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Ethological bases of infanticide: a state-of-the-art approach to mammals

Bases etológicas do infanticídio: uma abordagem sobre o estado da arte em mamíferos

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ABSTRACT

Considering that infanticide can oppose the interests between offspring and parents, as well as between the two sexes, the aggressive behavior of adults against infants is considered a fundamental part of the organisms' strategy. Thus, this article aims to describe the types of infanticide, explaining the advantages of each biparental infanticidal behavior. The research was carried out using the Publish or Perish© software, with keywords such as "ethology", "infanticide" and "mammals", in English, Portuguese and Spanish. After selection and discarding, we selected 51 works, including scientific articles, theses and dissertations, covering a period of 40 years. We organized them systematically, separating the references into two approaches: (a) physiological and (b) sociobiological/ecological. The results indicate that infanticide behavior in mammals can be influenced by different factors, such as environmental stress, hormonal pathways, mainly oxytocin and vasopressin. Furthermore, studies have shown that there are individual differences in the behavioral response to parental care and infanticidal behavior, influenced by both the genotype and the environment in which individuals were raised. Infanticide behavior can also be seen as an adaptive parental strategy to increase the chances of survival and future reproduction. Ultimately, our results highlight the complexity of mammalian infanticide behavior, pointing to the importance of considering physiological, sociobiological and ecological factors in its analysis and interpretation.

Keywords: Behavior. Lethal aggression. Parent-offspring conflict. Sexual conflict.

RESUMO

Considerando que o infanticídio pode se contrapor aos interesses entre a prole e os pais, assim como entre os dois sexos, o comportamento agressivo de adultos contra os infantes é considerado uma peça fundamental como estratégia reprodutiva dos organismos. Assim, o presente artigo visa a descrever quais os tipos de infanticídio, explicitando quais as vantagens de cada comportamento infanticida biparental. A pesquisa foi realizada utilizando o software Publish or Perish©, com palavras-chave, como "etologia", "infanticídio" e "mamíferos", em inglês, português e espanhol. Após a busca, selecionaram-se 51 obras dentre artigos científicos, teses e dissertações, destacando um período de 40 anos. Organizou-se de maneira sistemática, separando as referências em duas classes: (a) fisiológica e (b) sociobiológica/ecológica. Os resultados indicam que o comportamento de infanticídio em mamíferos pode ser influenciado por diferentes fatores, tais como estresse ambiental, vias hormonais, sobretudo a oxitocina e a vasopressina. Além disso, os estudos mostraram que há diferenças individuais na resposta comportamental ao cuidado parental e ao comportamento infanticida, influenciadas tanto pelo genótipo quanto pelo ambiente em que os indivíduos foram criados. O comportamento de infanticídio também pode ser visto como uma estratégia adaptativa parental para aumentar as chances de sobrevivência e reprodução futura. Em última análise, os resultados deste estudo destacam a complexidade do comportamento de infanticídio em mamíferos, evidenciando a importância de considerar os fatores fisiológicos, sociobiológicos e ecológicos em sua análise e interpretação.

Palavras-chave: Agressão letal. Comportamento. Conflito parental e prole. Conflito sexual.

INTRODUCTION

Infanticide can be described as a social behavior that characterizes the killing of the immature by the parents of the same group or involving individuals from different groups (Hrdy, 1979). Initially, infanticide was described as something controversial and confusing, sometimes as an "apparent disadvantage", leading to the belief that this behavior is not a product of natural selection, but rather an abnormal behavior or a pathological response to overpopulation (Alcock, 2011).

From the reproductive phase and their typical sexual behaviors, the population characteristics of the descendants are perpetuated. In some taxa, such as mammals, after reaching sexual maturity, individuals begin to allocate energy for reproduction (Andrade, 2021). Consequently, the parental investment applied to different species occurs through a set of processes, including behavioral ones, which invest time and energy dedicated to the development and care of offspring, optimizing their survival (Ricklefs & Relyea, 2016).

Parental care is an investment behavior, which aims to guarantee the fitness of offspring, increasing the probability of survival and reproductive success of the offspring (Peroni & Hérnandez, 2011). However, the quality and quantity of investment differ between species due to a myriad of factors, such as the availability of natural resources and/or the presence of agonistic interactions (Alcock, 2011). Thus, parental behavior is part of a spectrum of investments from parents to offspring, which begin during the formation of gametes and will influence the fitness of the offspring (Rymer & Pillay, 2018).

The relationship between energy allocation in the reproduction process requires organisms to adopt different strategies. In this sense, an example of optimization is the persistence of the couple's stability during the rearing of the offspring, since biparental care increases the chances of reproductive success (Machado, 2004, 2018). In mammals, the duration and intensity of biparental care for offspring varies between species and is related to resource ecology, reproductive behavior, and the risk of infanticide (Opie, Atkinson, Dunbar & Shultz, 2013). Overall, social monogamy, that is, living in pairs, is rare among mammals, corresponding to less than 3% of mammal species (Opie et al., 2013).

Among the behaviors directed at the group's offspring or infants, in addition to parental care, there is much discussion about infanticide committed by adults of both sexes.

The nature of this action is verified in several primate species, such as howler monkeys (Aguiar et al., 2005), langurs and gibbons, as reviewed by Ma, Brockelman, Light, Bartlett and Fan, and Opie et al. (2013), for example.

The occurrence of infanticide behavior can raise several questions about the factors involved or the reason for the expression. However, the infanticide can be seen as an alternative for the adult individual to increase the opportunity to survive by freeing themselves from expensive care, as may be the case for some females, as well as to reproduce, as may be the case for many males, accelerating the generation of another offspring. They therefore act as adaptive strategies (Lukas & Huchard, 2014).

In the context of relationships, intraspecific aggressiveness is characterized by violent behavior against individuals of the same species (conspecifics), increasing the chances of killing and injuring individuals. These acts include cannibalistic behavior, intergroup aggression, fratricide (common in birds, see Stinson, 1979), feminicide, infanticide, and other types of aggression (Andrade, 2021), which are commonly observed in several species of mammals, in which males often compete for resources among themselves and can kill descendants of the same species (Lukas & Huchard, 2014).

Furthermore, according to Andrade (2021), conflict between individuals from the same group involving the aforementioned aggressive behaviors can be seen as an advantage in the social position of the aggressors, because it gives the winner a monopoly over food and reproductive resources, in addition to protection and coping in favor of survival.

Given the variety of hypotheses found to explain infanticidal behavior, which can bring benefits to infanticides, both males and females, there are explanations that vary from those that confer advantages by foregoing the costs of care, to others that interpret it as an extreme form of obtaining food under stressful environmental or social conditions for parents.

More specifically, the hypotheses are: (a) competition for resources, especially in those species that live in social groups with hierarchies; (b) reproductive investment in which males may kill the offspring of females they did not mate with to induce a return to estrus; (c) when a new male takes control of a social group, he can kill the offspring that are not his descendants and also induce the return of estrus in females; (d) failure to identify offspring, whose infanticide may be an accidental result of a male not recognizing the offspring as his own, (e) or a female kills her own offspring, possibly due to stress, lack of maternal experience or other factors; (f) when dominant females kill the offspring of subordinates (see Parsons & Svensson, 2021).

In this sense, such hypotheses start from the assumption that infanticide is a consequence rather than a cause (Lukas & Huchard, 2014), and thus can be considered an evolutionary adaptation in certain ecological contexts, as it is used to improve the reproductive fitness of the individuals that practice it (Balme & Hunter, 2013).

Faced with the paradox in which infanticide can oppose parental care, the interests between parents and children as well as the interests between the sexes, aggressive behavior is considered a fundamental part of the organisms' strategy that can directly influence their individual fitness, making it possible that carriers of the variations have a greater chance of perpetuating their characteristics, leaving more descendants (Darwin, 1859; Izar, 2016; Andrade, 2021), spreading the "aggressive" variant.

The development of scientific knowledge requires an understanding of previous studies that served as a basis for the research carried out today, as well as for future research. Considering the multiple evolutionary and behavioral responses that are correlated to infanticidal behavior presented in different groups of animals, especially mammals (Lukas & Huchard, 2014), and the number of studies that sought to present such behaviors, it is necessary to compile and search common patterns between species.

The purpose of this literature review is to summarize the main scientific findings on infanticide, explaining the advantages of each infanticidal behavior observed between conspecifics, carried out by both sexes of mammals. It should be noted that cases of infanticide observed in humans and those in which adults of prey species kill the youngsters of their potential predators are outside the scope of this analysis.

MATERIALS AND METHODS

Data obtention and organization

To search for scientific studies that analyzed infanticide in mammals, we used the Publish or Perish© software (Harzing, 2007). Our methodology was based on the following keywords: (a) ethology, (b) infanticide and (c) mammals, in three languages: English, Portuguese, and Spanish. The selected studies were systematically organized by choosing references from various types, including: (1) scientific papers published in journals with ISSN (International Standard Serial Number), (2) PhD theses, (3) master dissertations, and (4) undergraduate theses, encompassing a total time frame of 40 years.

This research is based on the methodological assumptions of Ridley (2012), which considers that a systematic review synthesizes a certain 'number of conclusions' in a specific research field. To this end, the recording method of Prodanov and Freitas (2013, p. 135) was carried out, which "aims to identify the studies consulted, record their content, the reflections provided by reading, and organize the information collected" from the manuscripts with the following information: (a) theme; (b) authors; (c) year of publication; (d) brief summary, and (e) reference, so that the approach subthemes could be selected. Finally, to better organize the analysis of this review, the content found was divided according to two disciplinary contexts: (A) physiological, and (B) sociobiological and ecological.

Data analysis

Data analysis was carried out based on "Bardin's Content Analysis" (2011, p. 15), which consists of a "[…] set of methodological instruments in constant improvement, which apply to discourses (contents and contexts) extremely diversified".

Additionally, we adopted the criteria set out by Ridley (2012) to apply a systematic review of the bibliography found, adopting three steps to compile and select the studies: (a) creation of a search protocol; (b) literature search, and (c) exclusion and inclusion criteria. As a methodological instrument for this research, the databases followed the approaches above, optimizing knowledge management regarding this review to try to provide possible explanations on the topic.

RESULTS AND DISCUSSION

A priori, the search resulted in a total of 121 references. Of these, 51 were considered relevant to the research according to the selection of subjects from the disciplinary categories (physiology, sociobiology, and ecology), since the others, despite containing keywords or titles related to the main theme, did not contain content directed to the infanticidal behavior or description of the event. The studies were allocated to their respective areas with their subthemes, accounting for 14 studies for the (a) physiological approach and 37 studies for the (b) sociobiological

and ecological approach to infanticide in mammals.

Physiological approach

According to the physiological approach, the imbalance affects the harmony of the organism, causing problems in animal health, such as hormonal regulation related to social and parental behavior (Hierro, Heras, Rodríguez & Montalbán, 2014). Machado (2018) highlights that hormones such as oxytocin (hereafter, OXT) and vasopressin (hereafter, AVP) in mammals can promote different behavioral expressions.

In this example, OXT which acts on several muscles, such as the uterine wall, is also involved in promoting social behaviors, such as monogamy and parental care, which reduce the risk of infanticide, observed in both female and male primates (Opie et al., 2013). Variations in AVP expression, on the other hand, can inhibit paternal care by acting as an antagonist to OXT, stimulating an aggressive and infanticidal response, as observed in the prairie vole (Machado, 2018).

Different perspectives have been reported regarding the approach to infanticidal behavior in the light of endocrine analyses (Moreira, 2010). Studies like these have revealed key points about how this behavior has stood out in the face of adverse conditions, in addition to pointing out the relationship with the evolutionary history of the species (Cunha, Waureck, Souza, Genaro & Moreira, 2021).

Mammals have great brain plasticity, fully capable of reorganizations that are associated with individual experiences. These experiences, influenced by different environmental stimuli, enable the acquisition of knowledge acquisition, since they are reorganized in the nervous system and cause important changes, such as conformational changes in the brain, influencing the intensity of cellular connections (Sousa et al., 2017), processes that can modify mammal behavior.

Thus, Cunha et al. (2021) explained that aggressiveness is a factor regulated by a significant series of neurotransmitters, in particular serotonin, a neurotransmitter that acts mainly in the central nervous system. Furthermore, the authors described that the concentration of this neurotransmitter is related to the inhibitory or stimulatory effects on aggressive behavior and more than ten different receptors for serotonin have been found. Most of this neurotransmitter is found in the raphe nucleus, which are neuronal aggregates in the brainstem (Narvaes, 2013).

Hosken (2018) points out that stress is the trigger for aggressiveness and that responses to stress vary according to the species, contexts, and factors involved, which can be exogenous, such as social and environmental variables, resource availability, and ecological relationships. Related to imbalance in the body, stress causes a series of behavioral and physiological responses that trigger the failure of immunological, reproductive, and growth processes, as they are also mediated by endocrine responses (Yaribeygi et al., 2017).

It is noteworthy that in wild mammals, for example, when under stress, increased levels of glucocorticoid hormones are observed, which are characteristic of the stress response, which allow an animal to respond to unpredictable social, physical or environmental challenges (Reeder & Kramer, 2005).

The organism in the face of a stressor usually presents behavioral deviations, such as directed aggression, which includes cannibalism, infanticide, among other behaviors (such as stereotypies and self-mutilation). The result of the imbalance can be perceived through different pathways: (a) through neuroreceptors that are associated with the voluntary motor system, (b) the autonomic nervous system, or (c) the neuroendocrine pathway (Orsini & Bondan, 2006).

As described by Orsini and Bondan (2006), the processed information elicits motor responses and behavioral stimuli through nerve impulses. The stressor's impact activates the sympathetic autonomic nervous system, releasing catecholamines into the bloodstream. This, together with parasympathetic processes, facilitates the gradual resumption of organismal activities following alert state responses. The neuroendocrine pathway is considered the latest and occurs through hypothalamic stimulation triggered by the stressor, inducing the synthesis (through the release of hormones) of cellular reserves, such as amino acids and fatty acids, which are promptly mobilized for glucose synthesis (Orsini & Bondan, 2006).

The development of parental caregiving or infanticidal behaviors has been analyzed in mice. Olazábal and Alsina-Llanes (2015) addressed the fluctuation of oxytocin receptors and the action of this neurotransmitter in several brain regions, including the lateral septum, the cingulum and the paraventricular nucleus of the thalamus of males and females, pointing out relationships with behavioral responses. It was highlighted that (a) infanticidal or parental responses developed gradually in organisms, being absent in juveniles or non-adult individuals, and (b) decreases and increases (i.e., positive and negative relationship of variations) of oxytocin contributed to differences in these behaviors in different sexes and ages (Olazábal & Alsina-Llanes, 2015).

In wild and laboratory mice, it was considered the influencing factors in a case study where the groups began to express infanticidal behavior. The results showed the involvement of genotype, family group, and sex in regulating the behavioral response to offspring, namely: (a) wild mice differed notably from laboratory mice, committing infanticide, and the latter showed mostly spontaneous parental care behavior towards their offspring (Jukubowski & Terkel, 1982).

In the same study above, however, after wild mice cohabited with laboratory mice, in which there were males that took care of their offspring, the wild males expressed paternal behavior, while the wild virgin females continued to exhibit infanticide. The results, in turn, indicated that parental behavior in wild mice is not spontaneous, in addition to pointing out that domestic mice may present behavioral variations and biases for the study of animal behavior (Jukubowski & Terkel, 1982.).

The social structure and the degree of kinship between female *caititu* are determinant in the pattern of social behaviors (Fragoso, 2006). In an exploratory analysis of cooperative breastfeeding and its own offspring, a case of extra-group infanticide was observed by a female without offspring, killing one of the newborns on the farm during the studies, showing that females from unrelated groups can respond more aggressively (Packard et al., 1990). Therefore, kinship and familiarity with the offspring must be taken into account in studies on tolerance (Biondo & Bussad, 2004).

In summary, we analyzed the following studies aimed at the physiological approach, cited below in temporal order (Table 1). These studies describe the specific conditions in which physiological changes act on the regulation of parental care and infanticidal behavior, and bring together different mechanism explanations on how infanticidal behavior occurs.

Sociobiological and ecological approach

Taking into account that several external stimuli can be assimilated as stressors by the organism and can trigger physiological changes and behavioral changes (Orsini & Bondan, 2006; Hosken, 2018), sociobiology comes in handy as a discipline that studies and integrates the relationship between proximate (physiological) and ultimate (adaptive) explanations

in social behavior, also taking into account ecological factors and structural dynamics in populations, to explain how certain behaviors, seen as strategies, emerged and perpetuated themselves throughout evolution through natural selection (Dawkins, 1979; Suscke, 2014).

Using the ecological approach, we seek to understand the dynamics of the population by investigating possible variables – resulting from behavioral responses – in order to explore the participation of behavior in the quality of the organism's survival, aiming to evaluate its impacts on the population (Peroni & Hérnandez, 2011).

Thus, it is possible to highlight patterns or variations for what we call here infanticidal behavior, reported in several studies that aim to answer the question from an evolutionary perspective and on its individual, social and ecological functions (López, López, Methion & Covelo, 2018; Breedveld, Folkertsma & Eccard, 2019; Smith & Smith, 2019; Zhao et al., 2020). Through these studies it is understood that infanticidal behavior, or other related aggressive episodes, can occur from variable contexts such as those summarized below in Table 2.

Table 1
Physiological conditions associated with infanticidal behavior.

Physiological approach	
Stress	• It was reported that life in captivity is a stressful condition, in which the individual begins to express altered behavior, demonstrating aggression directed towards other organisms, including infanticide (Orsini & Bondan, 2006). • Pregnant female Swiss mice that suffered the effects of ionizing radiation showed an aggressive behavioral incidence of cannibalism, indicating fetal motor disturbance (Piúma, 2007).
Hormone profile	• Studies of fluctuations in neurohypophyseal hormones (vasopressin and oxytocin) in relation to social behaviors during pregnancy and birth of the offspring of the Eastern meadow vole and the montane vole, which pointed to oxytocin as a promoter of maternal care, reducing infanticide (Nicita, 2008). • Common marmoset pups exposed to sensory cues between contact or inhibition of stimuli between mothers and pups, in order to observe parental care as a potential for changes in behavioral and hormonal responses. Vocalization, vision, smell, and contact signals acted as physiological modulators of behavior in caring for offspring (Barbosa, 2009). • High levels of cortisol as a response to stress in wakefulness behavior to protect offspring against infanticide, made female black capuchin monkeys alert, intensifying care for their offspring (Moreira, 2010). • Progesterone acting in signaling as a potential activator of infanticidal behavior and inhibitor of parental care in male (Saltzman & Ziegler, 2014). • Behaviors, such as aggression, in spotted paca, were more frequent at night (Hosken, 2018).
Signaling	• Mating interest and nest protection in female rodents. The study points out that females associated familiarity with the risk of infanticide, increasing nest protection especially when there are males in the group and unknown males, through olfactory recognition (Eccard, Reil, Folkertsma & Schirmer, 2018). • Reduction in maternal care through the administration of purinergic receptor antagonists, Suramin and PPADS, in regions of their behavioral expression (medial preoptic area, bed nucleus of the stria terminalis and oxytocinergic neurons in the paraventricular nucleus and supraoptic nucleus), leading to changes in aggressive behavior by reducing neuronal activation by infusion of the receptor (Teodoro, 2018).

Sources: Orsini & Bondan (2006); Piúma (2007); Nicita (2008); Barbosa (2009); Moreira (2010); Saltzman & Ziegler (2014); Eccard et al. (2018); Hosken (2018); Teodoro (2018).

The evolutionary history of mammals shows that among many behaviors, "lethal aggression" is a relevant factor. The study by Gómez, Verdú, González-Megías and Méndez (2016) showed that the phylogenetic signal "lethal aggression", including predation, is found in about 5,020 extant mammals and 5,747 recently extinct mammals. However, the phylogenetic signal for lethal aggression presents evolutionary flexibility, indicating that it is possible for additional factors to modify the levels of aggression or friendly characteristics, as often observed in closely related species, such as chimpanzees and bonobos (Gómez et al., 2016; Lukas & Huchard, 2019; Rapchan, 2019).

Therefore, the phylogenies of a group expose the evolutionary relationships that promoted favorable or unfavorable conditions for survival, accentuating the possibility of propagating "infanticidal genes", since it is through descendants that the continuous permanence of the characteristics of the group is conceived (Moore, 2017). However, different factors, such as selection pressures, can promote changes to eliminative certain behaviors.

Table 2
Social, biological and ecological conditions associated with infanticidal behavior.

Sociobiological and ecological approach	
Reproductive strategy	• Extra-group males and the probability of conceiving victimized mothers, who would otherwise not be readily available (Parmigiani, Palanza & Brain, 1989; Coulon, Graziani, Allainé, Bel & Pouderoux, 1995; Pluhácek, Bartos & Vichová, 2006; Bezerra, Silva Souto & Schiel, 2007; Feh & Munkhtuya, 2007; Borries et al., 2011; Izar, 2016; Parsons & Svensson, 2021). • Sexually selected infanticide within the group to guarantee only their own offspring, since the next litter will be their descendants, being an adaptive male mating strategy (Lewison, 1998; Bellemain, Swenson & Taberlet, 2005; García-Diaz & Lizana, 2013; López et al., 2018). • Sexual and aggressive strategy from female leopards, gorillas, and rodents to young males, shaping socio-spatial ecology (Watts, 1989; Balme & Hunter, 2013). Episodes of aggressive attacks by females, acting as a co-strategic behavior aimed at potentially infanticidal males. Therefore, female aggression can prevent the reproduction of males with little fighting capacity, and their offspring in the group (Parmigiani et al., 1989).
Reproductive pressure/Social Dominance	• Infanticide acts among closely related mothers to benefit from decreased competition, allowing their daughters to be recruited (Dobson, Chesser & Zinner, 2000). • Episodes of aggression or death as a mechanism of reproductive suppression (Silva, 2014; Lukas & Huchard, 2019). • Consanguinity in the formation of groups, which generates changes in the social hierarchy, as recorded in chimpanzees (Durham, 2003). • Transfer of females from the group, when females are allocated to copulate with extra-group males, generating changes in the social hierarchy, modifying social interaction or modifying the establishment of dominance relationships in the group (Almeida, 2012; Silva, 2014).
Social system/ Presence of unrelated males	• Change in the social system of males with the presence of an allochthonous male (Pluhácek et al., 2006).
Investment	• Energy expenditure on offspring care varies according to the composition of the litter, since infanticide reduces intra-offspring competition for food, including the one driven by the sex of the offspring, whereas in rodents the cost of raising males can be higher than that of females (Baião, 2000), optimizing offspring care (Zhao et al., 2020). • Episodes of cannibalism, after committing infanticide, result in energy recycling, so as not to lose all the energy expenditure allocated to obtaining nutritional benefits (Parmigiani et al., 1989; Ebensperger, Botto-Mahan & Tamarin, 2000).
Competition	• Competition for resources in the community or between communities or when human interference occurs, which can be an important stressor (Aguiar et al., 2005; Rödel, Starkloff, Bautista, Friedrich & Von Holst, 2008; Lukas & Huchard, 2019). • Food competition between subadult males to ensure growth and survival, aiming for long term tenure in the group and social position, both maximize reproductive success (Agoramoorthy & Rudran, 1995). • Sexual competition, when males commit infanticide to reduce the number of future competitors by increasing the ratio of females to males. In this case, infanticide was observed in puppies at different ages (Machado, 2004).
Isolation or deprivation of stimuli	• When organisms do not perform their natural functions in nature, such as hunting, cutting, etc. (Cunha et al., 2021). The deprivation of stimuli from cohabitation is an important factor in the occurrence of a male taking care of his offspring and in inhibiting infanticidal behavior (Sartório & Vieira, 2001). Because the parental care system is dynamic and modulated by variables that act directly on the experiences of both the offspring and the partner (Vieira, 2003). Isolation or deprivation of natural stimuli can be observed in females of the Striped Mongoose, in which females with greater reproductive dominance evict, induce abortion and infanticide for social control of reproduction in the group as competition reproductive (Gilchrist, 2006). It was also observed that after abortion, females were allowed to rejoin the group. The explanation for abortion and infanticide was explained by stressful causes, such as expulsion from the group (Gilchrist, 2006).
Stress	• Stressful factors affect the relationships of animals with their community, as observed in human presence, or deprived of their natural habits in closed breeding systems or captivity, or in isolation from the group due to social motivations of the group itself. These present behavioral modifications, such as aggression, cannibalism, abortion, and infanticide (Aguiar et al., 2005; Gilchrist, 2006; Orsini & Bondan, 2006; Feh & Munkhtuya, 2007; Cunha et al., 2021).

Sources: Parmigiani et al. (1989); Agoramoorthy & Rudran (1995); Coulon et al. (1995); Lewison (1998); Dobson et al. (2000); Ebensperger et al. (2000); Sartório & Vieira (2001); Durham (2003); Vieira (2003); Machado (2004); Aguiar et al. (2005); Bellemain et al. (2005); Gilchrist (2006); Pluhácek et al. (2006); Feh & Munkhtuya (2007); Rödel et al. (2008); Borries et al. (2011); Almeida (2012); García-Diaz & Lizana (2013); Silva (2014); Izar (2016); López et al. (2018); Lukas & Huchard (2019); Zhao et al. (2020); Cunha et al. (2021).

Initially, infanticide was organized by Hrdy (1979) into five classes: (1) exploitation, (2) resource competition, (3) parental manipulation, (4) sexual selection, and (5) social pathology. The first four recognize infanticidal behavior as an adaptive value for the organisms that commit it. The fifth class, "social pathology", is associated with social stress, due to internal and external factors, such as human interference (Hrdy, 1979).

Discussions about parental investment highlight intriguing questions about behavior, as it seems to make no sense to invest energy with the offspring and, at a certain point, commit infanticide.

In this way, studies such as that by Balme and Hunter (2013) have pointed out to hypotheses about the benefits of infanticide, highlighting, for example, (1) the hypothesis of sexual selection as a reproductive strategy that enhances the fitness of males, the (2) hypothesis of predation, in which it is suggested that infanticide is a mechanism to obtain food. In the latter scenario, parents experiencing energy-related stress may resort to infanticide, resulting in the killing and potential consumption of their own offspring. In turn, the (3) hypothesis of competition for resources, in which the infanticidal practice provides the perpetrators or their descendants with greater access to resources, eliminating competitors.

The hypotheses allow us to understand that the functions and consequences of infanticide differ between populations, species, and contexts. Therefore, it is necessary to know everything from the life history of organisms to how the population dynamics occur, in order to determine whether or not it is advantageous to express the behavior (Balme & Hunter, 2013).

Supplementary Table

List of species mentioned in the text.

Name	Genus and/or species	Author of the species
Howler monkeys	*Alouatta* spp.	Lacépede, 1799.
Langurs	*Semnopithecus* spp.	Desmarest, 1822.
Gibbons	*Hylobates* spp.	Illiger, 1811.
Gibbons	*Nomascus* spp.	Miller, 1933.
The prairie vole	*Microtus ochrogast*	Wagner, 1842.
Mice and Swiss mice	*Mus musculus*	Linnaeus, 1758.
Caititu	*Dicotyles tajacu*	Linnaeus, 1758.
Eastern meadow vole	*Microtus pennsylvanicus*	Ord, 1815.
Montane vole	*Microtus montanus*	Peale, 1848.
Common marmoset	*Callithrix jacchus*	Linnaeus, 1758.
Black capuchin monkeys	*Sapajus nigritus*	Goldfuss, 1809.
Spotted paca	*Cuniculus paca*	Linnaeus, 1766.
Chimpanzee	*Pan troglodytes*	Blumenbach, 1776.
Bonobo	*Pan paniscus*	Schwarz, 1927.
Guatemalan black howler	*Alouatta pigra*	Gmelin, 1788.
Banded mongoose	*Mungos mungo*	Gmelin, 1788.

Source: The authors.

Furthermore, Agrell et al. (1998) documented that infanticidal behavior in mammals is an adaptive behavioral strategy, which confers reproductive success on the aggressor. The aforementioned authors emphasized that the infanticidal act brings benefits such as nutritional gains and potential mating partners to those who commit it.

For females, it saves investment in situations of scarcity, access to food, nesting sites, and communal gain of care for offspring, by eliminating young from other females that would compete for care, a behavior presented in neotropical primates, such as Guatemalan howler monkey (Parsons & Svensson, 2021) and marmosets (Bezerra et al., 2007).

CONCLUSION

Regarding the guiding questions of this review, there are several hypotheses that suggest advantages for infanticide behavior in different species of mammals. Some of these hypotheses include sexual selection as a reproductive strategy to increase the fitness of males and females, which allow obtaining nutritional gains and potential mating partners, access to resources for the aggressor's descendants, and saving resources by discarding the care of unviable offspring, whether for reasons of deviations in the offspring's development or environmental severity and scarcity of resources.

There is a possibility that factors such as stress, hormonal profile, cellular signaling and responses, reproduction and competition strategies influence the expression of infanticidal behavior, so it seems that there is no single causal factor for infanticidal behavior.

Moreover, the relationship between the different sexes and between parents and offspring can determine the allocation of non-genic resources, including care, disposal, and aggression towards the offspring. It can therefore be concluded that there is no single answer to the question, as several factors can influence the expression of infanticidal behavior in mammals during the period of infant occurrence.

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COMPETING INTERESTS

The authors declare that there are no conflicts of interest.

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