Infanticide across Apes: A Meta-Analysis of Life History Traits to Estimate Risk in Orangutans (*Pongo spp*.)

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Abstract

Infanticide is most commonly observed in species with slow life history traits, where females have long intervals between births, and as a way of increasing reproductive success males may force females to return to estrus sooner by killing their dependent offspring. Orangutans exhibit some of the longest inter-birth intervals (IBI) among mammals, making them a key system for evaluating the Sexual Selection Hypothesis. Orangutans, in particular, are known for their extensive parental care, and they are characterized by having the longest gestation length among primates after humans. In species with extended gestation and lactation lengths as well as delayed weaning, such as orangutans, the incentive for infanticide is expected to be especially strong because the dependent offspring suppress female fertility for prolonged periods. In this study, comparative data from both great apes (Hominidae) and lesser apes (Hylobatidae) are used to test whether variation in life history traits such as gestation length, weaning age, and inter-birth interval (IBI) can predict the likelihood of infanticide in orangutans, despite no occurrence having been documented in wild populations. Statistical models were applied to assess which life history traits in apes show higher probabilities of infanticide occurrence. There are many authors that claim that infanticide is an important selection pressure in orangutans, yet, there is no documentation of these events in the wild. Could it be that infanticide is not an important selection pressure for orangutans despite being a proven pressure for some of it's closest relatives? Or perhaps infanticide is occurring and the rural habitats that orangutans live in make it too difficult for humans to observe? The objective of this meta-analysis is less about proving or disproving the presence or absence of infanticide in orangutans, and more about analyzing if infanticide is occurring, why would orangutans be susceptible to it, under the assumption that it is occurring in wild populations for the purpose of this study.

Introduction

There are three species of orangutans within the genus *Pongo*, which include the Bornean Orangutan, the Sumatran Orangutan, and the Tapanuli Orangutan. All three of these arboreal species are endemic to Indonesia and Malaysia, exclusively on the islands Sumatra and Borneo. Orangutans are one of the Great Apes, which also include gorillas, bonobos, chimpanzees, as well as humans. Collectively these species are known as the Hominids. The lesser apes are within Hylobatidae, and this family includes gibbons and the siamangs. Apes are distinguished as primates that have hair instead of fur, fingernails as opposed to claws, opposable thumbs, high IQs due to their larger brain-to-body size ratios, binocular vision, and unlike monkeys they lack tails. (Center for Great Apes, n.d.). Generally the main difference between great and lesser apes is size, as great apes are significantly larger in body mass. Additionally, great apes exhibit sexual dimorphism, unlike the lesser apes (Blaxland, 2022). Most apes are known for being highly social, with the exception of the semi-solitary orangutan (O'Connell, 2018). Similar to humans, some species live in multi-male/multi-female groups, while other categories of social organization include solitary, male-female pairs, and one-male/multi-female groups. Adult male orangutans display an unusual phenomenon called bimaturism, which is a reproductive strategy where sexually mature males have one of two morphological forms: flanged or unflanged. Flanged males are distinguished by large cheek pads on both sides of their face, and a large throat sac, while unflanged males do not have these traits and are smaller in size. Although unflanged males are still sexually mature, adult females prefer to mate with the dominant flanged male. Bimaturism also plays a role in the semi-solitary characterization of the species, as the flanged adult male will remain solitary unless he is mating, and flanged males are intolerant of each other (Knott et al., 2007). The subadult males (unflanged) will associate with other subadult males and females, and adolescent females will often travel together. Adult females however will typically avoid mature males, and will invest lots of time into parental care, as infants are completely dependent on their mothers for at least two years. This type of intensive motherhood is a defining characteristic of their life history, distinguishing orangutans from other primates, and is often compared to humans (Orangutan Foundation International, 2019).

Image displays bimaturism in male orangutans. Unflanged male on the left and flanged male on the right. Photo by wildlife photographer, Tim Laman.

The objective of this meta-analysis is to estimate infanticide risk in orangutans based on life history traits associated with infanticide in other ape species. There are 27 members of the great and lesser apes on the IUCN Red List, all of which are either vulnerable, endangered, or critically endangered. Although infanticide has been theorized in orangutans by researchers and primatologists, no infanticides have been observed in wild orangutans. There are many authors that claim that infanticide is an important selection pressure in orangutans, yet, there is no documentation of wild infanticide for the species. Currently only 6% of all primate species have direct observations for infanticide, which translates to be around 36 species of primates with documented infanticide. (Dixson, 2013; Scott, 2019). Infanticide is defined as the killing of an infant by an individual of the same species (Hrdy, 1989). It is an adaptive strategy for males, with the sexual selection hypothesis (SSH) suggesting that by killing an unweaned offspring, the perpetrator is shortening the inter-birth interval of the mother, and by doing so he is increasing his reproductive fitness and decreasing the reproductive success of his competitors (Stumpf et al., 2008). If an infant is still reliant on its mother for milk, killing that infant means that the mother will commence her menstrual cycle sooner and be in estrus again, allowing a male to be able to have his own offspring sooner. Although there are no documented cases of infanticide in wild orangutans, several female mating and social strategies have been observed that are consistent with counterstrategies that primates with documented infanticide utilize. For example, polyandrous mating and postconceptive mating have been hypothesized to increase paternity confusion, and when males are uncertain of paternity, the likelihood of committing infanticide is reduced. In addition, female orangutans become increasingly socially isolated following parturition, which may serve to minimize encounters with males during periods of peak infant vulnerability. These behaviors suggest that, even in the absence of direct observations, infanticide risk may have acted as an important selective pressure in shaping orangutan reproductive strategies. Thus, male infanticide is not only a product of sexual selection but also a force influencing female social behavior, spatial patterns, and mating decisions (Scott, 2019).

Another example of reproductive strategies that could suggest the presence of infanticide is forced copulation. Orangutans exhibit relatively high levels of forced copulation among mammals (Knott et al., 2005). Due to the unflanged males not being the primary choice for copulation by females, the disadvantaged unflanged males obtain a large portion of their offspring by force. It is hypothesized that female resistance to copulation is contingent upon the costs of being fertilized by an undesirable male. (Knott et al., 2005) When a male cannot compete for a receptive female, forced copulation becomes an alternative tactic for reproductive success. Similarly, infanticide can be utilized as another alternative strategy for species with high male-male competition, used by males who lack mate access because it brings a female back to estrus once lactation stops suppressing ovulation. There are high levels of sexual conflict occurring between males and females because the males want to maximize the number of offspring they have while the females are looking for high-quality mates while simultaneously protecting their offspring. On top of that, orangutans are semi-solitary, amplifying the competition for a mate because reproductive opportunities can be rare.

Methods

This meta-analytical review was initially focused only on existing literature for infanticide only within the three species of orangutans, and from there the search was extended for databases available for all great ape species and lesser ape species. For the scope of this project the lesser apes were included in the meta-analysis in order to have a larger sample size, as well as a greater understanding of infanticide within the phylogenetic tree.

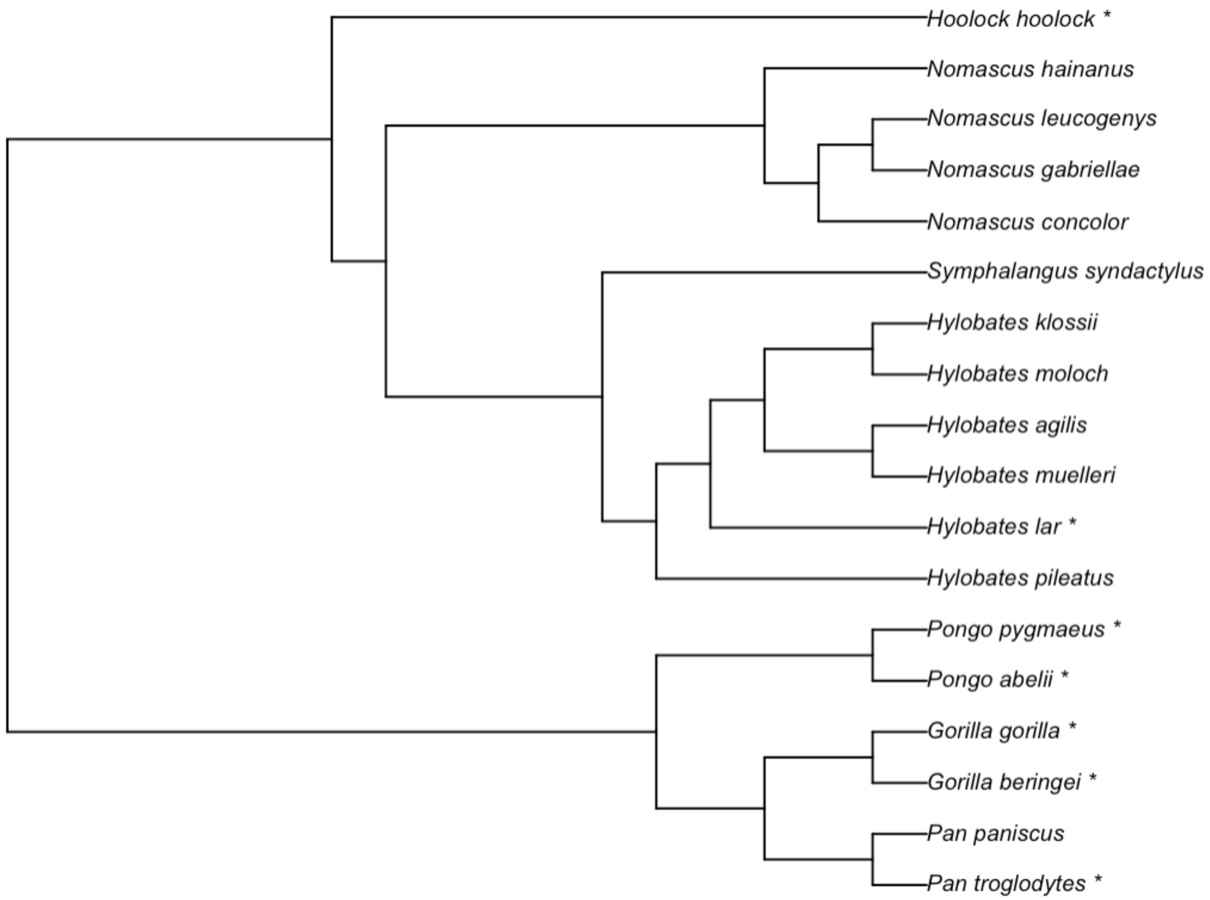


Figure 1. Phylogenetic tree of the ape species included in the study. *Indicates the eight species with either documented infanticide or predicted infanticide in the case of both Pongo species. (Due to uneven data availability, Hoolock tianxing, Hoolock leuconedys, Nomascus annamensis, Nomascus nasatus, Nomascus siki, Hylobates abbotti, Hylobates funereus, Hylobates albibarbis, and Pongo tapanuliensis have been excluded.)

I was interested in determining how traits associated with infanticide covary across primates, and in assembling the data, I was cognizant that study methods for each species may vary. Species were included if peer-reviewed studies reported with sufficient data were available. Due to uneven data availability, not all species—particularly among Hylobatidae and the Tapanuli Orangutan—were represented, which reduced the sample size to 18 rather than 27 total species of great and lesser apes. The life history data gathered is from four databases: The

Wisconsin National Primate Research Center, The Animal Diversity Web, AnAge Animal Ageing and Longevity Database, and The Journal of Human Evolution - Journal 47, Issue 6. The variables extracted from the databases included average gestation, average lifespan (both wild and captive), average female sexual maturity age, average weaning age, average interbirth intervals (IBI), as well as mating systems and social organization types. I chose to focus on these variables because they are key components of a slow life history, which increases infant vulnerability to infanticide.

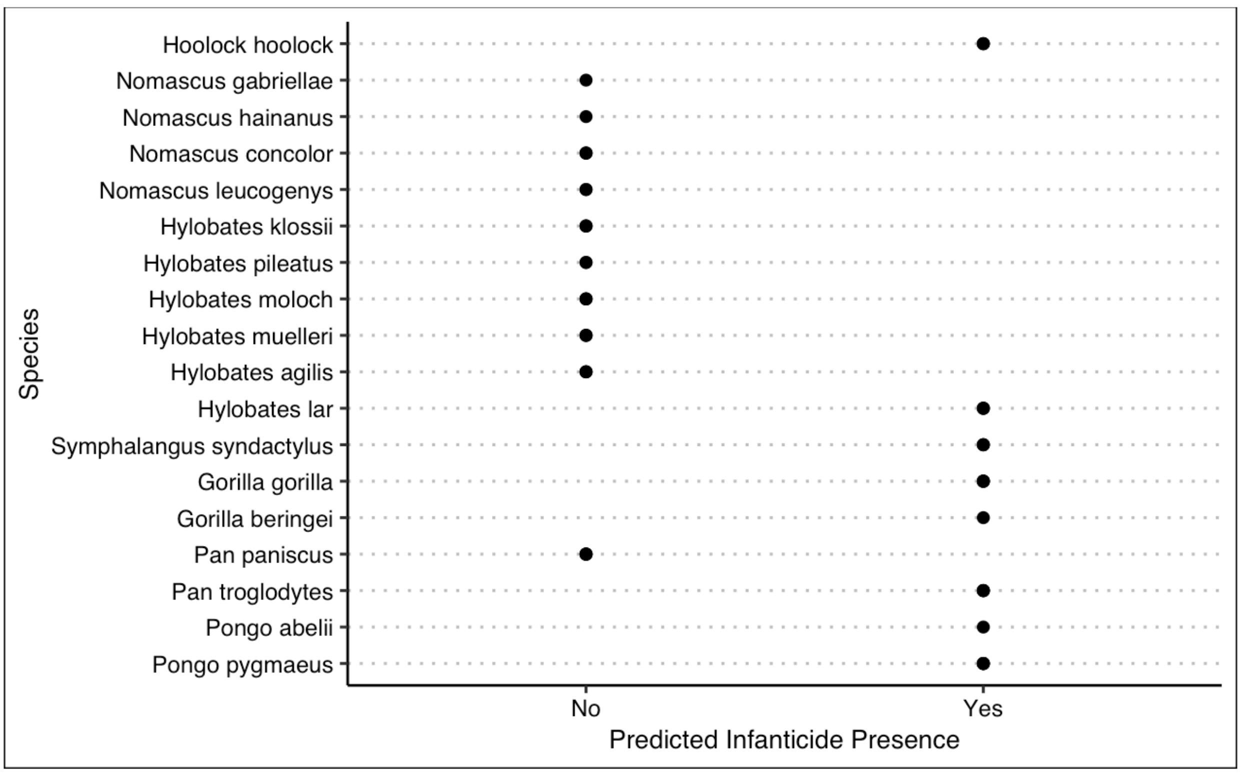
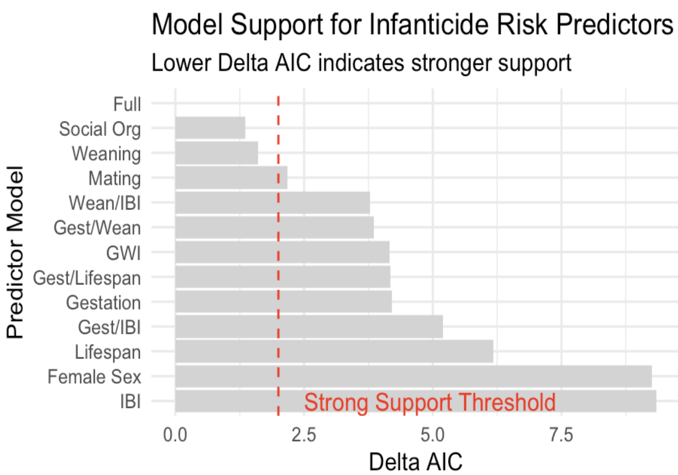


Figure 2. Displays species with documented infanticide presence. Out of the 27 ape species, only six have documented instances of infanticide. For the purpose of this study, orangutans are considered to exhibit infanticide in wild populations.

A series of Generalized Linear Mixed Models (GLMMs) were used in Rstudio with the Generalized Linear Mixed-Effects Models function (glmr) within the Linear Mixed-Effects Models package (lme4) to account for species as a random effect in order to evaluate the effects of life history and social variables on infanticide risk. A total of eight predictor variables were analyzed with the first five designated as the “Full Model” which included: average gestation length, average weaning age, average interbirth interval, social organization type, mating system type. The other three predictor variables tested were average female sexual maturity age, average lifespan, as well as conservation status according to the IUCN. All character variables were mutated to be factors, and infanticide was coded as binary (0 = absent, 1 = present). Each predictor variable was initially tested independently to evaluate its relationship with infanticide risk. Additional models were constructed to assess interactions within the variables in the full models based on life history traits hypothesized to influence infanticide occurrence. These interaction models included combinations of weaning age and IBI, gestation length and weaning age, gestation length and IBI, gestation length and lifespan, and a multivariate model including gestation length, weaning age, and IBI.

Results



	Model	AIC	Delta_AIC	Rank	Interpretation
1	full	21.32818	0.000000	1	Strongest support
2	socialorg	22.68790	1.359727	2	Strong support
3	wean	22.93061	1.602435	3	Strong support
4	mating	23.51041	2.182231	4	Moderate support
5	wean_ibi	25.10398	3.775799	5	Moderate support
6	gest_wean	25.17703	3.848850	6	Moderate support
7	GWI	25.49264	4.164467	7	Weak support
8	gest_lifespanC	25.51135	4.183173	8	Weak support
9	gestation	25.52829	4.200117	9	Weak support
10	gest_ibi	26.53241	5.204236	10	Weak support
11	lifespanC	27.50027	6.172097	11	Weak support
12	femsex	30.57747	9.249294	12	Unsupported
13	ibi	30.68272	9.354539	13	Unsupported

Figure 3. Model support for predictors of infanticide risk based on Akaike Information Criterion (AIC) comparisons among Generalized Linear Models. Lower ΔAIC values indicate stronger model support. The full multivariate model, which included gestation length, weaning age, interbirth interval (IBI), social organization, and mating system, received the strongest support with the lowest AIC value (ΔAIC = 0). Models including only social organization and weaning age also showed substantial support, as both fell within the strong support threshold of ΔAIC < 2 (red dashed line).

Figure 4. A table displaying each model and the corresponding AIC as well as ΔAIC, in order from most supported to least supported.

Model selection based on Akaike Information Criterion (AIC) indicated that the full multivariate model, which included gestation length, weaning age, interbirth interval (IBI), social organization, and mating system, provided the strongest overall support, with the lowest AIC value (AIC = 21.33, ΔAIC = 0). Models including only social organization (ΔAIC = 1.36) and weaning age (ΔAIC = 1.60) also received notable support because both fell within two AIC units of the top model. In contrast, models containing female sex ratio or IBI alone showed little support, with ΔAIC values greater than 9.

Overall, these findings suggest that infanticide risk is best explained by a combination of reproductive and social variables rather than by any single factor alone. However, the strong independent performance of social organization and weaning age indicates that social structure and maternal investment strategies may play especially important roles in shaping infanticide risk across species.

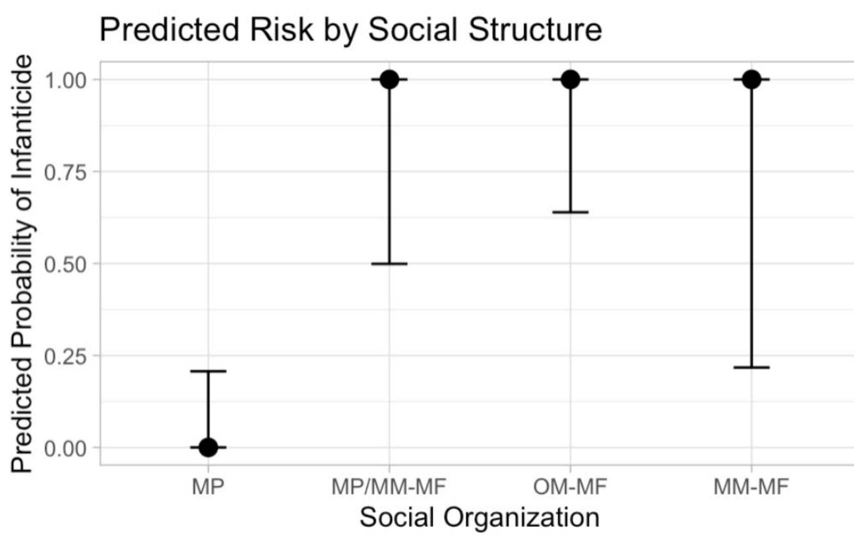


Figure 5. Predicted probability of infanticide risk across different social organization types derived from the Generalized Linear Model analysis. Values range from 0 (low or no predicted risk of infanticide) to 1 (high predicted risk of infanticide). Points represent model-predicted probabilities, and error bars indicate confidence intervals.

Predicted probabilities generated from the social organization model further demonstrated clear differences among social systems. Multi-male/multi-female (MM-MF), one-male/multi-female (OM-MF), and mixed MP/MM-MF systems all showed high predicted probabilities of infanticide risk, whereas monogamous pair (MP) systems showed very low predicted risk. Among the high-risk categories, the one-male/multi-female social organization exhibited the narrowest confidence interval, indicating greater precision and consistency in the model estimates. This pattern is notable because it aligns with the social organization observed in orangutans, indicating once again that their social organization could be a risk factor for infanticide.

Discussion

These results support theoretical predictions that infanticide is associated with reproductive strategies in which males can increase reproductive success by shortening female interbirth intervals. Additionally, the results suggest that social systems influence opportunities for infant protection, male competition, and paternity confusion, all of which may contribute to variation in infanticide risk across species. The results of this study suggest that infanticide risk in apes is shaped by a combination of reproductive, life history, and social factors rather than any single predictor alone. Model comparisons using Akaike Information Criterion (AIC) demonstrated that the full multivariate model received the strongest support, indicating that infanticide risk is best explained when multiple variables are considered together. While social organization and weaning age emerged as strong individual predictors, the results of the multivariate model highlights the importance of interactions among reproductive strategies, maternal investment, and social dynamics in influencing infanticide risk. Overall this supports the idea that complex behavioral phenomena such as infanticide cannot be adequately explained by isolated traits. The findings are also consistent with long-standing evolutionary theories regarding sexually selected infanticide in other primates. Species characterized by prolonged maternal investment, long interbirth intervals, and social systems with increased male competition may create conditions in which males gain reproductive advantages by eliminating dependent offspring, thereby accelerating the return of females to reproductive receptivity. Similarly, social organization may influence opportunities for infant protection, paternity confusion, and male control over access to female mates, all of which can alter the likelihood of infanticide occurring. The elevated predicted risk associated with one-male/multi-female and multi-male/multi-female systems aligns with these theoretical expectations and suggests that reproductive competition and social structure interact to shape behavioral strategies across ape taxa.

Although infanticide remains undocumented in wild orangutan populations, this absence of evidence might be due to lack of detection or observation rather than lack of occurance. Orangutans are semi-solitary, highly arboreal primates that occupy dense forest habitats, making direct behavioral observations difficult and infrequent. As a result, infanticide events may occur undetected, particularly because such behaviors are rare and often happen over short periods of time. Infanticide risk could still be biologically relevant to the abundance of the species even if direct cases are not observed in the wild.

These findings may also have important implications for conservation and management. Orangutans are critically endangered and already face substantial pressures from habitat loss, fragmentation, and reduced reproductive rates. Understanding the full scope of pressures that may influence reproductive success is therefore important for conservation planning. If social pressures, altered population density, or changes in male competition increase the likelihood of infanticide, then habitat fragmentation and human disturbance could indirectly affect population recovery by influencing social dynamics and infant survival. Incorporating behavioral ecology into conservation management may help improve predictions of population viability and reproductive success in endangered ape populations.

Several limitations should also be considered when interpreting the results of this study. Most importantly, the analyses are correlational and do not establish direct causation. Instead, they identify patterns of association among life history traits, social systems, and predicted infanticide risk across ape taxa. In addition, the relatively small number of species and the difficulty of observing infanticide in wild populations may limit the strength of conclusions that can be drawn. Future research incorporating larger comparative datasets, long-term field observations, and phylogenetic approaches may help clarify the mechanisms underlying these relationships and determine how ecological conditions influence infanticide behavior across primate species.

An important improvement to this study would be the incorporation of a phylogenetic comparative analysis rather than relying solely on Generalized Linear Models with species treated as a random effect. Because ape species share evolutionary histories, traits associated with infanticide risk may not be fully independent across taxa. Closely related species often exhibit similar life history strategies, reproductive patterns, and social systems due to shared ancestry, which can influence statistical outcomes in comparative analyses. Incorporating a phylogenetic tree into the analysis would allow evolutionary relationships among species to be explicitly accounted for and could provide a clearer understanding of whether infanticide risk is associated with inherited evolutionary traits rather than only present-day ecological or social conditions. A phylogenetic approach could therefore help clarify the genetic and evolutionary foundations of infanticide behavior and improve interpretations of how these behavioral strategies evolved across ape lineages.

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