest that emotional
mechanisms that regulate maternal behaviour and the mother-infant bond may underlie the latter observations. Consequently, a proximate mechanism for ICC could be the maternal anxiety triggered by separation from an infant [54]: mothers may carry corpses to avoid this ‘separation anxiety’ [61].

In agreement with previous studies [19,28], we found that climate, specifically temperature and climate type, did not influence ICC duration. We suggest that the climate hypothesis, which suggests that slow putrefaction in dry and cold climates enables extended ICC [27], can be rejected at this stage. Instead, we propose that extended ICC occurs in mothers who have a particularly strong bond with their infant at death (see above).

Finally, we turn to the ‘bigger’ evolutionary and comparative thanatology question about the implications of these findings for our understanding of the evolution of responses to death. Broadly, primates' responses to dead conspecifics seem to be promoted by social bonds [7]. As the mother-infant bond is the most significant bond among primates, prolonged ICC may represent the most extreme manifestation of that bond. Attentive thanatological behaviours have also been observed in other social vertebrates, particularly in proboscids, cetaceans and, possibly, corvids [2,62]. These taxa live in hierarchical, complex societies in which individuals recognize each other and base their behaviour on previous social interactions [63–67]. The mammalian taxa have prosocial tendencies and a slow life history strategy with low birth rates, strong mother-infant bonds, and extended maternal investment [2,68]. Attentive thanatological behaviours may thus have evolved in different social animals as a by-product of strong social bonds through parallel evolution and/or phylogenetic continuity [69]. If so, it is possible that early human mortuary practices arose as an extension of primates’ attentive thanatological behaviour [70].
Although our results indicate some evidence for predictors of ICC occurrence and duration, we acknowledge that the interpretation of these results is complicated by the range of possible explanations suggested by competing hypotheses. We are also aware, despite creating and using the largest database of ICC to date, that our interpretations are particularly limited for understudied primate species [52] for which neither absence nor presence of thanatological behaviours have been recorded. Our study highlights that the unsystematic recording of ICC is an important limitation for comparative thanatology. Thus, we encourage long-term sites to systematically record ICC and to make data publicly available through publication or data sharing projects such as ‘ThanatoBase’ (http://thanatobase.mystrikingly.com/).

Acknowledgments

We are grateful to Dr Dieter Lukas for helping us to adjust the Bayesian phylogenetic methods to our data and for explaining the mathematics behind this type of analyses. We thank Dr Jarrod D Hadfield for his advice on the threshold models. We are also grateful to Dr André Gonçalves for his insightful comments on an earlier version of the manuscript. Finally, we are thankful to Cara MacLeod for her contribution to the data collection.

The database and some results formed part of a dissertation submitted in partial fulfilment of the requirements of the degree of MSc of the University of London in September 2020.
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Table 1.
Hypotheses and predictions proposed to explain infant corpse carrying (ICC) tested in the paper. Shown are: the hypotheses; followed by a brief description; the predictors and direction of the predicted relationship; the level of explanation (within-species (WS), between-population (BP) and/or between-species (BS)); whether the predictor had any support for each response (occurrence or duration) and the direction of the relationship; and the references for the hypotheses (see ESM §1.1 for a full list).
<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Description</th>
<th>Predictor and relationship</th>
<th>Level</th>
<th>Support?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal behaviour</td>
<td>Strong selection on maternal investment and care of offspring can carry over post-mortem.</td>
<td><em>Infant dependency:</em> Infant age: ↑ICC for younger infants</td>
<td>WS</td>
<td>Duration: as predicted</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Mother-infant bond strength:</em> Infant age: ↑ICC for infants of intermediate ages (see text for details)</td>
<td>WS</td>
<td>Duration: as predicted</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Learning to mother:</em> Parity: ↑ICC for nulliparous and primiparous mothers</td>
<td>WS</td>
<td>No</td>
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<td></td>
<td></td>
<td><em>Maternal investment:</em> Inter-birth interval (IBI): ↑ICC in species with relatively longer IBIs</td>
<td>BS</td>
<td>No</td>
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<tr>
<td></td>
<td></td>
<td><em>Maternal experience:</em> Parity: ↑ICC in multiparous mothers</td>
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<td>No</td>
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<tr>
<td>Infantile cues</td>
<td>Infantile characteristics are attractive to primates, eliciting caring behaviour</td>
<td><em>Infant age:</em> ↑ICC for younger infants (but aborted foetuses will not be carried)</td>
<td>WS</td>
<td>Duration: as predicted</td>
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<td>Death detection</td>
<td>Cause of death: ↑ICC for non-traumatic (e.g. illness) vs traumatic deaths</td>
<td>Occurrence: as predicted</td>
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<tr>
<td>Putrefaction rate</td>
<td>Climate type and temperature: ↑ICC in dryer climates and/or colder habitats where putrefaction is slower</td>
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<td>Energetic costs</td>
<td>Terrestriality: ↑ICC in terrestrial species</td>
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<td></td>
<td>Travel distance: ↑ICC in species or populations with shorter daily travel distances</td>
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<td></td>
<td>Maternal rank: ↑ICC in high ranking mothers</td>
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<td></td>
<td>Body mass: ↑ICC in species with greater relative body mass</td>
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</table>
Summary of the information theoretic approach determining the predictors of ICC occurrence and duration (see text for details). Reported are: the intercept ($\beta_0$); the presence of particular predictors in each model (+); the deviance information criterion (DIC); the difference in DIC between the given model and the best model ($\Delta$DIC); and the weight ($w$) of each model.

<table>
<thead>
<tr>
<th>Response</th>
<th>Corresponding hypothesis</th>
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<th>Predictor</th>
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<th>$\Delta$DIC</th>
<th>$w$</th>
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<td>Living condition</td>
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