

On human parental investment termination

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Abstract

Neglect or murder of someone's own child is often viewed as an unnatural act. However, it is also seen in non-human mammals. From an evolutionary viewpoint it could be beneficial to terminate investment in a specific offspring, in order to invest in other current or future offspring. Abortion, resorption, infant neglect and infanticide are the means to accomplish this. We reviewed literature to see whether investment termination occurs under comparable circumstances in human and non-human mammals, and whether its occurrence can be explained evolutionary by the current investment termination models. The models predicting parental investment were the additive, contingent, male quality, competition for restricted resources, local resource enhancement, advantaged-daughter and the population adjustment model. All but the contingent and additive model could be distinguished based on characteristics of the infant most likely to suffer investment termination and of the caretaker that terminates investment. Important characteristics are resource availability, litter quality, parenthood certainty, environmental safety, caretaker condition, caretaker rank, infant fitness, infant sex, condition dependent sex, dispersing sex, equilibrium sex ratio and current sex ratio. Studies measuring at least some of these factors were scarce, none measured all. In most studies the additive/ contingent model best predicts the parental investment termination patterns observed, but this is also due to a lack of data required to test alternative explanations. The majority of primate studies on neglect were better predicted by an alternative, possibly maladaptive hypothesis; neglect occurs more often in primiparous females that lack maternal experience. No difference was observed between species with different breeding styles. The additive/ contingent model may be the best model of investment termination in all species, or most incomplete studies could fit to it because it is the broadest model. In order to test what is the case new studies are needed, measuring the described factors plus maternal experience.

Introduction

August 2010, Holland was shocked when 4 baby corpses turned out to be hidden in suitcases by their 25 year old mother, who had conceived and killed them in the past eight years. A month before this a 45 year old female was found guilty of killing 8 of her babies, and hiding them in her garden in France. These incidents sound gruesome and evolutionary maladaptive on first glance. Someone's progeny ensures the survival of genes, and the death of a child removes part of the parent's genes from the future gene pool. However, this behaviour is also seen in other non-human mammals and therefore there is reason to believe that it could be adaptive to terminate investment under some conditions.

In literature cases have been described of mammals committing abortion (Wickler & Seibt 1983; Baxter and Ward 1997), embryo resorption (England 1992), infant neglect (Rudnai 1973) and infanticide (Maestriperi 1991). In the case that some of these occurrences are not maladaptive, their evolutionary adaptive function could be explainable by considering parental investment decisions. It can, from a theoretical viewpoint, be beneficial to terminate investment in a specific offspring in order to invest in other current or future offspring (Trivers 1972; Trivers 1974; Alexander 1974; Hrdy 1979). Abortion, resorption, infant neglect and infanticide are the means to terminate investment in a specific offspring (Wasser & Barash 1983). We will review different models applicable to investment theory, and compare them to human and non-human mammalian literature on abortion, resorption, infant neglect and infanticide. Our aim is to see whether investment termination occurs under comparable circumstances in human and non-human mammals, and whether occurrences can be explained evolutionary by using investment termination models. In order to be able to compare different mammals their breeding group structure will be included, such that possible patterns will be more visible.

Ways to terminate investment

In order to identify investment termination it is necessary to understand the many ways this may occur. Parental investment can be terminated at different stages of infant development, by using different methods. We discriminate between two stages, the pre- and the postnatal stage. Prenatal investment termination has the advantage over postnatal investment termination that less investment is made, but the disadvantage of a higher environmental uncertainty. The balance between the two factors also depends on the gestation length of a particular mammal and the stability of the environment it lives in.

Prenatal investment termination

Termination of investment before birth can be caused by resorption or abortion. Resorption is the death and complete or partial cell lysis of an embryo. When resorption occurs the investment is partially reduced, as the absorption of the embryo provides nutrients. When nutrients cannot be resorbed anymore, or could never be, abortion will take place. Abortion is the expulsion of the embryo from the uterus. In animals that can give birth to more than one offspring at the same time, abortion or resorption can potentially take place for all or only part of the embryos (Landy 1986). In humans there is the additional possibility of intentional abortion through medical intervention. While resorption has a lower fitness cost than abortion because of the reuse of resources, both are less costly than terminating investment after birth.

Postnatal investment termination

After the infant has been born, investment can be terminated through infant neglect or infanticide. Infant neglect is when the caretaker ceases to provide care to an infant. Infanticide is the killing of an infant, which in the broad definition can also be committed by an unrelated individual. We will restrict the definition in this paper to killing by a caretaker, also called filicide, as we are investigating ways a caretaker can stop investment. Arguably neglect is from an evolutionary viewpoint preferable to infanticide when the caretaker does not gain resources by consuming the infant after infanticide (hrdy 1999). Neglected infants still have a chance to survive, for example when they are adopted by another individual. Also the act of killing consumes energy. The cases in which total neglect is not possible can form an exception in which infanticide is not an inferior method of investment termination. An example of this can be an infant who is independent enough to follow the caretaker around and induces a cost to the parent by doing so through, for instance, active suckling attempts.

When to terminate investment

The previous section elaborated on how parental investment can be terminated. However, it is also important to consider when it would be beneficial to terminate parental investment. In order to shed light on this 'when' question leading theories dealing with it will be examined. Life History Theory encompasses the flow of the lifespan of an individual, like the time to mature, when to reproduce and how long the lifespan is (Reznick 1985, 1992, Roff 1992, Stearns 1992, Schwarzkopf et al. 1999). According to this theory the total amount of investment is fixed for each individual, the decision is how to distribute this total investment, as investment in something lowers the amount left to invest in something else. A branch of Life History theory, Evolutionary theory of parental investment, uses this idea on parental decisions. Parental investment is defined as "...investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring" (Trivers 1972). This concept differs from parental care, as it considers both the cost of investment and the benefits gained, while parental care focuses on the benefits only (Clutton-Brock 1991). In other words parental investment theory encompasses the distribution of investment between offspring and self, while parental care focuses on the investment received by the offspring. Parental expenditure only focuses on the cost the caretaker incurs by providing parental care. We will use the definition of parental investment, as especially the trade-off between investing in a particular offspring, or in other current or potential future offspring is important from an evolutionary viewpoint. Using this paradigm we predict that a parent will terminate its investment in a specific offspring, if by doing so it will gain fitness from the capability to now provide added value to other current or future offspring.

Which species are likely to terminate investment

After considering how and when it would theoretically be beneficial to terminate investment in a specific offspring, it is time to elaborate on who will be most likely to do so. Not all mammals have equal reproductive strategies. Some factors, for example inter-birth intervals and litter size, are partially species-specific. A theory dealing with species-specific reproductive strategies is r/K selection theory. r/K selection theory is a product from Life History Theory that considers the trade-off between quantity and quality of offspring. It states that there is an inverse relation between fecundity and parental investment (Bogaert and Rushton, 1989 and Mac Arthur and Wilson, 1967).

The 'r' and the 'K' stand for the two extremes. The 'r' end stands for a large number of offspring and minimal parental investment in each individual, while the 'K' end stands for a minimal number of offspring and intensive parental investment in each individual. According to this theory the characteristics of the environment are determining whether selection is favoured for either 'r' or 'K' traits. (Pianca , 1970; Reznick et al., 2002). When everything else is equal, an unstable environment (e.g. fluctuations in the amount of food, high predatory rates) will favour selection of 'r-traits', such as large litters, short inter-birth intervals and low parental investment in each individual. Vice versa, a stable environment will favour selection of more 'K-traits', such as small litters, long inter-birth intervals and high parental investment in each individual. As prolonged parental investment will give rise to potential parental investment termination, a larger effect of investment termination strategies is expected in species that are found on 'the K side'. Ideally this review would therefore focus on 'K'-selected species, but as suitable literature is scarce 'r'-selected species will be covered as well.

Parental investment models

Parental investment models predict patterns of parental investment within a species. In order to consider these patterns, information on the investment of the parent in its offspring is needed. Therefore information on both parent and infant is important. In the previous sections we considered more universal theories on which species will most likely be the perpetrator of investment termination, and when is it expected to occur. These questions can be combined with the question which individual has the highest risk of becoming the victim, in order to create a parental investment model. These models can be used to make predictions on parental investment termination within a species. Different models concerning parental investment decisions are proposed, these can roughly be divided in the categories total investment driven, infant quality driven and population driven. Each model makes predictions on which individual will be the most likely to suffer investment termination under given conditions. This provides a clear way of testing these models against published studies of investment termination. These models are not mutually exclusive, yet it is likely a particular model will have a stronger influence under particular circumstances.

Total investment driven models

Total investment driven models assume that parental investment decisions are dependent on the total amount to invest. Especially the allocation of the total investment between the different offspring can change. In the case of a high amount of resources to invest in offspring resources can be allocated differently between young than in case of low resource availability. The total amount to invest in the current offspring is determined by multiple factors (also see table 1):

- The availability of resources, such as food and nesting space, is important because it forms a bottleneck to sustain the litter. For example, if there is not enough food to feed the whole litter it is impossible to keep all infants alive. Therefore, it is predicted that the more resources are available to the parent, the larger the total amount the parent is willing to invest.
- The quality of the offspring, such as the health and the size of the litter, can determine the willingness to invest. For example, house mice base their decision whether to fight an intruder off, on the size of their litter (Maestriperi and Alleva 1991). This leads to the

hypothesis that the higher the total quality of the offspring, the higher the total amount a parent is willing to invest.

- Parenthood certainty can be of importance in species where one of the caretakers is not certain he or she sired the offspring, in mammals this is often the male and therefore called paternity confidence. Willingness to invest in offspring, and therefore the total amount to invest in them, is predicted to go down if the likelihood someone else is the parent goes up (Anderson 2006).
- The safety of the environment can influence the total amount of investment a caretaker is willing to make; the more dangerous it is, the less likely offspring is to survive and therefore the smaller the likely returns of an investment. An example is the Bruce effect, where mice and voles abort their litter when scenting an unfamiliar, and therefore probably hostile, male (Bruce 1959; Richmond and Stehn 1976; Schadler 1981). Therefore, the safer the environment is, the higher the likely total parental investment in the offspring.
- The condition of the caretaker can be of influence, as when the caretaker is in poor condition a large investment can critically lower its survival and thus future reproduction chance. This is a shown effect in vervet monkeys, where time of weaning and survival chance of the infant where a function of the condition of the mother (Fairbanks & Mcguire 1995). Therefore, it is expected that a better condition of the caretaker results in a higher total parental investment in the offspring.
- There is debate whether previous investment has an influence on future investment decisions, which is also called the Concorde fallacy. The pro-argument is that the amount an animal already invested in his offspring can be used by this animal as a prediction method. This amount can be used to predict the amount of investment that would be necessary in the future to obtain a similar litter. The contra-argument is that, instead of previous investment, the worth of a product is important for future investment decisions. Most mammals probably do not use past investment to decide what to invest in the future, but look at the current fitness of the offspring (Coleman and Gross 1991; Arkes and Ayton 1999).

The above factors are assumed to influence the total amount an animal is willing to invest in its offspring. Given a total amount to invest, two different models have been proposed with different hypotheses on how this amount will be distributed between current offspring. These models are the additive and the contingent model (also see table 1).

The additive model

The additive model predicts that each offspring receives a proportion of the total investment based on its current fitness, where the strongest one obtains the highest investment and the weakest one the lowest. When the total amount that will be invested increases every offspring will receive more (Trivers 1974). If the total amount a parent is willing to invest in its current offspring is too low to sustain all offspring at least one individual will suffer. According to the additive model the individual with the lowest current fitness will be the first to suffer parental investment termination.

The contingent model

The contingent model challenges the fixed proportions assumption of the additive model. According to the contingent model the proportion each individual receives depends on the circumstances. If the total amount to invest is lower than the total amount necessary to sustain all offspring, the young with the highest current fitness receives the largest share. However if the total amount to invest is

higher than the amount necessary, the young with the lowest current fitness receives the highest share. By doing this the focus is on survival of as many offspring as possible in times of shortage. Contrary, in times of surplus the focus is on strengthening the weakest individuals, such that they can compete against unrelated individuals (Bugental & Beaulieu 2003). According to this hypothesis only in circumstances where the litter needs more investment to survive than the parent is willing to provide parental investment termination is expected. Therefore, the individual with the lowest current fitness will be the first to suffer parental investment termination.

By purely looking at which individual will suffer in the case of investment termination, the additive and contingent model cannot be discriminated. According to both models the weakest individual will be the subject of investment termination if the total investment is too low to maintain all offspring. Studies on resource allocation could tease these two models apart, but that is not within the scope of this review paper.

Infant quality driven models

Infant quality driven models predict that the characteristics, particularly the sex, of a specific infant determine parental investment decisions (also see table 1). These models are derived from the Trivers-Willard hypothesis. According to this hypothesis it is beneficial to invest most in the sex that, after the expected amount of investment, is likely to have the highest potential reproductive success (Trivers & Willard 1973). Differentiating between the sexes can both work prenatally, through different sex-ratios at birth, or postpartum, through different investment decisions based on sex. The different models proposed in this category are the male quality model and local resource competition models.

The male quality model

The male quality model suggests that one of the sexes has a more condition-dependent reproductive success. In other words, the amount of investment has more influence on the future reproductive success of one of the sexes. In mammals this is often the case for the males, as they have to be strong in order to compete for females. Therefore, caretakers in good condition, which is often measured by dominance rank, should invest most in the condition-dependent sex. In contrast caretakers in bad condition should invest most in the sex without condition-dependent reproductive success, as they also have a chance of reproduction if they are not in great condition (Trivers & Willard 1973). As an effect caretakers in bad condition will first terminate investment in the condition-dependent sex. Caretakers in good condition will invest less in the not-condition-dependent sex, which will therefore be more likely to suffer in case of investment termination. Nevertheless, the condition-dependent sex is at the highest risk of investment termination, as the caretakers in bad condition are more likely to have to terminate investment in some offspring than the caretakers in good condition. In order to test for this hypothesis it is important to measure both the sex of the infant that suffered investment termination, and the condition of its parent.

The local resource competition model

The local resource competition model discriminates between the sex that remains in its natal group, and the one that disperses. The model focuses on the difference in influence on the resources available to the parent. This model can again be split in three different hypotheses, the competition for restricted resources model, the local resource enhancement model and the advantaged-daughter model.

The competition for restricted resources model

The competition for restricted resources model focuses on the scarcity of resources. In species where one of the sexes stays (philopatric sex) and the other leaves, the philopatric sex will in the future compete for resources with its same-sexed caretakers. Therefore, it is beneficial to invest more in the sex that moves away and will not become competition, which are often the males (Clark 1978; Silk 1984; Bulmer 1986; Cockbum 1990; Gowaty 1993; Hiraiwa-Hasegawa 1993). Hence, if investment is terminated in an offspring it is likely to be of the philopatric sex. To test whether parental investment is terminated as predicted by this model, it is necessary to measure the sex of the infant suffering investment termination and which sex is philopatric.

The local resource enhancement model

In contrast, the local resource enhancement model focuses on the benefits of having close relatives in the group. In species where one sex is philopatric and the other leaves, only the sex that stays can in the future provide assistance, for example by assistance in conflict or assistance with raising future offspring. Thus, the sex that stays is likely to enhance the availability of resources to the parent later in life. Therefore, a similar investment in the philopatric sex will in the end be expected to have a lower net cost (Gowaty & Lennartz 1985; Lessels & Avery 1987). The sex that leaves will therefore be the one that is more likely to suffer from parental investment termination. To test for this model the sex of the infant suffering investment termination and the sex that usually leaves the group should be recorded.

The advantaged-daughter model

The advantaged-daughter model incorporates ideas from previous two models and adapts them slightly to focus on the caretakers rank. Because of the incorporation of rank this model is only applicable to species with a hierarchy. According to this model on one hand the philopatric sex provides benefits by being able to provide support. But on the other hand it competes for resources with all members of the group. Because of the scarcity of resources the philopatric sex will be in higher danger of aggression from unrelated group members. Higher ranking mothers will be more able to defend their offspring. Furthermore, offspring inherits the mothers' rank, which provides a benefit that increases with rank. Therefore, the sex that is preferred depends on maternal rank. High ranking mothers will prefer the philopatric sex, often the females, because they will benefit most of the rank inheritance and can provide support in the future. On the contrary, low ranking mothers will preferentially invest in the leaving sex, often the males, as they are less able to defend their offspring and the leaving sex is less likely to suffer from aggression from non-related group members. (Hiraiwa-Hasegawa 1993). Therefore, high ranking individuals will be most likely to terminate investment in the leaving sex, while low ranking individuals will be most likely to terminate investment in the philopatric sex. In order to test whether parental investment is terminated as predicted by this model, data on maternal dominance rank and the sex of her children suffering investment termination should be collected.

Population driven models

Population driven models assume that the characteristics of the population a caretaker lives in influence investment termination decisions (also see table 1). This category consists of only one hypothesis, the population adjustment model. The population adjustment model focuses on stabilizing the sex ratio within a population. According to this theory the rarer sex will be more valuable and provide a reproductive advantage based on the current sex ratio (Calhoun 1962). For

example, when there are twice as much males as females in a population where mating occurs one on one, producing females has an advantage as they will have a higher chance on mating, and thus reproducing, than males. The more the current ratio deviates from the optimal ratio, the greater the advantage is of producing the sex that is less than its equilibrium quantity. Therefore, investment termination is likely to happen in the sex that exceeds the equilibrium quantity. In order to test for this model the sex of the infants that suffer investment termination and the current sex ratio compared to the equilibrium sex ratio should be measured.

Overview of the models

Above we elaborated on the additive, contingent, male quality, competition for restricted resources, local resource enhancement, advantaged-daughter, and the population adjustment model. Except for the additive and the contingent model, all models can be discriminated based on paternal investment termination patterns. The below table summarizes these models. It focuses on which data concerning parental investment termination should be measured, and which patterns should be distinguished in order to discriminate between the different models. However models of different types are not necessarily mutually exclusive. For example the total investment driven models (1.) can agree with the male quality model (2.1a.) when litter quality is determined by the sex ratio. It is possible that in different species different investment models predict investment termination. It is also possible that multiple models operate at the same time, and which model prevails depends on the circumstances. When this is the case, it could be that within a species different models seem to control investment termination decisions in different populations.

Table 1, Models predicting investment termination according to specific factors

Type		Main factors	Model	Characteristics of investment termination
1. Total investment driven		Resource availability Litter quality Parenthood certainty Environmental safety Caretaker condition Fitness of specific offspring	1a. Additive model	Weakest individual (current lowest fitness)
			1b. Contingent model	Weakest individual (current lowest fitness)
2. Infant quality driven	2.1 Male quality model	Sex of the infant Condition of the mother Condition dependent sex	2.1a. Male quality model	Caretakers in bad condition: condition-dependent sex Caretakers in good condition: sex that thrives well on low investment
			2.2 Local resource competition models	Sex of the infant Dominance rank of the mother Dispersing sex
	2.2b. Local resource enhancement model	Works only on species where only one sex disperses. Sex that leaves		

			2.2c. Advantaged-daughter model	Works only on species with a hierarchy where only one sex disperses. High ranking caretakers: leaving sex Low ranking caretakers: philopatric sex
3. Population driven	Sex of the infant Equilibrium sex ratio Current sex ratio		3a. Population adjustment model	Sex that exceeds the equilibrium quantity

Data on investment termination in non-human mammals

In order to get an idea of the driving forces behind parental investment termination in humans, it can be helpful to first look at investment termination patterns in non-human mammals. Multiple studies have collected data on different forms of investment termination, often for other purposes than considering the specific models in this paper. We will provide an overview of the non-human mammalian data from studies considering factors useful for the purpose of this review.

Prenatal investment termination

Parental prenatal investment termination by means of resorption and abortion are discussed in this section. Studies on resorption are scarce, possibly because it is difficult to measure.

Resorption and abortion in coypu

In a research by Gosling (1986) the sex of resorbed offspring is measured in captive coypu, which are group living rodents with a polygynous mating system (Guichón et al. 2003). However, the sex of a resorbed embryo is hard to determine retrospectively. Gosling (1986) argues that if a specific sex is resorbed, there should be an inverse relation between the number of embryos resorbed and the number of viable infants of that sex. In his research, he does not find this relation for either of the sexes in coypu. Because he finds that the sex ratios at birth are skewed, he also examines sex specific parental investment termination through abortion. Comparing the proportion of litters with predominantly males and with predominantly females in each gestation stage indicates selective abortion of predominantly female litters, as the sex ratios were equal in early gestation, but skewed towards males in the last weeks. Females with larger fat reserves per embryo are shown to be more likely to abort predominantly female litters. Coypu also seem to abort small litters during the last part of pregnancy, whereas large litters are retained. However, this could also have been caused by young females producing on average smaller litters than old females. Summarizing, both sexes were equally likely to suffer investment termination through resorption. However, investment termination through abortion is possibly sex and maternal condition based. Females with more to invest per infant seemed more likely to abort litters with a high percentage of females. Finally, it was controversial if size of the litter or age of the female was a better predictor of abortion as both were correlated. Therefore the factors tested for resorption do not point to any model, and more should be tested. The characteristics tested for abortion point to the male quality (2.1a.) and the additive/contingent (1) model. The male quality model is supported by the observation of mothers with higher fat reserves, and thus a relatively good condition, are more likely to abort predominantly

female litters, the less condition dependent sex. However the opposite, mothers in bad condition aborting predominantly male litters, was not shown. The additive/contingent model was supported because of smaller litters, and thus lower litter quality, was a predictor of abortion.

Abortion in dairy cows and sheep

Research on parental investment termination has also been performed on domesticated dairy cows and sheep, both originally have a polygynous mating system. It is questionable how naturally captive farm animals behave, but for the sake of completeness the results are summarized in this overview.

In dairy cows body fat reserves are a predictor of abortion. Cows with extremely low fat reserves are 2.4 times more likely to abort during the early fetal stage than cows with an average fat reserve. (Lopez-Gatius et al. 2002; Silke et al. 2002). In other words, mothers in bad condition are more likely to abort, which points to the additive/contingent model. However, no infant characteristics have been measured. For example, when only predominantly male litters have been aborted, the male quality model would be supported instead. Therefore, too few factors have been measured in these studies to give a definite conclusion.

In sheep young maternal age (Quirke & Hanrahan, 1977), suckling other infant (Cognie et al. 1975), and heat stress (Alliston & Ulberg, 1961) are factors that increase the likelihood of embryonic loss. Lactating consumes energy and heat stress lowers body condition. Therefore, lactating and heat stress probably influence maternal condition negatively. Age, however, is not a direct influence. There is an indication embryos became abnormal under these circumstances, as transferring them to a normal host still resulted in a higher loss of these embryos than of average transferred ones. Therefore, there is an indication of low infant quality of the aborted embryos. Two studies, found respectively lactation and heat stress to be predictive factors. Because these factors can be expected to lower the maternal condition, occurrence of abortion in these studies are consistent with the additive/contingent model (1). The study that found young maternal age to be a predictor of abortion does not subscribe any of the current hypotheses. However, young mothers are less likely to have experience with raising infants than old mothers, which might be of importance.

Abortion in Hanuman langurs

In free ranging Hanuman langurs 7 abortions were witnessed during a 10 year period. Only 2 of these occurred in periods of group stability, the other 5 took place after takeover by males that committed infanticide of infants already in the group before they took over. This suggests the risk of abortion increases in times of violent male takeover (Agoramoorthy et al. 1988). Violent male takeover leads to a decline in environmental safety, therefore these occurrences of abortion are best described by the additive/contingent model (1).

Abortion in mice and voles

In rodents a similar phenomenon, known as the Bruce effect, occurs. Mice (Bruce 1959), pine voles (Richmond & Stehn 1976) and prairie voles (Schadler 1981) are likely to abort their litter when scenting an unfamiliar, and therefore probably hostile, male. The scent of an unfamiliar male decreases the likely environmental safety. Therefore, the circumstances under which these abortions are most likely to occur are best described by the additive/contingent model (1).

Summary

In table 2 details on the studies are summarized, stating for each animal the group structure during breeding and the outcomes of the study. Only the study by Gosling (1986) on coypu examined both infant and maternal characteristics. This study partially matches with the male quality model, as the sex that is less condition dependent, in this case females, has a higher incidence of abortion by females that have more to invest. However the contrasting effect, namely mothers that had less to invest being more likely to abort males, was not shown. The other studies consider when to terminate parental investment, but not who the victim was. They all point to the additive/ contingent model (1). However they could not have been in line with any of the other models, as sex of the infant was not measured. In the study on sheep by Quirke & Hanrahan (1977), and possibly in the coypu study, young maternal age predicted abortion.

Table 2, Studies on abortion and resorption with closest matching parental investment model

Animal	Breeding structure	Study	Type	Factors measured	Relations found	Closest matching model
<i>Coypu</i>	Polygynous	Gosling 1986	Resorption	Infant sex	none	none
			Abortion	Maternal condition (fat reserve) Maternal age Litter size Litter sex ratio	Big fat reserves predicted abortion of predominantly female litters, smaller litters or young mothers predicted abortion	Male quality model (2.1a.) Additive/contingent model (1)
<i>Dairy cow</i>	Polygynous	Lopez-Gatius et al. 2002	Abortion	Maternal condition (fat reserves)	Low fat reserves predicted abortion	Additive/contingent model (1)
		Silke et al. 2002				
<i>Sheep</i>	Polygynous	Quirke & Hanrahan 1977	Abortion	Maternal age	Young mothers were more likely to abort	None
		Cognie et al. 1975	Abortion	Maternal condition (lactating or not)	Lactating mothers were more likely to abort	Additive/contingent model (1)
		Alliston & Ulberg 1961	Abortion	Maternal condition (Heat-stress)	Heat stressed mothers were more likely to abort	Additive/contingent model (1)
<i>Hanuman langurs</i>	Matrilineal single- or multi- male groups	Agoramorthy et al. 1988	Abortion	Environment safety (aggressive male takeover)	Abortion was more likely during aggressive male takeover	Additive/contingent model (1)

<i>Mice</i>	territorial	Bruce 1959	Abortion	Environment safety(scent of unknown male)	Abortion was more likely after scenting an unknown male	Additive/ contingent model (1)
<i>Pine voles</i>	territorial	Richmond & Stehn 1976	Abortion			
<i>Prairie voles</i>	territorial	Schadler 1981	Abortion			

Neglect

In non-human mammals often only complete abandonment of the young is counted as neglect. This is done to have a distinct definition. Multiple studies on primates and other mammals, that have observed neglect either directly or concluded it retrospectively, will be covered in this section.

Neglect in cotton-top tamarins

A study on captive Cotton-top tamarins found multiple factors influencing the likelihood of neglect (Bardi et al. 2001). This same study also considered infanticide, which will be covered in the next section. Housing conditions of the subjects of this study were suboptimal, but it is nevertheless included in our review, as many factors were tested. Cotton-top tamarins are socially monogamous cooperative breeding primates in which both parents care for the young. Older infants also assist with taking care of their siblings, for example by carrying them. Data covering 10 years, in which 1093 live infants were born, were analysed during this study on a captive population. 50% of these infants was actively rejected, and thus neglected, before they reached one year of age. Stepwise multiple regression analysis was used to predict infant survival past 1 year of age with the minimal number of factors, where age of death was the dependent variable. Infant sex, year and season of birth, cage orientation and volume, how many young the couple have raised in total, and sires' experience were not predictors whether the infant was neglected or accepted. If siblings were present, infant neglect was less likely to occur. When the mother was inexperienced, neglect was more likely. Neglect was more likely with triplets, and thus a large litter size. Bad health condition of the mother made neglect more likely, the father's health condition was not as important. Young age of the parents increased the likelihood of neglect. These results can be explained using the additive/ contingent model (1). Infant neglect became more likely if the investment capacity per infant was lower, as was the case with no helpers, and bad health of the mother. Health condition of the father is less important, as it is the mother that lactates. It sounds as if the higher risk of neglect of infants that were born in triplets goes against the hypothesis, as it is an increased litter size. However in this case, three infants could be a lower quality than one or two, as two is the most common in the wild, and three could be more than sustainable. Child specific factors were not found to influence the likelihood of neglect, however weight and health of the infant were not considered, neither was the relation between the investment capacity and the sex of the infant. The factor inexperience of the mother, which made neglect more likely, cannot be explained by the additive/ contingent model. Probably inexperience, measured as maternal age, was important in the abortion studies on sheep and coypu as well (Quirke & Hanrahan 1977; Gosling 1986). This indicates the need of a new hypothesis, namely that it is important to have had previous experience with giving birth to an infant. It is also noteworthy that there is an extreme high percentage of infant neglect, possibly due to the housing conditions.

Neglect in Japanese macaques

Demographic data from captive Japanese macaques, collected over a period of 23 years, were analyzed (Schino & Troisi 2005). During this period 207 infants were born alive, of which 16, 7.7%, were neglected. An infant counted as neglected if it was rejected within a day after birth. The influence on neglect was calculated for the following factors: The sex of the infant, whether the mother was high or low ranking, whether the mother was sub adult, adult or older and whether the mother was primi- or multiparous. Inexperienced primiparous females had a reduced probability of successfully raising their infant; this was partially caused by higher rates of aggression towards low-ranking females. A mother being primiparous turned out to be a strong predictor for neglect (odds ratio 90), and the mother being low ranking was also a predictor (odds ratio 6). It could be argued that low rank decreases the maternal condition, because of the aggression. In that case an explanation would be that the individuals that have less to invest are the perpetrators of infant neglect. This would support the additive/ contingent model (1). However, being a primiparous mother was far more predictive of neglect than a low dominance rank was. This points to the same alternative hypothesis that previously showed up, namely that it is important to have had previous experience with giving birth to an infant. The sex of the infant and the age of the mother were not predictors of infant neglect. Since there was no bias towards an infant sex, the male quality model (2.1a), the competition for restricted resources model (2.2a), the local resource enhancement model (2.2b) and the advantaged-daughter model (2.2c) are contradicted by this data.

Neglect in sooty mangabeys

In a study of sooty mangabeys neglect, data are examined to see whether the factors infant sex and maternal parity predicted neglect (Maestriperi et al. 1997a). Sooty mangabeys are matrilineal primates living in a polygynous breeding group. Data records were analyzed of 9 Sooty mangabey families from unrelated matriarchs living in a captive environment. The data covered 26 consecutive years in which 535 infants were born. 7 cases of infant neglect by the mother were identified, which is 1.3% of the born infants. However, the actual number may have been higher, as an infant was only considered to be neglected if a caretaker witnessed a mother actively rejecting and abandoning an infant prior to death. Some of the 65 cases of unknown cause of death and 37 cases of stillbirth, where the infant was never observed alive, could also have been caused by infant neglect. Neglected infants were more likely to be firstborns, which was the case for 4 out of 7. The sex ratios of the neglected infants did not differ significantly between families. This indicates that maternal factors are more important than infant characteristics; however this conclusion is based on only 7 cases of infanticide. Because the sex ratios of neglected children did not differ between families, and rank presumably does differ due to matrilineal rank inheritance, the advantaged daughter model (2.2c) probably does not describe occurrence of infant neglect in sooty mangabeys. Like in the Japanese macaques, a relation is seen between maternal inexperience and a higher likelihood of infant neglect.

Neglect in pig-tail and rhesus macaques

Data records were analysed for 5 captive pig-tail macaque families over a period of 33 years (Maestriperi et al. 1997b). The factors examined were infant sex, maternal health and maternal experience. Of the 394 infants born 11 were reported to have died from maternal neglect. This 2.8% maternal infant neglect could again be an underestimation as 42 stillbirths and 46 unknown deaths were reported. Neglect was most likely to happen on the first days of infant life. Primiparous mothers were more likely to neglect, which was the case with 7 of 11 infants. Infant sex or health

state of the mother did not seem to influence occurrence of maternal neglect. Therefore the additive/contingent (1), male quality (2.1a), competition for restricted resources (2.2a) and the local resource enhancement (2.2b) model do not explain occurrences of neglect in this population. Again a relation between maternal inexperience and infant neglect is found.

The same correlation, between the mother being primiparous and an infant having a higher likelihood of neglect, was seen in pig-tail macaques (Dazey & Erwin 1976) and rhesus macaques (Hird et al. 1975). In pig-tail macaques there was a 30% rate of infant mortality were 30% was caused by injuries, but the inflictor was not recorded. In the rhesus macaque study 10.8% of the infants died before their thirtieth day of life and 6.9% after that, again the perpetrator was unknown. It is debatable whether the results of that study results should be considered, as they were obtained in captive groups in small enclosures, with high uncertainty on the exact circumstances. However, the results of the study are consistent with patterns of neglect observed in other groups and species.

Neglect in vervet monkeys

Infant neglect was measured in a captive sample of 160 Vervet monkeys during a period of 10 years (Fairbanks & McGuire 1995). Mothers were categorized to be of marginal, average, or prime reproductively, based on their age, weight and dominance rank. Dominance rank was only included in the prime reproductive group, which had to have a high rank and be of prime reproductive age. Females were marginal reproductive if they were either young or old, or had a low weight, factors that were shown to decrease fertility. The remainder of the females were categorised as average. Infant neglect was most common among the marginal reproductive group. In other words in this study relatively low maternal quality predicted infant neglect. This agrees with the additive/contingent model (1). However, no infant-specific factors were measured.

Neglect in lions and grizzly bears

Multiple small studies of lions and bears found a small litter size to predict infant neglect (Rudnai 1973; Tait 1980). 3 free ranging and 5 captive cases were described of lion females neglecting their litter when only one cub was left (Rudnai 1973). The same effect of small litter size was observed in 2 wild cases, both with a few weeks old healthy single grizzly bear cub as victim (Tait 1980). The proposed cause for these neglects was the litter size becoming too small, as the average litter size of lions and grizzly bears is 2-3 cubs (Packer & Pusey 1984). Rudnai (1973) and Tait (1980) calculated an increase in reproductive success would theoretically be obtained by following this strategy. These studies both focussed on the quality of all offspring together, and did not consider individual qualities of the cubs. This points to the additive/contingent model (1), as according to those models a smaller litter, and thus a lower litter quality, predicts a lower willingness to invest in the litter.

In addition, in wild lions neglect of the two weakest individuals of a litter of 3 cubs was described during a time of extreme prey scarcity (Packer & Pusey 1984). The criterion for being the weakest was that these two could not keep up during moving. The mother called the two cubs, but when they did not catch up, they were left behind. This case fits best with the additive or contingent model (1). However, important characteristics of the infants, like sex, were not assessed. Moreover, conclusions cannot be drawn from just one case.

Summary

The table 3 summarizes the main outcomes of the studies that were considered in this section. Summarising, studies that considered infant sex did not find a relation between the sex of the infant

and the likelihood of being neglected. Some studies found support for the additive/ contingent model (1). However, several studies pointed towards a different hypothesis of investment termination through infant neglect. As being a primiparous mother increased the likelihood of neglect, neglect could possibly be caused by maternal inexperience.

Table 3, Studies on infant neglect with closest matching parental investment model

Animal	Breeding structure	Study	Factors measured	Relations found	Closest matching model
Cotton-top tamarins	Socially monogamous cooperative	Bardi et al. 2001	Resources available (siblings present) Litter quality (litter size) Paternal condition (health condition sire) Maternal condition (health condition dam) Infant sex Infant birth date Cage size Couple experience Sire experience Dam experience Age of the parents	The fewer siblings present the more likely an infant is neglected. The lower the health of the mother, the more likely infant neglect is to occur. Triplets made neglect more likely. Young parents made infant neglect more likely.	Additive / contingent model (1)
Japanese macaques	Matrilineal Polygynous groups	Schino & Troisi 2005	Infant sex Maternal rank Age group mother Mother primi or multiparous	Being primiparous immensely increased the likelihood of neglect. Low dominance rank also increased the possibility	Alternative: Experience with having infants important
Sooty mangabeys	Matrilineal Polygynous groups	Maestriepieri et al. 1997a	Infant sex Mother primi or multiparous	Being primiparous increased the likelihood of neglect.	Alternative: Experience with having infants important
Pig-tail macaques	Matrilineal Polygynous groups	(Maestriepieri et al. 1997b)	Infant sex Mother primi or multiparous Maternal quality (health state of the mother)	Being primiparous increased the likelihood of neglect.	Alternative: Experience with having infants important
		Dazey &	Mother primi or	Being	Alternative:

		Erwin 1976	multiparous	primiparous increased the likelihood of neglect.	Experience with having infants important
Rhesus macaques	Matrilineal Polygynous groups	Hird et al. 1972	Mother primi or multiparous	Being primiparous increased the likelihood of neglect.	Alternative: Experience with having infants important
Vervet monkeys	Matrilineal Polygynous groups	Fairbanks & McGuire 1995	Maternal quality (combination of age and weight)	The 'marginal reproductive group' (lowest weight, highest or lowest age) were more likely to be neglected	Additive/contingent model (1)
lions	Polygynous	Rudnai 1973	Litter quality (litter size)	Litters of one infant were more likely to be neglected	Additive/contingent model (1)
		Packer & Pusey 1984	Resource availability (food) Infant quality (strength)	One case of neglect of two infants that fell behind during a period of food shortage	Additive/contingent model (1)
Grizzly bears	Solitary	Tait 1980	Litter quality (litter size)	Litters of one infant were more likely to be neglected	Additive/contingent model (1)

Infanticide

Infanticide by mammals, especially in primates, is often perpetrated by individuals other than the parent. However, there are studies that measured infanticide by the parent, which will be covered in this section.

Infanticide in cotton-top tamarins

In the study by Bardi et al. (2001) on which we elaborated in the previous section infanticide was measured as well, controlling for the same factors as neglect. Of the 1093 live births 12% was killed by a parent. Maternal inexperience made infanticide less likely. Bad health condition of the mother made infanticide more likely, the father's health condition was not as important. Young age of the parents also increased the likelihood of infanticide. The correlation between low maternal quality and a higher occurrence of infanticide can be explained by the additive/contingent model (1).

However the reason why younger mothers are more likely to commit infanticide cannot be explained by this model. A relation between young age of the mother and inexperience with raising infants can be expected. However, primiparous mothers were found to be less likely to commit infanticide. Still, this could be a by-product of fewer infants from primiparous mothers being alive, due to the high amount that is neglected in this group.

Infanticide in house mice and wood rats

House mice (Köning 1989) and wood rats (McClure 1981) cannibalise their pups one at a time as lactation progressed. This way, assuming the environment is unstable, a sustainable litter size can be determined more precisely, as the decision whether to terminate investment in a specific infant or not is delayed. At the same time the loss of prolonged investment in infants that will not be weaned is decreased by the additional food they provide. In the house mice study on average 2.7 pups per litter were subject of infanticide by consumption.

Food-deprived wood rat mothers were shown to commit infanticide, opposed to non-deprived ones (McClure 1981). In this species there was a significant bias towards killing males, in 11 out of 12 food deprived litters all male pups died before a female pup was killed. Instead of an equal ratio of males and females, as in the control group, the litters ended up consisting of 2.5 times as many females as males. In wood rats males are the sex that is condition dependent, as larger males are more successful in securing territories and attracting mates than small males. In the control group with unlimited access to food only one pup, a male, was neglected, probably due to nipple-shortage. An explanation for the mothers with unlimited food resources not differentially investing in males, as there were no female deaths, could be that there was no need to discriminate, as all pups could reach their optimal weight given the resources available (McClure 1981). This research therefore seems to point to the male quality model (2.1a).

Infanticide in golden hamsters and albino mice

Infanticide through cannibalism is proposed to occur due to a litter being too big in golden hamsters (Day & Galef 1977). Cannibalism within 5 days after parturition was measured, which was inferred from the number of pups still alive. Infants were also found to be consumed after death caused by something else than infanticide, but this number could be neglected when compared to death caused by maternal infanticide. Infanticide by the mother with subsequent eating occurs regularly in golden hamsters. 21 mothers produced 3 litters each and in 76% of the cases some degree of cannibalism occurred. In the 25 litters from a subsequent test in 88% of the litters cannibalism was observed. When data from the female that cannibalised her entire litter was excluded, 1.9 pups per litter were cannibalised on average per litter, with litters ranging between 4 and 14 pups. Litters that were assumed to be unlikely to survive because of certain characteristics were excluded from analysis, in order to avoid counting too many pups that died without infanticide being perpetrated. Handling, age of mother, experience with previous litters, number of pups and pup characteristics (birth weight, weight before disappearance, colour abnormalities, injuries) did not have an effect on maternal infanticide. There is reason to believe infanticide had the purpose of reducing the litter size to an optimal one. The evidence for this is that most maternal infanticide occurred within the first three days after parturition, and litter size after infanticide was approximately constant over three consecutive litters. This optimal litter size probably stayed equal in consecutive litters of each individual, due to the stable laboratory conditions. The optimal litter size hypothesis was confirmed by subsequent experiments, where litter size was varied artificially. In this study maternal factors, that increased the likelihood of infanticide in hamsters, were measured. However infant-specific factors, that were measured, birth weight, weight before disappearance, colour abnormalities and injuries, were not found to influence infanticide. This contradicts the additive/ contingent model (1), which was subscribed by the maternal factors. From the maternal viewpoint, given the circumstances, there is a total amount to invest, and if there are too many pups to sustain at a given moment, infanticide can be committed. Infant sex was not measured, but as the infanticide was litter size

driven, infant sex driven selection models predicting investment termination are unlikely to be suitable for these cases of infanticide. Therefore the male quality model (2.1a), the competition for restricted resources model (2.2a), the local resource enhancement model (2.2b) and the advantaged-daughter model (2.2c) are unlikely to match. The additive/ contingent model could still be the closest matching model if infant specific factors that were not measured increased the likelihood of being killed. Another model that could theoretically still fit is the population adjustment model (2.1a). However, none of the factors necessary to test for this model, which are infant sex, current and equilibrium sex ratio, were measured.

A similar effect of importance of litter size was seen in Rockland Swiss albino mice (Gandelman & Simon 1978). These mice typically give birth of on average 9 pups per litter. When litter sizes were increased by replacing them by foster litters of 12 or 16 young, the dams killed on average respectively 3 and 7 pups, adjusting their foster litters to standard size. Also they selectively killed the lightest pups. This result matches with the additive or contingent model (1). Nevertheless, as the study did not consider the sex of the infant, the other models cannot be excluded.

Infanticide in rats

In rats infanticide by the mother has been shown to occur when environmental safety decreases (Maestripiri 1992). When pup infanticide by an aggressive male has begun, the female ceases her attacks towards the male and joins him to consume the litter. Since the decision which individual to kill, and which to save, is not made when all pups are consumed, this is not a situation in which discrimination between the pups can occur. However, as an unsafe environment decreases the willingness to invest, these cases of infanticide roughly follow the additive/ contingent model (1).

Infanticide in Norway rats

In wild caught Norway rats there is an indication maternal rank influences decisions on when to commit infanticide (Boice, 1972). Low ranking rats committed infanticide of, and subsequently ate, more than 60% of their young, while high ranking individuals weaned all. This pattern is consistent with the additive/ contingent model (1), as the maternal quality influenced the likelihood of infanticide. In this study infant-specific factors were not measured, and thus none of the models can be excluded. However, since the subjects were caught during pregnancy, an alternative, maladaptive, explanation could be that low ranking rats are more susceptible to stress.

Summary

In table 4 data from the studies in this section is summarized. Most were most consistent with the additive/ contingent model (1) as the best predictor of infanticide. However, only two of the studies considered infant sex, of which one was better explained by the male quality model. Moreover there is only one study in this category that is not performed on rodents. Rodents have a different breeding group structure than humans; they are territorial which means only the female is close to the litter, opposed to at least one individual or a group of individuals, in socially monogamous cooperative or polygynous group living species. Also they have significantly more 'r'-selected strategies, like large litters and short inter-birth intervals, than the 'K'-selected humans. Therefore, potentially different systems have evolved, making the possibilities, of using these studies to predict patterns in humans, limited.

Table 4, Studies on infant neglect with closest matching parental investment model

Animal	Breeding structure	Study	Factors measured	Relations found	Closest matching model
Cotton-top tamarins	Socially monogamous cooperative	Bardi et al. 2001	Resources available(siblings present) Litter quality (litter size) Paternal condition (health condition sire) Maternal condition (health condition dam) Infant sex Infant birth date Cage size Couple experience Sire experience Dam experience Age of the parents	The lower the health of the mother, the more likely infanticide is to occur. Young parents made infant infanticide more likely. Maternal inexperience made infanticide less likely.	Additive/contingent model (1)
House mice	Territorial	Köning 1989	Resource availability(food)	Food deprived mice were more likely to commit infanticide	Additive/contingent model (1)
Wood rats	Territorial	McClure 1981	Infant sex Resource availability (food)	Food deprived Wood rats were more likely to commit infanticide, and male infants were more likely to be the victim.	Male quality model (2.1a)
Golden hamsters	Territorial	Day & Galef 1977	Handling Maternal age Experience with previous litters Litter size Infant quality (Birth weight Weight before disappearance Colour abnormalities Injuries)	Infanticide was more likely if the litter was larger than an individual dependent threshold.	Additive/contingent model (1)
Albino mice	Territorial	Gandelman & Simon 1978	Litter quality (litter size) Infant quality (relative weight)	The litter was reduced to an average size, killing the	Additive/contingent model (1)

				lightest offspring first	
Rats	Territorial		Environmental safety (attacking male that defeats female)	Infanticide of remaining pups if defending seems unsuccessful	Additive/contingent model (1)
Norway rats	Territorial		Maternal quality (dominance)	Low ranking rats more likely to commit infanticide	Additive/contingent model (1)

Data on investment termination in humans

Human data are even scarcer, as laboratory trials are unethical and it is harder to measure precise factors, since neglect and infanticide can stay hidden. The studies that did cover investment termination will be discussed in this section. Humans have a socially monogamous breeding structure. Even though sex specific intentional abortion, neglect and infanticide are known to occur in specific societies, discussing this is not within the scope of this review (Dickemann 1979). We will only cover investment termination in western societies. Sex specific investment termination in societies like feudal and post feudal but pre-industrial India, and the imperial period of traditional China, will not be discussed. Our reason to do so is that the incentive to raise males is far higher in these societies than in western societies, where our examples come from. This incentive can possibly overshadow other evolutionary mechanisms that are more important in western societies.

Pre-natal investment termination

In humans resorption has been described in twins, also known as the missing twin syndrome. Data have shown that a significant size difference between the infants, measured from crown to rump, was a risk factor for resorption of the smaller twin (Kol et al. 1993). A smaller infant could be seen as a weaker one. Also chromosomal or other physical abnormalities in one of the twins were shown to be a predictor of resorption (Weissman et al. 1994). Those two studies are most in line with the additive/contingent model (1), as infants with a lower quality, as measured in size or normality, were resorbed. Maternal age did not seem to influence the chance of embryonic resorption (Benson et al. 1994). The alternative hypothesis found in non-human mammals, that inexperience with having infants increases the likelihood of investment termination, is therefore not supported by these data.

The cases of spontaneous abortion of single infants fit best with the additive/contingent model (1), as, like in twin resorption, chromosomal abnormalities were a risk factor. In 50 to 61% of early stage abortions, occurring in the first or second trimester, these defects were found in the infant (Boue et al. 1975; Hassold et al. 1980). An even higher percentage of abnormalities have been reported by a study considering a period earlier in pregnancy (Boué et al. 1975). Other infant specific characteristics, which could have been important in the cases of the aborted infants that did not show abnormalities, and parental conditions, were not measured in these studies.

Although studies are scarce, they all agree the additive/contingent model (1) is the best predictor of abortion and resorption. However, none of the studies measured the sex of the lost infant, and thus the other models should not be excluded.

Neglect

In a data study on humans, neglect was most common in single father families, and more common in single mother families than in complete ones (Malkin & Lamb 1994). A single parent often has fewer resources than two parent families, and fathers have a lower parenthood confidence than mothers. Therefore the additive/ contingent model (1) explains the results of this study best. However infant characteristics were not measured.

Another study, which measured maltreatment, abuse and neglect taken together, of human infants, also found the additive/ contingent model (1) to be most in line with the data (Daly & Wilson 1981). Maltreatment was higher in parents with little, or unstable, resources and children with a handicap. However, again not many other factors, like sex, age and weight of the infant, were tested. Therefore other models cannot be excluded.

Infanticide

Research on infant death was performed in the United States over a period of 8 years, in which 34 million infants were born, examining data on infants that died before they became one year of age (Overpeck et al. 1998). They found young maternal age, single marital status, low education level and early birth of the infant to be predictive factors of infanticide. In other words, a mother short on resources, having a weaker than average infant, was more likely to commit infanticide. Also young infants were at a higher risk of infanticide, 50% of infants that were killed before becoming one year of age, died before they became 2 months of age. Therefore the additive/ contingent model (1) is the best predictor for these cases of infanticide. A drawback of this study is that only in 10% of the cases the relation, i.e. whether it was a natural parent, of the perpetrator to the infant was known. However previous studies have shown that during the first two weeks of life the mother is most likely to be the perpetrator (Jason 1983; Kunz & Bahr 1996). And in the remainder of the first year the father is the most likely committer of infanticide (Kunz & Bahr 1996; Dep. of Health 1997). Young maternal age also predicted infanticide. If young mothers are assumed to be maternal inexperienced this supports the need of experience hypothesis found in non-human mammals.

A data analysis performed in the United States, in which 3500 cases of parental infanticide occurred within 9 years, found an equal chance of male and female infants to be the victim during the first week of life. From the first week until fifteen years of age 55% of the victims were males (Kunz & Bahr 1996). Again risk of infanticide was higher for younger children. After the first week of life there is an increased risk of infanticide for boys, which points to the male quality model (2.1a).

Both studies in this section were not ideal to base conclusions on, since the one that is in line with the additive/ contingent model (1) did not test if the perpetrator was a natural parent. The other study, that found the male quality model (2.1a) to be the best predictor of parental infanticide, did not find an effect for the younger infants.

Summary

There is too little data to base solid conclusions on. Most studies are in line with the additive/ contingent model (1), but they measure too few factors to compare them to the other models. In one study the alternative need of maternal experience hypothesis best predicted the results, however another rejected it.

Conclusion and discussion

Studies measuring factors predicting investment termination are scarce, furthermore quite a few cover only 'r'-selected species. As 'r'-selected species have a reproductive strategy based on a large number of offspring and minimal investment per offspring, investment termination strategy is probably less important. None of the studies measured all factors necessary to discern the parental investment models; a majority only measured a few. No difference was observed between species of different breeding styles, but this could also have been caused by the limited amount of studies.

In most of the studies we reviewed, the additive/ contingent model was the best predictor of the parental investment termination patterns observed. It is possible that the additive/ contingent model best predicts the cases of investment termination in these species. An alternative explanation is that it is the broadest of the models, and therefore most incomplete studies could fit to it.

The majority of primate studies on neglect were an exception, as an alternative hypothesis prevailed. The data collected in these studies indicated a need of the mother being multiparous, and thus being experienced with having infants, before she was unlikely to neglect an infant. This could have an adaptive or a maladaptive cause. The adaptive explanation is consistent with the idea that it is inefficient to invest in offspring that is unlikely to reach reproductive age. It could be that the first infant is by definition unhealthy. For example when it is necessary for the birth channel to stretch by giving birth once, before an infant can pass without damaging. However it could also be a maladaptive by-product. For example of the flexibility obtained by learning skills later in life, which could make inexperienced mothers less likely to handle their infants right than experienced mothers.

We did not find enough studies that examined sufficient factors to test the data to the evolutionary models extensively. Therefore it is impossible to conclude if investment termination is evolutionary adaptive or maladaptive. Furthermore there is not enough data to sufficiently compare the human to the animal data. The additive/ contingent model seems to explain the few human studies best, however this conclusion is based on a few incomplete studies. A study by Resnick (1970) is in line with evolutionary maladaptiveness of investment termination through infanticide in humans. In this study on human perpetrators of infanticide 42% of females and 13% of males try to commit suicide after committing infanticide. As termination of investment in a specific offspring cannot provide an advantage if the freed resources are not reused, which happens if the parent commits suicide. However the same study indicates that these high suicide rates were not applicable for the majority of neonaticides, which is the killing of an infant within its first 24 hours of its life. Investment termination is a difficult topic due to its complexity.

One of the difficulties is determining whether behaviour is adaptive based on actions of individuals. This is difficult because a theoretically adaptive strategy can lead to wrong decisions due to the stochasticity of the environment. Pathological behaviour is evolutionary selected against, as it decreases the fitness of an individual. It is difficult to discriminate between mistakes in judgements of the environment and real pathological behaviour. For example behaviour of an animal in captivity that kills its offspring may be pathological, but it could also be the result of an adaptive strategy to delay reproduction in case of stress and wait for a better environment.

An at least as important difficulty is that investment termination is hard to monitor both in human and non-human mammals.

In non-human mammals, especially wild ones, abortion and resorption are hard to measure, as frequent scans are often not performed. But also infanticide and infant neglect can stay hidden in wild populations. For example carnivores, which are often nocturnal and wary of people, keep newborns hidden for first few weeks, and therefore death can often only be inferred (Packer & Pusey 1984). In captive studies neglect is sometimes inferred from records instead of specific observational research. It is questionable if this type of data is precise enough. For example in a study of 4 of the 7 sooty mangabey mothers that neglected also abused, but the victims were different infants (Maestriperi et al. 1997a). In another 5 of 11 pigtail macaque mothers both neglected and abused, also with different infants (Maestriperi et al. 1997b). It is questionable if in these studies neglect was not missed in cases of abuse and the other way around, as the criteria of both neglect and abuse was that it was observed "prior to death or removal".

In humans abortion or embryo resorption will be easier to measure as pregnancies are often monitored. However specific factors, like infant sex, will still be hard to measure in early losses that occur before the first echo. Studying neglect and infanticide has the obvious difficulty of cases that stay hidden. However there is an additional problem with studies of neglect in humans. In humans neglect and abuse often seem to co-occur (Mash & Wolfe 1991; McGee & Wolfe 1991; Pianta, Egeland & Erickson 1989; Zuravin 1988, Kaufman & Cicchetti 1989; McGee et al 1995). The co-occurrence could be a reflection of reality, but it could also be caused by weak definitions and therefore subjective division into categories. Studies often add together occurrences of multiple forms of maltreatment (different forms of neglect and abuse). Because the same data reflects multiple forms of maltreatment meta-analysis on just one of the types, in our case neglect, is impossible (Belsky 1993). Studies that looked at abuse and neglect separately show reason to believe these phenomena are guarded by different rules, for example abuse being repeated for most infants and neglect occurring only with selective infants (Crittenden 1981; Crittenden & Ainsworth 1989). Another indication that abuse is a separate phenomenon from neglect and infanticide is that only a minority of abuse cases are fatal, most inflict injuries on their children while continuing parental investment in them, opposite to neglect and infanticide where investment is terminated. Consistent with this, data indicates neglect and abuse rarely occur together in primates and are associated with different individual and behavioural profiles.

There seems to be a difference between patterns of investment termination through neglect in human and non-human primates. In primates abuse is more prevalent than neglect, contrary to humans (Maestriperi & Caroll 1998). But this can partially be due to unnatural environments in which the studied captive primates live. Also neglect occurs more often in non-human primates. However the definition of neglect is narrower for primates as only complete abandonment counts, whereas in humans a very broad definition is used. Therefore there is not necessarily a real difference in investment termination patterns between human and non-human primates.

In order to test whether occurrence of investment termination can be evolutionary adaptive and which decisions termination is based on, new research is needed. This research needs to consider more factors of the infant, the caretaker and the interaction between the two. A suitable paradigm of studying infanticide could be the use of artificially enlarged litters in rodents, as was done in the studies of Day and Galef (1977) and of Gandelman and Simon (1978). However, rodents and humans have very different breeding structures. It is unclear if breeding structure has an influence on investment termination decisions. However many rodents are 'r'-selected and possibly investment

termination decisions are less important than in 'K'-selected humans. A closer resembling breeding structure and reproductive strategy can be found in certain primates. An example would be cotton-top tamarins and marmosets, who are, like humans, socially monogamous cooperative breeders with small litters. In order to investigate parental investment termination in primates it would be beneficial to set up a meta-study to conduct the research during multiple small researches with different research aims. By doing this, observational data can specifically gathered, and thus data on all factors predicting investment termination, according to the different models, could be collected. A meta-study would solve the problem of the rarity of investment termination by collecting other data in the meantime. As maternal infanticide and infant neglect occurs for only a small percentage of the infants, and most primates have low birth rates already, existing demographic data were used for analysis. However, considering multiple groups could lead to faster data collection. This could have an added advantage that for example the effect of the factor rank could be measured easier, as more relatively high and low ranking individuals will be part of the sample. In humans it would be interesting to study infanticide and infant neglect as separate events within 24 hours postpartum, considering the maternal and infant factors from the investment theory models.

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