

On the adaptive significance of non-parental infanticide in mammals

Linking model predictions to empirical observations



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Abstract

Although it might sound counterintuitive, non-parental infanticide can be an adaptive strategy in mammals. Adult individuals may kill the offspring of conspecifics in order to obtain resources. Four hypotheses exist that try to explain under what conditions infanticide should occur. According to the sexual selection hypothesis, males kill the young of females to increase their chance of siring her future offspring. The resource competition hypothesis predicts that males or females kill young in order to increase their access to limiting resources such as territories, food or helpers. The cannibalism hypothesis predicts that young are killed in order to obtain food resources. The final hypothesis is the adoption avoidance hypothesis which predicts that young are killed in order to prevent spending time and energy in a unrelated young. The goal of this thesis is to investigate how well the predictions of the different hypotheses and associated models match empirical observations and to see if it would be possible to predict for a certain species whether or not it has the potential to be infanticidal. From this study I conclude that the predictions made by the hypotheses match fairly well with empirical observations depending on the studied species. Furthermore, I conclude that it would be very difficult to predict if a certain species has the potential to be infanticidal because infanticidal behavior is the combined result of a great number of factors. Future research should study the exact background of an infanticidal act more carefully before drawing any conclusions on what hypothesis can be applied.

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Introduction

Infanticide is the deliberate killing of the immature offspring of conspecifics and has been reported in over a 100 species belonging to at least 5 different orders and 18 different families (MacDonald, 2009).

At first sight, it seems surprising that a behavior that reduces the survival of infants can be adaptive and is therefore selected for by natural selection. However, numerous publications on the infanticide of infants by males and females attacking their own or a neighboring group suggest that infanticide is more than an pathological phenomenon.

Most of the explanations of non-parental infanticide in mammals are based on the assumption that the perpetrator gains something by committing infanticide. This may be nutritional gains when the infant is cannibalized (the exploitation hypothesis), increased breeding opportunity (the sexual selection hypothesis) or access to limited resources such as territories, food or helpers (the resource competition hypothesis). Furthermore, infanticide can be adaptive when it avoids the costly adoption of unrelated young (the adoption avoidance hypothesis) (Hrdy, 1979; Pierotti, 1991).

The goal of this thesis is to assess how well the predictions made by the previously described hypotheses and associated models fit empirical observations from both natural and experimental studies. Furthermore, I want to assess if it is possible to determine whether or not infanticide could occur in a certain species by comparing their characteristics to the predictions of the hypotheses.

The sexual selection hypothesis

Sexual selection occurs when sexes differ in their reproductive success due to differences in their mating success. The reproductive success of males is often limited by mating opportunities whereas the reproductive success of females is limited by resources. This may result in sexual dimorphism, where sexes differ in morphology or behavior. The members of the sex that are under strong sexual selection may compete among themselves over matings with females, which can result in infanticide (Freeman and Herron, 2007). By killing the young of another male, a male can increase his own chance of successfully siring offspring with the mother of the killed young. (Hrdy, 1977). The sexual selection hypothesis requires that males should not kill their own offspring, that by committing infanticide, a male shortens the interbirth interval (IBI) of the victimized female and that males should mate with the mother of the killed infant (Ebensperger, 1998).

That fathers should not kill their own offspring under the sexual selection hypothesis, makes sense from an evolutionary point of view because current offspring is of equal value to a father than any future offspring. Fathers could avoid accidentally killing of their own offspring by being able to recognize them or by not killing any young during the time that his own offspring is vulnerable to infanticide. Mennella and Moltz (1987) were able to test this prediction experimentally using Wistar rats. They used a group of male rats that remained sexually-naïve during the experiment and a group of rats that was allowed to mate with a female. Then the sexes were kept separate until a few days

before parturition. 10 days after parturition, the sexually-naïve group proved to commit infanticide significantly more than the sexual-experienced group. This observation confirmed the prediction that males rarely kill offspring that they might have sired.

The second prediction of the sexual selection hypothesis is that by committing infanticide, males must shorten the IBI of the victimized female. The IBI is the time period between the birth of the first and second infant of a female and consists of a lactation period, a waiting period for conception and the gestation period of the second infant (Figure 1). Infanticide has been confirmed to shorten the IBI of lions by 8 months (Packer and Pusey, 1984), 23 days in Wistar rats (Menella and Moltz 1987) and 14 months in wild geladas (Beehner and Bergman, 2008). This prediction also indirectly suggests that sexual selected infanticide should not occur in seasonally breeding species, since females of these species will not be

receptive until the next breeding season. However, infanticide among seasonal breeders has been observed in red deer (Bartoš and Madlafousek, 1994), Japanese macaques (Soltis *et al.*, 2000) and Hanuman langurs (Borries, 1997). Hrdy and Hausfater (1984) suggested that infanticide might occur in seasonally breeding animals when females who lose their litter, are more likely to breed successfully or produce a larger litter in the following breeding season. Borries (1997) showed that 82.9% of the males in the seasonally breeding Hanuman langurs had access to their victimized mother in the following mating season.

The final prediction of the sexual selected infanticide hypothesis is that the male should mate with the victimized mother. This prediction is well supported by observations in hanuman langurs (Sommer and Mohnot, 1985), wild geladas (Beehner and Bergman, 2008) and lions (Packer and Pusey, 1984).

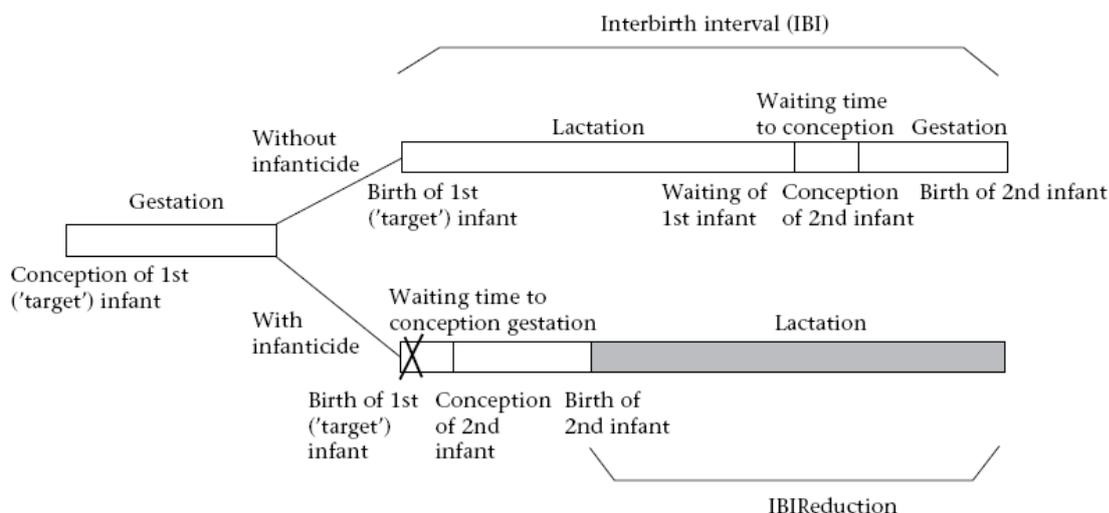


Figure 1. Schematic representation of an interbirth interval with and without infanticide. The top timeline represents a situation without infanticide whereas the bottom timeline includes infanticide (marked by 'X'). By committing infanticide, a male can shorten the IBI of the female with a period that is equal to the sum of 'age at first infant at infanticide', 'waiting time to conception' and 'gestation time'. The grey area marks this reduction in IBI. From Boyko and Marshall, 2009.

Modeling the sexual selection hypothesis

Although the predictions made in the previous section on when sexual selected infanticide should occur are logical, recent modeling by Boyko and Marshall (2009) suggest that sexually selected infanticide should occur under a much wider range of conditions. In their model, a male will receive a genetic payoff when he sires the next offspring of his victimized female. This payoff is being multiplied by the probability of paternity of the second offspring, which can be estimated by his dominance rank or residence status. According to the model then, a male should commit infanticide when there is no chance of paternity and the cost of committing infanticide are negligible. It should be noted that this is not a realistic assumption because an infanticidal male might even die in a confrontation with the parents of the infant (Sommer, 1988).

When a male however has a chance of paternity, the choice of committing infanticide is depended on the infant's age. This makes sense because the possible reduction in IBI is roughly equal to the remaining period of lactation, which decreases when infants become older. For example, the mean IBI of Ramnagar langurs is 2.4 years but only when males kill very young infants, they can reduce this IBI with a maximum of about a year (Borries, 1997). Since the possible IBI reduction is related to the duration of the lactation period, this also suggests that in species where the gestation/lactation ratio is high, it is less adaptive for a male to commit infanticide (Figure 2). Van Schaik (2002) developed a more elaborate view on this point of the model. He hypothesized

that in species where females have long lactation periods (i.e. low gestation/lactation ratio), post-partum mating (i.e. where the gestation and lactation periods overlap) is rare because this creates prolonged energetic and time budgeting problems to the female. As a consequence, these females face a higher risk of infanticide. However, in species where females have short lactation periods (i.e. high gestation/lactation ratio), post-partum mating is less costly and as a result, these species face a lower risk of infanticide. This can be explained by the fact that an infanticidal act on such a female does not necessarily bring her back into breeding conditions since she may already be pregnant with another young (Van Schaik, 2002).

A second prediction of the model is that when dominance rank and paternity are positively correlated, high ranking males should be the ones who commit infanticide. Evidence for this can be found in mice where 82% of the dominant ranked males committed infanticide on unrelated young whereas subordinate males committed infanticide in only 23% of the cases (Vom Saal and Howard, 1982) Subordinate males kill considerably less young because this will not increase their mating chance since dominant males get most of the matings in the breeding group.

The last prediction of the model is that infanticide becomes less adaptive when males in multi-male groups are more related to each other (Figure 2). This suggests that immigrant males should commit infanticide whenever this reduces the IBI and costs of committing infanticide are negligible because immigrants are presumed to be unrelated to the other males in the group. Broom *et al.* (2004)

showed in their model that this may be more complicated in primates. They expected low rates of infanticide to occur in species where immigrant males enter at the bottom of the dominance rank because these males have a low chance of winning a possible confrontation with the infants father. This might explain the low rates of infanticide in multi-male groups of Japanese macaques (Sprague *et al.*, 1998; Yamada and Nakamichi, 2006). Higher rates of infanticide by immigrant males may occur in species where males enter at the top of the dominance rank. Evidence for this can be found in Hanuman langurs (Borries, 2000) and sooty mangabeys (Fruteau *et al.*, 2010).

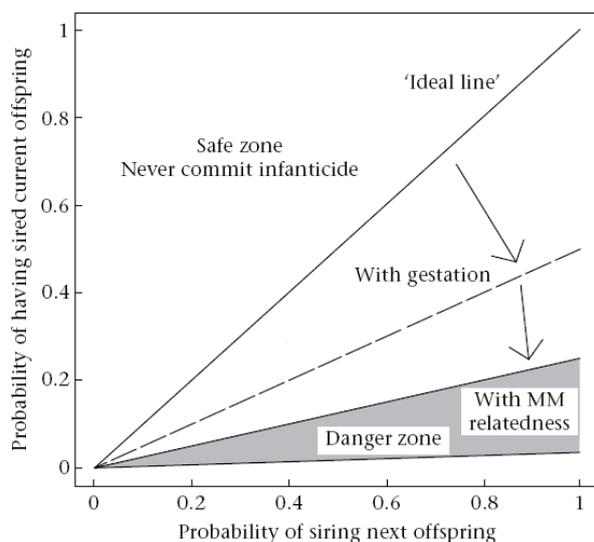


Figure 2: The conditions under which infanticide is adaptive under the sexual selection hypothesis. The ‘ideal line’ represents the case where a male’s estimated paternity in the current infant is equal to his estimated paternity in the next infant that he could conceive by a female when he commits infanticide on here current infant. Above this line, his chance of siring a next infant is lower than the chance of having sired the current infant. Under this ideal line, committing infanticide is adaptive but increased gestation and male-male (MM) relatedness decrease the conditions under which infanticide is adaptive. Modified from Boyko and Marshall. 2009.

The resource competition hypothesis

Where the reproductive success of males is mostly limited by access to females, is the reproductive success of females limited by access to resources (Freeman and Herron, 2007). The resource competition hypothesis states that by committing infanticide, females increase their access to limited resources such as territories or nesting sites (Hrdy, 1979). The resource competition hypothesis makes two predictions. First of all, infanticide should be more common when resources are limited due to crowding or food scarcity. And second of all, the sex that is most likely to present future competition for the limited resource should be the target of infanticide (Ebensperger, 1998). This last prediction may not be the norm in rodent species because by killing the entire nest, females save time by not having to sex their victims. (Sherman, 1981 cited in Ebensperger and Blumstein, 2007).

Infanticide in high density populations of European rabbits might be a significant factor of pup mortality (Rödel *et al.*, 2008). 12% of the nest mortality in a 5 year study was proved to be caused by infanticide. In 50% of these cases, another female build a new nest inside the chamber of the killed nest or gave birth in an adjacent chamber in the same burrow. Rödel *et al.* (2008) suggested that competition for breeding burrows is an explanation for the observed cases of infanticide in this species but that the reduced density might also increase the survival chance of the infanticidal female’s own offspring because it attracts less predators. Wolff and Cicirello (1989) showed that in a wild population of white-footed mice where only 30% of the

suitable habitat was occupied, females did not commit infanticide in order to obtain a territory. However, when strange pups were placed close to a female's own nest to create high-density conditions, females committed infanticide in 76% of the cases. In other words, females compete for territories at high densities but not at low densities because in the latter case there is enough space to create a territory (Wolff and Cicirello, 1989).

Although the resource competition hypothesis is usually associated with infanticide committed by females, it can in some cases also be applied to males. Observations of chimpanzees by Watts *et al.* (2002) showed that male chimpanzees killed infants of females that were presumed to be from a neighboring troop. The attacks were located on the border of the male's territory near a mast fruiting event of an important food species of the chimpanzees. By committing infanticide, males expanded their foraging range and thereby gained increased access to food for themselves, their mates and their offspring.

A final limited resource for the reproductive success of females are helpers in cooperative breeding species. Helpers are involved in babysitting, carrying and feeding pups in mongoose (Clutton-Brock *et al.*, 1998b). Helpers are subordinate females that have little chance of reproducing themselves and can increase their inclusive fitness by helping relatives to rear their young (Hamilton, 1964). Dominant females often kill the infants of subordinate females because the amount of food received by pups increases when more helpers are available (Clutton-Brock *et al.*, 1998a). When a litter is born to subordinates during the time period when the dominant female's litter is most

depended on other group member for food, the litter will not survive. However, if this litter is born after this period, it has a much greater chance of surviving (Clutton-Brock *et al.*, 1998a).

Modeling the resource competition hypothesis

Tuomi *et al.* (1997) designed a game theory model for the resource competition hypothesis in small rodents. In their model, two female choose either an infanticidal or a non-infanticidal strategy. The infanticidal strategy has energy and time costs at the expense of her reproductive success. When she successfully kills the litter of the other female, she gains reproductive success by reducing competition for resources, which she can invest in her own litter. The chance of a successful attack is depended on how well the other female is able to defend her nest. The model assumes a single attack cycle and so, no learning response. The model would be more realistic when a female could adapt her strategy to that of the other female.

The model shows that the optimal level of infanticide is dependent on the potential costs and benefits of the behavior. When potential benefits are high, for example when the competition for resources is high, high rates of infanticide are advantageous. Furthermore, when the costs of infanticide increase less sharply with increasing rates of infanticide, infanticide can also be advantageous. Both predictions imply that killing the closest neighbor is the best strategy because they are the likeliest competitors for resources. Furthermore, the energy and time costs of killing the litter of a neighbor are smaller than killing a litter that is located further away from the

infanticidal female's own nest. This is consistent with observations in white-footed mice (Wolff and Cicirello, 1989) and California ground squirrels (Trulio, 1996).

It is important to note that killing neighbors may not always be a good strategy. When a neighbor would never strike back when she loses her litter, killing the litter of a close neighbor is advantageous. This may occur when a female that lost her litter moves to another location (Wolff and Cicirello, 1989). However, when a neighbor is effective in defending her nest or when she always strikes back after losing her nest, killing a neighbor's litter or even any female's litter may be less advantageous because there is an increased risk for the infanticidal female to lose her own litter (Tuomi *et al.*, 1997).

Killing the closest neighbor's litter is also not a good strategy in group-living species where females are philopatric and males are recruited from outside the breeding group. Dobson *et al.* (2000) suggested that the most distantly related individuals in the breeding groups should become victim of infanticide first. They also hypothesized that when distantly related individuals are replaced by the infanticidal female's own daughters, the coancestry in the breeding group may increase and that because of this, the frequency of cooperative behavior may also increase. This may be only partly true for group-living black-tailed prairie dogs. Prairie dogs prefer being infanticidal within their own coterie, but because they are unable to recognize distant from close relatives and because they are unable to enter a nearby coterie, they sometimes kill close kin (Hoogland, 1995). This may still be an adaptive strategy because they

receive a larger foraging area, better helpers and a reduced risk of becoming victims of infanticide themselves in return (Hoogland, 1995).

The exploitation hypothesis

Cannibalism is in some species a common strategy in obtaining food resources. Infants are more likely to become victims of cannibalism than adults because they are easy prey. Infanticide is considered adaptive under the exploitation hypothesis when it provides the perpetrator with food resources (Hrady, 1979). The predictions of the exploitation hypothesis are that the infanticidal act should be followed by the consumption of the infant and that it is more common in energy-stressed individuals (Ebensperger, 1998).

Examples of the first prediction are numerous and include observations in chimpanzees (Hiraiwa-Hasegawa, 1992), chacma baboons (Saayman, 1971), polar bears (Stone and Derocher, 2006), cougars (Lesowski, 1963), black-tailed prairie dogs (Hoogland, 1995) and California ground squirrels (Trulio, 1996).

The second prediction of the exploitation hypothesis is that energy-stressed individuals should be more likely to kill and eat infants. This suggests that cannibalism of infants is common for lactating females, since this is the most energy demanding period in the life cycle of eutherian mammals (Gittleman and Thompson, 1988). This could explain the high rate of infanticide and cannibalism by lactating females in Colombian ground squirrels (Stevens, 1998), black-tailed prairie dogs (Hoogland, 1995) and California ground squirrels (Trulio, 1996).

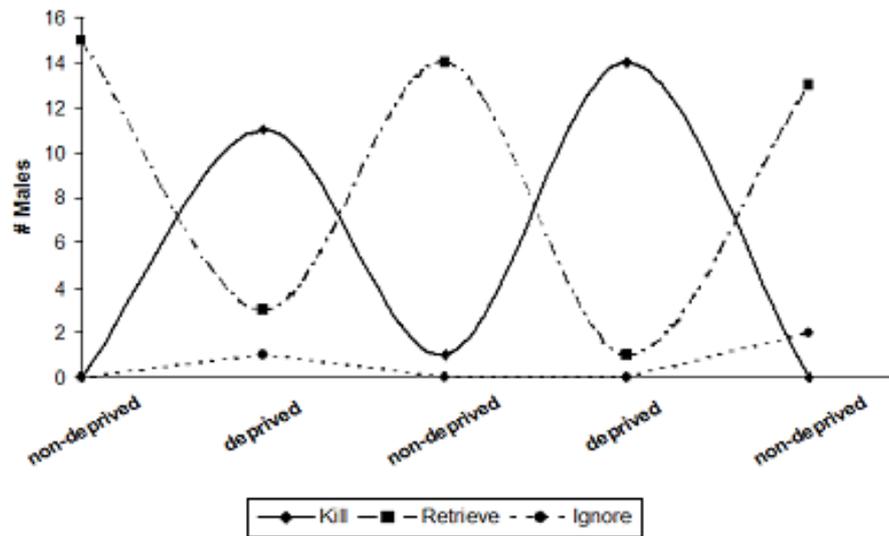


Figure 3: The effect of food deprivation on the behavior of non-killer male mice. During the non-deprived periods, males were allowed free access to food for 24 hours. During the deprived periods, males were food-deprived for 24 hours. The behavior of the males was scored as kill, retrieve or ignore. Created from Svare and Bartke (1978).

Energy-stress can also be the result of environmental conditions that affect the availability of food. Mongolian gerbils that were food-deprived for twenty-four hours in the laboratory, killed and ate newborn pups significantly more than the control group, suggesting that the occurrence of infanticide is related to the availability of food (Elwood and Ostermeyer, 1984).

Svare and Bartke (1978) hypothesized that hunger-induced infanticide is a reversible response to the availability of food. To test this, the behavior of 15 male mice was scored after a cycle of 24 hour free access to food and 24 hour deprived of food. Male mice showed to kill and eat significant more infants after the food-deprived periods and retrieved (e.g. normal parental behavior) significant more infants after the non-deprived periods (Figure 3).

Climate change may be a factor that induces infanticide in species that are non-infanticidal under normal environmental conditions (Derocher *et al.*, 2004). The reports for infanticide in polar bears

have increased recently due to prolonged ice free periods that result in reduced foraging areas. This may be an explanation for the observation of Stone and Derocher (2007) who witnessed an incident of infanticide by a male polar bear who appeared to be in poor physical condition.

The adoption avoidance hypothesis

Pierotti (1991) described the adoption of nonrelated offspring as a conflict in which offspring try to receive care from parents that are under selection to avoid giving this care. Selection for winning this conflict is expected to be stronger on the offspring since if they fail to receive care, they will die, whereas the costs for parents are much lower. In some cases, parents win the conflict and commit infanticide on the unrelated young to prevent investing time and resources in the young. The predictions of the adoption avoidance hypothesis are that infanticide should be more common in group-living species,

infanticide should be committed by the sex that bears the most cost of adoption and should be more frequent for species that have multiple offspring per litter (Pierotti, 1991). The adoption avoidance hypothesis is the least well studied type of infanticide in mammals. As a consequence, supporting studies for this hypothesis are inconclusive or circumstantial.

The first prediction of the hypothesis is that infanticide under the adoption avoidance hypothesis should be high for species that are group living or that live in patches close to each other because the chance of encountering a wandering young is then high. Although this makes sense, this prediction is also hard to distinguish from the resource competition hypothesis since it can be argued that group living contributes to more competition for resources as well as a higher risk of adopting unrelated young (Pierotti, 1991). Of the 30 species that show both infanticide and adoption, 27 are group-living (Pierotti, 1991). Examples include dingo's (MacDonald and Moehlman, 1984), walruses (Riedman, 1990), wild boars (Riedman, 1982) and lemmings (Boonstra, 1980). It can also be hypothesized that this type of infanticide is more common in precocial species (i.e. with mobile young) than in altricial species (i.e. with depended young) because the former are more likely to obtain care from unrelated parents (Elwood, 1992). This may be an explanation for the observation that females of altricial species sometimes retrieve unrelated young when they encounter them at unfamiliar territory (Fleming, 1979) whereas females of precocial species kill unfamiliar young (da Cunha Nogueira et al., 1999). However, because good comparative studies on

infanticide in altricial and precocial species are missing, no conclusive answer can be given about this particular prediction.

The second prediction of the adoption avoidance hypothesis is that infanticide should be committed by the sex that bears the highest cost of a possible adoption. In most cases this sex is the female since lactation is the most costly period in the lifetime of mammals (Gittleman and Thompson, 1988). Evidence for this is numerous; in 20 of the 21 species studied for this hypothesis, females were the primary sex that committed infanticide (Pierotti, 1991). Also, in all of these species, females were the primary caretakers (Pierotti, 1991). It should be noted that male care in canids and some species of rodents and primates are an exception to this rule since these males provide parental care in the form of food provisioning, thermoregulation, guarding or grooming (Woodroffe and Vincent, 1994; Gubernick and Teferi, 2000). However, these costs are not comparable to the energetically high costs of lactation borne by females.

The final prediction of the adoption avoidance hypothesis is that infanticide should be more common for species that have multiple offspring per litter, but only when a certain infant can be identified as unrelated. In 19 of the 21 studied species females produce multiple offspring, which results in a high change of offspring confusion. The two exceptions are humans and elephant seals. It should be noted that the latter breeds in dense aggregations where the chance of adopting unrelated infants is high (Pierotti, 1991).

Female elephant seals prevent the adoption of unrelated infants by attacking any infant that approaches them when they

already have an infant with them (Riedman and LeBoeuf, 1983). Female wild mice prevent killing their own offspring by killing alien pups when there are pregnant, adopting them when they are lactating and killing pups again after they weaned their own offspring (Soroker and Terkel, 1988). In black-tailed prairie dogs, lactating females are the main perpetrators of infanticide. These females distinguish unrelated young from their own offspring by killing them before they emerge from the natal den of another female (Hoogland, cited in Pierotti, 1991). A final strategy to prevent adoption of unrelated young has been observed in the cavy. Cavy females kill young that do not match the age of their own young but adopt them when they are of similar age (Künkele, 1987 cited in Ebesperger 1998).

Discussion

Of all the hypotheses that have tried to explain the occurrence of infanticide, the predictions of sexual selection hypothesis best fit empirical observations. This is partly due because most predictions are easy to test or observe. However, it is hard to determine a value for inclusive fitness which has been proposed to play a role in the decision of committing infanticide in multi-male groups. This is so because this value incorporates the number of related genes between a potential perpetrator and a related male and the probability that the related male sired the infant (Boyko and Marshall, 2009).

The resource competition is a much harder theory to prove because it can be argued that killing an infant always reduces the competition for resources. To successfully prove the resource

competition hypothesis, it must be showed that the resource is actually limiting and that by committing infanticide, an individual can increase its access to the resource. Only a small number of studies have successfully proven these conditions (Pierotti, 1991).

The cannibalism hypothesis is fairly well supported by empirical observations. However, only a relative large number of people that observed an act of infanticide followed by cannibalism failed to provide details on the physical body condition of the perpetrator. As a consequence, the cannibalism hypothesis cannot be applied with full confidence. Another factor that makes it difficult to contribute an act of infanticide to the cannibalism hypothesis is when the act also shows overlap with another theory. For example, when a female kills and eats an infant and thereby also increases her access to a limiting resource such as helpers or a burrow, the infanticide cannot be fully contributed to the cannibalism hypothesis.

The adoption avoidance hypothesis is by far the least studied hypothesis and is therefore not well supported with empirical observations. Future studies should lay more emphasis on proving that by committing infanticide, a female reduces the chance of adopting an unrelated young.

In cases of infanticide where no obvious advantages can be identified, the infanticidal act may simply be nonadaptive (i.e. neutral or maladaptive). Infanticide can be nonadaptive when it is the direct result of selection for another behavior (e.g. aggressiveness), is an accident or occurs as the result of habitat disturbance or social disturbance (e.g. frequent changes in group male membership in primates) (Boggess, 1979; Curtin and Dolhinow,

1978; Doidge et al., 1984). Nonadaptive infanticide is expected to be a rare occurrence because of the assumption that an infanticidal strategy must have some advantage over a non-infanticidal strategy in order to invade in a non-infanticidal population (Tuomi et al., 1997).

In general it can be argued that how well observations support the different hypotheses is to some degree depended on the different species (Ebensperger, 1998). This variation arises due the type of benefits that can be obtained but also due to environmental factors that result in reduced food availability for some species but not for others. Furthermore, the type and effectiveness of the different counterstrategies that species use to avoid becoming victims of infanticide can play a role in this. These counterstrategies include pregnancy termination, female aggression, group defense, avoidance of infanticidal individuals, multi-male mating and territoriality (reviewed by Ebensperger, 1998).

As for the second research question, I believe that it is nearly impossible to predict for a certain species, population or even a single individual (of whom infanticide has not been confirmed before) whether or not it has the potential to be infanticidal. This is due to the complex nature of the infanticidal behavior. Whether or not an individual is infanticidal is depended on its physiology (e.g. duration of the IBI, gestation/lactation ratio), its personality (e.g. does or does not strike back after becoming victim of infanticide), the environment (e.g. food scarcity), social factors (e.g. stability of the group due to immigrants, relatedness) and possible human disturbance.

In my opinion, researchers should study the exact background of an infanticidal act more carefully before drawing a conclusion on the underlying explanation. This is especially necessary in the case of the resource competition because it is easily invoked while good supporting studies are missing. When more elaborate studies on the background of infanticide arise, the predictions of the hypotheses and the associated models may prove to be even more accurate.

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