Factors Affecting Breeding in Captive Carnivora.

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ABSTRACT

Captive carnivores pose a challenge for conservationists and institutions alike, presenting many problems that range from diseases to poor welfare and unsuccessful breeding. Available databases of captive populations are rich sources of information that can help determine which factors can affect breeding success and the real potential of these populations in conservation programmes. Some species, such as tigers *Panthera tigris,* seem to preserve in captivity the same reproductive parameters seen in wild animals, making captive individuals extremely useful in the research of reproductive biology, that can be applied in evolutionary and physiological studies of the order Carnivora. Specific reproductive characteristics, mainly connected with the altriciality of the young, can make some species more prone to lose young in captivity than others, and these factors must be taken into consideration when developing *ex situ* conservation programmes. Infant mortality in captivity seems to be primarily caused by inadequate maternal behaviour, which can be connected to biological factors as well as to individual characteristics such as origin and rearing methods. Maternal infanticide, either passive or active, is also affected by biological and ecological characteristics of the species, and there may be an effect of the origin of the females, i.e. if they were wild-caught or captive-born. Housing conditions and individual history affect infant mortality, with females that suffered transfer between institutions exhibiting lower breeding success. Also, institutions with thriving research programmes presented higher infant mortality overall, independently of their latitude or management system, which can indicate an effect of human interference. Further research, both in the wild and in captivity, is needed to fully understand the factors affecting breeding success of captive carnivores.

To my dam, Judith.

In loving memory of
My father, Reinaldo, who sired me
My uncle, Elson, who fostered me
And our patriarch, Alfredo, alpha-male
You all left the group while I was away.

Goodbye.

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Chapter 1

Conservation and management aspects of carnivores in captivity.

Abstract

This chapter is a review of the conservation status of terrestrial carnivores and the challenges faced by conservation programmes. In average, a proportion of 58.6% of all families of terrestrial Carnivora are listed by IUCN in some level of threat. Conservation programmes are running to cover many species, both in the wild and captivity. The role of zoological institutions in conservation programmes is crucial, especially for those species with rapidly declining wild populations. Researchers face different challenges in the wild and captivity. In the wild, these are mostly related to conflicts between human populations and governments on the use of land assigned for conservation purposes. In captivity, zoologists face the lack of appropriate housing conditions and biological information on many species, as well as behavioural and physiological disorders caused by confinement. Conservation efforts must be interdisciplinary, with a stronger involvement from the human populations surrounding conservation areas and a direct effort from researchers and zoological institutions to exchange knowledge and set strict priorities prior to any practical investment.

1.1. *Introduction.*

Although the Order Carnivora[1] is not the most endangered mammalian order, it does contain some of the most charismatic species in the Animal Kingdom. This appeal has resulted in specimens being kept in hundreds of zoological institutions all around the globe, and species listed as threatened or endangered are frequently the subject of conservation and re-introduction programmes.

Managing predators or long-range foragers in captivity, however, is a very complex task. Not only are many wild species susceptible to diseases of

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[1]Although it appears that there is no evolutionary reason to exclude the families Phocidae and Otariidae from the Order Carnivora (e.g. Bininda–Emonds, Gittleman & Purvis 1999), in this work only terrestrial carnivores were included, due to fundamental differences in the housing, husbandry and management of aquatic and terrestrial mammals.

their domestic relatives, but also some have very specific environmental demands, which are, in many cases, close to impossible to recreate in captivity. The failure to achieve these standards may lead to welfare problems, such as stereotypies, that can lead to higher juvenile mortality (Clubb & Mason 2000), and jeopardise conservation programmes.

The role of zoos in conservation programmes is controversial (Schaller 1996). Nevertheless, many institutions claim that their main responsibility, when keeping endangered species, is to take part in captive breeding schemes, usually for subsequent re-introduction in the wild, in what is known as *ex situ* conservation (De Boer 1992). Only recently the World Conservation Union (IUCN) released the guideline policy for *ex situ* conservation, in which captive breeding is recommended under strict circumstances (IUCN 2002a). However, the results of many captive conservation programmes held by zoological institutions open to visitation were never scientifically assessed.

In the search for a better understanding of the factors that may affect breeding in captive mammals, carnivores can be a very adequate group to be looked at. The species differ largely in their life histories, including physical dimensions (Gittleman 1986a), diet (Van Valkenburg 1989), habitat use (Taylor 1989), geographical distribution (Wilson & Reeder 1993), and activity pattern (Gittleman 1986a). These factors have such an impact in husbandry techniques that species-focused guidelines for zoological institutions were urged since 1990 (Roberts 1990). Reproductive parameters are also very diverse within the order, from the age of independence of the young and the age in which the young open their eyes (Gittleman 1986a) to the general energy output in reproduction (Oftedal & Gittleman 1989), but most species are very altricial, which can prove to be a problem in captive conditions. The variety of social systems (Gittleman 1989), parental care (Baker 1994; Baker, Baker & Thompson 1996) and patterns of social communication (Peters & Wozencraft 1989; Gorman & Trowbridge 1989) have to be considered when housing groups, and mistakes can be punished by the death of a potential founder (e.g. Brocklehurst 1997; von Schmalz Peixoto 1998).

Another advantage of using carnivores as a model for this type of research is the relative abundance of institutional records. Apart from certain institutions dedicated to a single species, most of the zoos and aquaria of the world keep at least one species of the order (ISIS 2003). The overall lack of success of captive breeding programmes for carnivores (De Boer 1992) is an additional incentive to the use of these species for this research.

1.2. *Conservation status of the Order Carnivora.*

There are around 240 terrestrial species in 8 families of the Order Carnivora, and 109 species, or 45.42% of those, were classified as threatened in the last edition of the Red List from IUCN, making it the fourth most threatened mammalian order with more than 100 species (IUCN 2002b). Presenting this proportion as a pooled value, though, can be confounding: within families, the proportion of species reported as in some level of risk of extinction in the IUCN Red List ranges from 23.7% for the family Herpestidae to 75% in the small families of Ursidae and Hyaenidae, with an average of 58.6%. According to the IUCN Red List Categories and Criteria version 3.1 (2001), these species are, or will be in the near future, at risk of extinction if no action is taken place. Species are considered extinct (EX) when there is no reasonable doubt that the last specimen has died, confirmed by surveys in the historic range of the species, but when it still survives in captivity or artificial propagation, it is considered extinct in the wild (EW). The threatened species are classified as critically endangered (CR), endangered (EN) or vulnerable (VU) when at high risk of extinction, at different levels of threat, through loss of habitat or individuals. If the populational or geographical loss does not meet the statistical criteria for high risk of extinction, the species is evaluated as near threatened (NT). Data deficient species (DD) do not have enough support of adequate information on distribution and abundance to be evaluated safely, even when the species is well studied and many biological aspects are known. IUCN recognises the need for more accurate information on DD species and acknowledges that a threatened status may be appropriate. Widespread, abundant species are classified as least concern (LC), and some taxa were not evaluated (NE) for the Red List, once their abundance is evident. In the order Carnivora, the proportion of species in each category varies greatly between families, but those containing species with large body size seem to be more affected than families with medium to small body size (Figure 1.1). Body mass was one of the factors found to predict extinction in declining species (Purvis *et al* 2000). In a recent work, Cardillo *et al.* (2004) proposed a model which combines biological factors of carnivore species and human density in the areas in which they occur, explaining how a biologically sensitive species suffers higher impact of human population expansion.

Several carnivore species are subjects of *ex situ* conservation programmes, and many were reintroduced into their historical range. It appears, however, that many declining species, although in urgent need of direct conservation actions, have been overlooked. For example, in 165 reintroduction programmes of carnivores, only 28, or 16.9%, involved threatened species (Gittleman & Gompper 2001). This may reflect either the existence of multiple programmes for few threatened species (Mace *et al.* 2000) or the decision of programme managers to prioritise charismatic species over threatened ones that could benefit from these efforts (Balmford, Mace & Leader-Williams 1996). The importance of captive breeding programmes will be discussed in section 2.2.1.

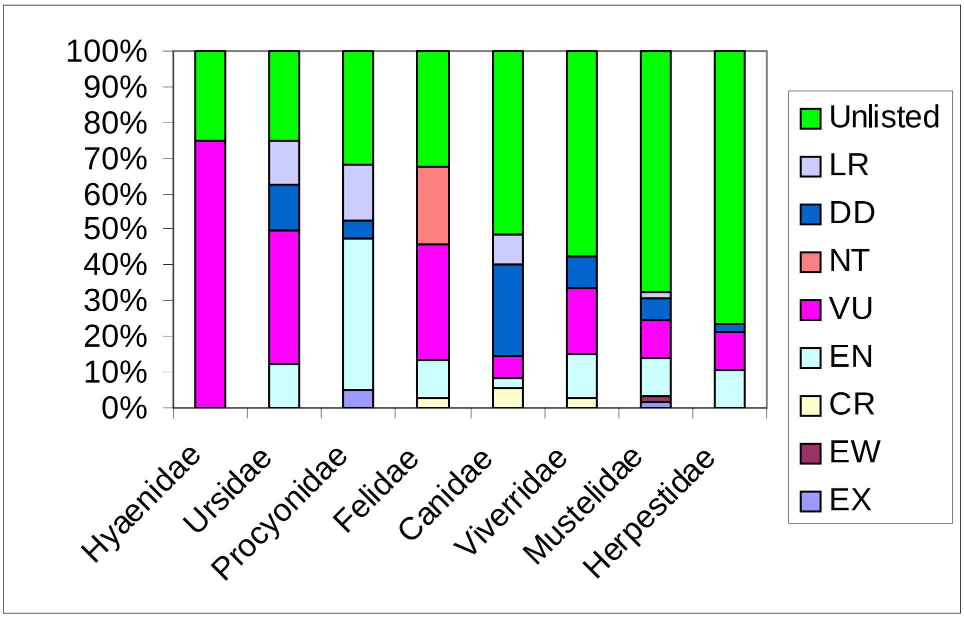

Figure 1.1: Proportion of species in each family of the order Carnivora that are unlisted or listed in diverse categories on the 2002 IUCN Red List. LR = low risk; DD = data deficient; NT = near threatened; VU = vulnerable; EN = endangered; CR = critically endangered; EW = extinct in the wild; EX = extinct.

The same situation occurs in zoological institutions around the world. While, on average, 75.3% of non-threatened carnivore species have bred more than 5 litters in captivity, worldwide, from 1986 to 1996, only 45.2% of the threatened species did so (see Chapter 2). Once again, these values vary among families (Table 1.1).

Table 1.1: Proportion of endangered species by family of carnivores, proportion of endangered species that bred at least 5 litters in captivity from 1986 to 1996 and proportion of non-endangered species that bred at least 5 litters in captivity from 1986 to 1996.

Family	Endangered species (%)	Captive-bred endangered species (%)	Captive-bred non-endangered species (%)
Canidae	50	50	61.1
Felidae	67.5	64	91.6
Herpestidae	23.7	0	20.7
Hyaenidae	75	66	100
Mustelidae	32.3	38.1	43.2
Procyonidae	68	15.4	100
Ursidae	75	83.3	100
Viverridae	42.4	0	31.5
Average	58.6	45.2	75.3

The present human-induced extinction crisis, which is developing at a rate 1000 to 10,000 times faster than the expected rate (Pimm *et al.* 1995), will soon claim many of these species, and it is an opportune moment to consider the actual potential of captive populations in the management of declining species.

1.2.1. *Zoos and conservation.*

The value of captive breeding in the conservation of endangered species has been discussed for several years. As early as 1979, Leyhausen argued that captive breeding could never be the solution for endangered species, since conservation efforts should consider the long term process of evolution, which would be lost in small captive populations. The most recent guidelines for *ex situ* management published by IUCN (2002a), however, points out that the goal of conservation is to maintain "biological interactions, ecological processes and function", through the management of wild populations and habitats, and the development of self-sustainable captive populations, aiming the production of individuals for reintroduction, when needed. Gittleman & Gompper (2001) affirm that the re-colonisation of habitats by declining species is a major goal of conservation efforts. Jalme (2002) pointed out the various aspects of captive breeding for conservation of avian species, which can be applied to many mammalian species: captive populations can replace wild populations in research and education, may provide genetic reservoirs to reinforce or found wild populations and can be a last resort for species whose wild populations cannot be maintained by other means. It is generally agreed, however, that *ex situ* conservation depends on high budgets, and must be used only as a support for ongoing *in situ* conservation programmes.

Comparing the budget of *ex situ* and *in situ* conservation programmes shows that the costs per capita for a efficient plan *in situ* are much lower than in captive breeding programmes, such as those for large mammals with scarce wild populations (Balmford, Leader-Williams & Green 1995). For instance, the costs of captive breeding programmes of larger felids are extremely high because of the species' requirements for large territories, the management of a large founder population (due to the higher level of homozigosity of predators) and the expenses with assisted reproduction techniques (ARTs), factors present also in other families of the order Carnivora (Conway 1986). Examining the costs of keeping several taxa, from invertebrates to vertebrates, it was found that body mass increases the costs, and the result was the same when examining only mammals; the need for much larger captive populations for smaller species, due to faster breeding and quicker loss of genetic variability, seems to eventually level costs between large and small species (Balmford, Mace & Leader-Williams 1996).

The IUCN warns of the danger of leaving the development of *ex situ* techniques until a species is on the verge of extinction, since it may be too late for the formation of a viable founder population (IUCN 2002a).

The genetic management of captive populations is of great concern in captive breeding programmes. Although loss of genetic variation through generations is inevitable, there are ways to minimise it: to select founders from different wild demes; reduce the time in captivity before re-introduction; and expand the period between generations if the population has to be kept in captivity. Also, different captive populations will lose different sets of alleles, and selecting individuals from different breeding programmes to start a reintroduced population allows a larger variation that would otherwise be possible (Mace 1986). Computer databases, such as ISIS and electronic studbooks, have been used to track genetic information from captive populations, and can be used to simulate loss of variation through successive generations, giving background to a safer and more effective conservation plans (Flesness & Mace 1988). One example of how effective the use of these new techniques can be is the very successful *ex situ* programme on Rodrigues fruit bats (*Pteropus rodricencis*): the introduced populations are stable, with a safe genetic variation and continue to subdivide, occupying new areas (Carroll & Mace 1988).

Some programmes have been less successful, and can reflect the need for a very careful planning. One example is the black-footed ferret (*Mustela nigripes*) that had almost disappeared due the eradication of the prairie dogs (*Cynomis* sp.), its main prey, from North American prairies. The last wild population was discovered in 1981, and a captive breeding programme was started, as a way to increase wild populations through re-introduction. Unfortunately, an outbreak of canine distemper, spread probably by the researchers, wiped out the wild colony. Now, captive propagation is the only method that can preserve this species. Some valuable lessons have been learned, such as keeping viable genetic diversity, and increasing and subdividing the captive population. Re-introduction efforts started in 1991 (Thorne & Oakleaf 1991), and through extensive research, the programme is starting to obtain positive results (Wolf *et al.* 2000a).

One particular programme is not achieving good results, even with the help of a large budget and several Assisted Reproduction Techniques: the conservation of the giant panda (*Ailuropoda melanoleuca*). Despite all efforts, more than half of the cubs born in 10 countries from 1963 to 1998 (226 individuals) died before 30 days after birth, and only 30% of the surviving cubs lived for 3 years in captivity. The slow breeding biology of the species and the inadequate behaviour displayed by hand-raised individuals are thought to be among the causes (Peng, Jiang & Hu 2001).

Conservation programmes should also consider problems of re-introduction. When re-introducing predators into areas where they have disappeared, prey populations can be easily affected once they are not prepared to defend themselves. Naïve prey populations were eliminated in the Pleistocene when faced by the first human hunters (Gittleman & Gompper 2001). In a study of the impact of re-colonising brown bear (*Ursus arctos*) and wolf (*Canis lupus*) populations on moose (*Alces alces*) groups in Europe and North America showed that naïve moose, which were unable to recognise predator cues, suffered higher predation-related mortality than experienced ones. Offspring predation, however, seems to elicit maternal hypersensitivity towards predator cues, contributing to subsequent increased survival rates. This shows that this species is swift in learning and adapting to changing predator populations, which may not have been true for the Pleistocene species eradicated by humans (Berger, Swenson & Persson 2001).

Naïveté can be also a problem for re-introduced predators. In the case of red wolves (*Canis rufus*), that were becoming extinct in the 1970s, the US Fish and Wildlife Service and Point Defiance Zoo started the Red Wolf Captive Breeding Program in Tacoma, Washington, in 1973. There are about

125 red wolves in captivity. They released captive-born animals in protected or rarely used areas, all individuals carrying a radio-collar. Meetings with neighbour human populations were held to enhance public recognition of the problem. Thirty-nine wolves were released and 12 died, three hit by cars and the others of "natural causes". To avoid further deaths, the population was tracked by radio, supplementary diet was provided when necessary and reproduction was, in some cases, assisted by recapturing wolves to pair and breed within acclimation pens (Moore & Smith 1990). A recent review of 116 re-introduction programmes showed that only 26% were classified as successful over time, although these values vary between years and countries. A series of measures to improve success in these programmes was suggested, such as identifying and removing the primary cause of decline and releasing large groups of animals (n>100) containing some wild-caught individuals (Fischer & Lindenmayer 2000). The release of wild-caught individuals together with a re-introduced population seems also to enhance the chances of success in African wild dogs, *Lycaon pictus* (Woodroffe & Ginsberg 1997), although some researchers put the blame of failure in re-introduction of captive-born African wild dogs on the lack of collaboration between captive breeding centres and nature conservation institutions (Frantzen, Ferguson & de Villiers 2001).

Conservation strategies have been used by The Jersey Wildlife Preservation Trust, Wildlife Preservation Trust International and WPT Canada, together with governmental organisations and zoos to research captive breeding and try to restore or create habitats to endangered species. The whole project involves also public education, personnel training and field research, with funding to captive and zoo-based breeding research and land purchase (Mallinson 1991).

Since *ex situ* techniques depend on captive founders, captive stocks are a fundamental part of any conservation programme. The role of zoological institutions in conservation programmes, however, goes beyond captive breeding. Physiological and behavioural research, fundamental for the understanding of the biology of species, and public education cannot be provided by any other source (Smith *et al.* 2002). Today, the focus is shifting for a better understanding of the impact of captivity on the welfare of the individuals, and the scientific community is beginning to recognise the importance of research with captive populations.

1.3. *Captive wild carnivores: conservation and husbandry.*

Keeping wild carnivores in captivity poses several challenges, from the security of big predators to welfare and conservation problems. Research is fundamental to identifying and overcoming these difficulties. Although most of physiological problems are now well known and can be avoided with simple measures, some behavioural dysfunctions are still unclear. This section is an overview of the most common problems of wild carnivores in captivity, and which solutions have been proposed to increase the welfare of these species.

1.3.1. *General health problems.*

Carnivores are susceptible to a variety of common feline and canine diseases, but some can be prevented through the use of commercial vaccines. Nevertheless, a few species can develop vaccine-induced diseases, and live strains must be avoided (Table 1.2).

Panleucopaenia is a common cause of death of zoo carnivores, and the presence of feral cats inside zoo facilities can be a permanent danger. One young male clouded leopard (*Neofelis nebulosa*) was found dead when 6 months old, victimised by panleucopaenia spread by feral cats during an epidemic of the disease (Geidel & Gensch 1976). Feline infectious peritonitis (caused by calicivirus) and panleucopaenia are responsible respectively for 6 and 4% of captive cheetahs (*Acinonyx jubatus*) deaths (Marker-Kraus 1997).

Pneumonia affects carnivores from bush dogs (*Speothos venaticus*) (Kitchener 1968) to fishing cats (*Felis viverrina*) (Jayewardene 1975), but can be treated if detected in early stages. Sand cats (*Felis margarita*) are highly sensitive to lung diseases, especially in cages with high humidity levels, but the most common infection is rhinotracheitis, spread commonly by feral cats. They are susceptible also to degenerative liver diseases and myocarditis (Sausman 1997). In felids, kidney diseases cause death of many individuals. They are the most common death cause in zoo-housed cheetahs over 6 months of age (Marker-Kraus 1997) and adult black-footed cats (*Felis nigripes*) (Olbricht & Sliwa 1997).

Table 1.2: Vaccines commonly used in captive wild carnivores and their limitations (from Roberts 1975; Scheffel & Hemmer 1975; Hulley 1976; Hinshaw, Amand and Tinkelman 1996; Deem *et al.* 2000).

Family	Vaccines used	Problems
Canidae	Canine distemper, canine infectious hepatitis, leptospirosis, parvovirus, rabies.	Cape hunting dogs (Lycaon pictus) can develop vaccine-induced distemper (must be used only chick-embryo-origin vaccine).
Felidae	Feline panleucopaenia (feline distemper), rhinotracheitis, calicivirus, rabies.	Should be used only killed vaccine to distemper. There is no vaccine to feline coronavirus (infectious peritonitis). Jaguarondis (Herpailurus yagouarundi) can develop vaccine - induced panleucopaenia, and Geoffroy's cats (Felis geoffroyi) can develop feline distemper.
Ursidae	Rabies	
Procyonidae	Canine and feline distemper annually. Rabies.	Kinkajous (Potos flavus) and red pandas (Ailurus fulgens) can develop vaccine-induced canine distemper from live vaccine. Red pandas are sometimes vaccinated against hepatitis and leptospirosis.
Viverridae	Canine and feline distemper annually.	
Mustelidae	Canine and feline distemper annually.	Ferrets (Mustela putorius) can develop vaccine-induced canine distemper. Susceptible to parvovirus.
Hyaenidae	Rabies and canine distemper annually.	

Parasitic infections are not, in general, life threatening, and can be easily controlled through antihelmintic oral solutions or vaccines. In nature, however, some species are susceptible to very specialised parasites that can lead to death. A female wild-caught maned wolf (*Chrysocyon brachyurus*), kept on Frankfurt Zoo, died of acute sero-glomerulo-nephritis. *Post-mortem* exams revealed that she had one kidney missing. This was caused by nematodes *Dioctophyma renale*, common parasites of maned wolves, that when untreated tends to destroy the kidneys (Faust & Scherpner 1975).

Malnutrition affects a large number of carnivores, due to the common mistake that feeding them solely with clean meat is sufficient to ensure good health. Felids feed largely on prey, but they consume not only the flesh, but also skin, cartilage, small bones and organs, such as liver and spleen. Giving whole carcasses instead of clean meat can prevent common nutritional problems like greenstick fractures and bone deformities (Ashton & Jones 1979). Nutritional deficiencies may be the cause of several bone deformities, but some species have a tendency to develop them. Bush dogs, like small domestic dogs, can suffer from bilateral patellar luxation, a painful condition that impeaches normal movement (Kitchener 1968).

Hand-reared animals can develop milk-induced diarrhoea that may lead to death, especially if the composition of the natural milk is not known, as in bush dogs (Kitchener 1968).

Other health problems range from hyperparathyroidism and encephalitis (Hulley 1976) to deaths by abdominal gas distension said to be caused by a sensitivity reaction, in the lack of a more accurate explanation (Murphy 1976).

Cancer occurs with some frequency in caged carnivores, and the causes of it are several. In the last years, however, veterinarians had discovered that vaccination can cause sarcoma in domestic cats (Esplin *et al*. 1993; Macy & Bergman 1995), and may be related to a local dermal inflammation resultant from the postvaccinal reaction (Macy & Hendrick 1996).

General health problems are responsible for a large number of deaths, but with appropriate veterinarian advice, most of these problems can be avoided or treated. It is important to say, however, that many of the zoological institutions included in this research do not have a veterinary doctor in their permanent staff, having an advisor that makes regular visits. Acute cases are usually treated by any veterinary surgeon available, who is sometimes not experienced in dealing with wild species. This could be the cause of the high numbers of deaths caused by these well-known conditions in some institutions.

1.3.2. *Reproductive physiological problems.*

Of all causes of poor breeding, low fertility is probably the easiest to identify. If a sexually mature couple, after obvious and repeated mating behaviour, fail to produce a pregnancy, infertility is immediately thought to be the cause. It is more complex, though, to define what is causing infertility in the first place.

Many factors can influence fertility in animals, apart from some obvious conditions, such as immaturity, old age, diseases and congenital abnormalities. In the wild, the three major suppressers of fertility are environmental factors (especially the variation on climate, day length and rainfall among seasons), lactation (which inhibits gonadotrophin, and then ovulation) and social dominance. In common marmosets (*Callithrix jacchus*), subordinate females had decreased gonadotrophin levels, and in naked mole-rats (*Heterocephalus glaber*), ovulation is suppressed in all females of a colony, except the "breeding queen". In both cases, removal of the infertile female from the presence of other females restores her fertility (Abbott 1988). External factors can also play a role in infertility. Environmental and industrial chemicals can influence reproductive fitness in animals, which is well illustrated by the effects of polychlorinated biphenols in a population of Baltic ring seals (*Halichoerus grypus*) (Holloway & Moore 1988).

Mellen (1991) found negative correlations between number of litters produced by small felids, and number of medical treatments, latitude distribution of the species, and group size, and a very positive correlation with husbandry style. In general, small cats kept in groups of more than a pair (one male and one female) were unlikely to reproduce, but the ones cared for by caretakers that spent more time talking and interacting with them produced more litters. Reproductive failure of apparently healthy individuals may lead to the conclusion that the individuals do not produce gametes. In research on sperm efficiency in black-footed ferrets (*Mustela nigripes*), species in which around 55% of adult males fail to sire offspring (even when 90% of the females are receptive), it was revealed that the sperm quality of fertile and "infertile" males was the same; failure was occurring due to a combination of behavioural (improper mating position, excessive aggressiveness) and physiological (underdeveloped testes, lack of ejaculation) factors (Wolf *et al.* 2000b).

Contrasting with the low fertility problem, some species are excellent breeders, and contraception becomes the problem. There are many solutions for excessive breeding. Some zoos used to castrate males or keep female brown bears (*Ursus arctos*) alone (Van Keulen-Kromhout 1976), instead of using other available methods. Lions (*Panthera leo*) breed so well in captivity that contraceptive procedures are a common place. Hormonal implants, injections or even tablets are given to females, but the development of mammary cancer is a serious drawback to this technique. Vasectomy of males is a relatively simple surgery, and its risks are much lower (Ashton & Jones 1979). A recent trend is to find ways of interrupting early pregnancy, as with the use of antiprogestin in zoo-housed bears (Jewgenow *et al.* 2001).

It may seem that excessive breeding would be a positive step towards the conservation of a species. However, it is not only detrimental to the health of the females, but the burden of many young may trigger brood-reducing behaviour in mothers, as it happens in rodents (Labov *et al. 1985)*, or lead to infanticidal episodes in males. The major problem, though, is the issue of re-housing the young adults properly. Rare species are always in high demand, but more common species, usually the ones affected by excessive breeding, may give rise to serious housing problems. The use of reversible contraceptive methods is crucial for conservation purposes, and avoids the need in the future of using drastic "culling" methods, such as euthanasia (Graham 1996).

One of the most important aspects of reproduction that must be taken into consideration in a conservation programme is concerned with genetic variability and inbreeding. Inbreeding increases homozygosity and can allow expression of deleterious genes. Mortality during first six months after birth is higher in inbred youngsters of red pandas and leopards (*Panthera pardus*) (Carlstead 1996). In leopards, inbreeding seems to increase the frequency of cub killing (Carlstead 1996). Bred in captivity for over a century and a half, zoo populations of cheetahs are highly inbred. This genetic homogeneity seems to be responsible for the high rate of infant mortality and the low life expectancy of captive-born individuals (Marker-Kraus 1997), although this could also be an effect of differences in management practices, for values vary significantly between zoological institutions (Wielebnowski 1996).

For many species there are studbooks, where each individual of the captive population is listed, along with all its genetic relatedness to other individuals. This type of detailed record allows institutions to match couples from different genetic backgrounds, minimising the effects of inbreeding. Many rare species, however, have very small captive populations, and some, like the Sri Lankan rusty-spotted cat (*Prionailurus rubiginosa phillipsi*), have their whole captive population originated from one pair of founders from Frankfurt Zoo (Dmoch 1997). In these cases, it is difficult to increase genetic variation, for it would imply in capturing new founders in the wild to start a conservation programme, that could be, in the end, unsuccessful. It seems, though, that inbreeding depression does not affect some species as seriously as it was thought some years ago, as in the cases of the Mexican wolf (*Canis lupus baileyi*) and the red wolf (*Canis rufus*), and this could be true to many other species (Kalinowski, Hedricks & Miller 1999).

In a captive breeding programme, having a pregnant female is a sign that only the first problem has been solved. Many gestations do not come to term, because of the high incidence of miscarriages, premature births and stillbirths among captive carnivores. For example, in cheetahs (*Acinonyx jubatus*), 20% of the cubs are stillborn, mainly because of premature births (Marker-Kraus 1997). In Okahandja Park, South-West Africa, brown hyaena (*Parahyaena brunnea*) pups at were born prematurely and died due the underdevelopment of lungs (Schulz 1966). In some species, to cross the threshold of 30 days after birth does not mean that the litter will survive. In the National Zoo, Washington, DC, USA, all the red panda cubs died before 130 days after birth, the mean age of death being 78.5 days, although the cause of these deaths were not reported (Roberts 1975).

The breeding biology of many species is not yet completely understood, and much research is still needed. Without this knowledge, the physiological causes of many of the problems listed above are mere conjecture. Furthermore, individuals demand particular treatments, so each case has to be minutely analysed. New techniques, such as non-invasive endocrinological methods, have been yielding valuable reproductive information, and can be used to survey the breeding status of captive females (Goodrowe *et al.* 2000). Maybe only the dynamic interchange of information between zoologists and veterinary surgeons can lead to a higher level of successful breeding.

1.3.3. *Reproductive behavioural problems.*

Captive breeding can be difficult due to inability of individuals to perform regular mating behaviour. Alternative patterns of sexual behaviour, such as masturbation and homosexuality, were recorded in the wild and cannot be described as abnormal, but their non-reproductive character may be a drawback for conservation programmes. Homosexuality is largely found among carnivores (Table 1.3), and masturbation has been recorded in several species. These behaviours promote sexual satisfaction without reproduction, but the individuals that perform them are also usually able to have, as long as a suitable partner is available, also regular reproductive activity (Bagemihl 1999). In the other hand, inadequate sexual behaviour may be originated from more complex mechanisms, like imprinting, and have long-lasting effects on the individuals, that can be unable to reproduce.

Behavioural inadequacies affecting reproductive performance may be attributed to deficient early rearing environments, the social milieu in which animals are kept in a long-term basis, or in the way potential mating pairs are put together (Lindburg & Fitch-Snyder 1994). In the case of the black-footed ferret described by Wolf *et al.* (2000b), 25% of unsuccessful breeding attempts were caused by the failure of males in adopting a proper mating position with the female. Inadequate mating behaviour is also among the causes of poor breeding success in captive giant pandas (Peng, Jiang & Hu 2001).

Table 1.3: Occurrence of homosexuality in carnivores (Bagemihl 1999)

Species	Gender	Type of behaviour	Level of occurrence	Observed in
African lion	M/F	Courtship, sexual, pair-bonding and parenting	Moderate	Wild, semiwild* and captivity
Cheetah	M/F	Courtship, sexual and pair-bonding	Moderate	Wild, semiwild and captivity
Red fox	M/F	Sexual and parenting	Incidental	Wild and captivity
Wolf	M/F	Courtship and sexual	Incidental	Captivity
Bush dog	M/F	Sexual and parenting	Incidental	Captivity
Brown bear	M/F	Sexual, pair-bonding and parenting	Moderate	Wild
American black bear	M/F	Sexual, pair-bonding and parenting	Moderate	Wild
Spotted hyena	F	Sexual	Moderate	Wild and captivity

* Such as large breeding centres or fenced nature reserves and protection areas.

1.3.4. *Infanticide.*

Infanticide has evolved as an ultimate mechanism of energy economy, or a way to minimise the others' fitness, improving the killer's own chances. Examples of nonparental infanticide in the wild include the nomadic lions in Serengeti, which expel and sometimes kill other males and eat their cubs (Schaller 1972). Killing other individuals' offspring may increase fitness by facilitating access to resources or enhancing breeding opportunities, and some species may have developed counterstrategies to minimise the occurrence of these events, such as termination of pregnancy, defence mechanisms against intruders and territoriality (Ebensperger 1998). Parental infanticide has different causes and benefits. In extreme situations, such as lack of food or threat of predation, mammals can respond by aborting or reabsorbing litters, or deserting or eating them if after birth. The benefits of these strategies may depend on the ability of the parents to produce another litter in the same season, on the cost of having another litter to the parent's reproductive value and on the probability of these youngsters, raised under adverse conditions, to breed when adults (Clutton-Brock 1991). Infanticide also allows the alteration of reproductive patterns at the expense of others, and parental investment can be suppressed in any stage between conception and weaning (Hayssen 1984). Different types of infanticide have different aetiology and adaptive values (Hrdy 1979), but its occurrence in captivity can be detrimental to the success of breeding programmes. The impact of infanticide on the breeding success of captive carnivores is not yet well researched, and will be discussed in detail in Chapter 6.

1.3.5. *Behavioural problems.*

Individual behaviour can be affected by captivity (Carlstead 1996), leading to poor welfare (Mench & Kreger 1996). Even daily husbandry procedures can elevate levels of stress hormones and lead to inappropriate behaviour (Mendl *et al.* 2001). For social species, captivity puts the stability of a group under pressure, as an individual cannot abandon the group if social interactions become too agonistic, and sometimes has to change its own behaviour in a way to survive. For example, at Nairobi Zoo, two deformed pups of a litter of African wild dogs (*Lycaon pictus*) were killed when they were four months old. The only survivor had to assume a permanent submissive posture towards others (Cade 1975). Disputes over hierarchy are to blame for many fighting episodes and some casualties. In a group of dholes *(Cuon alpinus*), disputes over hierarchy led to severe fights among animals of the same sex (Sosnovskii 1975) that have lived before in apparent harmony. In a more serious event, the same disputes between a tamed male ocelot (*Leopardus pardalis*) and another male led to the death of the latter (Leyhausen 1966). This could happen because of the change in status an individual may go through when entering sexual maturity.

Respecting the social structure adopted by a species in the wild can avoid some problems with zoo-housed groups, and can even help with captive breeding efforts. For example, cheetahs frequently have poor breeding in captivity. Although their behaviour in the wild is not completely unravelled, two factors are quite clear: 1) during much of lifetime, females are isolated from other adult conspecifics; 2) males move in hunting groups. Female isolation period goes from early pregnancy until the cubs are 16 months old, then again females are approached by males. In zoos, however, male and females are usually housed together, or at least in olfactory or visual contact, and this husbandry practice could be affecting the perception of the individuals of their housing condition (Benzon & Smith 1974). Other species are naturally solitary, and the attempt to house them in pairs or groups leads to severe injury of the animals, as it occurs with least weasels (*Mustela nivalis*) (Rosenthal 1971).

Whatever is the cause for excessive aggressiveness, there are reports of it in several species, especially felids. Table 1.4 displays some examples.

The development of stereotypies, a display of repetitive behavioural patterns with no apparent function (Mason 1991), in captive carnivores, seems to be related to the median home range size of the species (Clubb & Mason 2000). In carnivores, stereotypies are usually elicited by feeding, and pacing is the most common display. Changes in diet and feeding schedule can reduce pacing in cats (Mellen, Hayes & Shepherdson in press), and stereotypic pacing in leopard cats (*Prionailurus viverrinus*) was reduced 50% when the enclosure was provided with places to hide (Carlstead, Brown & Seidensticker 1993).

Table 1.4: Events of excessive aggressiveness in some Carnivora species in captivity.

Family	Species	No. of animals attacked	Event	Was the victim eaten?	Thought cause	Reference
Felidae	*Catopuma temmincki*	2	A male killed one female during introduction and, later, the female that was living with him.	N	Not available	Brocklehurst 1997.
Felidae	*Oncifelis geoffroyi*	1	A male killed a female.	Y	The animals were being fed live prey on the occasion.	Scheffel & Hemmer 1975.
Felidae	*Panthera onca*	1	A male preyed on a conspecific.	Y	Not available	Oliveira 1994.
Felidae	*Panthera tigris*	1	An introduced young male was killed by an adult male.	N	Competition among males. There were 4 females in the area.	Yost 1976.
Procyonidae	*Nasua narica*	1	One male was permanently under attack of females.	N	In the wild, females expel adult males from the groups.	Smith 1980.
Procyonidae	*Nasua nasua*	1	One introduced female was killed by 2 males and 7 females of a established group.	N	The group was stable, and the new female was introduced abruptly.	Von Schmalz Peixoto 1998.

Stereotypic displays can be also elicited by loud noises and cleaning procedures, as in fennec foxes (*Vulpes zerda*) (Carlstead 1991). An institution suffering frequent breeding failures has a good start towards improvement if it revises its current husbandry techniques, and checks more closely the relationship between keepers and animals.

1.4. *Thesis structure and hypotheses to be tested.*

This research aims to identify the factors affecting breeding success of captive carnivores, making use of the large amount of data already available from several sources. In this chapter, I review the conservation status of terrestrial carnivores, consider the importance of captive breeding, and present the most common challenges facing the management of captive carnivores. The subject and relevant questions of the next chapters are described below.

1.4.1. *Chapter 2: Using databases in the research of infant mortality in captive carnivores.*

In this chapter, I describe the available databases for zoo research, and the datasets on captive carnivores originating from them. I also present in detail a method of collecting and analysing this type of data, identifying the possible confounds and ways to overcome some problems. I suggest the use of relative indices as dependent variables and present the equations used in this research. I also test the variables used in multi-species analyses for possible effects of phylogeny and question the need to correct this issue.

1.4.2. *Chapter 3: Factors affecting breeding in captive tigers* **(Panthera tigris):** *a studbook research.*

In Chapter 3, I use the tiger studbook as a model to address the possibility of answering biological questions with record research. I point out that the tiger is a species with a large latitudinal range, thus excluding photoperiodic effects in breeding. Considering that there are abundant food and water in captivity, and that serious institutions have to provide adequate housing to their animals, it is not expected that biological parameters, such as litter size, differ from wild populations. There are genetic, phenotypic and geographical differences between the two subspecies in the studbook, so it is expected that the dataset will reflect this and express the need of subspecies-orientated husbandry protocols. I hypothesise also that there will be little or no effect of inbreeding levels in this species for, like several carnivores, it presents high levels of homozygosity in wild populations.

1.4.3. *Chapter 4: Biological factors affecting infant survival in captive carnivores.*

Here I use multiple datasets to predict, through statistical models, the possible effects of the natural history of the species on infant mortality in captivity.

If conditions in captivity are providing all the demands of a species, as it would happen with a wild population during phases of abundant resources, then the specific proportion of infant mortality in captivity should be similar or slightly lower to those values for a wild population, because of the absence of natural phenomena such as fires, flash floods and predation. Otherwise, it would imply that other factors, rather than resource availability, are affecting these species' breeding success in captivity. The variance in the proportion of infant mortality between species may indicate that biological parameters have an influence on infant survival. In that case, it is possible that species with slower development were more prone to lose infants.

1.4.4. *Chapter 5: Causes of mortality in young captive carnivores.*

The causes of death of young carnivores in captivity are described in this chapter, and I consider the factors that can make certain species more prone to particular ailments. Also, I investigate the occurrence of infant deaths caused by inadequate maternal behaviour. I hypothesise, based on published reports, that a significant proportion of infant mortality in some species of carnivores in captivity is caused by the female. If so, most deaths shall occur in the first few weeks after birth, especially in species in which the young develop at a faster pace, due to the costs of maternal care.

1.4.5. *Chapter 6: Maternal infanticide in captive carnivores.*

The impact of inadequate maternal behaviour on infant mortality of captive carnivores is discussed in Chapter 6, where I also describe the mechanisms involved in maternal infanticide.

I hypothesise that species with altricial young will present higher proportion of active infanticide, and that some of the variance of infant mortality among institutions may be accounted for the history of the females (e.g., if they were wild-caught or captive-born) and institutional protocols (such as translocations and male presence during rearing).

1.4.6. *Chapter 7: Increasing juvenile survival in captive carnivores: Practical considerations.*

Here I review the techniques of assisted reproduction and the solutions proposed by institutions to minimise infant mortality, with special focus on hand-rearing survival rates.

A high variance in the proportion of infant mortality between institutions may suggest the influence of local characteristics such as the origin of the females and the number of translocations they were subjected to. If inadequate maternal behaviour was responsible for a significant proportion of infant deaths, and high infant mortality is related to institutional and individual characteristics, then infant mortality in captive carnivores can be greatly reduced if certain measures were taken, such as avoiding female translocations, providing more adequate housing conditions and respecting photoperiodic needs of breeding individuals.

1.5. *Conclusion.*

Carnivores are rapidly disappearing from many areas in the wild, and some species are declining at alarming rates. Captive stocks can help research and conservation efforts, but a change of priorities is needed, enhancing the focus on declining species rather than more abundant, but charismatic, ones. Conservation efforts need to be multidisciplinary, integrating several areas of science with local populations and governments, and a realistic approach of objectives and practical issues has to be addressed prior to any investment on the area.

The maintenance of carnivore species in zoological and research centres is yet cause of concern, and many techniques are still in their first attempts. A better communication between researchers around the world may lead to higher success, and the shifting role of zoos, from entertainment spaces to educational and research units, lifts the expectations for more successful integrative conservation programmes.

Chapter 2

Using databases in the research of infant mortality in carnivores.

Abstract

For many decades, zoological institutions have been keeping records of their animal stocks, many times with extreme detail. Main sources of information are the *International Zoo Yearbooks* published by the Zoological Society of London; the *International Species Information System*, created in 1978 by the American Association of Zoo and Aquaria; and Species Studbooks, kept initially as regional records of institutions and now available for many endangered species worldwide. Institutions keep private records of their collections and compile, many times, detailed information on individuals, including medical records and transfers. These data were very seldom used as bases for researching particular aspects of captive animals, due to the risk of bias and other statistical challenges. These problems can be overcome with the use of appropriate data collection and statistical analyses.

2.1. *Introduction.*

Population records for captive wild species have been kept since 1932, with the appearance of the first studbook for the European bison (*Bison bonanus*) (Glatston 1986), and gained a more standardised approach in 1960, when the *International Zoo Yearbook* (IZY) was first published by the Zoological Society of London (Olney 2003). In the 1970s, researchers at Minnesota Zoological Parks developed a computer-based questionnaire in which institutions could load data from their own collections[2]. This system gave rise to the International Species Information System (ISIS), and grew beyond American borders to be used by a large percentage of the Western zoos (Flesness 2003).

[2] A collection is the total of individuals of the same species kept by a zoological institution; in some cases, institutions may keep separate collections for different subspecies, especially when the subspecies are subject of conservation programmes.

Meanwhile, curators and keepers with particular interest in one species or other, started compiling information from their own institutions and others that kept the same species in studbooks, making the number of species covered by these records grow exponentially through the decades. The basic format of the studbooks still follows the guidelines of the first attempts, but nowadays there is a more accurate account of details such as inbreeding levels, and electronic communication between institutions allowed for a better coverage of the captive population (Glatston 1986).

Zoo records have been used as a tool in the research on species conservation, animal breeding, behaviour and welfare since their standardisation in the 1980s (Flesness & Mace 1988). New methods of collection and analysis of data have been used in recent years to overcome some of the confounding factors found in the first years of data collection, and the reliability of data is getting higher due to standardised methods and the use of computer programmes.

In this chapter, I review the sources of information on zoo animals and their problems, and make use of analytical methods aimed to overcome these challenges. I describe the collection methods of the datasets used in the next chapters for statistical modelling, as well as the relative indices calculated by formulae to overcome statistical confounds. The aim of this chapter is to demonstrate that the records of captive populations, although not flawless or complete, can be safely used for statistical modelling as means of testing biological hypotheses when collected and analysed carefully.

2.2. *Captive population databases.*

The population of carnivores kept in zoological institutions and research or breeding centres is restricted, both in species and individuals. The number of individuals and collections reported to databases, however, has been growing since the beginning of record keeping. One example is the number of collections and individuals published annually by the *International Zoo Yearbooks*: from 1986 to 1996, the number of collections has grown steadily, although the number of individuals has not followed the same slow rise throughout the years (figure 2.1). The *IZY* published the census of individuals and list of multiple births for the last time in 1996, when many studbooks and the ISIS were already collecting and organisisng most of institutional records. In posterior editions, the *IZY* printed just the list of studbooks and studbook keepers. The slight decline on the number of collections and individuals reported when the last full list was published may reflect the tendency of institutions to send reports directly to international data systems, such as studbooks or to the ISIS, instead of the Zoological Society of London, or may indicate the existence of copyright issues, held by commercial data systems such as ISIS, preventing the full publication of these lists for free access.

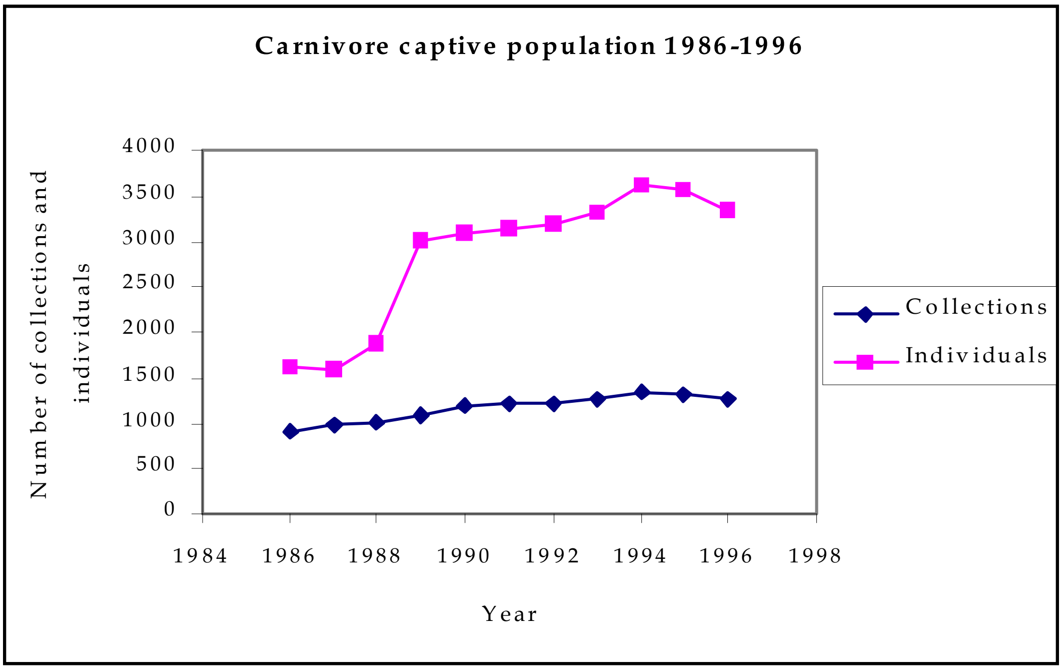

Figure 2.1: Number of collections and individuals of 35 declining Carnivora species reported to the *International Zoo Yearbooks* from 1986 to 1996. Some institutions keep subspecies in separate collections.

Nowadays, most individuals are numbered and coded, and the information from different sources is, in general, either repetitive or complementary (Glatston 1986). For example, a female in Zoo A, identified by the number 1234, may have her breeding records in the *IZY* from 1980 to 1996, and in the international studbook of the species, which also contains more detailed information of her life history, from 1984 to 2002. The decision of which repetitive data to be discarded (in this case, from 1984 to 1996) is at the discretion of the researcher. As the identity of the female is certified, complementary data, such as enclosure size and number of nesting dens, may be available on published papers and reports, or even in the institution's archives. Repetitive data can be used to crosscheck different data sources. Researchers face some challenges when collecting information, and those not attached to an institution may find their requests for data denied or subjected to copyright.

Each one of the available sources (the *IZY*, the International Tiger Studbook, zoological records collected through questionnaires and data published in papers and reports) was collected in slightly different ways, although most requested the same basic information. Institutional responses, however, may differ greatly and result in incomplete or scattered data. Overall, information on individual origins, births, deaths, enclosure characteristics and collection size will be provided by all databases. More detailed information, such as cause of death, medical treatments, transport-related issues (such as quarantine time and relocations) and aspects of husbandry (diet, number of keepers, use of contraceptives and manipulation of group size, to mention some), are rarely reported in standardised databases, but these data can be found in published reports or be requested directly to the institutions through questionnaires.

Recent efforts to keep an integrated and unique source have been proven fruitless, especially with the implementation of commercially exploited databases, such as the ISIS. The ISIS has been trying to standardise data collection and treatment, but records are not often retroactive and older datasets are still incomplete or may be unreliable. Data organised by the ISIS have restricted access (see Section 2.2.3).

For this research, I made use of three sources or institutional records: the studbook of tigers (*Panthera tigris*); the published records on the *International Zoo Yearbooks*; and individual reports from 19 collections. Due to copyright guidelines of the International Species Information System, it was not possible to access more detailed data, apart from the annual census published in the World Wide Web (ISIS 2003).

2.2.1. *Captive populations of carnivores and their implications for long term conservation.*

In Chapter 1, the role of captive populations in species conservation was discussed, and some examples of successful programmes that used *ex situ* techniques were described. But captive populations are restricted, and populational researchers frequently question if these small populations are actually self-sustainable on a long-term basis. One of the possible problems is the loss of genetic variability that can affect the viability of captive populations, and therefore compromise breeding programmes.

The minimum viable size of an animal population has been the subject of great controversy in the last years. Conservation researchers disagree on the adequate values, especially when comparing research on wild and captive populations. When considering only captive populations, for example, researchers may project species persistence, which involves genetic variability, for the immediate future (e.g. Earhardt *et al.* 2001), while researchers in the wild may project species persistence for 40 or 50 generations up to into perpetuity (Reed *et al.* 2003). Surveys on numbers of rare species in captivity show that these populations are far from reaching adequate numbers calculated for the wild (Table 2.1). In addition, a study on 13 species of carnivores suggested that the loss of genetic variability in captivity ranges from 3.1% (on the cheetah *Acinonyx jubatus*) to 22% (on the African hunting dog *Lycaon pictus*) over one generation (Earhardt *et al.* 2001). Considering that the average generation for these 13 species is 7.27 years, in only 100 years 13 generations will be produced and genetic variability may be severely reduced if not closely monitored and controlled.

Table 2.1: Minimum viable adult population size in the wild (MPVa), minimum viable adult population size in the wild corrected for 40 generations (MPVc), generation time in years (T) and population size in captivity (PC) in 2003 for five species of carnivores (Reed *et al*. 2003; Earnhardt *et al.* 2001; ISIS 2003).

Species	**MVPa**	**MVPc**	**T**	**PC**
Acinonyx jubatus	831	4036	5.9	1732
Canis lupus	1403	6332	7.05	896
Lycaon pictus	500	2229	-	476
Panthera leo	1023	5792	6.23	886
Panthera tigris	326	2377	7.5	253

In some species captive populations may recede, once they are not able to successfully breed in captivity and founders die of old age. For instance, the studbook keeper for the brown hyaena (*Parahyaena brunnea*) published a warning, in the 1970s, that the captive population of this declining species would disappear in the next decades (Shoemaker 1978; Shoemaker 1983). The numbers of captive individuals for the species published by the *International Zoo Yearbooks* from 1986 to 1996 seem to confirm the decline, while other large declining carnivores are apparently thriving (figure 2.2).

Captive populations can play a crucial role in conservation efforts, if genetically and demographically well managed. Institutions, on the other hand, should provide the most accurate information possible, since studbook keepers need this information to recommend breeding pairs with minimal genetic loss.

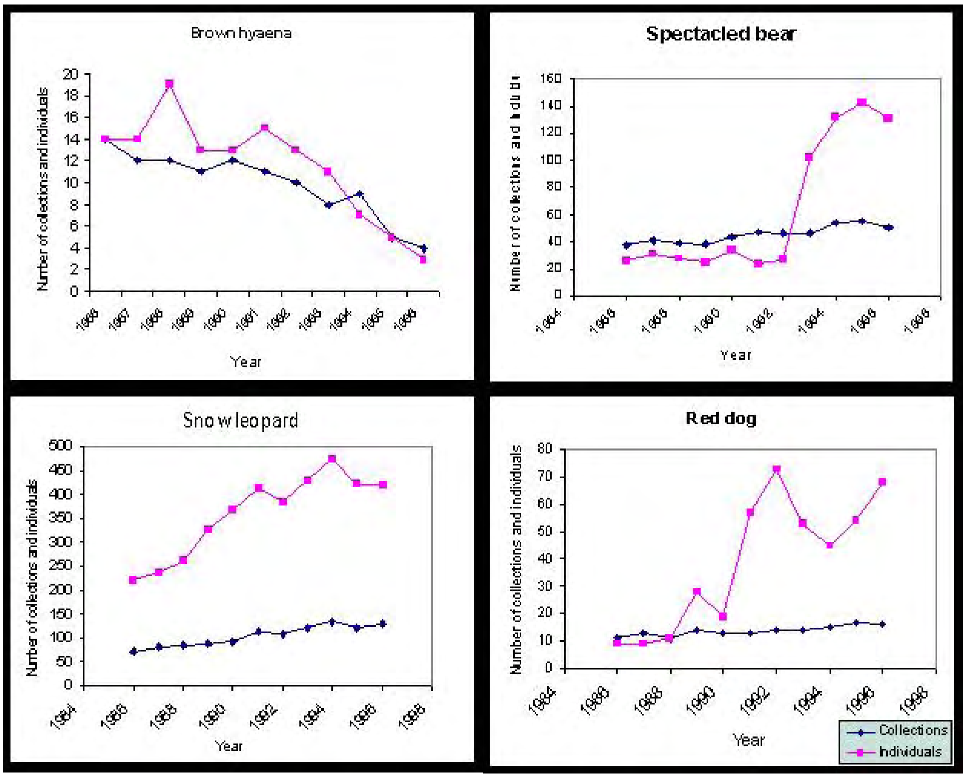

Figure 2.2: Number of collections keeping brown hyaenas (*Parahyaena brunnea*), spectacled bears (*Tremarctos ornatus*), snow leopards (*Uncia uncia*) and red dogs (*Cuon alpinus*), and total number of adult individuals reported to the *International Zoo Yearbooks* from 1986 to 1996.

2.2.2. *The International Zoo Yearbooks.*

The *International Zoo Yearbook (IZY)* was created by the Council of the Zoological Society of London in 1959, when an amount of £ 2000 was allocated to sponsor a publication aiming at zoological institutions worldwide (Olney 2003). For its first edition, Sir Zolly Zuckerman, then the Honorary Secretary of the Zoological Society, contacted personally hundreds of institutions around the world asking for papers and listings of animals and births, managing to receive information from more than 200 institutions (Morris & Jarvis 1960). From this date to 1996, the Zoological Society of London had been publishing, every year, the censuses of animals in captivity and the records of multiple births in captivity. This database today contains information from more than 600 zoos and aquaria worldwide, covering hundreds of species from all taxa, including some invertebrates. The records are pooled by institution by year, and the census are restricted to rare species, but it contains the number of young born and number of young which died before completing 30 days of age.

When the studbooks started covering most of the species presented in the *IZY*, the publishing of listings was abolished, and now the *IZY* publishes the list of studbook keepers, for those willing to contact them. Being absolutely free of charge, any institution wishing to add its information to the database was welcome to do it, and as a result a very large collection of data is available for the years in question. The *IZY* also published detailed information on collaborating institutions, including total number of species held and annual attendance. According to the Conservation Breeding Specialist Group from the World Conservation Union, there were over 5,000 zoological institutions registered in several associations of zoos and aquaria in 1996 (www.cbsg.org), and just over 1,200 reported to the *IZY* in that year. Non-English speaking countries report in even lower proportion: from the 120 institutions registered in Brazil in 1996 (www.ibama.gov.br), only nine contacted the *IZY.*

The main advantage of the *IZY* records is the amount of data, covering most of the captive population of vertebrates and the lack of bias towards wealthier institutions; its disadvantages include the impossibility of calculating litter sizes (for the data are pooled by institution and the number of breeding females is not reported), the possible failure to report stillbirths and observational mistakes (such as the failure of noticing young that were eaten by the dam before the litter was observed). Nevertheless, the *IZY* information is still the most reliable source for the calculation of the proportion of infant mortality in zoological institutions.

2.2.2.1. *The International Zoo Yearbooks datasets.*

There were two datasets collected for this research from the *International Zoo Yearbooks*: the first contains all births and infant deaths before 30 days of age, from 1986 to 1996, for 98 species of carnivores (see Appendix 1); the second contains the characteristics of all the 535 institutions (62% of all zoos and aquaria registered in the Zoological Society of London) that provided information used to calculate the values for Appendix 1 (see Appendix 2).

The dataset on births contained information on how many young were born and died before 30 days of age every year in each collection, adding to a total of more than 9000 reported events. A proportion of mortality was calculated for each species in each zoo, and from this the median proportion of mortality was calculated for each species, as seen in Appendix 1. There is also information on the origin of the collection, if wild-caught or captive-bred, but as the information is pooled, if a collection has only one wild-caught individual, it will be listed as captive-bred. The number of breeding females in each collection was not reported.

As the database from the *IZY* is not available in electronic format, and the input of data had to be done manually, only information from the last 10 years' published listings was collected. Also, by the end of the 1980s, most members of international organisations of zoo and aquaria followed standard husbandry practices, providing a similar diet, preventive medicine and maintenance routine, and so minimising the effect of these factors in the difference of results between institutions.

The main problem of this dataset is the impossibility of calculating the number of young per female, since all births in a given collection are pooled together, independent of the number of breeding females. Also, infant deaths are only counted when happened before 30 days after birth. From this dataset, it was possible to calculate the median proportion of infant mortality for each species that was used, together with life history information on carnivores collected by Gittleman (1983, 1986a, 1986b), to investigate biological factors that may affect breeding success in captive carnivores. Using the information presented in Appendix 2, it was possible to investigate the breeding performance of particular institutions and test the hypotheses that species from temperate areas may be affected by the latitude of the institution they are kept (cf. Chapter 4).

2.2.3. *The International Species Information System.*

The International Species Inventory System (ISIS) was created by Ulysses Seal and Dale Makey in 1973 as a means of standardising data collection for their research on comparative endocrinology of wild animals (Seal, Makey & Murtfeldt 1976). Its user-friendly interface and relative simplicity of data input quickly made the system interesting to other institutions, and in 1989, with its name changed to International Species Information System, it became the first worldwide collection system specifically designed for zoo records, holding the status of an independent organisation, with a Board of Trustees (Flesness 2003).

Presently, ISIS has more than 200 institutional members worldwide, but up to 90% of its members come from North America or Western Europe (figure 2.3). Its contents, however, are only fully available to its members, who are charged high prices to join. In 2003 these values range from US$ 955 to US$ 6355 for institutions (depending on the annual attendance) and US$ 955 to researchers. Independent conservation researchers (such as members of Taxon Advisory Groups or Conservation Specialist Groups) and studbook keepers are granted free access for data concerning only one species. ISIS and most studbooks are interconnected, and access to unpublished information may be subjected to the same copyright laws.

Poorer institutions can opt for an alternative form of payment, called General Operating Budget. To use this option, the institution has to calculate the general operating budget, including donated services from the government; the fee will be 0.1% of the budget of the institution to a minimum of US$ 440.

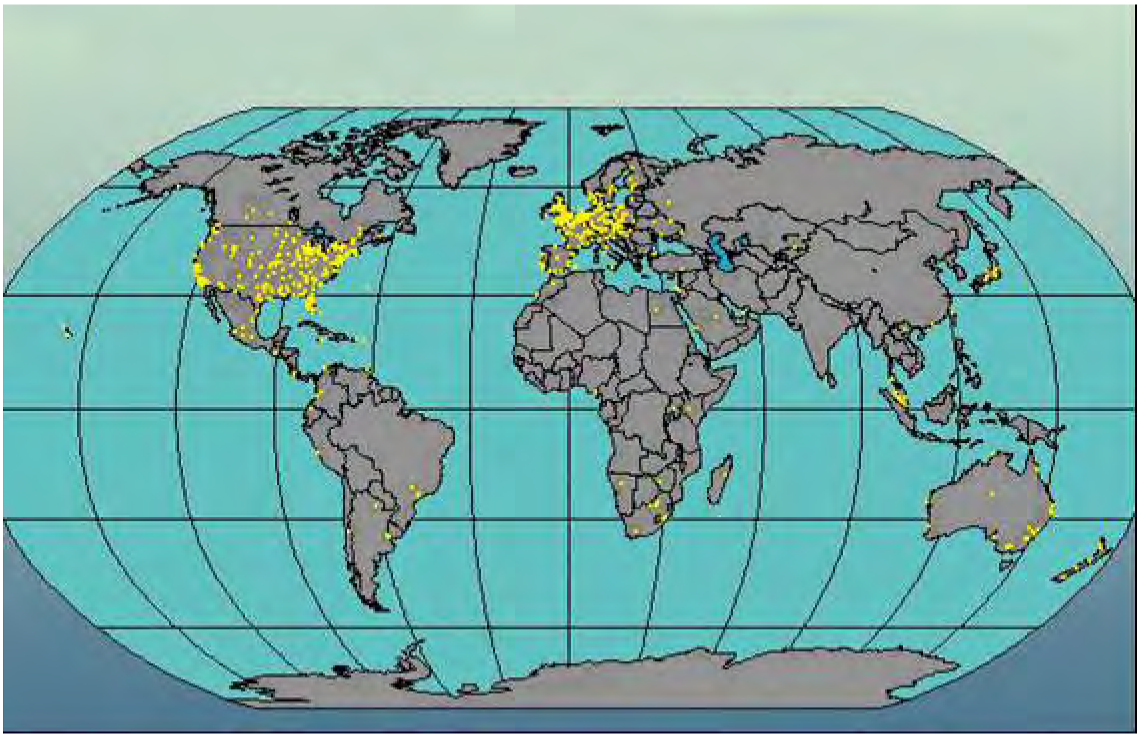

Figure 2.3: Distribution of institutional members of the International Species Information System (ISIS) in 2004, from www.isis.org.

Membership to ISIS includes a package of computer programmes that allow institutions to keep records and upload them online to the ISIS website (www.isis.org). These programmes were developed for the specific needs of record keeping by institutions. ARKS (Animal Records Keeping System) is the simplest of programmes and is suitable for maintaining simple specimen records; MedARKS (Medical Animal Records Keeping System) offers several options to keep veterinary records of collections; and SPARKS (Single Population Animal Records Keeping System) was developed specific for veterinary records, studbooks and Species Survival Plans, and have special features that allow genetic and demographic analyses (Flesness 2003). SPARKS is provided free for studbook keepers, and is the only ISIS computer programme that can be purchased by non-members. SPARKS provides a simple touch-button form which has preset options for some items, while allowing the input of original data for aspects such as name of the individual, parental identification or more detailed medical notes. SPARKS does not cover housing information or husbandry details.

The great advantage of ISIS is allowing a large amount of data to be immediately available for its members, and the homogeneity of information that is collected through its software packaging. Its disadvantage, however, involves the general bias found in zoological records (Rieger 1979), which leads institutions to tend to report more successful events than the unsuccessful ones. For example, an institution may not report the single stillborn young of a given female in one year, but report the successfully risen young born to the same female in the following year (Rieger 1979). This procedure can lead to mistakenly high breeding success levels to both the female and the institutions. Also, because of the large amount of options offered by its softwares, such as SPARKS, zoo staff tends to leave some of these options in their default positions. For example, SPARKS has an option to describe the cause of death of individuals, which is held in the default answer "by unknown means". Analysis of the tiger information from the studbook kept by Sarah Christie at London Zoo revealed that 88.16% of the events were described as this category.

The expensive membership fees of ISIS automatically bias its information as coming from wealthy institutions, hence the majority of members being located in North America and Western Europe. Traditional institutions, such as the Zoo Negara in Kuala Lumpur, Malaysia, which have been sending records for free to the Zoological Society of London, cannot spare resources for the fees and is out of the database, even when they keep and breed successfully some declining species, such as the Malayan sun bear (*Helarctos malayanus*) and the Persian lion (*Panthera leo persica*), among others.

For this research, ISIS was approached, through London Zoo, to give permission for the use of its records for tigers (*Panthera tigris*). Unfortunately, the access was denied because there was no connection between this research and any official conservation group at the time. However, the tiger studbook keeper, Ms. Sarah Christie (in 2000), provided her information for this research. The specific problems of this dataset will be discussed on section 2.2.4.1.

2.2.4. *International studbooks.*

The studbook system was created in the end of the 18th century, to keep breeding records of domestic stock, and started to be applied for wild species in 1932 (Glatston 1986). For some species of the order Carnivora, however, studbooks were not created until much later. For example, the first studbooks for the maned wolf (*Chrysocyon brachyurus*), bush dog (*Speothos venaticus*) and spectacled bear (*Tremarctos ornatus*) were published simultaneously in 1975, after their first appearance in the *IUCN Red Data Book* of 1972 (Roeben 1975).

Studbooks are primarily used, for captive populations of wild species, as the source of data for genetic and demographic management, while other sources, such as ISIS and surveys, are used for regional collection planning. ISIS data were once considered unsuitable for genetic management due to significant discrepancies with more detailed studbooks (Earhardt *et al.* 1995). The reply stated that studbooks also contained errors, especially on parental identity, but agreed that the raw data from ISIS needed thorough examination before analysis (Flesness *et al.* 1995).

The obvious suggestion for integrating both studbooks and ISIS in a single source was first made in 1986 (Glatston 1986) and was recently reiterated by an appeal to avoid duplication of data collection. The author points out, however, that before this can happen, ISIS has the challenge of becoming a more "open" system, allowing wider access to researchers and facilitating the subscription by the 500 institutions worldwide that are still not members (Flesness 2003).

In any case, studbooks are very useful tools in animal management, and the quality of data is improved by the personal involvement of the studbook keeper with the information. Once one institution sends a record to a studbook, the keeper will annually remind, sometimes three or four times, for the institution to keep sending records (Glatston 1986).

2.2.4.1. *The Tiger Studbook dataset.*

The dataset extracted from the electronic tiger studbook kept by Sarah Christie at the Zoological Society of London, was collected using the software SPARKS, from the International Species Information System (ISIS). It contains all births and infant deaths in 116 institutions mainly in the Northern hemisphere, during the period from 1986 to 1996. The records refer to two subspecies: the Sumatran (*P. tigris sumatrae*) and the amur or Siberian tiger (*P. tigris altaica*).

The dataset contains 249 litters born from 126 females (28 Sumatran and 98 Siberian), and there is additional detailed information for 43 females. There are data on the number of young born, date of birth, offspring that died up to 6 months old, date of death, litter size, litter rearing method (if reared by parents or by hand), inbreeding level and parental identity. There was no information on enclosure area or housing conditions (see Appendix 3). The cause of death of young is reported in less than 12% of the events. Studbook information is, as long as possible, checked by the studbook keeper. Mrs. Sarah Christie pointed out that older data might present some problems such as unreported litters, especially stillbirths. The identity of the female was reassured whenever possible. In any case, the data from the tiger studbook represent a large sample of the captive population, and the values calculated from it, such as proportion of infant mortality, litter sizes and peak of births, were used to investigate reproductive parameters of tigers in captivity, check subspecific breeding differences and test the hypotheses that inbreeding levels do not affect breeding success in captive tigers.

2.2.5. *Published records.*

Since the first publication of the *International Zoo Yearbooks,* curators of collections have been publishing small records and notes on the breeding and rearing of wild animals in captivity. For decades, these reports were purely descriptive of the events, and usually contain detailed information on several aspects of husbandry. Many of these reports give details not only on parental identity, date of birth and cause of death of young, but also on the housing conditions, diet, cleaning routines and isolation protocols. All the basic information found in studbooks is usually described, and when the young were removed for hand-rearing, also the techniques used and results obtained with the procedure.

Published records were used successfully before to produce a dataset for the research on stereotypic behaviour in captive carnivores, yielding significant results (Clubb 2001). The level of detail of the reproductive data presented in published papers and notes is higher than in the other, more formal, databases. Nevertheless, it is not possible to use this type of dataset to produce a general view of the proportion of infant mortality, since there is a strong bias towards successful reproduction on these records.

2.2.5.1. *The bibliographical dataset.*

Following the methodology described by Clubb (2001), several bibliographical searches were performed using electronic resources available at the University of Oxford, such as the Web of Science and the Oxford Electronic Reference Library (ERL) databases. The results were scrutinised for descriptions of the births of individual litters. In addition, all volumes of the *International Zoo Yearbooks* and the periodical *Zoo Biology*, where these reports are common, were examined. Papers that present pooled values for several litters or that did not clarify parental identity and date of births were not included in the dataset. This dataset differs from that compiled by Clubb (2001), which contains papers describing stereotypical behaviour in captive carnivores rather than breeding events. The dataset contains information from 141 papers and notes on captive breeding of carnivores, and presents data on: litter size; date of birth and death of young; parental age, origin and rearing method; area of enclosure; number of dens; area of dens (when available); cause of death of young; and isolation protocol for pregnant females (see Appendix 4). It also contains data on removal for hand-rearing and the cause for it. The dataset comprises 69 species, and has information on 447 litters born from 212 females between 1961 and 2000. There was no information on female body weight. Table 2.2 summarises the bibliographical data presented in Appendix 4.

Table 2.2: Species, number of litters, number of zoological institutions keeping the species and number of females summarised from the data compiled from bibliographical sources.

Family	Species	Number of litters	Number of zoos	Number of females
Canidae	*Alopex lagopus*	2	1	2
Canidae	*Canis familiaris*	1	1	1
Canidae	*Canis latrans*	2	1	1
Canidae	*Canis lupus*	9	3	3
Canidae	*Cerdocyon thous*	6	2	2
Canidae	*Chrysocyon brachyurus*	20	9	13
Canidae	*Cuon alpinus*	4	2	4
Canidae	*Dusicyon vetulus*	1	1	1
Canidae	*Lycaon pictus*	4	2	2
Canidae	*Otocyon megalotis*	1	1	1
Canidae	*Speothos venaticus*	5	3	3
Canidae	*Vulpes corsac*	5	1	2
Canidae	*Vulpes zerda*	7	3	4
Felidae	*Acinonyx jubatus*	22	13	16
Felidae	*Caracal caracal*	5	3	4
Felidae	*Catopuma temmincki*	22	2	5
Felidae	*Felis bengalensis*	8	2	2
Felidae	*Felis margarita*	10	2	2
Felidae	*Felis nigripes*	8	2	3
Felidae	*Felis pardalis*	1	1	1
Felidae	*Felis silvestris*	29	4	8
Felidae	*Herpailurus yaguarondi*	4	2	2
Felidae	*Leopardus geoffroyi*	15	4	6
Felidae	*Leopardus tigrinus*	7	2	3
Felidae	*Leopardus wiedii*	3	2	2
Felidae	*Leptailurus serval*	2	1	1
Felidae	*Lynx lynx*	10	3	7
Felidae	*Neofelis nebulosa*	15	4	5
Felidae	*Panthera onca*	4	2	3
Felidae	*Panthera pardus*	1	1	1
Felidae	*Panthera tigris*	9	3	3
Felidae	*Prionailurus viverrinus*	4	2	2
Felidae	*Uncia uncia*	11	4	5
Herpestidae	*Atilax paludinosus*	2	1	1
Herpestidae	*Cryptoprocta ferox*	1	1	1
Herpestidae	*Galidia elegans*	3	1	1
Herpestidae	*Helogale parvula*	14	2	3
Hyaenidae	*Crocuta crocuta*	4	3	3
Hyaenidae	*Parahyaena brunnea*	3	1	1
Mustelidae	*Amblonyx cinerea*	11	3	3
Mustelidae	*Arctonyx collaris*	1	1	1
Mustelidae	*Eira barbara*	3	2	2
Mustelidae	*Enhydra lutris*	9	4	5
Mustelidae	*Gulo gulo*	1	1	1
Mustelidae	*Lutra canadensis*	3	2	3
Mustelidae	*Lutra lutra*	7	2	4
Mustelidae	*Lutra perspicillata*	8	3	7
Mustelidae	*Meles meles*	2	1	1
Mustelidae	*Mellivora capensis*	2	1	2

Family	Species	Number of litters	Number of zoos	Number of females
Mustelidae	*Mustela nigripes*	2	1	1
Mustelidae	*Pteronura brasiliensis*	12	1	2
Procyonidae	*Ailurus fulgens*	9	3	4
Procyonidae	*Nasua narica*	4	1	4
Procyonidae	*Nasua nasua*	2	1	2
Procyonidae	*Potos flavus*	6	3	3
Ursidae	*Airulopoda melanoleuca*	11	6	7
Ursidae	*Helarctos malayanus*	12	3	5
Ursidae	*Tremarctos ornatus*	11	4	4
Ursidae	*Ursus arctos*	2	2	2
Ursidae	*Ursus maritimus*	11	4	4
Viverridae	*Arctictis binturong*	13	5	5
Viverridae	*Arctogalidia trivirgata*	1	1	1
Viverridae	*Fossa fossa*	1	1	1
Viverridae	*Genetta genetta*	1	1	1
Viverridae	*Hemigalus derbyanus*	1	1	1
Viverridae	*Paradoxurus hermaphroditus*	4	1	1
Viverridae	*Prionodon linsang*	1	1	1
Viverridae	*Viverra civetta*	9	1	3
Viverridae	*Viverra zibetha*	2	1	1

The main problem with this dataset is the lack of standards in data collection and presentation. As most of the reports follow the author's discretion, some papers will contain more detailed information than others, and the dataset will not present all variables for all species. Nevertheless, many of these papers contain data that is not available in any other source, such as detailed maternal behaviour, cause of death of the young and some husbandry protocols. The bibliographical dataset was used to investigate the causes of death of young captive carnivores and test the hypotheses that some biological factors, such as altriciality, may influence the occurrence of maternal infanticide.

2.2.6. *Zoological institution records.*

Zoological institutions keep records for all their specimens, including breeding notes that are fundamental for the management of collections. Recent records are usually readily available to the registrars of the collections, once the notes on many individuals that have been in exhibition for a long time may be needed for medical purposes. Most institutions, nowadays, are transferring the data from record books to computer programmes such as SPARKS, sometimes to the detriment of some detail of information.

Traditionally, institutions keep records in a diary format, recording every single event on the life of the specimen, from vaccinations and ailments to notes on unusual behaviours (such as stereotypical pacing, excessive aggressiveness towards the keeper or changes in appetite). Female oestrous and mating are recorded when observed, as are the births and deaths of young. The animal keepers have the responsibility of keeping these records, and standardisation of the data varies greatly among institutions. Some data are fundamental and can be found, in different formats, in all institutional records, and provides a more detailed view of the conditions in which the animals are kept.

2.2.6.1. *Dataset collected through questionnaires.*

For this present research, 135 zoological institutions worldwide, corresponding to over 15% of zoos and aquaria registered at the Zoological Society of London, were contacted and invited to complete an electronic questionnaire. The questionnaire, a Microsoft Excel Workbook, asked for information in studbook format, with parental identification, date of birth, litter size, number of young dead, date and cause of death, and method of rearing, i.e. if the young were mother- or hand-reared (see sample in Appendix 5). Additional information on enclosure size, number of dens per enclosure, number of keepers and age, and origin of the breeding individuals was requested. As required by the institutions prior to sending the information, the identity of the females and the institutions had to be preserved and could not be printed in the dataset, being replaced by codes (Appendix 6).

To make this dataset congruent with the others in this research, and to facilitate the collection of data by the collaborating institutions, only the data from 1986 to 1996 were requested.

This dataset is restricted to nine species: red panda *Ailurus fulgens*, meerkat *Suricata suricatta,* tiger *Panthera tigris*, snow leopard *Uncia uncia,* wolf *Canis lupus*, oriental small-clawed otter *Amblonyx cinereus,* brown-nosed coati *Nasua nasua,* polar bear *Thalarctos maritimus* and maned wolf *Chrysocyon brachyurus*. The choice of species tried to reflect the diversity of habits and habitats of the Order Carnivora, and was also based in the possibility of acquiring information on the largest possible number of females, which is more probable in species with larger captive populations.

Unfortunately, only 16 institutions, comprising 31 collections, answered the request for filling the questionnaires, a response rate of less than 12%. Another 6 institutions agreed to participate but, to this date, did not return the questionnaires despite occasional reminders. Only two institutions declined participation due to lack of staff or management transition.

The dataset from the 31 collections contains 148 litters from 63 females of nine species. The cause of death of the young was reported in 61.5% of the cases.

The main drawback in this dataset was the very low level of response from the institutions, which made this dataset the smallest collected. Also, the complexity of the data discouraged the appropriate filling of the questionnaire, due to the need of reading protocol books frequently stored away in the institutions archives and the high time demand. A larger dataset, apparently, would need to be collected personally in each institution. Nevertheless, reliable information on the number of keepers, cage area, number of dens and distance travelled by the female is available in this dataset, allowing the hypotheses that husbandry protocols have an effect on the breeding success of captive carnivores to be tested.

2.2.7. *Summary of data.*

To avoid data duplication, the variables extracted from different sources were not the same, in a way to complement the information required for analysis. Also, complementary information was taken from other sources, such as range of latitude (Wilson & Reeder 1993), conservation level (IUCN 2002b) and biological information (Gittleman 1983, 1986a, 1986b). A summary of the variables extracted from each source and the level of duplication can be seen on Table 2.3.

For the analysis in Chapters 4, 5 and 6, some variables regarding the biology of the species were used. From Gittleman (1986a, 1986b), the variables were: gestation length; weaning age; age when the young open their eyes; female body weight; species body length; type of zonation (e.g. terrestrial, arboreal, aquatic); type of vegetation (e.g. open grassland, forest, desert); and type of diet (e.g. carnivorous, omnivorous, vegetarian). The data on delayed implantation comes from Mead (1989), and the information on juvenile mortality in the wild was presented by Gittleman (1983) in his unpublished doctoral thesis.

Table 2.3: Summary of the data used in this research, the variables extracted from each one, the sources of data, the chapters in which they were used, and the level of duplication found between datasets.

Dataset)	Variables (sources)	Duplication	Chapter
Appendix 1 (98 species)	Proportion of infant mortality, number of zoos holding the species (*IZY* vols. 26-35); conservation level (IUCN 2002b); range of latitude distribution (Wilson & Reeder 1993)	Basic dataset; encompasses the largest amount of data.	4 & 7
Appendix 2 (535 zoological institutions)	Number and type of species held, number of veterinarians and staff; presence of research staff; size; annual attendance; type of management (*IZY* vols. 30-35); latitude (calculated with software).	Complementary to the data on Appendix 1. The index of zoo performance (see section 2.3.3) was calculated using the proportion of infant mortality from Appendix 1.	4 & 7
Appendix 3 (1 species; 249 litters; 126 females)	Zoo; date of birth of litters; sire and dam; place of birth, rearing, number of transfers and age of dam; number and sex of young born and dead; age and cause of death of young; type of litter rearing; inbreeding level of the young (Mrs. Sarah Christie, International Tiger Studbook Keeper)	Over 90% of the births reported in the studbook are also reported on the *IZY*, although the studbook reports litters separately. From this dataset was possible to calculate female breeding success instead of infant mortality.	3
Appendix 4 (69 species; 447 litters; 212 females)	Zoo; origin, rearing and age of dam; litter size; number of dead young; cause and age of death of young; few present cage area, number of individuals per cage and number of dens; presence of male (141 papers published in several scientific journals from 1961 to 2000)	Some of the written reports are accounted for in the *IZY* and studbook datasets. The analysis was done exclusively with variables from this dataset, and the proportion of infant mortality was calculated for each female.	5 and 6
Appendix 6 (9 species; 148 litters; 63 females)	Age of sire; age, origin and rearing of dam; distance travelled by the dam; litter size; number and age of dead young; few present cause of death of young; number of keepers; few present cage area and number of dens (electronic questionnaires sent to institutions)	All the litters were accounted for in the *IZY* dataset, but it was possible to calculate female breeding success. Bonferroni corrections were applied when necessary.	7

2.3. *Methods of collection and analysis of zoological records.*

As seen in the previous sections, animal records can present many discrepancies between different sources. This is understandable since different databases have information from different groups of collections (for example, there are 535 institutions in the *IZY* dataset, but only over 200 in the ISIS census for 2003), although subgroups of data may overlap. They can provide, nevertheless, large samples of captive populations and can be crosschecked, in a way of verifying data reliability. For example, the overlapping information between *IZY* and the tiger studbook can be checked for the total of animals born every year or number of animals held. During the compilation of the datasets used in this research, discrepant data, comprising less then 1% of the total, were discarded. Also, pooled reports in the annual *IZY Records of Multiple Births* (represented by (b), to signify that a litter of unknown size died immediately after birth and was consumed by the dam) and incomplete data (e.g. when the number of dead animals was not printed by mistake) did not enter in the final datasets. This method of "cleaning" the data helps to minimise errors and is often used when preparing demographical datasets for human populations (Chatfield 1991). The input of data into electronic datasets must be meticulously made, and simple sums of columns and rows suffice to avoid typing errors.

There is not a standard way to treat animal records. Frequently these records are used on the research of inbreeding effects (e.g. Laikre *et al.* 1996 on brown bears *Ursus arctos*, and Wielebnowski 1996 on cheetahs *Acinonyx jubatus*), but were also used to calculate the effect of housing (Carlstead *et al.* 1999), individual behaviour (Carlstead, Mellen & Kleiman 1999) and rearing experience (Ryan *et al.* 2002) on breeding success, with very significant results. Care must be taken, however, on the multiple analysis of the datasets to assure that they represent a significant range of variance on the populations before any conclusions are made.

2.3.1. *The bias of data: adjusting the numbers.*

Zoological records tend to be biased for institutions that perform research and have breeding pairs, and perhaps even for those who managed to successfully produce young, once unsuccessful reproductions are, sometimes, not reported to international record keepers (Rieger 1979). Also, the cryptic nature of many species, together with the design of some enclosures, does not allow keepers to be aware of all births. Many females in captivity are overweight, and pregnancy can pass unnoticed, as it has happened with the oriental small-clawed otter *Amblonyx cinerea* (Leslie 1970).

In this way, these samples from animal databases are likely to represent observed births in wealthy zoos that are successful in breeding carnivores. The low participation of zoological institutions of poorer countries, as seen in the case of Brazilian zoos, is an example of this bias. Still, these institutions have very different characteristics that can be tested in the search for the factors that affect infant survival in captive carnivores.

2.3.2. *Record research and sex ratio.*

Zoological databases for captive populations could be excellent sources for the research on sex ratio of many species. In this research, however, it was found that this type of data was not reliable in the datasets analysed.

Many birth reports contain young of undetermined sex, which were observed but could not be handled up to the time of publication. Researchers discard litters that contain unsexed individuals (Faust & Thompson 2000), but it has been pointed out that there are occasions where the mother consumes some young of a large litter right after birth. This could easily pass unnoticed by keepers, and the reported litter would be included in the analysis (Rieger 1979; Christie, pers. comm.). In the datasets used in this research, the proportion of young of undetermined gender varies greatly (Table 2.4). Within the dataset collected from the *IZY*, the variation is also high between families, being the proportion of unsexed young higher in the families Procyonidae, Mustelidae and Herpestidae, which contain small species frequently housed in groups. In species with communal rearing of the young, common in these families, manipulation of the young is discouraged and it is difficult to identify the gender before 30 days of age.

Table 2.4: Total number of young born, young of undetermined sex and proportion of young of undetermined sex in the several datasets used in this research.

Dataset	Taxa	Number of young born	Young of undetermined sex	Proportion of young of undetermined sex
Bibliographical dataset	69 species	1144	513	44,84%
Tiger studbook	*Panthera tigris*	670	70	10,44%
Census of multiple births from the *IZY* vols. 26-35	Felidae	11595	2282	19,68%
	Ursidae	2083	568	27,26%
	Viverridae	788	246	31,22%
	Canidae	7891	2474	31,35%
	Hyaenidae	406	138	33,99%
	Procyonidae	3605	1278	35,45%
	Mustelidae	4067	1735	42,66%
	Herpestidae	3372	2088	61,92%

Although the proportion of unsexed young is relatively low in the tiger studbook, the studbook keeper, Mrs. Sarah Christie, pointed out that this data is not reliable and she was still in the process of confirming the gender of the surviving individuals. The questionnaires sent to the zoological institutions asked for this information, but only one of the institutions provided this data.

2.3.3. *Relative indices as dependent variables.*

In a zoological institution there are many factors that may have potential effects on the behavioural and physiological condition of the animals. Because of this, it is appropriate to calculate relative indices that consider the possible husbandry differences between institutions, allowing the effect of other factors to be analysed. The following equations were developed for this research and are tailored to overcome specific problems of the datasets collected and analysed here.

The basic measurement on the research of infant survival is the proportion of young that died before 30 days of age, as published in the database from *IZY.* For the species, infant mortality will be the median of the proportion of mortality of each institution or female (equation 2.1), once there could be an effect of husbandry techniques or individual differences.

$$I = median[(\delta / \beta)_{\alpha\eta}...(\delta / \beta)_{\alpha\infty}]$$

Equation 2.1: Infant mortality in a species (I), where δ = total number of young dead ; β = number of young born in the in the same period of time; and $\alpha\eta\ldots\infty$ = each one of the collections or females in the database.

Breeding success can be measured in many different ways. Some authors calculate breeding success including unsuccessful mating attempts, in order to assess male energy expenditure (Ilukha, Harri & Rekila 1997), and others consider infant survival a good measurement of successful breeding (Durant 1999).

For this research, females of the same collections were not considered independent, due to husbandry practices. To overcome this problem, an index of infant survival, or breeding performance, was calculated (equation 2.2). The result balances the possible confounding effect of husbandry when testing the effect of biological factors.

$$B = \frac{\beta - \delta}{\psi * \phi}$$

Equation 2.2: Female breeding performance (B), where β = total number of young born in a given period of time in an institution; δ = total number of young dead in the same period; ψ = number of years of the given period of time and ϕ = number of breeding females in that institution for the same period of time.

To understand if institutional characteristics are affecting infant survival, and taking into consideration that species have different I values, the institutional performance (equation 2.3) will give an overview of how the institutions are with all species of carnivores, of local range or imported, independent of the environmental factors, such as photoperiod, that could affect breeding in foreign species.

$$Z = \sigma / \zeta$$

Equation 2.3: Institutional performance (Z), where σ = Number of species in an institution with higher infant mortality than the value of I for the species; and ζ = total number of Carnivora species held in that institution.

The use of relative indexes to overcome statistical pitfalls such as pseudoreplication (Hurlbert 1984) can help focus analytical efforts in measuring the effect of known factors.

2.3.4 *Testing for phylogenetic effects.*

One of the major problems when working with several species is the possibility of phylogenetic effects in the results. Until the end of the 1970s, researchers usually took a straightforward approach when dealing with traits of several species, regardless of taxonomic levels, which led to erroneous generalisations (Harvey & Pagel 1991). A classic example is presented by

Harvey & Clutton-Brock (1985): a study presented results for mammals when 82% of the species used in the analysis were rodents, which made the results valid only for this taxon rather than all mammalian species. Ignoring phylogenetic effects in comparative studies can lead to type I and II errors, and if the data reflects a structure phylogeny, with little independence, the results can be misleading (Gittleman & Kot 1990).

To avoid these problems it is paramount to establish the independence of data and examine which percentage of the variance in the data is accounted for at different taxonomic levels (Gittleman & Luh 1992). There are several methods for checking this relation, including nested analysis of variance (Harvey & Clutton-Brock 1985) and autocorrelation statistics such as Moran's *I* (Gittleman & Luh 1992).

In this research, some comparative analysis was used in the search of whether biological aspects affected reproductive success in captive carnivores. A problem that rises in the data collected from zoological institutions is that it is not possible to cover the majority of major taxa, once not all species are kept in captivity. There are, however, data on other families of Carnivora, although not as abundant as Felidae. However, analyses of certain aspects of breeding in close taxa do not imply that these results are unimportant or invalid; care must be taken not to generalise results in a varied group such as the carnivores, but these results may point out patterns within families or, in special cases, within a species.

Table 2.5 presents a nested analysis of variance including the biological variables used in statistical models in this research. Most of these variables show independence from the genus level or below, and as phylogenetic methods reflect a more extreme form of analysis (Gittleman & Luh 1992), it was decided that a straightforward method would be adequate in this case.

Table 2.5: The percentage of variance in the data accounted for at successive taxonomic levels by each variable used for testing hypotheses. The results are based on a two-level nested ANOVA with unequal sample sizes. Apart from the age of young opening their eyes, most variance resides below the level of genus, and the response Proportion of Infant Mortality in Captivity is mostly specific.

Taxonomic level:	**Family**	**Genus**	**Species**	**Genus and below**
Variable:				
Gestation length	0	79.67	20.33	100
Proportion of infant mortality in captivity	0.58	71.97	27.45	99.42
Weaning age	30.21	0	69.79	69.79
Female weight	45.35	0	54.65	54.65
Opening eyes	67.03	27.44	5.52	32.96

It is important to point out that the results in this research shall not be generalised for all Carnivora species. For each test, the taxa more likely to behave as the results point out will be specified.

2.4. *Conclusion*

Captive population records have been helping to understand specific demands for better management practices, that can affect breeding success, genetic variability and, ultimately, the long term survival of captive populations. Conservation efforts should, before spending too many resources in *ex situ* programmes, consider the actual possibilities of captive populations with the help of animals databases. Research would benefit, however, from the creation of a single system of data management, incorporating records from studbooks, ISIS and detailed information from the collections, but also from a better, wider access to the databases already available.

At present, the reliability of the data is still low, but there are precautions that can be taken to minimise the error and allow relevant analysis to be performed.

This research is based in a very small sample of the total information available, for thousands of species, in the databases described in this chapter. With the technological advancements rapidly being adopted by institutions all over the world, data quality and quantity will rise. Even today, these resources must be better explored, because captive populations can decline within a decade. Conservation efforts involving captive populations are very recent, and unless the real status of these populations is known now, some species may not have the genetic backup to start new populations in the near future.

Chapter 3

Factors affecting breeding in captive tigers (Panthera tigris)*: A studbook research*

Abstract

Data from the International Tiger Studbook was analysed, comprising 249 litters born from 126 females of Siberian (*Panthera tigris altaica*) and Sumatran tigers (*P. tigris sumatrae*) from 116 institutions, mostly of the Northern hemisphere. Births peaked in the month of May; the average litter size was 2.72 cubs per litter, and the average age of breeding females was 6.2 years. Female age did not have a statistically significant effect over litter sizes or proportion of infant mortality. In average, young died before the end of the third week. The median proportion of infant mortality in this dataset was 68%. There was no significant difference between Siberian and Sumatran subspecies in the number of litters produced by each female, in the interbirth interval or in the female's average number of litters per reproductive year. Also, there was not a subspecific difference in the proportion of infant mortality and heterozygosity. Sumatran tigers produced smaller litters and less young in 10 years. Sumatran cubs died significantly earlier than Siberian cubs. In both subspecies, litter size had an effect on infant mortality, and infant mortality was higher in litters born in the autumn. Institutions with a history of poor breeding of other Carnivora species also performed poorly with tiger breeding, but there was no effect of ongoing research on infant mortality. There were no detectable effects of inbreeding or female origin in infant mortality, although a larger sample size would be required.

3.1. *Introduction.*

Tigers (*Panthera tigris)* comprise the largest captive population of all declining species of the order Carnivora. Today, with over 1,000 individuals, including subspecific hybrids, the species is held in more than 400 collections (ISIS 2003). All five persistent subspecies (Siberian or Amur tiger *P. t. altaica,* Amoy tiger *P. t. amoyensis*, Indo-Chinese tiger *P. t. corbetti,* Sumatran tiger *P. t. sumatrae* and Bengal tiger *P. t. tigris*) are kept in separated collections and supervised by studbooks (Olney & Fisken 2003).

In this chapter, studbook data from two subspecies of tiger, *P. t. altaica* and *P. t. sumatrae*, were compiled and analysed, so as to compare reproduction parameters in the captive population with wild populations. Also, the effect of certain aspects of the biology of the species and husbandry conditions in the reproductive success of females was tested through statistical models (see section 3.4). The results reaffirm the importance of record research in the management of captive populations and may help the development of more effective husbandry protocols.

3.2. *Tiger status and conservation in the wild.*

According to the World Conservation Union (IUCN), the species as a whole is endangered, with an observed continuous decline through loss of habitat and poaching, and do not possess any subpopulation with more than 250 mature individuals. Three subspecies (Siberian, Amoy and Sumatran tigers) are singled out as critically endangered, meaning that they are at extreme risk of extinction. In the case of the Siberian tigers, the population of mature individuals was estimated at less than 250, and at less than 50 individuals for the Amoy tiger (IUCN 2002). During the 20th century, three subspecies became extinct: the Bali tiger *Panthera tigris balica* in the 1940s, the Caspian tiger *P. t. virgata* in the 1970s, and the Javan tiger *P. t. sondaica*, as recently as the 1980s (Jackson 1998).

International conservation efforts started in 1994, when the Global Tiger Forum, a conference from 11 countries where the tiger occurs, took place in India. However, since the 1970s, smaller regional programmes started warning about the rapid decline of the species and campaigns were set up against the use of tiger parts, to try to stop commercial poaching (Weber & Rabinowitz 1996).

The maintenance of a commercially exploited species in poor countries faces many problems. For example, the profits of poaching tigers are very high, especially for the people living in poor conditions and without an economically viable alternative to support themselves (Saberwal 1996). Poaching activities on tiger populations peaked in the beginning of the 1990s, when the demand for tiger parts grew due to an increase in the use of traditional Chinese medicine, and only stopped growing after intense governmental intervention (Karanth & Madhusudan 1997). In 1995, researchers predicted, through mathematical models, total extinction of the species in the wild in just over one decade, if poaching was not drastically reduced (Kenney *et al.* 1995).

Human populations usually surround natural reserves, and cattle are frequently raised within the range of the tiger population. Cattle predation by tigers is an economical problem in rural areas in China (Zhang *et al.* 2002), Bhutan (Dorji & Santiapillai 1989) and India (Veeramani, Jayson & Easa 1996). Human-tiger conflicts over space due to the growing human population and the development of lands have been reported in Russia (Tkachenko 1997) and India, where there are reports of human casualties by tigers (Sukumar 1994; Veeramani, Jayson & Easa 1996, Saberwal 1996).

It has been suggested that extinction of small populations occurs by loss of genetic variability and fluctuations in demographic factors, and that population sizes are the main predictor of population extinction over time (Lande 1988). However, detailed statistical analysis of published and unpublished population reports for 10 species of large carnivores suggested that conflict over space between humans and these species is the main cause of mortality in wild populations; farmers and settlers at the edges of nature reserves were responsible, accidentally or not, for the majority of the mortality in large carnivores. Conservation efforts should thus focus largely in this aspect, especially in the case of small reserves with wide-ranging species (Woodroffe & Ginsberg 1998).

The use of land surrounding tiger territories by people can also affect tiger population over time. For example, cub survival is higher in areas with few or no roads than in areas with primary and secondary roads. Also, human disturbance reduces prey consumption and time spent on prey site, leading the animals to wander even further in their ranges (Kerley *et al.* 2002).

Humans can also compete with tigers directly for prey. In Nepal, one tiger lost ten kills to humans in an eight-month period; the tiger was driven away from the kills by humans, which then removed the carcasses from the reserve area (Sunquist & Sunquist 1989).

The effect of human-tiger conflict in tiger conservation is very strong and should be addressed at the beginning of any conservation programme. The political implications of this issue were the focus of discussion among conservation scientists in the end of last decade. In India, local human populations are generally unsupportive of conservation actions. Tigers are seen as dangerous animals that kill cattle and villagers, and nature reserves are often full of resources which the people lack (Saberwal 1996). The Indian government and conservation groups, working as part of an international effort, support the creation of a few completely inviolate areas for tiger conservation, which means relocating people and heavily securing the protected area to inhibit poaching, before the total disappearance of the species in the wild (Karanth & Madhusudan 1997). In any case, human-tiger conflict seems to be leading these carnivores to either total extinction in the wild within the next two decades, or to their confinement to small isolated populations that will not persist in the long term.

In the Royal Chitwan National Park, in Nepal, conservation efforts have been in practice for decades, and have focused frequently in the human populations surrounding the Park. As a result, tiger density in the park is the highest of the world, and the carnivore's presence seems to have also improved the population of other species in the park (Gittleman *et al.* 2001).

3.3. *Tiger conservation in captivity.*

While wild tigers are quickly and inescapably disappearing, the attention of researchers has been turning to the captive population and its potential to preserve the species. For two subspecies, the Siberian and the Amoy tigers, the reported captive population exceeds estimated numbers in the wild (Table 3.1).

Captive breeding programmes for all tiger subspecies are run in more than 200 institutions around the world (Olney & Fisken 2003), since the viability of the captive population, for some, seems higher than the small, scattered remnants of wild populations. For instance, the Amoy tiger is the most critically endangered of these subspecies, with a wild population estimated as less than 50 individuals scattered in isolated pockets of habitat. It has been suggested that the subspecies is very close to extinction, and the captive population, although coming from only 6 wild-caught founders, may be the only alternative for Amoy tiger survival (Tilson, Traylor-Holzer & Jiang 1997).

Table 3.1: Estimated numbers in the wild and reported captive populations of tigers *Panthera tigris*; captive population numbers do not include individuals of unidentified gender (Jackson 1998; Olney & Fisken 2003; ISIS 2003)

Subspecies	**Estimated wild population in 1998**	**Captive population in 2000 (studbooks)**	**Captive population in 2003 (ISIS)**
P. t. altaica	360 – 406	466	365
P. t. amoyensis	20 – 30	51	Not available
P. t. corbetti	1227 – 1785	26	88
P. t. sumatrae	400 – 500	162	143
P. t. tigris	3176 – 4556	206	244
Totals	5183 – 7227	911	840

In the case of Sumatran tigers, official efforts started only in 1994, with the publication of the Indonesian Sumatran Tiger Conservation Strategy by the Ministry of Forestry of Indonesia. This document gave rise to a great number of multinational programmes, although researchers have pointed out how *in situ* and *ex situ* programmes must collaborate closely, for an international effort of this magnitude to be effective (Tilson *et al* 1997).

One specific problem faced by *ex situ* programmes is the limitation of resources, especially related to housing. In a survey of 1990, an estimated 1000 spaces existed in institutions worldwide, for tigers of all subspecies. Dividing them equally between subspecies would benefit the preservation of individual subspecies, while allocating more spaces to the subspecies with higher genetic variability would help the conservation of the species as a whole (Maguire & Lacy 1990). The development of assisted reproduction techniques, such as cryogenic preservation of gametes and embryos, can help solve the problem by allowing the production of embryos from the present population; preserved, these could be implanted, when needed, in surrogate mothers (Donohue *et al.*1990). Tigers have been intensively researched in these aspects and the first technical protocols are achieving positive results (e.g. Byers *et al.* 1990; Donohue *et al.* 1992; Donohue *et al.* 1996; Crichton *et al.* 2003).

Recently, researchers have discussed new priorities on tiger conservation. Earlier approaches focused on keeping a viable population for each of the five tiger subspecies in the wild, but genetic analysis showed that there is very little difference between the four continental subspecies of tiger, and only the Sumatran tiger, an island subspecies, has significant genetic differences from the continental subspecies (Ginsberg 2001).

Conservation *ex situ* has been the subject of controversy among researchers. Some view zoological institutions as Noah's Ark (the "Ark Paradigm") and believe that all declining species can be preserved through re-introduction of zoo-bred animals (Gippoliti & Carpaneto 1996); others sensibly point out the high costs of this type of programme, adding that they should be used in extremely rare situations and the indiscriminate re-introduction of captive-bred animals can be responsible for disease outbreaks in wild populations (Snyder *et al.* 1996). For a species, such as the tiger, whose ecological demands of large areas and abundant prey lead to conflict with human populations, re-introduction programmes have to be very carefully planned and managed, or the new populations will face the same pressures of the original ones, and also disappear. As pointed out recently by researchers, captive breeding and re-introduction programmes for large carnivores cannot bring about population recovery if the species has declined because of habitat destruction (Woodroffe 2001).

A species as high in the trophic chain as the tiger may soon enough be displaced by its human competitors, and may become exclusive to zoological institutions and breeding centres. This captive population, if well managed, can persist for long periods of time with minimum loss of genetic variability. It is important, though, to understand the biological patterns of this population for optimal management, especially related to husbandry techniques.

Studbooks are fundamental for conservation programmes and have been used as sources of reliable data for the research into several aspects of captive breeding in carnivores (c.f. Chapter 2), and also can provide data to the construction of mathematical models and simulations that can be applied for wild populations (Wildt, Howard and Brown 2001).

The importance of studbooks to the conservation of large carnivores is exemplified by the management plan for the African lion subspecies in North American zoos. Of the two subspecies identified in the captive stock, *Panthera leo krugeri* and *P. l. nubicus,* only *P. l. krugeri* had breeding potential to take part in a future *ex situ* conservation programme. Furthermore, with the widespread occurrence of feline immunodeficiency virus (FIV) and canine distemper in North America, the species survival plan recommended only tested individuals to be included in breeding loans and programmes, in an attempt to contain the spread of these diseases (Shoemaker & Pfaff 1997).

Biological information on captive populations may help to understand the biology of the species in the wild, at least for some species. For example, one of the most endangered of Carnivora species, the giant panda *Ailuropoda melanoleuca* has more than two decades of records in studbooks. In one study, researchers monitored the breeding biology of six wild female giant pandas. The results were compared with data from studbooks, in aspects such as litter size, interbirth interval and reproductive life span and found no difference between captive and wild counterparts (Zhu *et al.* 2001).

3.4. *Hypotheses to be tested*

I use the tiger studbook as a model to address the possibility of answering biological questions with record research. I point out that the tiger is a species with a large latitudinal range (Wilson & Reeder 1993) and does not seem to be strictly seasonal (Byers *et al.* 1990; Smith & MacDougal 1991), thus excluding photoperiodic effects in breeding. Considering that there are abundant food and water in captivity, and that serious institutions have to provide adequate housing to their animals, it is not expected that biological parameters, such as litter size, differ from wild populations. There are genetic, phenotypic and geographical differences between the two subspecies in the studbook (Ginsberg 2001), so it is expected that the dataset will reflect these differences on some biological parameters and express the need of subspecies-orientated husbandry protocols. I hypothesise also that there will be little or no effect of inbreeding levels in this species for, like several carnivores, it presents high levels of homozygosity in wild populations (Shivali, Jayaprakash & Patil 1998).

3.5. *Methods.*

In this research, data from the Tiger International Studbook were compiled and statistically analysed using the computer programmes MINITAB v. 13 and SPSS v.11. The dataset extracted from the electronic tiger studbook kept by Sarah Christie at the Zoological Society of London, was collected using the software SPARKS, from the International Species Information System (ISIS). It contains all births and infant deaths in 116 institutions mostly in the Northern hemisphere, during the period from 1986 to 1996. The records refer to two subspecies: the Sumatran (*P. tigris sumatrae*) and the amur or Siberian tiger (*P. tigris altaica*).

The dataset contains 249 litters born from 126 females (28 Sumatran and 98 Siberian) over 10 years (1986-1996), and there is additional detailed information for 43 females, such as place and date of birth, parentage and number of transfers. There are data on the number of young born, date of birth, offspring that died up to 6 months old, date of death, litter size, litter rearing method (if reared by parents or by hand), inbreeding level and parental identity. There was no information on enclosure area or housing conditions (see Appendix 3). The cause of death of young is reported in less than 12% of the events. There was no data on female body weight.

Studbook information is, as long as possible, checked by the studbook keeper. Mrs. Sarah Christie pointed out that older data might present some problems such as unreported litters, especially stillbirths, and that the data on the gender of the young may be unreliable, misleading sex ratio calculations. The identity of the female was reassured whenever possible. Although the interbirth interval could be calculated for 64 females, many institutions house animals of different genders separately, only occasionally gathering them for breeding, while others do not allow females to breed more than once a year. Housing protocols can therefore influence this result.

The dependent variables for regressions were the proportion of infant mortality for each female (***I***, calculated by equation 2.1, cf. Chapter 2), transformed by the arcsine of the square root; female breeding performance (***B***, see equation 2.2); the overall breeding success of the institution (***Z*,** see equation 2.3) and the absolute litter size.

For the statistical tests, litters with uncertain numbers of individuals were not considered. The discarded data comprised 0.76% of the information available on the studbook. Young of undetermined gender comprised 10.44% of the dataset; however, as pointed out by Mrs. Sarah Christie, this information should not be relied on.

As the tests done in this chapter refer to the same population, it is necessary to correct for multiple tests. In this work, the method used was described by Legendre & Legendre (1998), which adjust values for multiple analyses but still allows lighter effects to be detected. All p-values presented in this chapter are adjusted. Data used in the analysis of average litter sizes were calculated separately for each female. Data on breeding age of dam, age of young at death and breeding season used pooled females. Institutional characteristics were collected from the *International Zoo Yearbooks* and can be found in Appendix 2.

3.6. *Results.*

3.6.1. *Description of reproductive parameters in the sample.*

3.6.1.1. *Births*.

In the tiger studbook, recorded births occurred mostly during Spring and Summer, peaking in the month of May (figure 3.1).

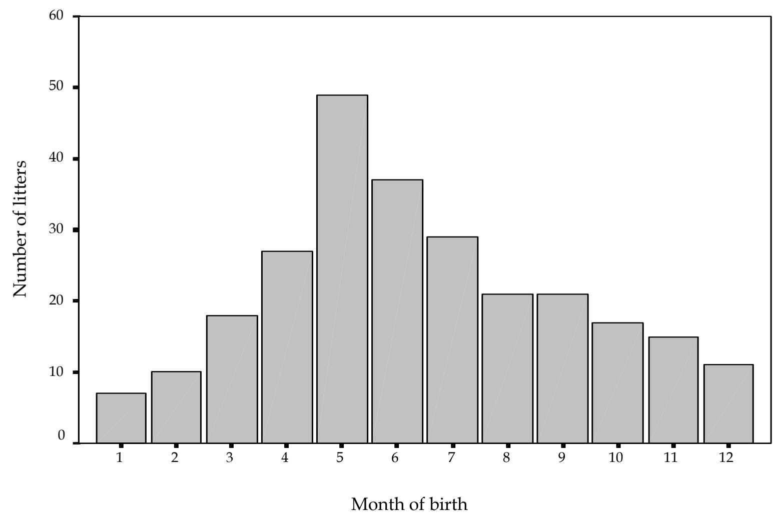

Figure 3.1: Absolute frequency of births of tiger litters in 116 Northern hemisphere institutions over ten years, by month (N=262).

In a study in Nepal, there was no evidence of breeding seasonality in wild tigers. The number of new litters appears to peak around the beginning of Summer and once again, less remarkably, in the beginning of Winter, but the difference is not statistically significant (Smith & MacDougal 1991). In the studbook data, the apparent peak during Summer months may be caused by active management of the institution: as it is known that gestation length in tigers averages 104.1 days, or approximately three and a half months (Gittleman 1986b), males and females are kept separated and introduced to each other in the end of Winter, enabling litters to be born during Summer, when the number of visitors is higher.

From the 116 institutions present in this dataset, 107 have known latitude. Most of them, however, are located between 35 and 55 degrees of latitude (Figure 3.2). Tigers occur between the latitudes of 62 ° N and 10 ° S (Wilson & Reeder 1993), so it was decided not to include latitude as a factor in this analysis, once it is unlikely that results would be significant.

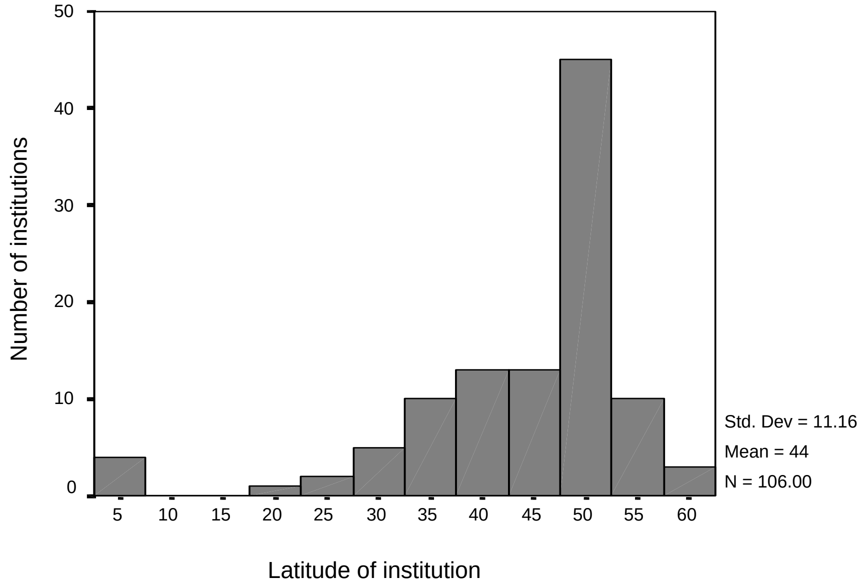

Figure 3.2: Absolute frequency of zoological institutions present in the International Tiger Studbook according to the latitude of their location (N=106).

3.6.1.2. *Litter size.*

In this dataset, litter sizes ranged from one to seven cubs (average of 2.72 ± 1.17 cubs per litter, N=126). Figure 3.3 shows the absolute frequency of litter size; most of the litters have less than four cubs.

In a wild population in Nepal, litter sizes also ranged from one to seven cubs, but seldom more than three (Sunquist 1981). In another study in the same population, litter sizes ranged from two to five cubs, with an average of 2.98 (Smith & MacDougal 1991). The average litter size in the wild for the species, calculated from published material, is from 2.5 (Gittleman 1986b) to 3 (Gittleman 1989).

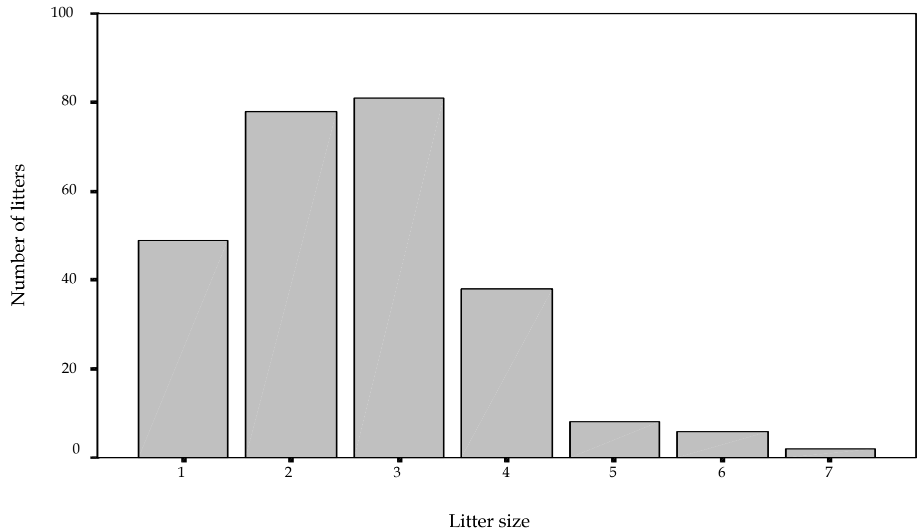

Figure 3.3: Absolute frequencies of litter size on captive tigers from 116 Northern hemisphere institutions (N=262).

Table 3.2 summarises this data from the wild providing sample sizes when available. In studies made previously in zoos, the average litter size reached 2.8 (Sankhala 1967).

Table 3.2: Summary of litter sizes found in wild tiger populations. Sample sizes are provided when available.

Source	Place	Litter size (N)	Sample size
Kerley *et al.* 2003	Russia	2.4±0.6	16 litters
Sunquist 1981	Nepal	2.52	22 litters
Smith & MacDougal 1991	Nepal	2.98	49 litters
Gittleman 1989	Several	3	Not available
Gittleman 1986a	Several	2.5	Not available

3.6.1.3. *Breeding age of dam.*

On average, the captive female tigers produced more litters when 6.2 years (± 2.96, N=241), but females bred from 2 to 16 years of age (figure 3.4). There is very little information on these aspects in wild tiger populations, but oestrus was once observed in a 30 months old female in Nepal (Sunquist 1981). Other study in the same area revealed a mean age of first reproduction as 3.4 years (Smith & MacDougal 1991). In zoos, first mating was observed in females between three and six years old (Sankhala 1967). In this study, there are few reports of 2 years old females producing young, but this information is usually based in estimated age of dam and cannot be relied on. In one event, however, a female with known date of birth bred before 24 months of age, but this is probably a very rare phenomenon. Management decisions may affect the distribution of births, because studbooks keepers tend to take older animals out of the breeding stock (Christie 2000).

There was no significant effect of the age of dam over litter sizes (One-way ANOVA: $F_{15,\ 227} = 0.976$, $p = 0.48$) or the proportion of infant mortality (One-way ANOVA: $F_{15,\ 226} = 1.323$, $p = 0.18$).

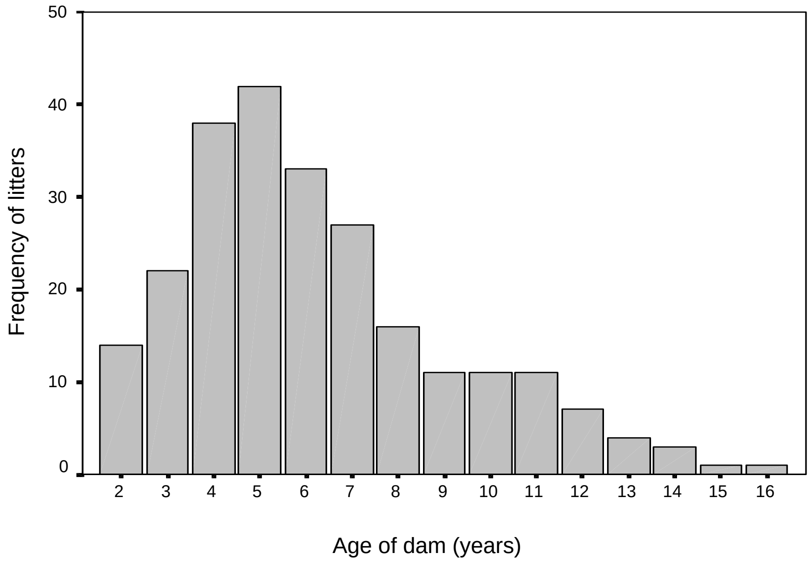

Figure 3.4: Absolute frequencies of breeding age of captive female tigers, in number of litters (N=262). Females are pooled in the analysis.

3.6.1.4. Age *of death of young.*

Most infant deaths in this database occurred in the first week of life (Figure 3.5), and on average the young died before the end of the third week (average week of death = 2.1 ± 2.1).

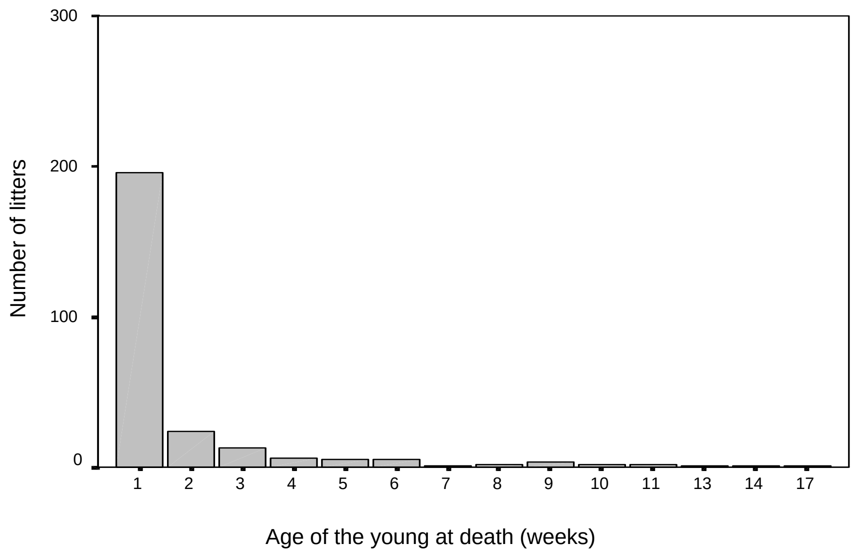

Figure 3.5: Absolute frequencies of age of death of tiger litters in captivity (N=262).

3.6.1.5. *Proportion of infant mortality.*

In this dataset, the median proportion of infant mortality is higher than the median proportion calculated from the database from the *International Zoo Yearbooks* (section 2.2.2.1, in Chapter 2), which contains information from 230 institutions. The median infant mortality calculated from the studbook, for the first 30 days, was 68%, against 37% of the *International Zoo Yearbooks* dataset. In the *IZY* there is no information on the number of litters and females, and the proportion of mortality was calculated by collection (i.e. all young born by year independently of number of females or litters). In this dataset, the proportion of infant mortality for each female was calculated, and the median for the sample was taken.

In Nepal, cub mortality in the wild was recorded as 34% for the first year (Smith & MacDougal 1991), and 31 - 43% for the first two years (Sunquist 1981). In India, first year mortality in tiger cubs was calculated around 38% for the first year, but because of the difficulty of knowing actual litter sizes in the wild, it could be as high as 50% (Sunquist 1981).

3.6.1.6. *Differences in reproductive parameters between subspecies.*

There was no evidence of significant statistical difference between Sumatran and Siberian tigers in the number of litters produced by each breeding female (t_{124} = -0.748, p = 0.46). Also, no significant differences between these two subspecies were found in the interval, in years, in which each female had litters recorded in the studbook between 1986 and 1996 (t_{112} = 0.208, p = 0.84) or the female's average number of litters per reproductive year (t_{112} = -0.238, p = 0.81). Both the proportions of infant mortality (t_{124} = 1.471, p = 0.14) and heterozygosity - or inbreeding level - (t_{32} = 0.721, p = 0.48) did not differ significantly. However, Sumatran tigers appear to produce smaller litters (t_{124} = -1.705, p = 0.09, η^2 = 0.05) and to have produced fewer cubs in total during these 10 years ($t_{81.4}$ = -2.778, p = 0.007, η^2 = 0.035) than the continental subspecies. Sumatran cubs died significantly earlier, in average, than Siberian cubs ($t_{123.9}$ = -2.770, p = 0.006, η^2 = 0.023).

3.6.2. *Factors affecting infant mortality.*

3.6.2.1. *Litter size.*

Litter size had an effect on the median proportion of mortality of young (transformed by arcsine of the square root), especially when corrected for females (regression: $F_{1,124}$= 77.129, p= 0.000). Litter size explains 37.8% of the variance in the proportion of infant mortality. The fitted line plot can be seen on Figure 3.6. The relation of litter size and infant mortality in other species will be discussed in section 3.6.3.

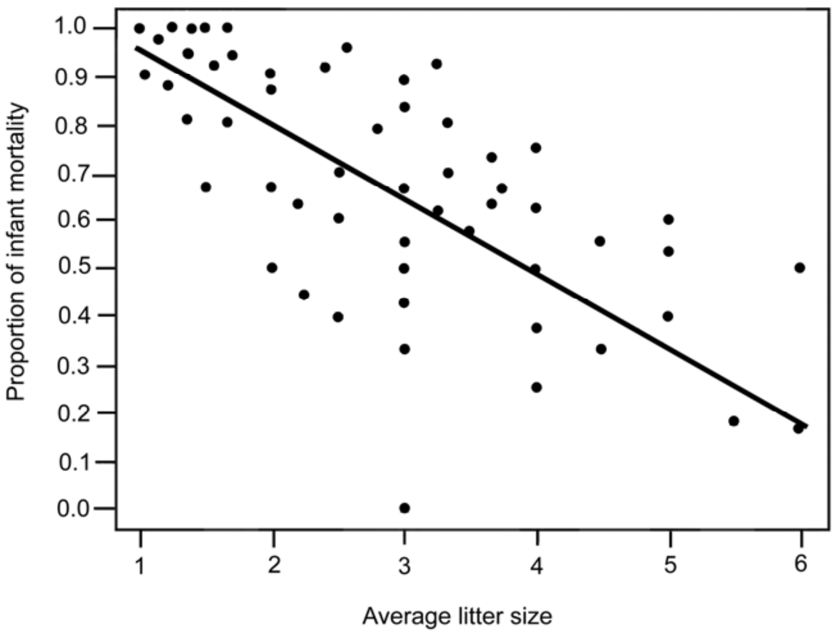

Figure 3.6: Regression plot for the effect of average litter size for female tiger, on the median proportion of infant mortality. Each dot represents one female tiger. The data plotted was not transformed.

3.6.2.2. *Season of reproduction.*

The median proportion of infant mortality is higher in litters that are born in autumn than in other seasons, for autumn litters are smaller than litters born in any other season, when corrected for the latitude of the institutions (One-way ANOVA: $F_{3, 258} = 3.95$, $p = 0.036$; see Figure 3.7).

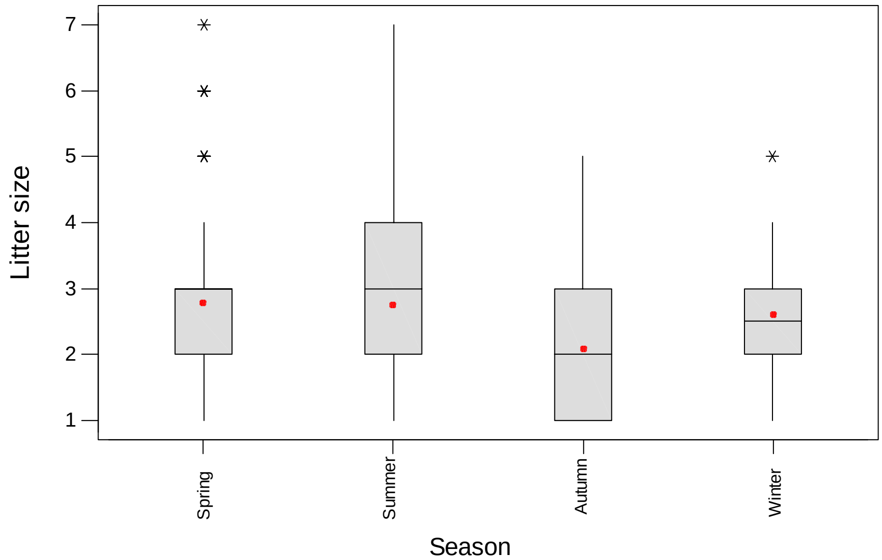

Figure 3.7: Litter size in captive tigers in each season of the year. Solid circles represent means, lines represent medians and stars represent outliers. The data plotted has pooled females.

3.6.3. *Factors affecting institutional female breeding success.*

3.6.3.1. *Institutional characteristics.*

Institutions that presented low breeding performance with species of the Order Carnivora in general (see Chapter 4) also scored poorly for breeding success in tigers (Regression: $F_{1, 81} = 9.28$, $p = 0.015$), but there was no statistically significant difference between breeding success in institutions that did and did not perform research with their animals, when the p-value was corrected, as seen overall for the order in Chapter 7 (One-way ANOVA: $F_{1, 81} = 3.74$, $p = 0.17$, see figure 3.8). The higher proportion of infant mortality in this dataset, when compared to the tiger dataset from the *International Zoo Yearbooks*, may reflect the prevalence of institutions with overall poorer carnivore breeding success in the studbook, and may be related to institutional husbandry protocols. The studbook dataset also contained a higher percentage of institutions performing research (45.8%) when in comparison with the institutions listed in the dataset of the *International Zoo Yearbooks* (28.5%). The studbook excludes hybrids individuals and those of unknown subspecies, and institutions with researchers are more likely to be able to identify with certainty the subspecies of their individuals.

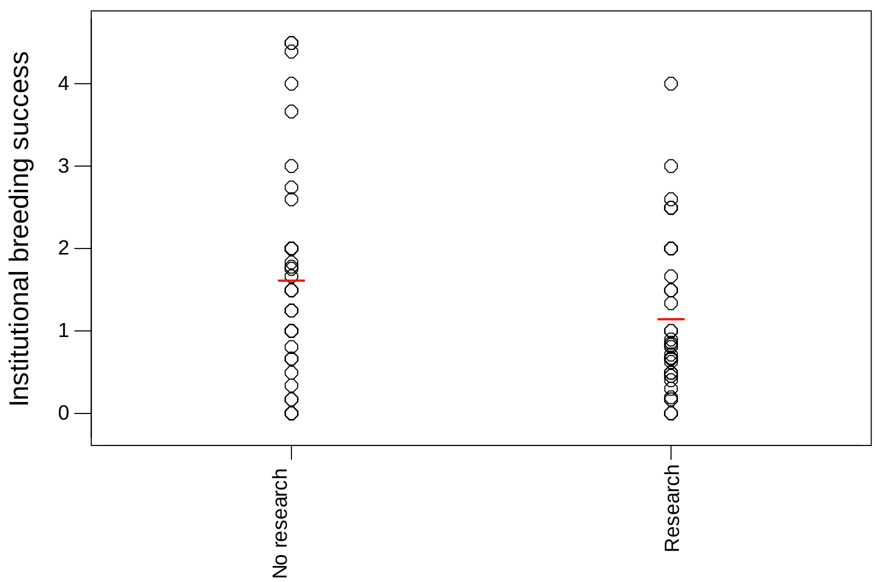

Figure 3.8: Breeding success of female tigers kept in institutions with (N=38) and without (N=45) research groups.

Unfortunately, it was not possible to collect information regarding the institutional experience on tiger reproduction, because breeding efforts are frequently informal at the beginning at are usually not reported to studbook keepers until some positive results are obtained (Christie, pers. comm.).

3.6.3.2. *Female characteristics.*

There is no detectable effect of inbreeding level in individual females' breeding success, although a larger sample would be needed to increase test power (Regression: $F_{1,40} = 1.24$, $p = 0.4$, R-Sq = 3%). There was no evidence that wild-caught females performed worse than captive-born ones, but it must be considered that there are only nine wild-caught females in the sample, against 35 captive-born, and the power of the test is low (One-way ANOVA: $F_{1,42} = 0.32$, $p = 0.5$, power = 0.07). The dataset did not contain information on female body size, and there was no sample size large enough to investigate the effect of the age of dam on breeding success. For the reasons discussed before, it was not recommendable to perform tests on sex ratio.

3.7. *Discussion.*

3.7.1. *Reproductive parameters in captivity and in the wild.*

The reproductive parameters of gestation length and litter size found in the tiger studbook data were, in general, congruent with the data collected in the wild, suggesting that this species preserves much of its reproductive patterns in captivity.

The peak of births during summer found in this research may reflect more the husbandry techniques applied by institutions than the actual existence of a breeding season, and a previous research using data from the

Siberian tiger studbook for North America, seasonal analysis also showed a peak of births between April and June (Seal *et al.* 1985). Although seasonality is uncertain in tigers as a species (Byers *et al.* 1990; Smith & MacDougal 1991), a study on seven captive females indicated that oestrus and follicular cycles started in late January and ceased in early June, suggesting that Siberian tigers, at least, may be induced ovulators and seasonal breeders (Seal *et al.* 1985). Season did not seem to affect semen viability in five captive Siberian tigers monitored throughout the year, but serum concentrations of thyroxin and triiodothyronine were lowest during summer, and testosterone was higher in autumn and early winter (Byers *et al.* 1990). Unfortunately, there are no studies on seasonality on Sumatran tigers, and further research is needed for the species as a whole, if possible using larger sample sizes.

3.7.2. *Subspecific differences and implications to captive breeding.*

As it was said before, there are few genetic differences among the four continental subspecies of tigers; continental subspecies, however, differ greatly from the Sumatran subspecies, and this fact is leading to a change in conservation priorities for tiger subspecies (Ginsberg 2001). Subspecific hybrids happen frequently in the captive population (Olney and Fisken 2003) and also in some wild populations. For example, conservations efforts on a wild tiger population in India led to the introduction of a hybrid Siberian-Bengal tiger in an attempt to increase tiger numbers; two decades later, genetic analysis of this population showed a prevalence of Siberian tiger markers in the reserve population (i.e. subspecific hybrids), but as the hybrids were fulfilling the ecological role in the area and were unlikely to migrate to other areas, and the population would not support the removal of hybrids, the population was left in this way (Wayne & Brown 2001).

A recent review of the factors affecting the persistence of carnivore species pointed out aspects that make some species more prone to extinction: small populations; island endemics; higher trophic levels; slow life histories; complex mating displays and social structure; large home ranges; and large body sizes, which correlate with many of the previous aspects (Purvis, Mace & Gittleman 2001). Although both subspecies present the same basic characteristics, Sumatran tigers may be more vulnerable to extinction pressures because of their natural distribution (an island), smaller populations, and reduced litter sizes and female reproductive output. This may indicate that a tailor-made conservation approach is needed for the subspecies, instead of applying to Sumatran tigers the same protocols used for the Siberian subspecies.

3.7.3. *Factors affecting breeding success.*

Infant mortality in the dataset from the *International Zoo Yearbooks* was similar to that found in wild populations, and even smaller than the 50% rate suggested by Sunquist (1981). In the studbook dataset, however, infant mortality during the first month was extremely high (68%), but may reflect bias in the data, as discussed in Chapter 2. Further investigation, using a broader dataset, would be useful to determine the actual infant mortality rates for the species in captivity.

Of the factors that could be related to infant mortality in captive tigers, litter size seems to have a very strong effect. The fact that litter size was negatively correlated with infant mortality in captive tigers was not expected, because litter sizes are usually positively related with infant mortality in several mammalian species, such as the common marmosets *Callithrix jacchus* (Rothe, Darms & Koenig 1992) and other Callitrichidae (Jaquish, Gage & Tardif 1991), and snowshoe hares *Lepus americanus*

(O'Donogue 1994). Infant mortality can be affected also by birth weight, which is negatively correlated to litter size in mammals such as the snowshoe hare (O'Donogue 1994) and the Zambia giant mole rat *Cryptomys mechowi* (Scharff *et al.* 1999).

Litter sizes can be related to the age of death of young. For example, in captive common marmosets, perinatal infant mortality was prevalent, and stillbirths and abortions were related to litter size: most abortions occurred in singleton pregnancies, while most of stillbirths occurred in quadruplets (Rothe, Darms & Koenig 1992). Also, in a study of several species of Callitrichidae, litter size also influenced infant survivorship; survival to maturity was higher in singleton and twins than in triplets, while perinatal mortality was higher in singletons and triplets than in twins, suggesting some influence of sibling competition and maternal care (Jaquish, Gage & Tardif 1991).

An indication of what could be influencing the relation of litter size and infant mortality in captive tigers was found in other species of mammals. Litter sizes were positively correlated with maternal body fat (or nutritional status) in Virginia opossums *Didelphis virginiana* (Hossler, MacAninch & Harder 1994) and raccoon dogs *Nyctereutes procyonoides* (Kauhala & Helle 1995). In raccoon dogs, litter sizes were correlated with the abundance of prey and population density, which affected directly the fat reserves of females, but mortality before maturity, albeit high, was not correlated with litter size (Kauhala 1996). In cheetahs *Acinonyx jubatus*, maternal food intake and maternal fat reserves were positively correlated with cub growth rate up to a physiological limit (Laurenson 1995). Cub birth mass and maternal mass also affected positively infant survival in polar bears *Thalarctos maritimus*, and maternal condition affected infant survival during the first year; lack of food, and its direct effect on maternal fat stores, can be crucial during lactation and may be the main cause of mortality in polar bear cubs (Derocher & Stirling 1996). This may suggest that female tigers that had larger litters were in a better nutritional and health status, and were able to raise the cubs successfully. One confounding factor in captive tigers, though, is the husbandry protocol that some institutions adopt: in many zoos, cubs are removed immediately after birth for hand-rearing, especially after a maternal infanticide event (e.g. Hughes 1977). This way, larger litters could have at least some individuals "rescued", while small litters, especially those of singletons or twins, could be killed almost instantly, before the intervention of zoo staff. A more detailed database would be needed to rule out the influence of human intervention on cub survival in captive tigers.

Researching infant mortality in 18 species of canids in captivity, Ginsberg (1994) found that there is a strong correlation between extensive institutional breeding experience and pup survivorship, explaining up to 77% of the variance. Species bred in captivity for a long time will have higher infant survival.

In this research, there was an effect of the season of the year in litter size, with smaller litters occurring during autumn months. If litter sizes are related to female body fat and nutritional conditions in tigers, it would be informative examining female weight fluctuations in captive conditions, and a decrease in body fat would be expected by the end of the summer and beginning of autumn.

In any case, it is possible that there is a real relation between litter size and cub survival in tigers in captivity. It was suggested that the relation between infant survival and litter size can be affected by population dynamics, and change overtime. In a long-term study with Columbian ground squirrels *Spermophilus columbianus*, litter sizes were large during the phase in which the population was growing, and infant survival increased with litter size; when the population was decreasing, the average litter size fell from 4 to 3, and larger litters suffered higher mortality, which can be related to changes in resource availability (Festa-Bianchet & King 1991). As resources are theoretically abundant and do not change over time in captivity, the captive population could be behaving as a population in growth phase.

The relation found between institutions that had overall poor carnivore breeding and those who were not breeding tigers successfully suggests the influence of husbandry techniques in infant mortality. Some of the aspects that may be involved are hand-rearing techniques, housing conditions and the provision of a well-balanced diet, but this data was not available.

There was no detectable effect of inbreeding levels in infant mortality of captive tigers. The effect of inbreeding depression in tigers is not yet fully researched, and opinions on the subject differ. Inbreeding depression can be reflected in many aspects of reproduction, such as litter size, infant survival and spermatozoa quality. A study in the Royal Chitwan National Park in Nepal monitored 22 breeding females and 14 breeding males for 16 years, and found that the inbreeding rate of this population, one of the largest in the Indian subcontinent, is 2% per generation. This suggested that, if low levels of heterozygosity affect the species, many tiger populations would be vulnerable to inbreeding depression (Smith & McDougal 1991).

In recent years, the idea that captive tiger populations may have low genetic variability due to inbreeding has been researched with the aid of technological innovations, and the results point in a different direction. For instance, a DNA fingerprinting study in 22 tigers from a wild population in India revealed that its level of genetic variability (22.65%) did not differ from levels analysed in museum skin samples collected between 50 and 125 years ago (21.01%). This may indicate that the low genetic variability found in this subspecies was not caused by the population bottleneck of the beginning of the 20th century (Shankaranarayanan *et al.* 1997).

In a study on the effects of inbreeding in captive Indian tigers, semen was collected for analysis of spermatozoa quality and fertilizing ability, one of the measures of inbreeding depression in mammals. The majority of samples fell within the estimated optimal values for the species, suggesting that high homozygosity does not cause inbreeding depression on the species (Shivali, Jayaprakash & Patil 1998). This type of research, however, is extremely new and much work is still needed to get to more accurate results.

3.8. *Conclusion.*

Captive tigers seem to preserve natural reproductive parameters, and research with these populations can prove very valuable to the study of wild populations. Studbooks can provide reliable data, and individual institutional records can help to unravel factors that affect the reproduction on the species.

Conservation efforts should integrate research in both captivity and the wild, in a complementary way, since certain factors were not yet researched in wild populations due to the obstacles of data collection; this information can be crucial for the maintenance and protection of surviving wild populations.

It is important to stress the urgent need of a more collaborative interchange of information between the several groups participating in the conservation of tigers, to preserve remaining populations in the wild, once the reintroduction of large predators can face many challenges. A multidisciplinary approach can facilitate the understanding of the causes of species decline and, with the help and participation of the human populations surrounding tiger reserves, achieve more positive results towards the persistence of the species in the wild.

Chapter 4

Biological factors affecting infant survival in captive carnivores

Abstract

The proportion of infant mortality in 98 species of captive carnivores was calculated from the *International Zoo Yearbooks* (Vols. 26-35). Infant mortality in carnivore species in captivity was significantly affected by the developmental characteristics of the species such as the age when young open their eyes, gestation length and weaning age. Specific body weight did not have an effect on infant mortality in captivity as it had on the juvenile mortality of carnivores in the wild. Species with delayed implantation of embryos did not have lower infant mortality in captivity. Declining species presented higher infant mortality than abundant ones, but the rates of juvenile mortality differ greatly between wild and captive populations. Species from temperate or cold climate had higher infant mortality when kept outside of their natural latitudinal ranges, although this effect was not significant for tropical species, even those with restricted distribution. Infant mortality in captive carnivores was also significantly affected by the specific type of diet and zonation, but there were not significant effects of activity patterns or habitat vegetation of the species on infant mortality in captivity.

4.1. *Introduction.*

The evolution of species is driven by adaptation to habitats. Some species spread through large areas, encompassing more than one ecosystem; others became highly specialised in only one, sometimes frail, habitat. Species that occupy different habitats must not only have flexible strategies to explore resources, but also be able to reproduce in the most varied conditions. Highly specialised ones, however, are restricted to places that present optimal conditions.

The process of reproduction has a complex structure that could be influenced by many factors, whether biological or environmental (cf. Ch. 1). For captive reproduction programmes, it may be tempting then to try and control enclosure conditions. Given the diversity of species and their particular demands, it is unlikely however that there is a panacea-like compilation of guidelines to be developed, and many programmes cannot afford experimental failures.

Although some research has been made on breeding success of mammals in captivity, and the effects of biological factors on infant mortality, most of them are focused on primates (e. g. Birrell et al. 1996; Courtenay 1988; Debyser 1995a; Debyser 1995b; Debyser 1995c; Mooney & Lee 1999). In the order Carnivora, this aspect has been researched mainly in the cheetah *Acinonyx jubatus* (Beekman et al. 1999; Benzon & Smith 1974; Marker & O'Brien 1989; Wielebnowski 1996), arctic foxes *Alopex lagopus* (Bakken 1992; Bakken 1993; Bakken 1994; Ilukha, Harri & Rekilä 1997) and black-footed ferrets *Mustela nigripes* (Biggins et al. 1998; Thorne & Oakleaf 1991). Species are not usually randomly chosen for this type of research. The captive population of the cheetah is one of the oldest and better recorded of all captive carnivores, and databases yield decades of breeding information (Marker-Kraus 1997). Arctic foxes are farmed for their fur, and higher breeding success leads to more profit (Bakken 1992). Finally, black-footed ferrets, being extinct in the wild, depend on low mortality rates to produce individuals for reintroduction programmes (Thorne & Oakleaf 1991). Also, the biology of these species was already well described (cf. cited authors). For other species, especially those with many, at present, unknown biological characteristics, research is extremely scant.

Conservation programmes have been developed for several species of carnivores, and those depending on captive populations are listed in Table 4.1. It is important to notice that the Species Survival Commission of the World Conservation Union, in its technical guidelines for *ex situ* conservation programmes (IUCN 2002a), decided that all species classified as Critically Endangered (CR) or Extinct in the Wild (EW) should be subjected to *ex situ* conservation in a way to restore wild populations, but many resources have been applied in programmes for species that are not listed. Some critically endangered species, such as the Iberian lynx *Lynx pardina* and the Malabar civet *Viverra civettina*, do not have a breeding captive population until present. The IUCN also points out that the investment on *ex situ* programmes should take into consideration research results, and many species were not researched properly yet.

4.1.1. *Hypotheses to be tested*

Carnivore life history traits have been used in the understanding of complex biological processes such as energy expenditure in reproduction or extinction risk (Oftedal & Gittleman 1989; Purvis *et al.* 2000). Here I use multiple datasets to predict, through statistical models, the possible effects of the natural history of the species on infant mortality in captivity.

If conditions in captivity are providing all the resources for a species, then the specific proportion of infant mortality in captivity should be lower than in the wild, because the young do not risk dying of starvation (Kauhala & Helle 1995; Rogers 1987; Sklepkovych 1989), predation (Ralls & White 1995; Steiger *et al.* 1989; Van Heerden *et al.* 1995) or hunting (Lode 1995; Payne & Root 1986; Takeuchi & Koganezawa 1994).

Due to the great diversity of life history traits of the Carnivora (Gittleman 1986a, 1986b), it is expected that the variance in the proportion of infant mortality between species will indicate which are thriving in captivity (Debyser 1995a, 1995b, 1995c) and which biological parameters have an influence on infant survival (Birrell *et al*. 1996; Courtenay 1988; Mooney & Lee 1999). As altricial young are more fragile than precocial ones (Hayssen 1984; Hrdy 1979; Packer & Pusey 1984; Wolff 1997; Wolff & Peterson 1998), it is possible that species with slower development were more prone to lose infants. Arctic species are affected by photoperiod (Curlewis 1992; Jallageas *et al.* 1994; Lincoln 1998) and may present higher infant mortality when housed outside the species' range of distribution.

Infant mortality can be directly related to resource availability, through competition, predation and curtailed maternal investment (Clutton-Brock 1991), and high infant mortality in captivity may indicate that optimal conditions were not provided by the institutions (Debyser 1995a; Marker-Kraus 1997; Promislow & Harvey 1991). Species with elaborate nutrition, such as insectivores (Ashton & Jones 1979; Donoghue & Langenberg 1994; Price *et al.* 1999), and those with complex environmental needs, which need multi-environment enclosures (Carlstead & Shepherdson 1994; Lyons, Young & Deag 1997), are expected to breed poorly in captive conditions.

Table 4.1: Conservation programmes involving captive populations of carnivores. IUCN categories are from version 3.1 (IUCN 2001). Types of programmes: Managed captive populations = individuals tracked by studbooks and breeding depends on space availability; Captive breeding = extensive breeding loans with the purpose of enhancing captive population; Reintroduction = extensive captive breeding aiming reintroduction of new individuals in the wild.

Species	IUCN Status (IUCN 2002b)	Type of programme	Reference
Acinonyx jubatus	VU C2a(i)	Managed captive populations, captive breeding	Balmford, Mace & Leader-Williams 1996
Ailuropoda melanoleuca	EN B1+2c, C2a	Managed captive populations, captive breeding	Balmford, Mace & Leader-Williams 1996; Peng, Jiang & Hu 2001
Ailurus fulgens	EN C2a	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Amblonyx cinereus	LR/nt	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Canis lupus	The subspecies reintroduced are not listed	Managed captive populations, captive breeding, reintroduction	Balmford, Mace & Leader-Williams 1996; Berger *et al.* 2001
Canis rufus	CR D	captive breeding, reintroduction	Moore & Smith 1990; Woodroffe & Ginsberg 1997; Gittleman & Gompper 2001
Chrysocyon brachyurus	LR/nt	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Enhydra lutris	EN A1ace	captive breeding, reintroduction	Gittleman & Gompper 2001
Lycaon pictus	EN C1	Managed captive populations, captive breeding, reintroduction	Balmford, Mace & Leader-Williams 1996, Gittleman & Gompper 2001
Mustela nigripes	EW	Managed captive populations, captive breeding, reintroduction	Thorne & Oakleaf 1991; Balmford, Mace & Leader-Williams 1996; Gittleman & Gompper 2001
Neofelis nebulosa	VU C2 a(i)	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Panthera leo persica	CR C2a(ii)	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Panthera tigris	EN C2a(i)	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Puma concolor coryi	CR D	captive breeding, reintroduction	Gittleman & Gompper 2001
Speothos venaticus	VU C2a	Managed captive populations	Balmford, Mace & Leader-Williams 1996
Ursus arctos	Not listed	captive breeding, reintroduction	Berger *et al.* 2001, Gittleman & Gompper 2001

4.2. *Methods*.

4.2.1. *The dataset: species and variables used.*

The dataset used in this chapter was described in section 2.2.2.1 and is presented in Appendix 1. From the 98 species of carnivores that bred in zoos between 1986 and 1996, 85 species were analysed using biological, ecological and geographical data compiled by Gittleman (1983, 1986a, 1986b), Mead (1989) and Wilson and Reeder (1993), as predictors to infant mortality in captivity. The conservation status of the species was extracted from IUCN (2002b). Table 4.2 summarises the variables derived from each one of the sources.

Table 4.2: Summary of the biological, ecological and geographical variables, and their sources, used in statistical analysis in this chapter.

Type of data	Variables	Source
Developmental Biology	Gestation length, litter growth rate, age of young opening the eyes, weaning age and age of independence	Gittleman 1986a, 1986b
Ecological	Type of diet, type of vegetation of habitat, type of preferred zonation, activity pattern	Gittleman 1986a, 1986b
Juvenile mortality	Juvenile mortality in the wild	Gittleman 1983
Embrionic diapause	Presence and length of delayed implantation of embryo	Mead 1989
Geographical	Northernmost and southernmost latitudes of species distribution	Wilson & Reeder 1993
Conservation status	Decline of wild populations of the species	IUCN 2002b
Infant mortality in captivity	Median proportion of infant mortality in captivity	*IZY* Vols. 26-35

Not all variables were available to the 98 species presented in Appendix 1. Table 4.3 displays which species were included in each one of the statistical analyses of this chapter.

Table 4.3: Species included in the statistical analysis using different groups of variables collected from published databases (Gittleman 1983, 1986a, 1986b; Mead 1989; Wilson & Reeder 1993). DB = developmental biology; ECO = ecological; JM = juvenile mortality; ED = Embryonic diapause; LAT = geographical. Specific variables are displayed in Table 4.2.

Family	Species	DB	ECO	JM	ED	LAT
Canidae	*Alopex lagopus*	•	•			•
Canidae	*Canis aureus*		•			
Canidae	*Canis lupus*	•	•	•		
Canidae	*Canis mesomelas*		•			
Canidae	*Cerdocyon thous*		•			
Canidae	*Chrysocyon brachyurus*		•			•
Canidae	*Cuon alpinus*		•			
Canidae	*Lycaon pictus*	•	•			•
Canidae	*Nyctereutes procyonoides*		•			
Canidae	*Otocyon megalotis*		•			
Canidae	*Speothos venaticus*		•			
Canidae	*Urocyon cinereoargenteus*		•	•		
Canidae	*Vulpes rueppelli*		•			
Canidae	*Vulpes velox*		•			
Canidae	*Vulpes vulpes*	•	•	•		•
Canidae	*Vulpes zerda*	•	•			•
Felidae	*Acinonyx jubatus*		•			
Felidae	*Caracal caracal*	•	•			•
Felidae	*Felis chaus*	•	•			•
Felidae	*Felis margarita*		•			
Felidae	*Felis nigripes*		•			
Felidae	*Felis silvestris*	•	•			
Felidae	*Herpailurus yaguarondi*		•			
Felidae	*Leopardus pardalis*				•	
Felidae	*Leopardus tigrinus*		•			
Felidae	*Leptailurus serval*		•			•
Felidae	*Lynx lynx*	•	•	•		•
Felidae	*Lynx rufus*	•	•	•		•
Felidae	*Oncifelis geoffroyi*		•			
Felidae	*Panthera leo persica*	•	•	•		
Felidae	*Panthera onca*	•	•			
Felidae	*Panthera pardus*	•	•			
Felidae	*Panthera tigris*	•	•	•		
Felidae	*Prionailurus bengalensis*	•				
Felidae	*Prionailurus viverrinus*		•			
Felidae	*Puma concolor*		•			
Felidae	*Uncia uncia*		•			•

Family	Species	DB	ECO	JM	ED	LAT
Herpestidae	*Atilax paludinosus*		•			
Herpestidae	*Cynictis penicillata*		•			
Herpestidae	*Helogale parvula*		•			
Herpestidae	*Mungos mungo*		•			•
Herpestidae	*Suricata suricatta*	•	•			•
Hyaenidae	*Crocuta crocuta*	•	•	•		
Hyaenidae	*Hyaena hyaena*	•	•			
Hyaenidae	*Proteles cristatus*		•			
Mustelidae	*Amblonyx cinereus*				•	
Mustelidae	*Eira barbara*				•	
Mustelidae	*Enhydra lutris*	•	•		•	
Mustelidae	*Gulo gulo*	•	•		•	
Mustelidae	*Ictonyx striatus*	•	•		•	
Mustelidae	*Lutra canadensis*	•	•	•	•	
Mustelidae	*Lutra lutra*	•	•		•	
Mustelidae	*Martes flavigula*		•		•	
Mustelidae	*Martes foina*				•	
Mustelidae	*Martes martes*		•		•	
Mustelidae	*Martes zibellina*	•	•		•	
Mustelidae	*Meles meles*	•	•		•	
Mustelidae	*Mephitis mephitis*	•	•	•	•	
Mustelidae	*Mustela erminea*		•	•	•	
Mustelidae	*Mustela eversmanni*				•	
Mustelidae	*Mustela lutreola*	•	•		•	
Mustelidae	*Mustela nigripes*				•	
Mustelidae	*Mustela nivalis*	•	•		•	
Mustelidae	*Mustela putorius*		•		•	
Mustelidae	*Mustela vison*		•		•	
Mustelidae	*Pteronura brasiliensis*				•	
Mustelidae	*Vormela peregusna*		•		•	
Procyonidae	*Ailurus fulgens*		•	•	•	•
Procyonidae	*Bassariscus astutus*	•	•			
Procyonidae	*Nasua nasua*					•
Procyonidae	*Potos flavus*		•			•
Procyonidae	*Procyon lotor*	•	•	•		
Ursidae	*Helarctos malayanus*		•		•	
Ursidae	*Melursus ursinus*		•		•	
Ursidae	*Tremarctos ornatus*				•	•
Ursidae	*Ursus americanus*	•	•	•	•	•
Ursidae	*Ursus arctos*	•	•	•	•	
Ursidae	*Ursus maritimus*		•	•	•	•
Ursidae	*Ursus thibetanus*	•	•		•	•
Viverridae	*Arctictis binturong*		•			•
Viverridae	*Civettictis civetta*		•			
Viverridae	*Genetta genetta*	•	•			
Viverridae	*Genetta tigrina*	•	•			
Viverridae	*Paguma larvata*		•			
Viverridae	*Paradoxurus hermaphroditus*		•			

Although tests did not point the need for phylogenetic analysis of this data (section 2.3.4), it is important to remember that there can be some bias towards certain taxa in different analyses.

4.2.2. *Reproductive biology and infant survival.*

To choose which variables were more adequate to test the hypothesis that the biology of species affects infant survival of carnivores in captivity, a stepwise regression (forward method) was used on the biological database of carnivores (Gittleman 1983, 1986a, 1986b). Biological aspects of the species that are related with the level of development in which the young are born and the post natal growth (gestation length, litter growth rate, age of opening the eyes, weaning age and age of independence, all transformed by natural log) were tested against the median proportion of infant mortality (***I***) for the captive populations published on the *International Zoo Yearbooks* between 1986 and 1996 (equation 2.1). Also, the same variables were tested by the "best subsets" regression method, in a way to identify the best model to be applied in the multiple regressions. These variables were used in a fully factorial general linear model using the software MINITAB v.13, and all the p-values presented in this chapter are adjusted for multiple analyses.

4.2.3. *Delayed implantation.*

Information on delayed implantation (DI) from several species, from Mead (1989), was transformed to codes. The information available was presented as an objective measure for only two species (in months of delay), but for all others it was presented in a subjective form (absent, suspected, unknown duration, short duration and long duration). It was then considered that the DI length of those species represented in months was equivalent to 'long duration', for they consist in more than 70% of the total gestation time.

The code then was as follows: 0 = absent; 1 = suspected; 2 = unknown duration; 3 = short duration and 4 = long duration. This variable was then tested against the value I, through an analysis of variance (ANOVA).

4.2.4. *Captive infant mortality in declining species.*

The IUCN Red List categorises species according to subtle threat levels, such as 'lower risk, least concern', 'critically endangered' and 'extinct in the wild'. Some species are classified as 'data deficient'. For this test, due to the small sample size, there are not degrees of freedom enough to allow the analysis with the full 5-level IUCN code used by Purvis *et al.* (2000). A two-level code was then used, assigning a value of 1 if the species is listed as 'lower risk' or higher, or 0 if not listed. Data deficient species were not considered. Again, the dependent variable in the analysis of variance was the value ***I.***

4.2.5. *Photoperiod and latitudes.*

Based in this influence of latitude in the biology of temperate species, specific infant mortality was tested against the latitude of the zoological institutions. Information on the distribution of species was collected from Wilson and Reeder (1993). The extreme points of latitudinal distribution of each species were found in maps, and the latitude of each locality was found with the aid of a geographic positioning software, Earth Explorer 2.5 (Motherplanet Inc.). The species considered for this test were those with a range of latitudinal distribution smaller than 50 degrees (for example, from 20° N to 50° N), and that were kept in more than 30 institutions. Species were considerate Arctic if the lower latitude of distribution was above 23°, therefore having no population between the Tropics, and Tropical if many populations were found in this area. The list of species can be seen in Table 4.3. Code values were attributed to institutions, depending whether they were outside (0) or inside (1) the natural range of the species.

4.2.6. *Nutrition and zonation*.

Information on type of diet, activity patterns, type of preferred vegetation and zonation from Gittleman (1986a, 1986b) was tested against a coded value of infant mortality in captivity through a logistic regression (LOGIT). The response variable on a logistic regression has to be categorical, so to transform the dependent variable into a categorical variable, the upper and lower quartiles of ***I*** values for all the 98 species of carnivores in captivity was calculated, together with the median ***I*** for the order. If the specific ***I*** fell below the lower quartile of the order, it was coded 1. If it fell between the lower and upper quartile for the order, it was coded 2; and it was coded 3 if it fell above the upper quartile for the order.

Diet types were piscivorous; herbivorous; carnivorous; omnivorous; and insectivorous. Activity patterns were nocturnal; diurnal; crepuscular; nocturnal and crepuscular; and arrhythmic. Habitat vegetation categories were open grassland; forest; grassland and woodland; dense brush or scrub; desert; woodland; and aquatic. Types of zonation were aquatic; terrestrial occasionally arboreal; arboreal; terrestrial; and arboreo-terrestrial.

4.3. *Results.*

4.3.1. *Reproductive biology and infant survival.*

The variables that seem to have some influence on juvenile mortality rates are age of opening eyes (OE), gestation length (GL) and, with a weaker response, weaning age (WA). Gestation length values correlate both with weaning age (regression: $F_{1,\,48}$= 12.10, p= 0.001) and with the age of opening eyes (regression: $F_{1,\,47}$= 10.45, p= 0.002).

The variables OE and GL seem to have a linear effect on juvenile mortality rates in captivity, while WA almost presents a quadratic effect (GLM on transformed data: OE: $F_{1,\,33}$= 5.36, p= 0.027; GL: $F_{1,33}$= 5.29, p= 0.028; WA^2: $F_{2,\,33}$= 3.48, p=0.071). However, this model will only explain 17.32% of the variance of infant mortality rates. Figure 4.1 shows the plotted the raw data used in this model.

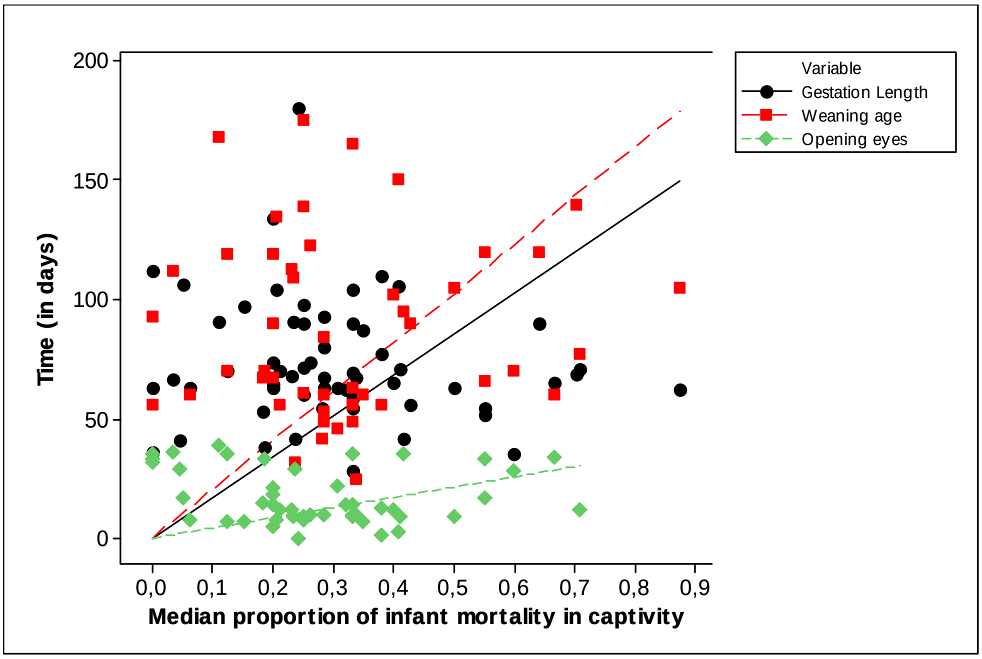

Figure 4.1: Developmental biology data of carnivore species plotted against the median proportion of infant mortality in captivity. Each colour represents a variable, and each dot represents a species. The species have values in all variables. Lines represent expected values.

Specific female body weight did not have a significant effect on the proportion of infant mortality in captive carnivores (One-way ANOVA: $F_{1, 67} = 0.256$, $p = 0.5$) as it had on the juvenile mortality of carnivores in the wild presented by Gittleman 1983 (One-was ANOVA: $F_{1, 14} = 12.72$, $p = 0.003$).

The possible, if weak, effect of these factors may indicate a tendency of higher mortality rates in altricial species, although a more complete database would be needed to enhance test power. It is important to remark, however, that many other factors may be affecting infant mortality, and it is unlikely that there will be a model to explain a much higher percentage of the variance.

4.3.2. *Delayed implantation.*

Overall, species with delayed implantation do not seem to be performing in captivity differently from those without this mechanism, although a larger sample size is needed, to increase test power (One-way ANOVA: $F_{4, 25}=0.30$; $p=0.876$; power=0.8225). Nevertheless, as infant mortality varies greatly between institutions, this test did not consider the effects of photoperiod (for the effects of latitude of institution, see section 4.3.4 below) on infant mortality of species with delayed implantation.

4.3.3. *Captive infant mortality in declining species.*

Declining species presented higher infant mortality in captivity than non-endangered species (One-way ANOVA: $F_{1, 96}=7.62$, $p=0.007$; Figure 4.1). Juvenile mortality rates in the wild differ significantly from infant mortality rates in captivity (t-test: $t=3.48$, $N=16$, $p=0.003$). This could indicate that factors affecting these values in the wild may be exacerbated by, or different to those of, a restricted environment.

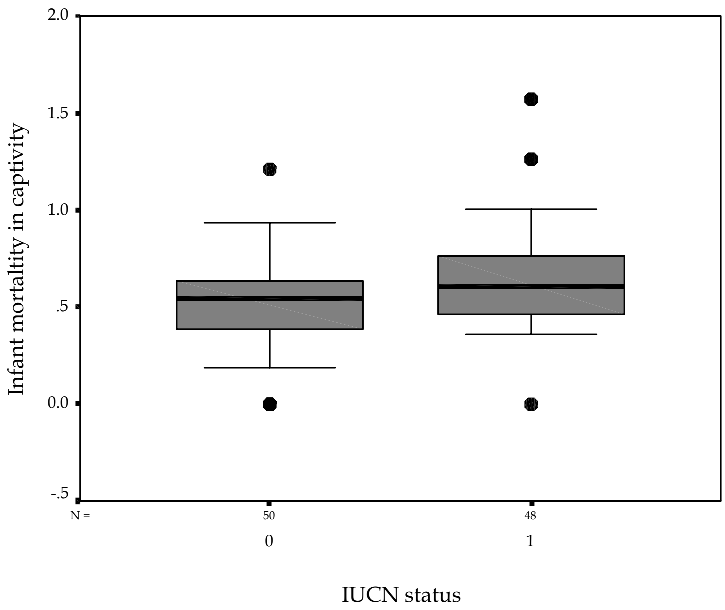

Figure 4.2: Infant mortality in captivity of non-endangered (N=49) and endangered (N=49) species of carnivores.

4.3.4. *Photoperiod and latitudes.*

Infant mortality was significantly higher when restricted distribution Arctic species (lower latitude of distribution < 23°) were kept in institutions outside their natural range of distribution (One-way ANOVA: $F_{1,\ 812}$=4.84, p< 0.03), as it can be seen in Figure 4.2. Species with restricted distribution, but primarily tropical or subtropical, were also tested, and there was no effect of latitude in infant survival (One-way ANOVA: $F_{1,\ 756}$=1.10, p> 0.1; power = 0.96).

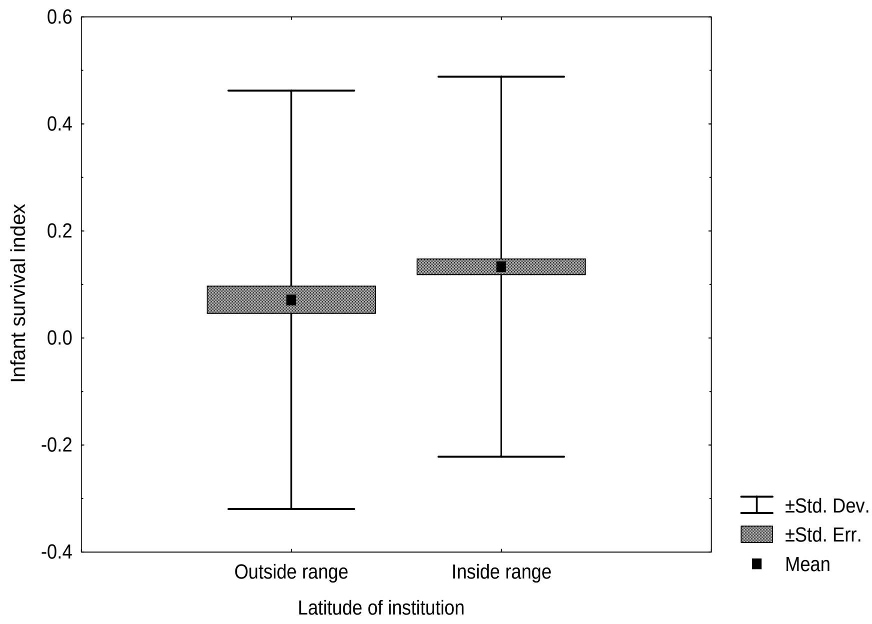

Figure 4.3: Index of infant survival of captive low distribution carnivores kept in institutions outside (N=240) and inside (N=572) their natural range of distribution.

4.3.5. *Nutrition and Zonation*.

There was a significant effect of type of diet (LOGIT: Z_{64}=-1.97, p = 0.05, odds ratio = 0.52) and zonation (LOGIT: Z_{70} = -2.26, p = 0.02, odds ratio = 0.46) on infant mortality in captivity. The type of diet of species with higher infant mortality was insectivorous, and piscivorous species performed better (Figure 4.3). Aquatic species suffered smaller infant mortality than all other types of zonation, and arboreal-terrestrial species presented higher proportion of young mortality (Figure 4.4).

There were not statistically significant effects of activity patterns (LOGIT: Z_{64}=-1.51, p = 0.13, odds ratio = 0.74) or habitat vegetation (LOGIT: Z_{66}=-0.95, p = 0.34, odds ratio = 0.91) of the species on infant mortality in captivity.

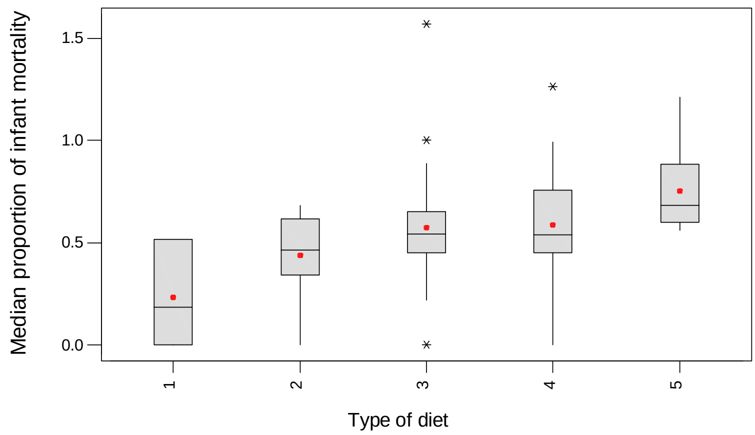

Figure 4.4: Median proportion of infant mortality according to the type of diet: 1= piscivorous (N=3); 2= Herbivorous (N=7); 3= carnivorous (N=28); 4= omnivorous (N=21); 5=insectivorous (N=9).

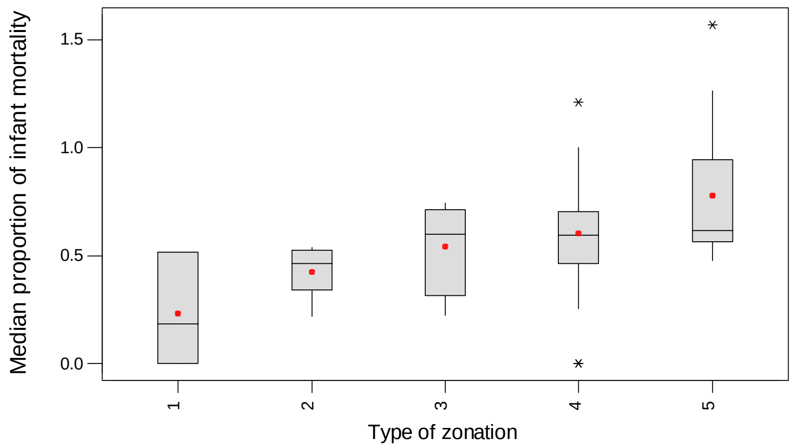

Figure 4.5: Median proportion of infant mortality according to the type of zonation. 1= aquatic (N=3); 2= terrestrial occasionally arboreal (N=7); 3=arboreal (N=4); 4= terrestrial (N=50); 5= arboreo-terrestrial (N=10).

4.4. *Discussion.*

4.4.1. *Reproductive biology and infant survival.*

The biology of reproduction is diverse within the Order Carnivora. As a result of the large morphological, ecological and behavioural variation in the order, some aspects of the breeding biology of carnivores can present extremely different values. For example, birth weight ranges from three grams to almost two kilos, litter size from one to eight cubs and lactation period from 30 to 730 days (Gittleman 1986). Databases containing specific information can allow a better understanding of dependent processes, such as the energy output during reproduction (Oftedal & Gittleman 1989), or supply models that may predict variation of certain phenomena, such as extinction risk in endangered species (Purvis *et al.* 2000).

Mortality rates, clustered by age or sex, have been suggested as a valid tool in the study of evolution and ecology of mammals (Promislow & Harvey 1991). Infant mortality rates (the proportion of young that died before certain age) are frequently used as an alternative to the traditional measure of breeding success (number of young per mature female per year), especially in large database research, where the number of females is not always available (cf. Courtenay 1988; Debyser 1995a, 1995b, 1995c). One advantage of using proportion of infant mortality instead of female productivity is that the latter method usually counts all females of the population studied, regardless of the fact that some females do not reproduce, either because of reproductive suppression or, in captive populations, because they are under contraceptive medication or do not have breeding opportunities.

In captive populations, infant mortality *per se* is a problem, and can jeopardise captive breeding programmes (cf. Chapter 1). Even though there is yet no detailed research on the most common causes of infant deaths in captive carnivores[3], diseases are reported to be the cause of death in many occasions (e. g. Geidel & Gensch 1976; Jayewardene 1975; Kitchener 1968; Olbricht & Sliwa 1997; Sausman 1997). Although the actual influence of maternal infanticide is not yet known, cannibalism and maternal neglect are profusely reported in several species (e. g. Coimbra-Filho 1966; Hess 1971; Leslie 1971; Michalowski 1971; Murphy 1966; Scheffel & Hemmer 1975). In captive cheetah, most of the mortality before 6 months of age results from maternal infanticide or neglect (Marker-Kraus 1997).

One aspect that may facilitate both the onset of diseases and the occurrence of infanticide[4] is the level of altriciality of the young. Carnivores may be considered altricial if compared to ungulates (Grand 1992), but there is great variation within the order (Gittleman 1986). Having in mind that altricial young are more prone to die of exposure, contract diseases and be eaten by the dam (or by other adults) than precocial ones (Hayssen 1984; Hrdy 1979; Packer & Pusey 1984; Wolff 1997; Wolff & Peterson 1998), it is possible that species with more immature young will present higher levels of infant mortality in captivity, as it was found in this research.

4.4.2. *Delayed implantation.*

Delayed implantation (DI) is a mechanism through which an embryo is kept in diapause after fertilisation, allowing the gestation length to be longer than the expected for the female body weight. This pause can last from a few days to 10 months, and occurs in several species of four families of terrestrial carnivores (Mustelidae, Ursidae, Ailuropodidae and Ailuridae). The ecological importance of delayed implantation is still controversial, and in need of further investigation. It was suggested, though, that DI could favour litter survival, either through the synchronisation of births, in species with alloparental care of the young, or allowing the female to give birth in the

[3] A detailed analysis of the causes of infant death in captive carnivores can be seen on Chapter 5.
[4] For the aetiology of infanticide and its relation to altriciality, see Chapter 6.

beginning of spring, thus giving time for the young to be independent through winter (Mead 1989). Delayed implantation can also be affected by photoperiod, as in European badgers *Meles meles* (Woodroffe & MacDonald 2000), which varies with latitude and, consequently, with the zoological institution. The lack of a significant effect of delayed implantation in this research can be due to the stronger effects of other factors and may reflect the homogeneity of resources throughout the year for captive carnivores. Information on this aspect for a larger number of species, or more detailed data on the species with known delayed implantation, is needed to rule out any effect of this biological characteristic on infant mortality in captive carnivores.

4.4.3. *Captive infant mortality in declining species.*

Declining species are often subjects of conservation programmes in zoos, and much research is realised in institutions for the validation of biochemical tests, most commonly non-invasive techniques of monitoring the breeding status of individuals (Brown, Terio & Graham 1996; Graham *et al.* 1993; Monfort *et al.* 1997; Schwarzenberger *et al.* 1996; Whitten, Brockman & Staviski 1998). It was suggested that species listed on the IUCN Red List have particular biological aspects that increase the chances of a population not being able to sustain itself, such as a slow life history and small geographical range size. Furthermore, there can be an effect of human activity, speeding up the process of extinction. Juvenile mortality was not identified as one of the predicting factors (Purvis *et al.* 2000).

As much effort is put into the breeding success of declining species of carnivores in zoological institutions, and juvenile mortality does not appear to be a threat for these species in the wild, infant mortality in captivity should be homogeneous between endangered and non-endangered species, or even higher in the latter. As the results showed that endangered species, although not presenting higher juvenile mortality in the wild, are performing worse in captivity, it may be the case that captivity conditions and husbandry protocols are influencing the breeding success in institutions.

4.4.4. *Photoperiod and latitudes*.

Changes in photoperiod are believed to be responsible for the regulation of several seasonal phenomena in mammals, especially in species from cold and temperate climates (Lincoln 1998). An example of how crucial photoperiodic regulation is for some species can be found in the lesser mouse lemur (*Microcebus murinus*). In this species, exposure to daylight for periods shorter than 12 hours leads to a general reduction of activity, sexual or behavioural, and the reverse happens when daylight lasts more than 12 hours. Individuals kept in a regimen of five months of long photoperiod followed by three months of short photoperiod ('accelerated seasonal rhythm') had a significant reduction in the number of months of their life span, although still living the same number of seasonal cycles (average of 5, with maximum survival of 9-10 cycles) as the individuals kept in normal photoperiod, although there was no effect on breeding success (Perret 1997).

Photoperiodic control of reproduction occurs in several species. For example, in the brush tail possum (*Trichosurus vulpecula*), changing photoperiod from long to short-day can hasten the onset of breeding activity, and it is advised for institutions involved in conservation to do so (Gemmell & Sernia 1995). Species that suffer this type of breeding control and are kept in institutions outside their natural distribution range can show inversion of season, as it is seen in Himalayan tahrs (*Hemitragus jemlahicus*). Captive specimens kept in the southern hemisphere have their breeding season six months apart from those kept in the northern hemisphere (Pare, Barrette & Prescott 1996). For some captive North Pacific pinnipeds, such as California sea lions (*Zalophus californianus*) and Pacific harbour seals (*Phoca vitulina* *richardsi*), birth timing seems to be tightly regulated by photoperiod, and varies with the latitude of the institutions in which they are kept. In California sea lions, shorter birthing periods occur at higher latitudes. The effect is as subtle as a subtraction of 0.6 days in the pupping season for each degree of latitude added (Temte 1993).

Photoperiodic breeding control occurs through the action of pineal-secreted hormone melatonin, which is released during dark hours (Bittman 1993). The length of nocturnal melatonin secretion reflects changes in the photoperiod, and regulates the pulsatile secretion of gonadotrophin-releasing hormone (GnRH) from the hypothalamus, inducing changes in luteinizing hormone (LH) secretion. LH is responsible for the alternation of occurrence of ovulation in females, and influences sperm production in males (Malpaux, Thiery & Chemineau 1999). In mink (*Mustela vison*), seasonal variations in photoperiod interfere with the pulse frequency of LH release (Jallageas *et al.* 1994).

Other important hormonal change caused by photoperiod concerns the release of prolactin (Curlewis 1992), peptide that stimulates milk protein synthesis and growth of mammary glands, and that seems to play a crucial role eliciting maternal behaviour (Randall, Burggreen & French 1997). There is evidence of the action of prolactin in eliciting nesting behaviour in wolves *Canis lupus* (Mech *et al.* 1996), domestic pigs (Boulton *et al.* 1997; Lawrence *et al.* 1994), and domestic rabbits (Gonzalez-Mariscal *et al.* 2000). It was suggested the involvement of low levels of prolactin with lack of nursing behaviour, and infanticide (McCarthy, Curran & Siegel 1994; Peters, Sist & Kristal 1991). Thus, inadequate photoperiods could eventually lead to higher infant mortality, through poor nutrition and lack of maternal care.

In this research, infant mortality was higher when Arctic species (*Alopex lagopus, Vulpes vulpes, Lynx lynx, L. rufus, Uncia uncia, Ailurus fulgens* and *Ursus maritimus*) were housed in institutions located in subtropical or tropical areas. Tropical species did not present higher infant mortality when housed in temperate areas. Photoperiodic-controlled environments have been used recently to manipulate reproduction in captive Palla's cats *Otocolobus manul* (Brown *et al.* 2002), black-footed ferrets *Mustela nigripes* and Siberian polecats *Mustela eversmanii* (Branvold, Biggins & Wimsat 2003), and results point out the urge to develop specific protocols to be followed by institutions involved in *ex situ* breeding programmes. The results of this research may indicate that artificially controlled photoperiods are extremely necessary for Arctic species housed outside of their range to breed successfully in captivity.

4.4.5. *Nutrition and zonation.*

To provide appropriate accommodation and nutrition to wild species is a constant concern for institutions. Inadequate nutrition can lead to severe health problems, and many physiological and behavioural problems can emerge from inappropriate enclosures (cf. Chapter 1).

The results found in this research point out to the fact that species with complex ecological demands, such as a diet of insects and a elaborate environment, have higher infant mortality in captivity than species with less complex demands, such as a diet of fish or aquatic habits. This may indicate the level of difficulty in the husbandry of these species and that the institutions are not yet giving appropriate conditions for young to thrive.

Nutritional deficiencies are usually a more immediate threat to the health and welfare of captive mammals. Highly carnivorous species, such as many felids, often do not receive enough calcium and vitamins from clean meat, i.e. with no cartilage, skin or fat, needing to eat whole carcasses to maintain health (Ashton & Jones 1979). Herbivorous and insectivorous species, whose low-calcium diet depends on food diversity, can suffer malnutrition because of the difficulty of providing a diverse and palatable diet in captivity (Donoghue & Langenberg 1994). In this research, nine insectivorous species (*Cynictis penicillata, Helogale parvula, Meles meles, Mephitis mephitis Mungos mungos,* *Otocyon megalotis, Proteles cristatus Suricata suricatta* and *Vormela peregusna*) presented higher levels of infant mortality. Insectivorous species require high levels of protein in captivity, and most of the dry food pellets in offer do not have appropriate protein contents. Institutions can usually raise one or two species of insects as live prey for insectivores, but this works more as a behavioural stimulus that nutritional supplement (Price et al. 1999). Many institutions do not meet the nutritional requirements of many species with complex diets because of the lack of information on their natural feeding habit (Dierenfeld 1997) and this may be reflected in the results.

Carnivore species that occupy both terrestrial and arboreal environments also bred poorly in captivity. Seven species used in these analyses (*Bassariscus astutus, Leopardus pardalis, L. tigrinus, Martes flavigula, M. martes, Oncifelis geoffroyi* and *Prionailurus viverrinus*) are small and very mobile, requiring platforms and branches in the enclosure, while two (*Helarctos malayanus* and *Melursus ursinus*) have larger sizes, making the provision of climbing areas more difficult.

The conditions of accommodation can affect captive animals in many aspects. For example, most felids are terrestrial and use taller vegetation as shelter or observation points. In captivity, platforms or other elevated structures are usually the most utilised area of the enclosure. Individuals with access to these structures spent more time resting or observing the surroundings than those in flat enclosures (Lyons, Young & Deag 1997). It was suggested that enclosure type and conditions could indirectly influence reproduction, through modulation of stress, social maintenance, and occurrence of play behaviour (Carlstead & Shepherdson 1994).

The conditions of captivity can play a role in the reproductive output of these species, and it is important that specific demands are reached by the institutions in a way to reduce infant mortality. The costs of providing such conditions to highly-demanding species should be taken into account in the design of any captive breeding programme.

4.5. *Conclusion.*

Biological characteristics of species can serve as predictors of breeding success in captivity. Species with complex environmental and biological demands, which are difficult to be reproduced in constrained spaces and limited resources, presented higher infant mortality rates even when this is not true for wild populations. The actual effect of husbandry techniques is unclear, but differences on performance of the same species from one institution to the other suggest that some protocols may be more efficient than others. However, the permanence and homogeneity of resources in captive conditions may affect positively the reproductive output of species with delayed implantation, once the diapause would not be needed in these conditions.

If the aim of institutions is to drastically reduce infant mortality in captive carnivores, it may be necessary to review husbandry protocols, especially those concerning housing and dietary demands of the species. Special attention should be given to photoperiodic control in the enclosures of Arctic species, when housed in lower latitudes, and to the nutritional and spatial demands of the species. Some species, however, will be naturally more prone to die in younger ages due to their slower development, because they have a longer period in which they are exposed to several factors, such as diseases and conspecific aggression that may cause death.

Chapter 5

Causes of mortality in young captive carnivores.

Abstract

Data collected from published papers served to the analysis of the causes of infant deaths in captivity for 29 species of carnivores. In this dataset, 17% of young deaths had unknown causes. The three main causes of death are related to inadequate maternal behaviour (maternal cannibalism, infanticide and neglect). Around 9% of young died under hand-hearing attempts, and in the majority of cases the young were removed from the mother after displays of aggression or abandonment. In general, young died in the first days *postpartum* and mortality decreased substantially after one week. Perinatal mortality was caused by stillbirths and inadequate behaviour, and all deaths that occurred after 30 days were caused by infectious diseases. There is no statistically significant evidence that the median age of death of infants or their cause of death are related to the taxonomic family of the species. Species with larger home ranges seem to be slightly more prone to lose young due to infectious diseases. There was no evidence that occurrence of stillbirths was affected by the zonation of the species, although a larger sample would be needed to increase power. Stillbirths were significantly more frequent in species with piscivorous and carnivorous diets than in vegetarian, omnivorous or insectivorous species. Mortality caused by inadequate maternal behaviour, such as by infanticide or neglect, was not connected to the type of habitat preferred by the species, but it was significantly higher in species which prey on small and very small animals. Species with faster development, i.e. with shorter lactation and with young that open their eyes early have higher proportion of mortality caused by the dam, indicating the interruption of maternal investment in captivity. While diseases and stillbirths can be greatly reduced by prophylactic vaccination and proper nutrition, adequate maternal behaviour depends on the welfare of nursing females, which can only be reached by the provision of adequate conditions for each species.

5.1. *Introduction.*

As seen in the previous chapters, infant mortality in captive carnivores may represent a drawback to breeding programmes aimed at the conservation of declining species. Mortality of young captive carnivores is reportedly caused by several factors, from infectious diseases to inadequate maternal behaviour, and research on the subject is usually descriptive rather than analytical (e.g. Marker & O'Brien 1989; Munson 1993; Maia & Gouveia 2002).

The investigation of the causes of infant mortality can be an important tool for understanding local threats to wild populations. For example, in one study on the causes of death of harbour seal pups in three regions in Washington, USA, several differences between populations were found. Neonatal mortality ranged from 12% to 26%, and the primary causes of death were predation by coyotes *Canis latrans*, premature parturition or starvation, depending on the location (Steiger *et al.* 1989). This type of information can help to find better solutions for the management of wild populations.

In this chapter, information on known causes of death in captive young carnivores is described and analysed in the search for factors that, if taken into consideration, could help alleviate the incidence of infant mortality of these species in captivity.

5.2. *Causes of death of young wild carnivores.*

It can be very difficult to determine the cause of death of carnivores in the wild. In a three-year study of 10 packs of African hunting dogs *Lycaon pictus* from the Kruger National Park, the cause of death was established only in a small number of cases: the two main causes found were predation by lions *Panthera leo* and disease, responsible for, respectively, 32.3 and 9.7% of the mortality in both adults and juveniles; several pathogens were found in over 95% of captured animals, and infant mortality exceeded 70% (Van Heerden *et al.* 1995).

To determine the mortality in neonates (up to 30 days of age) in the wild is very difficult for certain species, in special those of small size and that nest in burrows. For instance, in a study on breeding success of the meerkat *Suricata suricatta*, infant mortality was calculated from the time of emergence of the burrow until 6 moths of age, since it is very difficult to observe the actual number of young born in this species (Clutton-Brock *et al.* 1999). Other shy species may pose the same challenge. Gittleman (1983) compiled juvenile mortality data in wild carnivores, which is available for only 19 species, mostly terrestrial species with medium to large body sizes.

Research on the mortality of young carnivores in the wild has been yielding valuable information on the effect of ecological factors on population numbers. Resource competition, predation and human intervention appear to have a strong effect on infant mortality of young wild carnivores.

The availability of resources is related to juvenile mortality in several species of wild carnivores. In several populations of raccoon-dogs *Nyctereutes procyonoides* in Finland, the availability of berries is directly related to juvenile survival through autumn and winter (Kauhala & Helle 1995). Starvation was found to be the main cause of death of young wild Arctic foxes *laopex lagopus* in Sweden, and it was related to the decrease in numbers of microtine rodents, their primary prey (Sklepkovych 1989). Food scarcity was also responsible for most of black bears *Ursus americanus* cub deaths in Minnesota, USA (Rogers 1987).

Predation is a common cause of infant mortality in many ecosystems. Large canids, such as the coyote *Canis latrans* and introduced red foxes *Vulpes vulpes,* account for most of the few known deaths of juvenile and adult San Joaquin kit foxes *Vulpes macrotis mutica* in California (Ralls & White 1995). In Poland, reported causes of death of young wild badgers *Meles meles* were predation by raptorial birds and large carnivores, and in smaller scale road accidents and viral epidemics, especially rabies (Ruprecht 1996).

Intra-specific aggression seems to be the reason why female grizzly bears that harvest spawning trout at Yellowstone National Park, USA, lose more dependent cubs; high concentration of bears in trout-spawning areas increase the frequency of aggressive encounters with unrelated adults (Mattson & Reinhart 1995). Infanticide followed by cannibalism was registered in Alaskan brown bears *Ursus arctos*, though unrelated adults killed only four cubs in 19 summers of observations (Hessing & Aumiller 1994). Infanticide by related adults and juveniles followed by cannibalism was also recorded in Arctic foxes, when there was a drastic reduction in prey numbers in Sweden, but it was an isolated event in five years of observations (Sklepkovych 1989).

Besides resource competition and predation, other ecological factors can lead to the loss of infants and adults alike. For example, the dens of polar bears occasionally collapse in exceptionally warm weather, leading to the death of the mother and cubs (Clarkson & Irish 1991). With the rise in global temperature, these events can become much more frequent because of the higher levels of rain in late winter; together with the increased nutritional stress, this would have a devastating effect to the polar bear *Ursus maritimus* populations, especially for those in the southern boundaries of the range, such as Hudson Bay (Stirling & Derocher 1993).

Anthropical activities, such as trapping, shooting and road accidents, are responsible for many juvenile deaths in species such as the red fox *Vulpes vulpes* in central Japan (Takeuchi & Koganezawa 1994), the introduced American mink *Mustela vison* and native polecats *M. putorius* in France (Lode 1995), European lynx *Lynx lynx* in Poland and Belarus (Jedrzejewski *et al.* 1996), and European badgers in Poland (Ruprecht 1996). Trapping or shooting can cause up to 98% of infant mortality in harvested populations, such as the raccoon *Procyon lotor* populations in Wisconsin, USA (Payne & Root 1986).

Captive populations are safe from many of the causes of mortality of wild carnivores, such as predation, lack of resources or hunting, so it is expected that infant mortality in captivity reach lower proportions than those found in wild populations. In fact, from 16 species that had known proportion of mortality both in the wild and in captivity, only the polar bear *Ursus maritimus* and the spotted hyaena *Crocuta crocuta* presented higher infant mortality in captivity than in the wild, and at least half of the institutions housing brown bears *Ursus arctos* and Canadian otters *Lutra canadensis* did not report a dead young from 1986 to 1996 (Table 5.1).

Table 5.1: Juvenile mortality in the wild (Gittleman 1983) and median proportion of infant mortality in captivity (*IZY* Vols. 26-35) in 16 species of carnivores.

Family	Species	Juvenile Mortality (Gittleman 1983)	Infant mortality in captivity
Canidae	*Canis lupus*	0.44	0.2
Canidae	*Vulpes vulpes*	0.76	0.33
Canidae	*Urocyon cinereoargenteus*	0.68	0.28
Ursidae	*Ursus arctos*	0.18	0
Ursidae	*Ursus americanus*	0.28	0.11
Ursidae	*Ursus maritimus*	0.20	0.67
Procyonidae	*Ailurus fulgens*	0.52	0.20
Procyonidae	*Procyon lotor*	0.42	0.20
Mustelidae	*Mustela erminea*	0.83	0.12
Mustelidae	*Mephitis mephitis*	0.66	0.31
Mustelidae	*Lutra canadensis*	0.46	0
Hyaenidae	*Crocuta crocuta*	0.16	0.38
Felidae	*Lynx lynx*	0.32	0.23
Felidae	*Lynx rufus*	0.53	0.06
Felidae	*Panthera leo*	0.67	0.40
Felidae	*Panthera tigris*	0.57	0.33

5.3. *Causes of death of young captive carnivores.*

In captivity, under generally controlled conditions, many external causes of mortality in neonates are eliminated, and the remaining causes can be determined more readily. For example, in Prague Zoo, Czech Republic, the reproduction of Pallas' cats *Otocolobus manul* was registered twice, but both litters died within two months due to parasitic or bacterial diseases (Volf 1999). In Denver Zoological Gardens, USA, four wild-caught adults Pallas' cats tested positive for *Toxoplasma gondii* antibodies, and six young born to them died of toxoplasmosis-related conditions (Kenny *et al.* 2002). In a survey of North American zoos, diseases were also responsible for a large number of deaths of young captive cheetahs *Acinonyx jubatus* (Munson 1993). Another survey on cheetahs, this time covering over 100 years of records, suggested a larger participation of behavioural aspects on infant mortality: several reports of death "by devouring" or "weakness" may point out to events of maternal infanticide and neglect (Marker & O'Brien 1989). A similar record research on the maned wolf *Chrysocyon brachyurus* studbook revealed parental involvement in 67% of pup deaths, while infectious diseases were responsible for only 9% of the mortality (Maia & Gouveia 2002).

5.3.1. *Hypotheses to be tested.*

The causes of death of young carnivores in captivity are described in this chapter, and factors that can make certain species more prone to particular ailments are considered.

As seen in Chapter 4, life history traits can predict breeding success in captivity: altricial species that demand complex husbandry practices are more prone to lose young than easily manageable ones. There are indications that maternal infanticide is responsible for many infant deaths in captive carnivores (Bakken 1994; Laurenson 1993; Maia & Gouveia 2002; Marker & O'Brien 1989). As young in captivity are safe from most of the risks found in the wild, it is expected that inadequate maternal behaviour accounts for a large proportion of infant deaths in captivity. If so, most deaths shall occur in the first few weeks after birth, especially in species in which the young develop at a faster pace, due to the high costs of maternal care (Clutton-Brock 1991; Hrdy 1979; Labov *et al.* 1985). Species with large home ranges are heavily affected by captivity (Clubb & Mason 2003) and may be predisposed to contract diseases through poor nutrition or poor welfare.

5.4. *Methods.*

The dataset used for this analysis was the bibliographical dataset collected from 141 published papers (Appendix 4, described in section 2.2.5), which served for the analysis of causes of death in 29 species. Relative frequencies of known causes of death were calculated for each female and the median proportions were calculated for the species, being used as dependent variables in regressions. Average litter sizes, average age of breeding and average age of death of young were calculated for each female. Multiple analyses were performed using variables chosen through stepwise regression, forward method, from the datasets compiled by Gittleman (1983, 1986a, 1986b): juvenile mortality, home range sizes, age when young open their eyes, weaning age, type of vegetation in the habitat, type of diet and type of zonation. All proportional values were transformed by the arcsine of the square-root and other continuous variables were log-transformed. Table 5.2 displays the species used in the analysis of this chapter.

Table 5.2: Species used in the analysis of causes of death of young captive carnivores, with number of litters, dams, zoos holding the species, young born and young dead. The data was collected from 141 published papers (Appendix 4).

Family	Species	Litters	Dams	Zoos	Young born	Young dead
Canidae	*Canis lupus*	9	2	2	33	14
Canidae	*Cerdocyon thous*	6	4	2	25	9
Canidae	*Chrysocyon brachyurus*	20	13	8	49	19
Canidae	*Vulpes zerda*	10	7	3	23	8
Canidae	*Lycaon pictus*	4	2	2	24	8
Felidae	*Acinonyx jubatus*	22	15	12	66	17
Felidae	*Caracal caracal*	5	4	2	14	6
Felidae	*Felis margarita*	10	2	2	42	24
Felidae	*Felis nigripes*	8	3	2	13	8
Felidae	*Felis silvestris*	29	7	3	107	58
Felidae	*Leopardus tigrinus*	7	3	2	9	3
Felidae	*Lynx lynx*	10	7	3	23	8
Felidae	*Neofelis nebulosa*	15	5	4	31	14
Felidae	*Oncifelis geoffroyi*	15	5	3	34	17
Felidae	*Prionailurus bengalensis*	8	2	2	21	7
Felidae	*Uncia uncia*	11	5	4	28	17
Felidae	*Panthera tigris*	9	7	5	26	25
Herpestidae	*Helogale parvula*	14	3	2	51	20
Hyaenidae	*Crocuta crocuta*	4	3	3	6	2
Mustelidae	*Amblonyx cinereus*	11	3	3	28	21
Mustelidae	*Enhydra lutris*	9	5	4	9	9
Mustelidae	*Pteronura brasiliensis*	12	2	1	33	26
Mustelidae	*Meles meles*	2	2	1	3	1
Procyonidae	*Ailurus fulgens*	9	5	3	16	8
Ursidae	*Ailuropoda melanoleuca*	11	7	5	15	10
Ursidae	*Helarctos malayanus*	12	5	3	12	1
Ursidae	*Tremarctos ornatus*	11	4	4	17	12
Ursidae	*Ursus maritimus*	11	4	4	21	16
Viverridae	*Arctictis binturong*	13	5	5	33	12

5.5. *Results.*

5.5.1. *Causes of death and age of young.*

In this dataset, the cause of death was unknown in an average of 17% of young. Throughout 25 species, the three main causes of death are related to inadequate maternal behaviour (maternal cannibalism, infanticide and neglect), as it can be seen in Figure 5.1. Around 9% of young died under hand-hearing attempts, and in the majority of cases the young were removed from the mother after displays of aggression or abandonment. Most reports did not provide the exact date of removal of the young for hand-rearing.

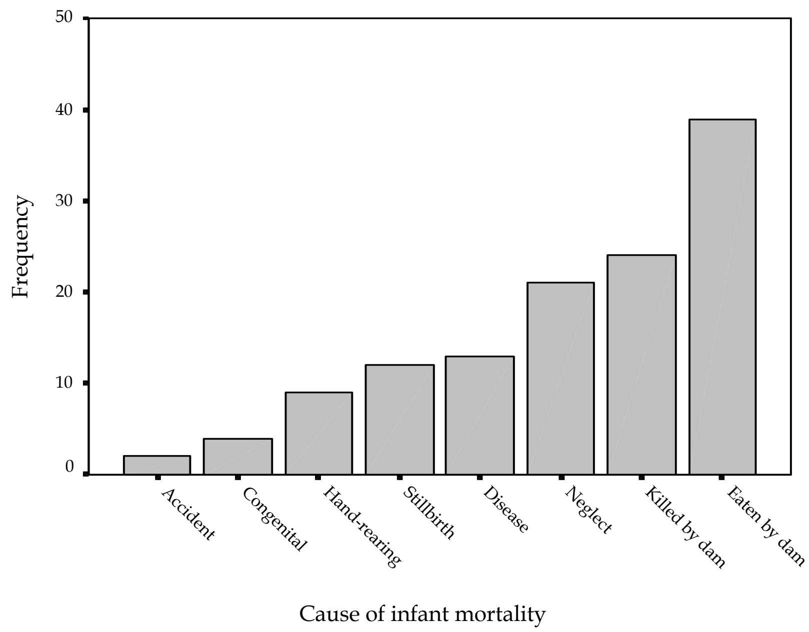

Figure 5.1. Absolute frequencies of cause of death in young captive carnivores (N = 364 young of 29 species).

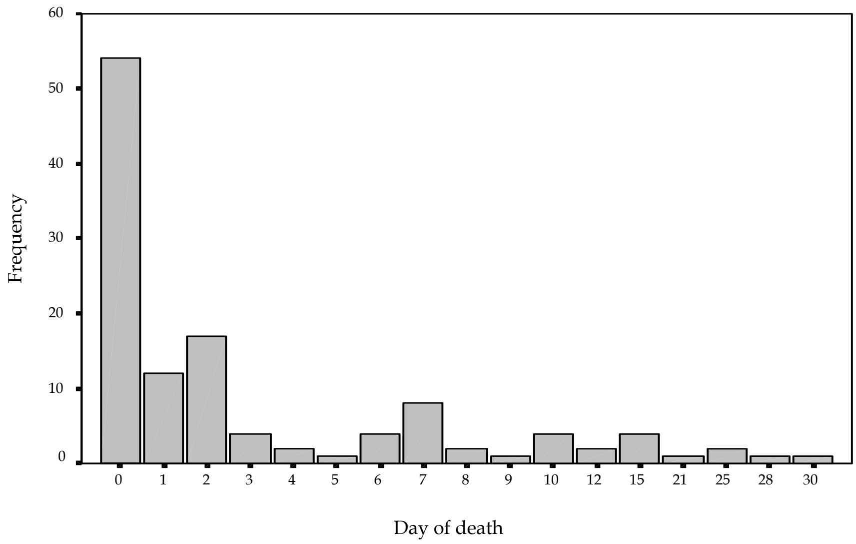

Figure 5.2. Absolute frequencies of age (in days) of death of young captive carnivores (N = 364 young of 29 species).

In general, young died in the first days *postpartum* and mortality decreased substantially after one week (Figure 5.2). *Postpartum* mortality was mainly caused by stillbirths, and inadequate maternal behaviour accounted for deaths up to two weeks of age (Figure 5.3); all deaths that occurred after 30 days were caused by infectious diseases (One-way ANOVA: $F_{3, 60} = 10.66$, $p = 0.000$). Reports did not specify when the young were removed for hand-rearing.

There is no statistically significant evidence that the median age of death of infants (One-way ANOVA: $F_{5, 74} = 0.98$, $p = 0.44$, power = 0.71) or the cause of death (LOGIT: $Z_{126}=-1.79$, $p = 0.21$, odds ratio = 0.66*)* are related to the taxonomic family of the species.

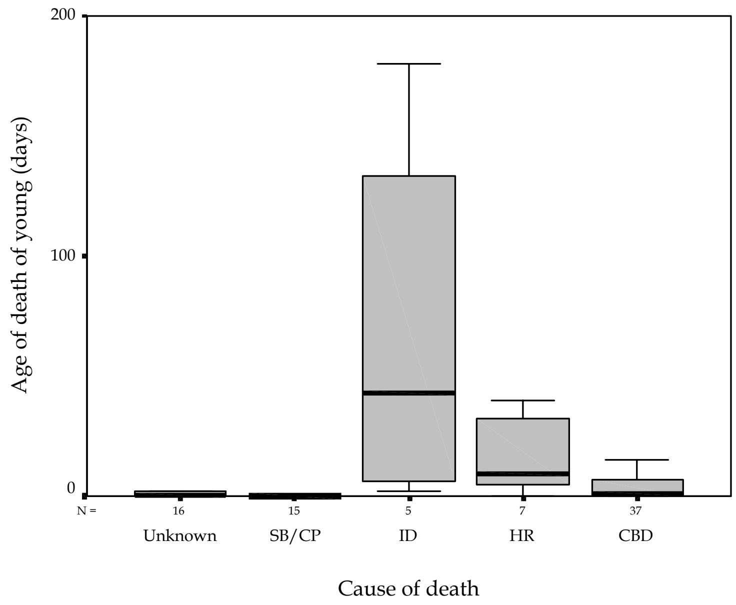

Figure 5.3: Age of death of young captive carnivores in days according to the cause of death, N = 364 young of 29 species. SB = stillbirth; CP = congenital problems; ID = infectious diseases; HR = under hand-rearing; CBD = maternal involvement (infanticide or neglect).

5.5.2. *Ecological factors as predictors of the cause of death of young captive carnivores.*

In captivity, carnivore species with larger home ranges seem to be slightly more prone to lose young to infectious diseases, and the regression explains 50% of the relation (Regression: $F_{9} = 6.07$, $p = 0.06$, R^2 adj. = 50%, figure 5.4). There was no evidence that occurrence of stillbirths was affected by the zonation of the species, although a larger sample would be needed to increase power (One-way ANOVA: $F_{5,\ 14} = 2.38$, $p = 0.09$, power = 0.26). However, stillbirths were significantly more frequent in species with piscivorous and carnivorous diets than in vegetarian, omnivorous or insectivorous species (One-way ANOVA: $F_{4,12} = 3.47$, $p = 0.04$).

Mortality caused by inadequate maternal behaviour, such as by infanticide or neglect, was not connected to the type of habitat (open land, sparse vegetation, dense vegetation or aquatic) preferred by the species (One-way ANOVA: $F_{3, 16} = 0.89$, $p = 0.4$), but it was significantly higher in species which prey on small and very small animals (One-way ANOVA: $F_{2, 14} = 7.20$, $p = 0.05$).

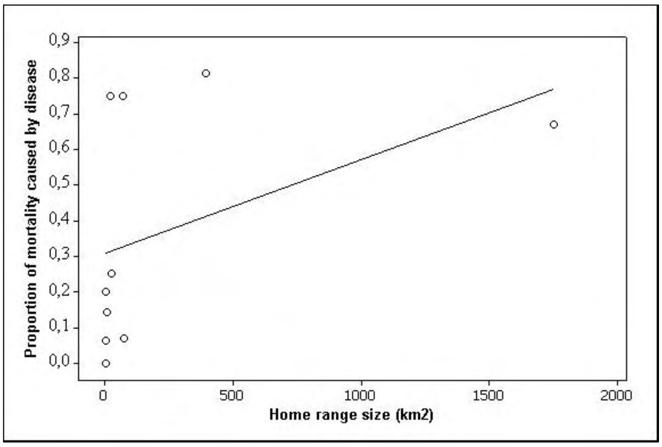

Figure 5.4: Graph of home range sizes (in km²) versus the occurrence of fatal infectious diseases in infants of 10 species of carnivores (data not transformed).

Weaning age (WA) seemed to have a negative effect on the proportion of mortality caused by the dam in this dataset, and a weak effect of the age in which the young open their eyes (OE) was also detected; the model explains 42% of the variance (GLM on transformed data: WA: $F_{1, 13}= 609.15$, $p=0.032$; OE: $F_{1, 10}= 6.68$, $p= 0.073$, Figure 5.5).

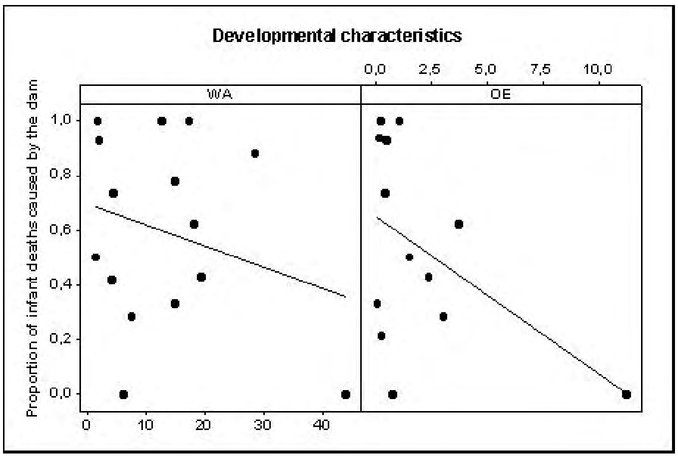

Figure 5.5: Scatterplots of developmental characteristics (WA = weaning age in weeks; OE = age of opening eyes in days) of 15 species of carnivores in relation to the occurrence of infant deaths caused by the dam in captivity. The data plotted was not transformed.

5.6. *Discussion.*

It seems that infant mortality in captive carnivores is frequently caused by inadequate maternal behaviour, so its several aspects will be analysed in detail in Chapter 6.

In this dataset, the young that survived birth were the most vulnerable to all causes of death during the first two weeks. In the wild, the observation of young carnivores is the most difficult during this period, and therefore most researches do not analyse this aspect. In captivity, however, similar results to this research were found: a survey on the mortality of captive African hunting dogs *Lycaon pictus* from 1983 to 1995 showed that the majority of infant deaths (57.5%) occurred before the end of the first week, decreasing to 14.9% between two weeks and 1 year of age (Van Heerden *et al.* 1996).

The actual number of stillbirths and the factors that may influence it in the wild is largely unknown. However, the phenomenon has been recorded frequently in captive carnivores. In farmed blue foxes, stillbirths occurred in 5.9% of the births, and 11.4% of the young died of infectious diseases before weaning (Ilukha, Harri & Rekila 1997). In domestic dogs of the Boxer breed, stillbirths and infections accounted for the majority of deaths (van der Beek *et al.* 1999).

The analysis of the present dataset suggested a relation between the type of diet of species and the occurrence of stillbirths. Nutrition can be an important factor to the health of young carnivores. An experiment compared weight gain and growth rates of young caged mink fed with products made with different technologies of preservation; kits fed with food prepared with a new technique of preserving raw animal by-products through fermentation decreased in weight and had lower growth rates compared to the ones fed with the traditional products (dried pellets) or fresh animal products (Urlings *et al.* 1993). In foxes, taurine deficiency causes the heart to dilate, and may lead to decreased breeding success and even death, being the effect more pronounced in younger animals (Moise *et al.* 1991).

Nutritional deficiencies can also facilitate stillbirths by depressing immune responses and allowing the onset of infections. For example, canine herpesvirus and feline herpesvirus-1 cause abortion or neonatal deaths in domestic dogs and cats, and may infect, many times undetected, wild related species (Smith 1997). Experiments with mink *Mustela vison* and ferrets *Mustela putorius* revealed that females contaminated by *Campylobacter jejuni* either aborted the kits or had stillbirths, even when they survived previous infections with the same bacteria, mainly because of the development of severe placentitis (Bell & Manning 1990).

Certain diseases are widespread in domestic animals but can affect wild carnivores, leading to lower breeding success. In farmed silver foxes *Vulpes vulpes,* the presence of parvoviral antibodies was found to cause small litter size and to facilitate the infection of cubs by other microorganisms; treating affected females with adequate antibiotics significantly reduced the number of abortions and neonatal deaths (Mizak, Rzezutka & Matras 1998).

Diseases were the only cause of death after the critical period of 30 days. Many pathogens can cause septicaemia in young carnivores, but very little is known about the epidemiological mechanisms in wild species, even in captivity. All research in this area has been done in domestic species and those farmed for commercial purposes.

In domestic dogs, neonatal mortality is usually related to septicaemia caused by pathogenic microorganisms such as staphylococci and streptococci, which cause sudden death within the first week after birth, frequently without any previous symptom. Researchers developed a metaphylatic protocol to identify the presence of any pathogen in vaginal smears of the mother and the facilities where the animals are, 20 days after birth, and appropriate antibiotics are given to the mothers for 7 days before the calculated date of birth; puppies receive the same treatment for 3 days after birth, and mortality from septicaemia was almost null in treated animals (Miljkovic *et al.* 1995). Research in Nigeria connected infant sudden death in domestic dogs to acute systemic infections by the Infectious Canine Hepatitis (ICH) virus, which killed puppies up to 12 weeks old without previous symptoms (Ojeh *et al.* 1989). It was suggested that inbreeding levels in domestic puppies had a very strong effect on the occurrence of neonatal infections (van der Beek *et al.* 1999).

Microorganisms can lead to asymptomatic deaths, and viral infections can affect infant survival even before they can be detected by any tests, and therefore may not be diagnosed as the cause of death in many occasions. Experiments with domestic cats showed that early infection with FIV, which is transmitted from the mother to kittens on birth or through nursing, may lead to neurological damage and poor growing within 12 weeks of birth, even before the full development of immunodeficiency (Johnston *et al.* 2002). Also, weanling kittens infected with feline leukaemia virus, which is widespread in domestic cats and eventually causes death, consumed and spent less energy, lost weight and developed a permanent growth impairment as early as the 4th day after inoculation, before the phase in which it can be detected by tests and much before the development of the bone marrow stage of the infection (Hartke *et al.* 1995).

Nowadays, most wild species can be vaccinated against domestic species common diseases, and there are alternative therapies for diseases that do not have specific vaccines. For example, one of the main causes of death in captive newborn mink kits is pneumonitis, or Aleutian disease, caused by the Aleutian Disease Virus (ADV). Although an ADV epidemic can be responsible for a large number of deaths in farmed mink, it can be controlled by the administration of antibody-specific gamma globulin, which is particularly effective in highly infected individuals (Aasted, Alexandersen & Hansen 1988).

In this dataset, there is a weak effect of the species average home range size in the frequency of infant mortality caused by diseases. This could be related to the effect of housing conditions in the health of individuals. Housing conditions are known to affect breeding success in carnivores (Carlstead & Sheperson 1994) and improper keeping can lead to poor welfare (Carlstead 1996; Clubb & Mason 2004). It was also found that species with large home ranges are more prone to develop stereotypies and breed poorly (Clubb & Mason 2003). Stereotypies not only reduce general welfare of the individuals but can lead to sometimes severe friction wounds (Spendrup & Larsson 1998).

Some characteristics of the enclosure, such as type of flooring and access to hygiene can also affect the health of the animals. Necropsies and histopathologic analysis showed that most red wolf *Canis rufus* pups had infected lesions in their feet, caused by the combination of inadequate substrate and poor hygiene (Acton, Munson & Waddell 2000). Depending on the design of the enclosure, perfect hygiene cannot be performed and parasites can be a permanent problem, re-infecting treated animals and infecting young at birth (Fowler 1996).

The influence of inadequate maternal behaviour in captive carnivores has been noted in other studies, but results can be contradictory. For instance, in one study maternal infanticide was found to be the main cause of mortality in farmed silver fox cubs, occurring in 75.9% of the deaths (Braastad & Bakken 1993); other research showed that only 0.3% of the infant deaths in silver foxes were caused by the dam (Ilukha, Harri & Rekila 1997). Infanticide in this species is highly related to social competition: infanticidal females that were removed from the view of conspecifics raised their young normally (Bakken 1992, Bakken 1993), showing that husbandry decisions may be crucial to the occurrence of maternal infanticide.

It can be difficult to record deaths by maternal aggression when the event was not observed, and maternal neglect can be only assumed in *post-mortem* examination when the young display signs of starvation and general lack of care. In captive African hunting dogs, the cause of death could not be determined in the majority of cases of neonatal deaths, but it was supposed that around 42% of neonatal mortality was caused by exposure. Around 15%

of the dead animals, including both juveniles and adults, presented signs of trauma caused by conspecifics (Van Heerden *et al.* 1996).

It has been suggested that carnivores are more prone to commit infanticide due to their carnivorous diet and altricial young (Packer & Pusey 1984). In this dataset, species that prey on small and very small animals presented higher proportion of deaths caused by of inadequate maternal behaviour, independent of which form it takes. Analysis also suggests the influence of prey size in active maternal infanticide, as will be discussed in Chapter 6.

In Chapter 4 it was suggested that species with altricial young present higher levels of infant mortality in captivity, because species with slower development are exposed to all causes of mortality, including those cause by the dam, for a longer period. In fact, this study suggests that species with faster development, i.e. that open their eyes and wean earlier, are more prone to die due to inadequate maternal behaviour, and that most of these deaths occur in the first weeks after birth. These results may reflect the mechanism of brood reduction, where maternal investment is reduced or interrupted to enhance either the fitness of the surviving young or the female's own capability for further breeding (Clutton-Brock 1991). Maternal investment is higher during lactation and young can especially demanding in small felids (Oftedal & Gittleman 1989); maternal infanticide and neglect were the main causes of death, in this research, in captive populations of *Caracal caracal* (100%), *Oncifelis geoffroyi* (88%), *Leopardus tigrinus* (67%), *Felis margarita* (42%) and *Felis nigripes* (38%). This type of strategy is commonly used when resources are low or there is the imminent danger of losing the brood (Clutton-Brock 1991), conditions which supposedly do not exist in captive conditions. It is possible that some species perceive captive environments as sub-optimal and react by interrupting reproductive investment, but further research, considering each species' characteristics, would be needed to fully understand the adaptive strategies involved.

5.7. *Conclusion.*

Infant mortality in captive carnivores occurs usually within a critical period before 30 days of age; after this period, the young are still vulnerable to infectious diseases, but many of those can be prevented through vaccination of other prophylactic measures. Certain characteristics of the species can make them more prone to some ailments, through poor nutrition or inadequate housing. Species that predate on small animals and have high-maintenance young have a tendency to display inadequate maternal behaviour, such as active infanticide and abandonment, and may perceive captive conditions as sub-optimal, thus interrupting maternal investment. Further research is necessary to understand the adaptive value of this strategy for each species and to develop possible solutions to reduce infant mortality in captivity.

Chapter 6:

Maternal infanticide in captive carnivores

Abstract

Most of infant mortality in many captive carnivores is caused by inadequate maternal behaviour. A dataset collected from 141 published papers yield information on the frequencies of three types of maternal behaviour fatal to infants (cannibalism, active infanticide and abandonment) in 29 species of carnivores. These values were tested against life history traits that could be predisposing species to perform these behaviours more frequently. Species that prey on larger animals tended to kill but not consume the young, but there was no significant evidence that species with smaller prey do consume the young. Species with slower growing litters showed a higher incidence of active infanticide without cannibalism.

Species weaning age and the age in which the young open their eyes did not influence the occurrence of active infanticide, followed or not by cannibalism. The proportion of passive infanticide reported for each species was strongly influenced by interbirth interval, but there was no significant effect of weaning age. Overall, wild-caught females presented slightly higher levels of maternal infanticide, passive or active, than captive-born ones independent of the species. Throughout the order Carnivora, there was a slight effect from the origin of the female (if wild-caught or captive born) in the type of infanticide: wild-caught females performed more passive infanticide and captive-born performed more active infanticide. The activity pattern of the species had a significant effect in the type of infanticide performed, with arrhythmic species presenting higher levels of active infanticide and diurnal species neglecting young more often. Overall, there was no statistically significant effect of the presence of the male in the incidence of maternal infanticide in species with exclusive maternal care (i.e. when the male does not care for the young), but a larger sample would be needed to increase test power. Brood reduction strategies seem to differ greatly between species of carnivores in captivity, but the decision on curtailing maternal investment may depend on the female's welfare, which can be affected by individual histories and husbandry practices.

6.1. *Introduction.*

Maternal behaviour seems to play a crucial role in the survival of captive-born carnivores, for most of the reported infant mortality is caused by maternal aggression or neglect, especially in species with expensive maternal care, such as small felids (Chapter 5). To control the impact of these phenomena in captive breeding, it is necessary to understand the adaptive role of infanticide and the conditions in which it is more prone to occur.

Infanticide, by related or unrelated adults, has different adaptive values depending on specific social and environmental conditions, as can be seen in Table 6.1; in the wild, maternal infanticide can occur under many conditions, as long as social or ecological pressures drive the females to opt for it (Hrdy 1979).

Maternal infanticide occurs when the female kills her own offspring, and was recorded in the wild in some species of the Order Carnivora, such as lions *Panthera leo* (Rudnai 1973), polar bears *Ursus maritimus* (Van Keullen-Kromhout 1976) and red foxes *Vulpes vulpes* (MacDonald 1980). It has been suggested that females may use this strategy to avoid further investment in a litter that will probably not survive (Hrdy 1979; Hausfater & Hrdy 1984). Certain species use maternal infanticide largely as a means of manipulating litter size or sex ratio (Labov *et al.* 1985; Wolff 1997).

The role of inadequate maternal behaviour in parental manipulation has been discussed only in recent years. Hrdy (1979) and Bakken (1994) pointed out that parental manipulation might occur at any level during the breeding process, from the destruction of gametes and abortion to the neglect or killing of young, the last two being caused by inadequate maternal behaviour. Maternal infanticide presents, then, both passive (neglect) and active (killing) expressions. The mother may ignore the young and allow them to die of starvation or hypothermia, or kill her young by direct action, such as biting or removing the young from the nest (Hayssen 1984). Both mechanisms can be applied in maternal litter manipulation - where selected youngsters are killed while others are raised normally - or under severe lack of resources or threat of predation - through the termination of the whole litter (Clutton-Brock 1991). The benefits of these strategies may depend on three factors: a) the ability of the parents to produce another litter in the same season; b) the cost of having another litter to the parent's reproductive value; and c) on the probability of these youngsters, raised under adverse conditions, to breed when adults (Hayssen 1984).

The female will, in many cases, reabsorb nutrients by eating the young (Hrdy 1979). Some authors call the cannibalisation of the offspring Cronism, in reference to mythological Greek god Kronos, who ate all his children (In MacFarland 1981: 55-58). There is evidence in nature, although scant, of maternal infanticide followed by cannibalisation. For example, remains of partially eaten cubs were found in the frozen floor of a den of polar bears (*Ursus maritimus*) in the wild (Van Keulen-Kromhout 1976). As seen in Chapter 5, many Carnivora species have nests in burrows, are nocturnal and/or are extremely cautious of humans, and there are not many observations of these behaviours in the wild. Packer & Pusey (1984) reviewed the occurrence of infanticide in carnivores, with special focus in male infanticide strategies. There are some observations of infanticide in wild large carnivores, such as lions and brown bears, but it is related only to litter abandonment; active maternal infanticide was not mentioned in this research, but the authors point out for the lack of data on nocturnal and solitary species (Packey and Pusey 1984).

Until the 1980's, maternal infanticide was generally regarded as an abnormal or "unnatural" behaviour displayed only under the stress of captivity or extreme crowding (Calhoun 1962; Lorenz 1966; Labov *et al.* 1985), mostly due to the lack of research in the wild. For example, one of the causes of maternal infanticide in captivity was thought to be the low level of domestication in some species, such as silver foxes *Vulpes vulpes* (Bakken

1994). The occurrence of infanticide in domestic species such as rabbits *Oryctolagus cuniculus* (Sambraus 1985), pigs *Sus scrofa* (Lammers & De Lange 1986), and cats *Felis catus* (Feldman 1993) seems to disprove this hypothesis.

Infanticide is said to be more prone to occur among carnivores, perhaps because of their predatory feeding habits and altricial young (Packer & Pusey 1984). In captivity, despite the fact that there are many published records of maternal infanticide for almost all families of the Order Carnivora, the subject was mostly studied in commercially exploited species (e.g. Bakken 1994; Pyykonen *et al*. 1998; Korhonen & Harri 1988). Although potentially useful, records from zoological institutions have been under used in the research on breeding success, in particular referring to the impact of inadequate maternal behaviour in *ex situ* conservations programmes.

In this chapter, an overview of the adaptive value and occurrence of maternal infanticide in captivity is made. Statistical analysis of data from captive populations is used to tests the hypotheses that life history traits can predict the type of maternal infanticide displayed by a species under sub-optimal conditions, and that the characteristics of individual females, such as the rearing method or place of origin, can affect the female's decision to interrupt maternal investment.

Table 6.1: Classes of infanticide (Hrdy, 1979).

Classes	Types	Function/ Methods	Advantages
Exploitation	1) As a food resource 2) As a buffer protection 3) As a "mother toy"	1) Cannibalism 2) Using as a distraction 3) Excessive or inadequate alloparenting	1) Food; protein 2) Escape; defence 3) Possibly training
Resource competition	1) Directly related to rearing 2) Indirectly related to rearing 3) Milk "theft" 4) Burrow "theft" 5) Xenophobia 6) Brood reduction	1) Nest sites 2) Parental food supply 3) Killing new-borns from other females 4) Killing new-borns from other females 5) Killing infants from an unrelated or alien female 6) Killing own young passively (exposure, starvation)	1) & 2) Increase in the average the access to resources to the killer & descendants 3) The female will nurse the killer's young 4) The killer will take the mother's burrow 5) Increases the opportunities of killer's lineage 6) Allocation of parental efforts to one young that is more prone to survive.
Parental manipulation	Destruction of offspring: 1) Imperfect or debilitated 2) Non-defective	1) Premature; defectives 2) a) Under poor conditions b) In the presence of danger c) When there is a previous offspring	1) The cost is too high for a doubtful outcome. 2) a) & b) The risks are so high that the effort is not justified. c) Allocation of resources after a high investment in a stronger litter.
Sexual selection	Performed often by males, some forms by females.	1) Killing other male's offspring 2) Killing other female's offspring 3) Reabsorbing foetuses in the presence of strange males	1) Eliminates the rival's offspring and reduces the interval for another (the killer's) 2) Eliminates the rival's offspring and increases the chance of male's services 3) Eliminates an offspring that would be eventually killed ('Bruce effect').
Social pathology	Considered maladaptive and typical of human-disturbed locations (zoos and urban areas). Abnormal.	1) Disturbed by noise, light, and/or smells, captive females devour their offspring right after birth. 2) In poor conditions or in the lack of resources, an increase in aggressiveness lead to cannibalism, and infants of all ages are more vulnerable.	1) It could be a reflex of the selected mechanisms of parental manipulation discussed above, which are still at work in captivity. 2) Self-preservation mechanisms that could save one's life in extreme situations.

6.2. *The adaptive value of maternal infanticide.*

According to Hrdy (1979), maternal infanticide, passive or active, can be explained either as a tool for maternal manipulation (including the manipulation of sex ratio) or as a social pathology triggered by conditions of captivity. Wolff (1997) suggested that there are aspects that predict which species will commit infanticide: territorial females, altricial, non-mobile young and risk of predation are common to all that use this strategy, which is the case of many rodents and most terrestrial carnivores.

Mothers can cull young as a form of manipulation of litter size or sex ratio. In rodents, females that have very large litters may kill and commonly eat some young, thus reducing the number of young to the average of the species and nourishing the survivors properly (Labov *et al.* 1985). In many species, male pups are usually more demanding and at higher risk of being culled in harsher conditions (Labov *et al.* 1985). Maternal manipulation of the sex ratio can occur through differential abortion of the two sexes or a tendency to neglect, or respond less, to the begging and demands of the most costly sex (Eshel & Sansone 1994).

Infanticide occurs in species whose populations can be regulated by intrinsic, or behavioural, mechanisms. Territoriality, gender segregation, dispersal and reproductive suppression are also intrinsic regulation mechanisms that can reduce population growth before resource limitation (Wolff 1997).

Experiments with silver foxes showed that primiparous vixens had a higher percentage of infanticide when compared to multiparous ones, and those infanticidal females, when kept in the next year on visual and spatial isolation from the others, performed adequate maternal behaviour (Bakken 1992; Bakken 1993). This evidence links inadequate maternal behaviour, in this species, to social competition, rather than to any other mechanism (Braastad & Bakken 1993).

Whatever is the adaptive value of maternal infanticide, it is a very extreme strategy used sparingly in the wild, and its occurrence in captivity is generally viewed as social pathology of the individual. However, the frequency in which it is performed by captive carnivores and the fact that infanticidal females may, when housed in better conditions, perform adequate maternal behaviour, may indicate that females perceive the conditions in captivity as sub-optimal.

6.3. *Maternal infanticide in captivity.*

Many captive carnivore females present behavioural problems in the care of young. Published reports are common and many institutions remove the young of certain species for hand-rearing right after birth. Although hand-rearing has been reported to in several species (see Appendix 4), there are official guidelines in which species shall be preferentially removed to be raised by hand. The decision of removing young from the care of the female is largely at the discretion of the institution's staff and is usually based in personal experiences and anecdotal reports of infanticide, with little empirical support (Wharton & Mainka 1997).

Poor maternal care can seriously threaten the success of a captive breeding programme. Certain species do not respond well to hand-rearing, either through intolerance to milk replacements or through the lack of a proper behavioural development, especially in species with a sensitive socialisation phase (cf. Chapter 1). There is abundant evidence of maternal infanticide in zoo-housed carnivores, with examples in several families of the order (Chapter 5).

Although there is very little information to compare the occurrence of maternal infanticide in the wild and in captivity, the frequency with which it occurs in captive conditions is remarkable. For example, in captive cheetahs (*Acinonyx jubatus*), cub abandonment is said to be very common, but it was only observed in the wild in very rare occasions, when prey are virtually non-existent (Laurenson 1993).

Zoological institutions can be an excellent source of information in the research of the causes of maternal infanticide. Data such as proportion of deaths caused by the dam, age of killer and offspring and husbandry routines are essential for the understanding of the phenomenon and are scarce in the wild (Braastad & Bakken 1993).

6.3.1. *Husbandry techniques and maternal infanticide.*

To unravel the factors behind the high frequency of maternal infanticide in zoos, the conditions in which the animals are kept must be looked at. Noise level, the proximity and quantity of visitors and the design of the enclosure are some of the aspects of captivity that seemed most likely to lead to episodes of infanticide.

The effect of husbandry on captive carnivore females was already evident and had led to the practical recommendation, among fur farmers, of removing infanticidal females from the stock, because they would continue to kill offspring while kept in the same conditions (Bakken 1994). Experiments showed, however, that these females can raise offspring when put in visual isolation from other females (Bakken 1994; Ilukha, Harri & Rekilä, 1997).

Noise levels were also known to be a source of disturbance to animals in exhibition. For example, bears seem to prefer smaller mothering dens than those provided by zoos. Small rounds dens are insulated from outer noises and allow the mother to hear the cubs (Van Keullen-Kromhout 1978). Female red pandas seem to be very disturbed by human presence and noise levels, and keep moving the cubs from one place to another, but the problem can be solved by roping the area and providing multiple nest boxes (Roberts 1975). Felids are said to require seclude and quiet to have cubs, and mothers could be prone to neglect or eat cubs when disturbed or stressed (Laurenson, Wielebnowski & Caro 1995).

High noise levels seem to disturb polar bears more than other ursids, maybe because of their natural silent environment. On all occasions polar bears bred successfully in captivity, noise was carefully avoided. Although regular noise levels do not seem to disturb brown bears, one female killed her cubs after an incident where people invaded the zoo and used iron sticks to bang the bars of her cage (Van Keulen-Kromhout 1976).

Breeding or cubbing dens are an important aspect to be design in an enclosure. In nature, some species move their young to post-natal dens, such as the raccoon *Procyon lotor* (Judson, Clark & Andrews 1994), or abandon their previous cubbing dens when threatened, even when this movement may affect the female's breeding success (Swenson *et al.* 1997). One indication of the importance of multiple cubbing dens is perhaps the act, performed by many captive carnivores, of moving the young around the enclosure. Unsuccessful mothers usually perform cub-carrying (Foreman 1997; Callahan & Dulaney 1997), an act once mistaken as the female's desire of displaying the offspring to the visitors (Leslie 1971). Female bears sometimes do not accept a breeding den in a zoo, and behave restlessly after the cubs are born, carrying them around and eventually neglecting or eating them (Van Keulen-Kromhout 1976). In one event, a female spotted hyaena *Crocuta crocuta* started carrying her cub when one of the five lions that were moved through the service corridor of the enclosures pounded on the door of the cubbing den (Kinsey & Kreider 1990). Excessive cub-carrying is regarded as a warning signal of potential inadequate maternal behaviour, and for some species, such as snow leopards *Uncia uncia*, it is recommended to remove the cubs immediately after the display of this behaviour by the female (Wharton & Mainka 1997).

Providing the female with safe dens and the adequate requirements for the species can be successful. A good example occurred at Buffalo Zoo. A study about the cause of poor mothering of a female spectacled bear *Tremarctos* *ornatus* tested several depths of bedding for the cubbing den. There is no information on the maternal behaviour of this species in the wild, but this observation in captivity showed that this female nursed her cubs not sitting or laying alongside, like other ursids, but laying on top of them. Previous litters were crushed to death, but with the bedding at 1 m of depth, the female prepared an oval nest with a deep middle depression where the cub was resting. The female then lay down on top of the nest to feed the young (Aquilina 1981).

Disturbances during parturition and early rearing are thought to elicit neglect of the litter or infanticide in some females. A strict hands-off policy during these times may result in a higher survival rate, especially with younger, less experienced females, which should give birth in familiar surroundings; the male rather than the female should be moved to another location during parturition and early rearing (Foreman 1997). For example, female giant otters *Pteronura brasiliensis* react to disturbance by lying flat on the floor, covering their teats and preventing the cubs from feeding; frequent repetition of this behaviour could be critical (Hagenbeck & Wunneman 1992). At Carl Hagenbecks Tierpark, in Germany, a female managed to rear two cubs after all sources of disturbance, including staff, were removed, and several nest boxes were provided for the female, and the institution recommends males to be separated from the females when cubs are present (Hagenbeck & Wunneman 1992).

There is a lack of information on many important aspects of the breeding biology of the species in the wild. This may have led to repeated mistakes in the management of more demanding species. For example, since the 1920s the maned wolf *Chrysocyon brachyurus* had been considered completely solitary, and there are not many observations of breeding in the wild (Rosenthal & Dunn 1995). Although paternal care is common among the Canidae, the role of male maned wolves in the caring of the young is unknown. Because of high juvenile mortality in mother-reared pups, the species survival plan used to recommend that the offspring should be removed for hand-rearing (Rosenthal & Dunn 1995).

A short experiment, however, suggested that males spend as much time as the females in the company of the young, sharing the duty of "guarding" the pups; pup survival up to 6 months increased if the sire was introduced right after birth and kept with the dam (Bestelmeyer 1999). Because of similar experiences in other institutions, the Species Survival Plan for the maned wolf now recommends that zoos either leave the male with the females and pups from the time of the birth or introduce the male shortly after birth (Bestelmeyer 1999).

Information from captive populations of carnivores may provide clues to which species are more prone to commit maternal infanticide, and from this result it can be possible to work towards husbandry protocols aiming to reduce female disturbance and providing optimal conditions for young to thrive.

6.3.2. *The impact of maternal infanticide in conservation programmes.*

Captive populations of rare carnivore species are often the subjects of conservation programmes, and institutions taking part in conservation efforts frequently keep records of births and causes of mortality (Chapter 2).

One of the few species to have some of these records analysed was the cheetah *Acinonyx jubatus*. Analysis of data from 3 breeding centres in North America showed that 48.5% of 33 cub deaths were caused by abnormal maternal behaviour (Laurenson, Wielebnowski & Caro 1995). Another study, using records from 1829 to 1994, showed that 44% of deaths in captive cheetah before 6 months of age (n=364) were caused by aggression, trauma, maternal neglect, exposure or being eaten by the dam (Marker-Kraus 1997).

Less extensive research in other species also shows the relatively high proportion of deaths caused by mothers. Records from 8 institutions that keep rusty-spotted cats, collected between 1976 and 1994, showed that in 11 out of 17 registered deaths the young had been killed and eaten by the mother (Dmoch 1997). At Cincinnati Zoo, mortality in Pampas cat *Oncifelis colocolo* kittens is primarily a result of injuries inflicted by the dam (Callahan & Dulaney 1997).

Although subject to intensive breeding programmes, the giant panda *Ailuropoda melanoleuca* poses a challenge for institutions. From the seven young born in 1989, only one was hand-reared to sexual maturity, and inadequate maternal behaviour caused all but one death (Bingxing 1990).

Some records are not explicit about the cause of death in the young. Analysing data from leopards *Panthera pardus*, Shoemaker (1982) found a high number of deaths caused by "weakness" or "by devouring", which could mean that females were neglecting or eating their cubs.

Usually, when faced with a frequently infanticidal species, institutions remove young for hand-rearing right after birth, or keep mother and young under observation to remove the young if its weight drops, which is the case with the cheetahs in Wassenaar Wildlife Breeding Centre (Beekman *et al.* 1997). The effects of hand-rearing in the behaviour of the adult individual are controversial, and must be specifically researched. An experiment with domestic cats suggested that hand-reared females have a much lower breeding success than mother-reared ones (Mellen 1992).

The high proportion of maternal infanticide found in Chapter 5 indicates that this behaviour have an impact in potential captive breeding programmes, reducing the output of new individuals and perhaps compromising their breeding capability through the possible long term effects of hand-rearing.

6.4. *Hypotheses to be tested.*

Statistical analysis of data from captive populations is used to test the hypotheses that life history traits can predict the type of maternal infanticide displayed by a species. As maternal investment is usually curtailed in times of scarce resources, when the welfare of the breeding female is low (Clutton-Brock 1991; Hrdy 1979; Hayssen 1984; Labov *et al.* 1985; Wolff 1997), it is possible that captive female carnivores are behaving as they would be under sub-optimal conditions. Active infanticide is more likely to occur during lactation, when energy output from the mother is higher (Clutton-Brock 1991; Oftedal & Gittleman 1989), and is probably more frequent in species with more demanding young (Oftedal & Gittleman 1989; Packer & Pusey 1984). Passive infanticide is more likely to occur when maternal investment is smaller (Clutton-Brock 1991), so species with lower mother-infant energy transfer are supposedly more prone to abandon their cubs. The welfare of carnivores is highly affected by captivity (Clubb & Mason 2003), thus it is expected that the characteristics of individual females, such as the rearing method or place of origin, can affect the female's decision to interrupt maternal investment. Also, husbandry protocols and housing conditions can affect directly the welfare of nursing females (Carlstead & Shepherdson 1994; Bakken *et al.* 1999), but can be adjusted to minimise the impact of inadequate maternal behaviour in the breeding success of captive carnivores.

6.5. *Methods.*

The dataset used for this analysis was the bibliographical dataset collected from published papers (described in section 2.2.5), which served for the analysis of maternal infanticide in 29 species. Data collected directly from zoological institutions (described in section 2.2.6) did not present detailed data on causes of infant mortality and were not suitable for the analysis.

Relative frequencies of the type of infanticide (killed by dam, eaten by dam or neglect) were calculated for each species, using the median of these proportions for each female, and used as dependent variables in regressions. Also, the type of infanticide (if active or passive) was used as a dependent variable to check the effect of categorical individual characteristics of the females through a binary logistic regression. A summary of the species used in the analysis and the sample sizes, together with the relative frequencies of infanticide, is displayed in Table 6.2.

Average litter sizes and the proportion of infant mortality were also calculated for each female. The origin of the females, as reported in the published records, was included in one analysis. There was some information on housing conditions, such as cage area and number of dens, but they were not used in the analysis of maternal infanticide because sample sizes were not large enough, after adjusting for species and females. Multiple analyses on the effects of life history traits were performed using the variables chosen through stepwise regression from the dataset compiled by Gittleman (1986a, 1986b, 1989). All proportional values were transformed by the arcsine of the square-root and other continuous variables were log-transformed.

Table 6.2: Species used in the analysis of the types of maternal infanticide in captive carnivores, with number of litters, dams, zoos holding the species, proportion of active infanticide (KBD), proportion of infanticide followed by cannibalism (EBD) and proportion of passive infanticide (NEG). The data was collected from 141 published papers (Appendix 4).

Family	Species	Litters	Dams	Zoos	KBD	EBD	NEG
Canidae	*Canis lupus*	9	2	2	0,9286	0,3571	0,5714
Canidae	*Cerdocyon thous*	6	4	2	0,7778	0	0,4445
Canidae	*Chrysocyon brachyurus*	20	13	8	0,7368	0,7368	0
Canidae	*Vulpes zerda*	10	7	3	0	0	0
Canidae	*Lycaon pictus*	4	2	2	1	0,3529	0,3529
Felidae	*Acinonyx jubatus*	22	15	12	1	1	0
Felidae	*Caracal caracal*	5	4	2	0,4167	0,4167	0
Felidae	*Felis margarita*	10	2	2	0,375	0,25	0
Felidae	*Felis nigripes*	8	3	2	0,4286	0,2857	0,1428
Felidae	*Felis silvestris*	29	7	3	0,67	0,67	0
Felidae	*Leopardus tigrinus*	7	3	2	0	0	0
Felidae	*Lynx lynx*	10	7	3	0,8571	0,3571	0,2142
Felidae	*Neofelis nebulosa*	15	5	4	0,8823	0,7647	0,1176
Felidae	*Oncifelis geoffroyi*	15	5	3	0,2857	0,2857	0
Felidae	*Prionailurus bengalensis*	8	2	2	0,2143	0,2143	0
Felidae	*Uncia uncia*	11	5	4	0,8	0,8	0
Felidae	*Panthera tigris*	9	7	5	0,9048	0,0476	0
Herpestidae	*Helogale parvula*	14	3	2	0,3333	0	0
Hyaenidae	*Crocuta crocuta*	4	3	3	0,1538	0	0
Mustelidae	*Amblonyx cinereus*	11	3	3	0,62	0,5	0
Mustelidae	*Enhydra lutris*	9	5	4	0,5	0	0,5
Mustelidae	*Pteronura brasiliensis*	12	2	1	1	0	0
Mustelidae	*Meles meles*	2	2	1	0,8333	0,8333	0
Procyonidae	*Ailurus fulgens*	9	5	3	0,9375	0,125	0
Ursidae	*Ailuropoda melanoleuca*	11	7	5	0,4167	0	0
Ursidae	*Helarctos malayanus*	12	5	3	0,9286	0,3571	0,5714
Ursidae	*Tremarctos ornatus*	11	4	4	0,7778	0	0,4445
Ursidae	*Ursus maritimus*	11	4	4	0,7368	0,7368	0
Viverridae	*Arctictis binturong*	13	5	5	0	0	0

6.6. *Results.*

6.6.1. *Biological factors.*

Species that prey on larger animals tended to kill but not consume the young (One-way ANOVA: $F_{2, 14} = 7.54$, $p = 0.04$), but there was no significant evidence that species with smaller prey do consume the young (One-way ANOVA: $F_{2, 7} = 3.8$, $p = 0.1$, power = 0.47). Species with slower growing litters showed a higher incidence of active infanticide without cannibalism (Regression: $F_{1, 9} = 1.18$, $p = 0.05$, R^2 adj. = 28%), as it can be seen in Figure 6.1.

In this dataset, there was an effect of weaning age (WA) and age in which young open their eyes (OE) on the incidence of deaths caused by the dam in each species (section 5.5.2), but these variables did not influence the occurrence of active infanticide, followed or not by cannibalism (GLM on transformed data: WA: $F_{1, 12} = 1.47$, $p = 0.4$; OE: $F_{1, 14} = 1.18$, $p = 0.6$, R^2 adj. = 40%). The proportion of passive infanticide reported for each species was strongly influenced by interbirth interval (Regression: $F_{1, 12} = 11.68$, $p = 0.005$, R^2 adj. = 45%, Figure 6.2) but there was no significant effect of weaning age (Regression: $F_{1, 13} = 1.38$, $p > 0.2$, R^2 adj. = 10%).

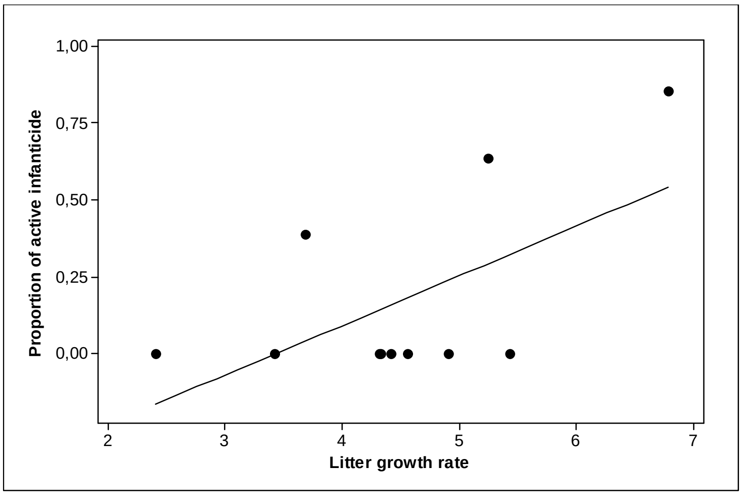

Figure 6.1: Regression plot of the effect of specific litter growth rate on the proportion of infant deaths caused by maternal active infanticide not followed by cannibalism, in 10 species of carnivores. The data plotted was transformed.

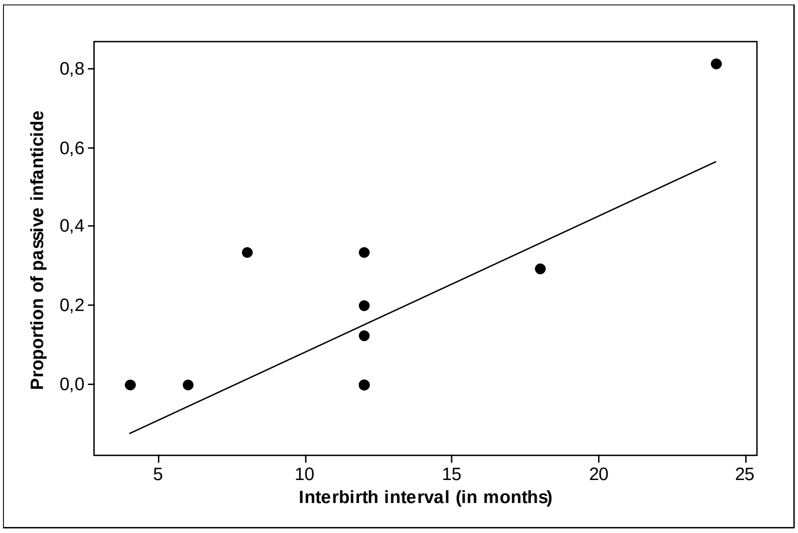

Figure 6.2: Regression plot of the effect of interbirth interval in the proportion of infant deaths caused by passive infanticide in 9 species of captive carnivores. The data plotted is not transformed.

6.6.2. *Individual differences and ecological factors.*

Overall, wild-caught females presented slightly higher levels of maternal infanticide, passive or active, than captive-born ones independent of the species (t-test: $t = 1.84$, $p = 0.06$, $df = 63$, Figure 6.3).

Throughout the order Carnivora, there was a slight effect from the origin of the female (if wild-caught or captive born) in the type of infanticide, although this is undetectable if other factors are added to the model: wild-caught females performed more passive infanticide (PI) and captive-born performed more active infanticide (AI), as it can be seen in Table 6.3. In the complete model, only the activity pattern of the species had a significant effect in the type of infanticide performed, with arrhythmic species presenting higher levels of AI and diurnal species neglecting young more often.

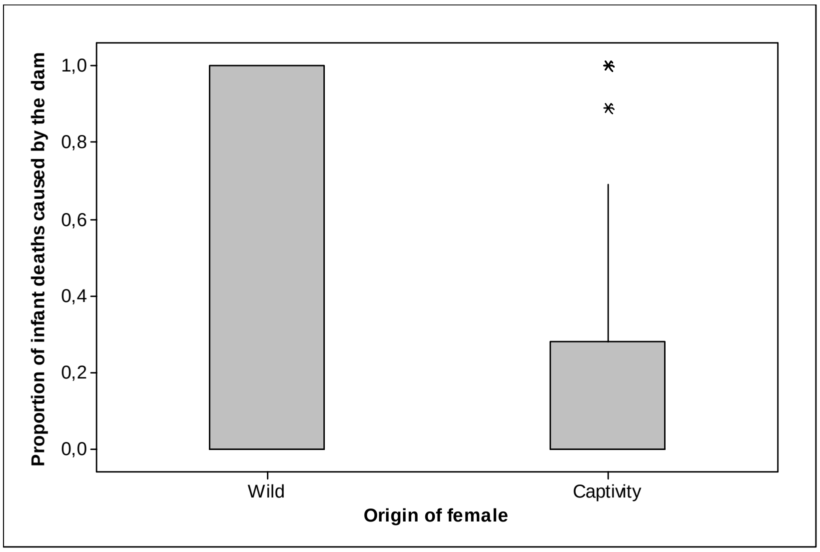

Figure 6.3: Proportion of mortality caused by inadequate maternal behaviour in wild-caught (N = 60) and captive-born (N = 27) females of 29 species of carnivores in captivity.

Overall, there was no statistically significant effect of the presence of the male in the incidence of maternal infanticide in species with exclusive maternal care (i.e. when the male does not care for the young), but a larger sample would be needed to increase test power (One-way ANOVA: $F_{1, 250}$ = 0.02, p = 0.89, power = 0.27).

Table 6.3: Logistic regression results with categorical variables of female characteristics and specific ecological requirements of captive carnivores; the dependent variable is the type of maternal infanticide (passive or active).

	Model 1		*Model 2*		*Model 3*	
Variable	**B**	**Wald**	**B**	**Wald**	**B**	**Wald**
Constant	-0.56	2.39	12.74	0.11	12.56	0.11
ORIGIN	4.19	0.04*	-8.12	0.04	-8.15	0.05
REARING	-	-	-1.55	1.11	-1.49	1.03
ACTIVITY	-	-	-1.76	4.55*	-1.79	4.46*
DIET	-	-	-	-	0.11	0.082
Model Chi-Square [df]	6.337 [2]*		12.564 [3]**		12.646 [4]**	
Block Chi-Square [df]	-		6.227 [1]		0.082 [1] *	
% corrected prediction	63.6		78.8		78.8	
Nagelkerk's R²	0.24		0.43		0.44	

* p< 0.05; ** p< 0.01

6.7. *Discussion.*

6.7.1. *Husbandry requirements and individual differences affecting maternal infanticide in captive carnivores.*

In this dataset, wild-caught females performed infanticide more often than captive-bred ones, though the latter were more prone to actively kill the young, while the former abandoned the cubs more often. The effect of the environment on encaged animals has been discussed in other studies, and some researchers affirm that stress from captivity can increase the occurrence of abnormal behaviour (Carlstead & Shepherdson 1994; Bakken *et al.* 1999). It is possible that wild-caught individuals are more sensitive to the conditions in captivity and therefore perform more infanticide. Carlstead and Shepherdson (1994) suggest some techniques that can be useful to reduce stress in captivity, and were useful to raise success breeding in captivity, focused basically on three aspects: special perception, such as providing platforms and windows to expand the view as well as places to "hide" from the public; feeding behaviour, to avoid pre-feeding stereotypical behaviour and to increase foraging time; and welfare, making sure that individuals have ways to control microclimate and are always interested in the environment.

A controversial suggestion, though, is that the animals should be trained for husbandry, to improve their relationship with human keepers. In a later work, Carlstead (1996) supports the idea that unconscious selection to tameness may lead to dangerous changes in natural behaviour; for instance, in malamute pups *Canis lupus lycaon*, unrestrained aggression and the absence of some threat displays seem to be result of a selection for neoteny. Inadequate environment or hand-rearing could lead to abnormal behaviour in species with sensitive periods (i.e., imprinting, socialisation) (Carlstead 1996). Unfortunately, this subject is not yet well researched.

It has been suggested that human interference, especially those related to research efforts in the wild, can increase the occurrence of cub abandonment in black bears *Ursus americanus* (Goodrich & Berger 1994), brown bears *Ursus arctos* (Swenson *et al.* 1997), and grey wolves *Canis lupus* (Ballard, Whitman & Gardner 1987). This could be reflected in the tendency of wild-caught females abandoning their litters in captivity.

Individual differences in the response to stress can predict which females will be more prone to commit infanticide. A study was performed to expose farmed silver foxes to stimuli that trigger stress-induced hyperthermia (SIH), phenomenon regulated by the HP axis, while measuring the time and intensity of their responses. Infanticidal females were more sensitive to stressors and responded quicker to the stimuli, while non-infanticidal ones had weaker responses. It was suggested that infanticidal behaviour could be predicted, and eliminated from the stock, by selecting breeders with lower levels of SIH (Bakken *et al.* 1999).

In the wild, threatened females will kill or leave their offspring to die after perceiving that there is no safe place to hide the young, or when there is only one surviving cub on a litter, because the risk of raising a single cub is too high, and it is more profitable try again (Packer & Pusey 1984).

There is a lack in research on the factors that can make species more prone to one or other type of infanticide. In this dataset, it was found that species with arrhythmic pattern of activity, i.e. that can be equally active during the day and the night, such as the grey wolf, performed active infanticide more frequently, and diurnal ones were more prone to abandon the litter. Species with diurnal activity are frequently at higher risk of predation than nocturnal or arrhythmic ones, as happens with baboons *Papio sp.* (Cowlishaw 1994) and striped skunks *Mephitis mephitis* (Lariviere & Messier 1997). Some species, such as the red-bellied lemur *Lemur rubriventer*, may have adjusted their activity pattern from exclusive diurnal to arrhythmic, or cathemeral, as a strategy to avoid predation by diurnal raptors (Overdorff

1988). If diurnal species are at higher risk of predation, leaving the litter alive may serve as a "buffer protection" (Hrdy 1979), as the young can be found by predators that could otherwise prey on the female; also, killing the young could attract predators through auditory or olfactory cues.

Unfortunately, it was not possible to calculate the effect of female age in maternal infanticide, once the data was available for very few females. Also, as discussed in Chapter 2, the dataset did not have reliable data to analyse sex ratio. Further research is recommendable to elucidate these points.

6.7.2. *Biological factors affecting maternal infanticide in captive carnivores.*

In Chapter 5, it was found that species that prey on small or very small animals perform more infanticide, active or passive, than those with larger prey (Section 5.5.2). Analysing infanticidal events separately, it was found that species with larger prey tend to actively kill the young, but not consume them. Prey size, in carnivores, has several ecological and morphological correlates, such as home range size, limb length and limb dexterity (Gittleman 1986a, 1986b; Harris & Steudel, 1997; Iwaniuk, Pellis & Whishaw 1999). Killing techniques, adapted to the type and size of prey, are the result of craniodental adaptations and differ greatly between taxa. Solitary predators, such as felids, usually kill prey with one single deep bite, while canids and hyaenids, social hunters, tend to kill with multiple shallow bites (Biknevivius & Van Valkenburgh 1996). In this dataset, the species that did perform more active infanticide without cannibalism were both group-hunting grey wolves, wild dogs and spotted hyaenas (prey "nibblers"), and the solitary tigers and cheetahs (prey "crushers"). This indicates the possible influence of feeding preference in this result: infants would be too small to consume out of starvation times. Further research is needed to look into the species that do consume the young and the possible connection with prey size and feeding preference.

In this research, active infanticide was also more frequent in species with higher litter growth rates (LGR). This is predictable once LGR can be a measure of maternal energy output, through energy transfer in lactation (Oftedal & Gittleman 1989), and females are more likely to withdraw maternal investment, partially or totally, to a litter through infanticide when they perceive sub-optimal conditions (Clutton-Brock 1001; Hayssen 1984; Hrdy 1979; Packer & Pusey 1984; Wolff 1997).

In captivity, the present research showed that species that open the eyes and wean at later ages are more prone to die from all causes (Chapter 4), while species that open the eyes and wean earlier, and therefore are highly demanding on the first weeks after birth, are more susceptible to be killed as a result of inadequate maternal behaviour (Chapter 5). These factors, however, did not predict the occurrence of the type of infanticide, i.e. if active or passive, suggesting that the decision of abandon or kill the young depends on other factors. Altriciality is thought to be a factor predicting the occurrence of infanticide in carnivores (Packer & Pusey 1984); together with territorial females, it is a condition for a species to perform infanticide as a intrinsic population regulator, but all Carnivora are altricial if compared, for example, with Artiodactyla species (Wolff 1997). Altricial young represent, at birth, a low maternal investment if compared to precocial ones; fast-developing species, however, represent a very high maternal investment (Zevelloff & Boyce 1986). It is possible that, among Carnivora species that perform infanticide, fast development, rather than altriciality, predicts frequency of infanticide, at least in captive populations.

Frequency of reproduction, reflected in the length of the interval between births in the species, had a strong effect in the occurrence of passive infanticide. Species that presented high frequency of neglect were grey wolves, Malayan sun-bears, spectacled bears, crab-eating foxes and wild dogs. Grey wolves and wild dogs are communal carers (Gittleman 1986a), dividing the energetic expenditure of raising the young between many. It is known that young desertion is more likely to be performed when the investment by the deserter is low (Clutton-Brock 1991). Brood desertion is common in ursids, and females are known to abandon a cub if it is the only survivor from a litter, once it is more profitable to raise a whole litter than to nurse the survivor (Clutton-Brock 1991). Other factors, however, may be involved in the interruption of maternal care. For example, in vervet monkeys (*Cercopithecus aethiops sabaeus*), infant mortality due to poor maternal care or abandonment was higher for females in poor body condition, while females in prime condition rejected their own young, that survived through alloparental care, to shorten the interval between conceptions (Fairbanks & MacGuire 1995). Unfortunately, there was not enough data in this study that allowed to check the influence of individual characteristics of the females, such as origin and housing conditions, in the occurrence of maternal infanticide.

6.8. *Conclusion.*

Maternal infanticide in captive carnivores is related to the level of maternal investment demanded by each species, with fast-developing young being more prone to be killed than slow-developing ones. The type of infanticide performed is also predicted by species characteristics: species that hunt large prey killed the young but did not eat them, while species with long intervals between conceptions tended to withdraw maternal care instead of actively killing the young. Each form of maternal manipulation of the litters will reflect the species' adaptation to balance maternal investment and resource availability within their environmental and social settings.

As the decision of interrupting maternal investment depends on the perception of the mother on resource availability, the welfare of the individual is crucial to successful breeding. The high frequency of maternal infanticide in captive populations of carnivores suggests that females perceive captivity conditions as sub-optimal, which can seriously damage the output of adult individuals by *ex situ* breeding programmes. This effect seems to be stronger in wild-caught females, unused to human manipulation, than in tamer captive-born ones. Further research is needed, however, to fully understand the influence of husbandry techniques and housing conditions in species prone to commit maternal infanticide.

Chapter 7

Increasing juvenile survival in captive carnivores: Practical considerations

Abstract

There are few studies on the impact of husbandry practices in the breeding success of captive carnivores. Questionnaires were sent to institutions asking for details of practices and housing conditions of nine species of carnivores, and 16 institutions provided data on 148 litters from 63 females. Overall the order Carnivora, institutions that perform research presented a higher proportion infant mortality than institutions that do not perform any kind of research activity. The distance travelled by the female was positively correlated with the proportion of infant mortality, while the number of dens and the available area for each female (adjusted for each species) were negatively correlated with the proportion of infant mortality. Transferring the females from one institution to other, or from the wild to any institution, can affect infant mortality even when not considering distances; the latitude of the zoo or the number of keepers in contact with the animals do not seem to affect infant survival. In this dataset, the two hand-reared females had a lower proportion of infant mortality than mother-reared ones, although a larger sample would be needed. Also, institutions that have scientific staff and run research programmes had higher infant mortality overall, independently of their latitude or management system, which may indicate an effect of human interference, although further research is needed. It is recommended that breeding loans between institutions do not include females, and that direct manipulation of animals in studies are avoided until further understanding of the impact of these practices on breeding success.

7.1. *Introduction.*

Captive carnivores pose a challenge for conservationists and institutions alike, presenting many problems that range from diseases to poor welfare and unsuccessful breeding (Chapter 1). Available databases of captive populations are rich sources of information that can help determine which factors can affect breeding success and the real potential of these populations in conservation programmes (Chapter 2). Some species, such as tigers *Panthera tigris,* seem to preserve in captivity the same reproductive parameters, such as litter size, lack of seasonality and breeding age, seen in wild animals, making captive individuals extremely useful in the research of reproductive biology, that can be applied in evolutionary and physiological studies of the order Carnivora (Chapter 3).

Specific reproductive characteristics can make some species more prone to lose young in captivity than others, and these factors must be taken into consideration when developing *ex situ* conservation programmes; for example, the effect of photoperiod in Arctic species should be taken into consideration when housing these species closer to the Tropics (Chapter 4). Infant mortality in captivity seems to be primarily caused by inadequate maternal behaviour, which is more frequent in fast developing species and wild-caught females; proper husbandry and well-designed enclosures can reduce the other causes of death (Chapter 5). Maternal infanticide, either passive or active, is also affected by biological and ecological characteristics of the species, but may be the result of poor maternal welfare as it is more frequent in wild-caught females (Chapter 6). It is important thus to research the effect of husbandry protocols and housing conditions in the breeding success of captive carnivores. Record research in the subject poses some problems: for example, data collection has to be restricted, once the many factors present in captive environments cannot be all accounted for, and the detail and reliability of the data varies between institutions.

In this chapter, an overview of studies relating husbandry and housing conditions to the welfare and reproductive success of captive carnivores is done. Records from institutions were used in the attempt of determining the effect of some of these conditions in the proportion of infant mortality in captivity, taking into consideration the results found in previous chapters.

7.2. *Welfare and breeding success in captive carnivores.*

Research has suggested that breeding success is strongly affected by the female's welfare, and non-invasive techniques to assess the adaptation of individuals to husbandry protocols can be very useful in reducing the impact of stress in reproduction (Wielebnowski 1999). Environmental enrichment techniques have been tested and applied in several species, such as the giant panda *Ailuropoda melanoleuca* (Swaisgood *et al.* 2001), the bush dog *Speothos venaticus* (Ings, Waran & Young 1997) and the kinkajou *Potos flavus* (Blount & Taylor 2000) with the aim of enhancing well-being and reducing unwanted behaviours, such as stereotypical movements, with positive results. Poor welfare and unsuccessful breeding attempts were connected in a study with captive clouded leopards *Neofelis nebulosa* in North American zoos, where behavioural problems, such as stereotypies and excessive aggressiveness are regarded as indicators of chronic stress, which can be detected by non-invasive corticoid monitoring (Wielebnowski *et al.* 2002).

Research with captive animals can point towards solutions to improve the welfare of individuals, and consequently increase breeding success. For example, a study on captive sloth bears *Ursus ursinus* showed that variation on physical and social captive environments affects activity patterns in this species, including the occurrence of stereotypies, and further studies may be helpful to identify which factors can be controlled to improve reproductive success and welfare (Forthman & Bakeman 1992).

In the subject of captive breeding, new techniques focus on the identification of oestrus, once it is difficult to perceive in some species and successful breeding frequently depends on the introduction of the male to the female while she is liable to accept mating. One example is the study of behavioural and physiological cues of oestrus in the cheetah *Acinonyx jubatus*, which uses laboratory techniques, such as cytology, non-invasive hormonal analysis, and ethological observations to determine the precise moment when females come into oestrus (Graham *et al.* 1995; Brown *et al.* 1996; Bircher & Noble 1997). Cheetahs are said to have a "silent" oestrus, which has led to unsuccessful introductions of males to females, but non-invasive endocrinological studies have yield good results in correlating physiological values with behavioural displays that can indicate the actual reproductive status of the females (Wielebnowski & Brown 1998). Oestrus is also difficult to determine in giant pandas, and researchers had found that there are chemical cues in the female's urine that trigger *flehmen* displays in males, the knowledge of which can be used to detect heat in females without the need of laboratorial analyses (Swaisgood, Lindburg and Zhang 2002).

The introduction of new males to females is crucial in captive breeding, and the welfare of the individuals has to be taken into consideration. Introduction protocols have been developed aiming the reduction of aggressive episodes that frequently lead to the injury of one of the animals, as it happens with clouded leopards *Neofelis nebulosa* (Law & Tatner 1998).

Research in zoological institutions has yielded valuable results in the diagnosis of pregnancy through non-invasive methods, which avoid direct manipulation of the animals. For example, it is difficult to determine early pregnancy in giant pandas without collecting blood samples of the females; a study, however, validated a method of diagnosing early pregnancy through urinary steroid concentrations and also showed that the species has delayed implantation, which can lead to mistaken calculations of gestation length (Chaudhuri *et al.* 1988).

It has been suggested that captive wild animals should be trained for husbandry, although it was pointed out that selecting for tameness might lead to the loss of important natural behaviours in certain species (Carlstead 1996). Although the subject was never researched, reports on the breeding success of tamed females suggest that closer interactions with known keepers reduce stress and promote adequate maternal behaviour in certain species, such as cheetahs (Florio & Spinelli 1967; Florio & Spinelli 1968; Tong 1974), giant pandas (Bingxing 1990; Zhang *et al.*2000) and clouded leopards (Fellner 1965). The effect of the origin of the female on the frequency of inadequate maternal behaviour in captive carnivores (Chapter 6) seems to support this view, although further research is necessary. Nevertheless, it is a safer policy for institutions to give preference to captive-born females, used to husbandry routines, as founders in *ex situ* programmes, and invest in the use of non-invasive monitoring techniques in breeding research, to minimise the stress in the individuals.

7.3. *Hand-rearing, fostering and inadequate maternal behaviour.*

Most institutions prefer to let the mothers to raise their cubs, and put up a policy of very little interference while there are young under care, but sometimes it is necessary to remove the infants for hand-rearing, usually after episodes of neglect or aggressive behaviour (Edwards & Hawes 1997). Removal of the young right after birth is recommended by the species survival plan for the maned wolf *Chrysocyon brachyurus* when the female seems agitated or is weakened (Rosenthal & Dunn 1995). Other reasons for the removal of the young include unsuitable enclosures with no dens; manipulation of group structure; neonatal illnesses; taming of individuals for educational purposes (making them accustomed to direct handling); and elimination of parasitic infections that would otherwise persist in the group (Read & Meier 1996).

Hand-rearing techniques have been tried and tested in many species and protocols have been established for a number of species, such as brown hyaenas *Parahyaena brunnea* (Volf 1996), otters *Lutra lutra* (Sikora 1996), Mexican margays *Leopardus wiedii glaucula* (Edwards & Hawes 1997), cheetahs *Acinonyx jubatus* (Bircher & Noble 1997) and ferrets *Mustela putorius* (Manning & Bell 1990), among others. In any case, hand-reared young are prone to develop certain ailments, especially related to improper nutrition, as it was noticed in hand-reared polar bear *Ursus maritimus* cubs which developed rickets; nutritional supplements were introduced, but one of the cubs was left with a permanent femur deformity (Kenny, Irlbeck & Eller 1999).

Other option is to give the neonates to foster mothers, usually of the same species, or a closely related one. For example, Asian golden cats *Catopuma temmincki* kits were successful reared by a domestic cat, although the fostered young had half of the weight of mother-reared ones before weaning (Louwman & Oyen 1968). Sometimes fostering can lead to unwanted results: a neglect giant panda cub was given to a foster giant panda dam that had a 3 weeks-old cub; the dam killed the foster young some days after introduction, and in the attack stamped her own young to death (Bingxing 1990).

Removing the young from their mothers is a decision to be taken only after analysing each individual case in detail, and realising that the young would certainly perish if left with the dam (Read & Meier 1996). However, since sometimes the young have to be removed, it is necessary to develop safer protocols that increase the survival of hand-reared or fostered captive carnivores.

7.3.1. *Hypotheses to test.*

Infant mortality is, overall, predicted by the level of altriciality of the species, but can be affected by institutional latitude in Arctic species (Chapter 4). Inadequate maternal behaviour was responsible for a significant proportion of infant deaths and is more common in species with fast development of the young (Chapter 5), but as this phenomenon is based on the female's decision to continue or curtail maternal investment, it can be triggered if the female perceive captivity conditions as sub-optimal, as it seems to happen more often in wild-caught individuals (Chapter 6). The high variance in the proportion of infant mortality between females and institutions suggests the influence of factors such as institutional latitude (Lincoln 1998), husbandry practices (such as number of keepers and if the animals are subject to research) (Bingxing 1990; Florio & Spinelli 1967; Florio & Spinelli 1968; Mellen 1991; Tong 1974; Wielebnowski *et al.* 2002; Zhang *et al.*2000), available area and nesting places (Clubb & Mason 2003; Roberts 1975; Van Keullen-Kromhout 1976), and the origin and the number of translocations females were subjected to, which can lead to stress and reduce breeding success (Forthman & Bakeman 1992; Ings, Waran & Young 1997; Swaisgood *et al.* 2001; Wielebnowski 1999).

7.4. *Methods.*

For this chapter, the dataset used in the search of husbandry factors affecting breeding success of captive carnivores was collected through electronic questionnaires (Appendix 5) sent directly to zoological institutions in Europe, North America and Australia (as described in section 2.2.5.1). From this, the proportion of infant mortality was calculated for each female, and paired with each individual's characteristics (such as origin and rearing) and housing conditions. In the general analysis, which involved all 9 species, the individual available area was calculated dividing the size of the enclosure by the number of individuals kept, and this result was divided by the average body weight for each species, in a way to adjust the value for the size of the animals. There were data on the origin and rearing of only 35 females. Table 7.1 summarises the data collected from the zoological institutions (Appendix 6). Multiple regression analyses were done using the arcsine of the square root of the infant mortality for each female. Cage areas were log-transformed.

Table 7.1: Species, number of litters, number of collections keeping the species and number of females summarised from the data collected through questionnaires from zoological institutions.

Family	Species	Number of litters	Number of collections	Number of females
Mustelidae	*Amblonyx cinerea*	8	2	2
Procyonidae	*Ailurus fulgens*	11	3	7
Canidae	*Chrysocyon brachyurus*	15	4	9
Canidae	*Canis lupus*	13	5	5
Procyonidae	*Nasua nasua*	11	1	6
Felidae	*Panthera tigris*	22	6	9
Herpestidae	*Suricata suricatta*	62	7	19
Felidae	*Uncia uncia*	3	1	1
Ursidae	*Ursus maririmus*	3	2	2

For the binary logistic regression, the proportion of infant mortality was transformed in a dummy variable: values below the median for the sample were coded 1, and above, 2.

To calculate the distance travelled by the female, information on the individuals transfer between institutions or between the local of capture and the institutions was transformed in kilometres. These values were found with the aid of the software Earth Explorer (Motherearth Inc.). Otherwise, the number of transfers to which the females was subjected was used in a logistic regression model.

The number of dens was given by the institutions and represents the number of nesting places present in the enclosure. The number of keepers represents the number of persons responsible for *in loco* husbandry, such as feeding, capturing (for changing enclosures, for example) and cleaning the cages. It is a common practice of institutions to delegate some enclosure to the care of particular staff, for it is believed, anecdotally, that the animals suffer less stress, and are more manageable, if they are used to the keeper.

To research the impact of animal manipulation on the breeding performance of captive carnivores, the datasets used were collected from the *International Zoo Yearbooks* (see section 2.2.2; Appendices 1 and 2). Relative institutional performance indices, ***Z***, were calculated (equation 2.3) using the proportion of infant mortality for each species and each zoo, and institutions were rated according to the proportion of the species that were breeding above or below the median proportion of mortality for the species (***I***, Appendix 1). Institutions were rated as "performing research" if the *IZY* related them as having research departments, academically qualified staff (such as PhDs and MScs) or were involved in conservation programmes. For the general linear model, categorical variables were used for the latitude of the zoos (tropical or temperate) , since some species have photoperiodic control of reproduction, and the management regimen (private, governmental or zoological society/charity), because only 17% of private zoos develop research programmes, while 35% of non-private zoos employ highly qualified staff and perform some type of research.

7.5. *Results.*

Overall the order Carnivora, institutions that perform research presented a higher proportion infant mortality than institutions that do not perform any kind of research activity; there was no significant effect of the latitude of the institution or the management regimen (Table 7.2, Figure 7.1).

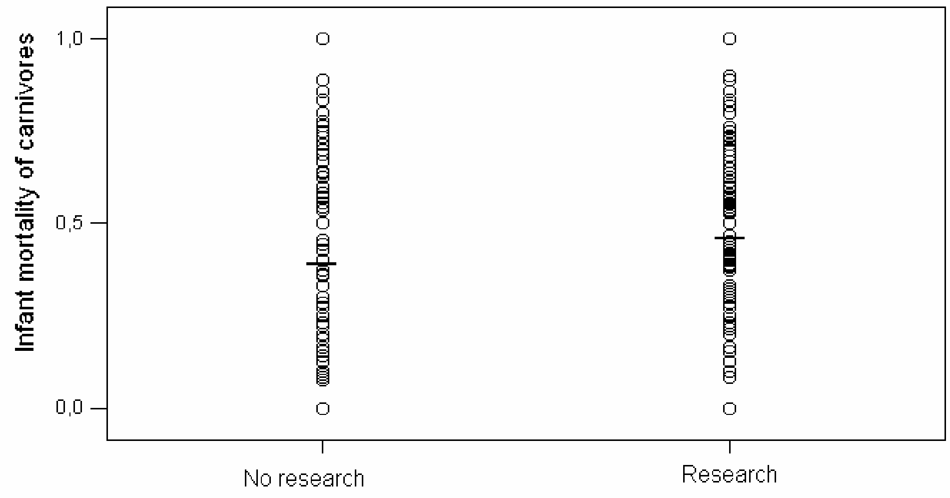

Figure 7.1: Relative proportion of infant mortality in 98 species carnivores housed in 461 zoological institutions with (N = 151) and without research facilities (N = 310). Solid lines represent means.

Table 7.2: General linear model (GLM) of the effect of latitude of the zoo (LAT), presence/absence of researchers (RES) and management regimen of the institution (MAN) on the institution's success in breeding carnivores.

Variable	DF	F	P
LAT	1	0.26	0.611
RES	1	6.31	0.012
MAN	2	0.06	0.942

The distance travelled by the female was positively correlated with the proportion of infant mortality (Figure 7.2), while the number of dens and the available area for each female (adjusted for each species) were negatively correlated with the proportion of infant mortality (Table 7.3, Figure 7.3). The multiple regression model with all three predictors produced R^2 (adj.) = 21%, $F_{3, 63} = 5.384$, p = 0.008.

Table 7.3: Correlations and results from the regression analysis of distance travelled by the dam (DTD), number of dens in the dam's enclosure (NAD) and relative available area (AIA) on the proportion of infant mortality (PIM) in captive carnivores.

Variable	Correlation with PIM	B	β
DTD	2.403	0.270	0.341*
NAD	- 2.748	- 0.485	- 0.390**
AIA	- 2.146	- 1.174	- 0.245*

* p< 0.05; ** p< 0.001

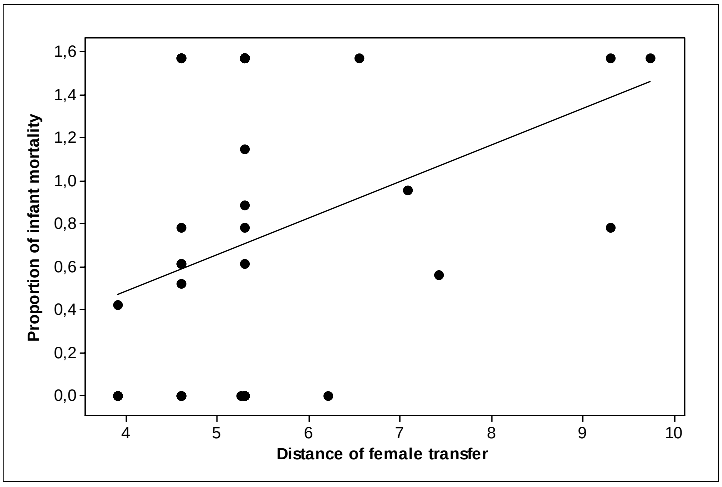

Figure 7.2: Scatterplot of the median proportion of mortality in 66 litters from 45 females of 9 species of captive carnivores in relation to the distance travelled by the female (log-transformed).

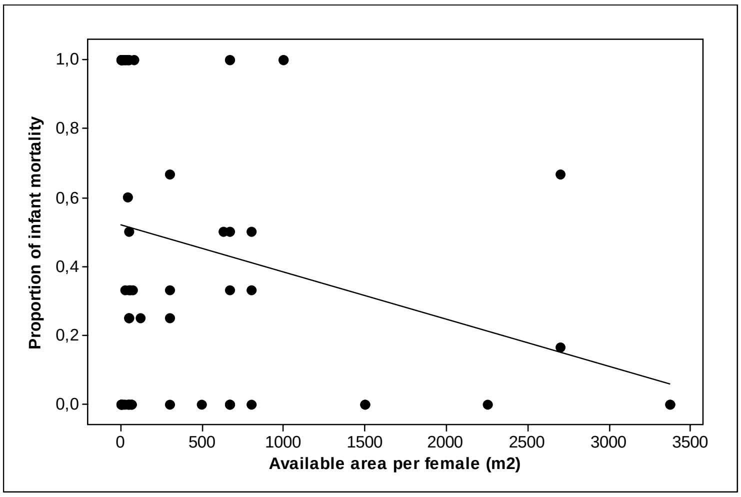

Figure 7.3: Scatterplot of the proportion of mortality in 74 litters of 39 females of 9 species of captive carnivores in relation to the relative available area per female (m^2).

Transferring the females from one institution to other, or from the wild to any institution, can affect infant mortality even when not considering distances; the latitude of the zoo or the number of keepers in contact with the animals do not seem to affect infant survival (Table 7.4).

Table 7.4: Logistic regression results with categorical variables related to husbandry practices on captive carnivores; the dependent variable is a binary measure of infant mortality per female (148 litters from 60 females of 9 species).

	Model 1		**Model 2**		**Model 3**	
Variable	B	**Wald**	B	**Wald**	B	**Wald**
Constant	- 0.16	0.319	1.813	2.953*	2.232	1.199
LATITUDE OF ZOO /SPECIES RANGE	- 0.022	0.002	- 0.733	1.483	- 0.817	1.033
DAM TRANSFER	-	-	- 1.152	3.791**	- 1.234	2.898*
No. OF KEEPERS	-	-	-	-	- 0.049	0.04
Model Chi-Square [df]	0.002 [1]		4.116 [2]*		0.040 [3]	
Block Chi-Square [df]	0.002		4.113 [1]**		0.040 [1]	
% corrected prediction	54.2		59		59	
Nagelkerk's R^2	0.02		0.15		0.15	

* p<0.1; ** p<0.05.

In this dataset, the two hand-reared females had a lower proportion of infant mortality than mother-reared ones, although a larger sample would be needed; with this sample, a one-way ANOVA test provided $F_{1, 34} = 3.82$, $p = 0.059$ (Figure 7.4).

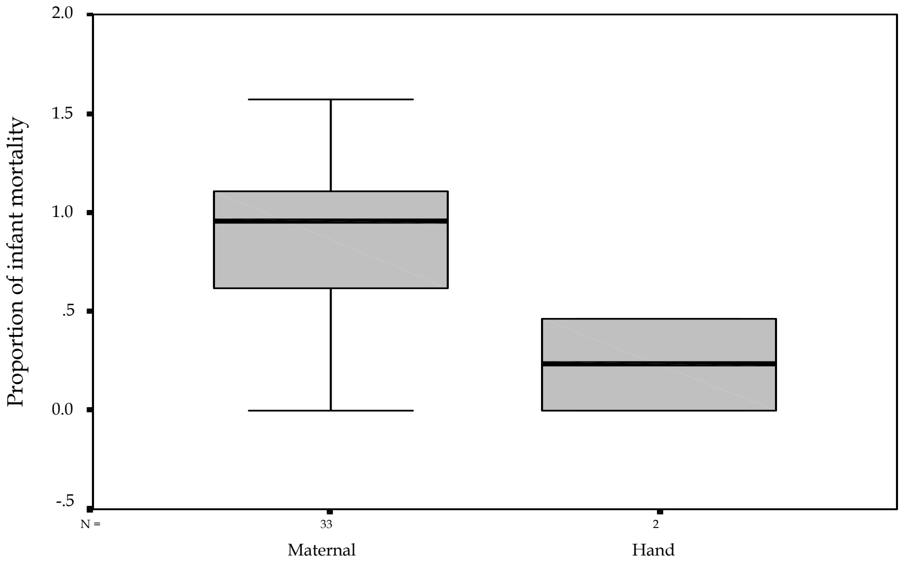

Figure 7.4: Proportion of infant mortality in mother-reared and hand-reared female captive carnivores.

7.6. *Discussion.*

7.6.1. *Housing conditions.*

There is a significant effect of the presence of researchers in the breeding success of captive carnivores, with females housed in institutions performing research presenting higher infant mortality. Research in zoological institutions has been growing since the beginning of the 1980s (Benirschke 1987; Finlay & Maple 1986; Stoinski, Lukas & Maple 1998) and it generally involves the direct observation and manipulation of animals or, at least, changes in the environment (Appleby 1997; Robinson 1998). Recently, researchers have been pointing out the need for non-invasive techniques for metabolical monitoring of stress (Wielebnowski 1999; Wielebnowski *et al.* 2002) and breeding (Graham *et al.* 1995; Brown *et al.* 1996; Bircher & Noble 1997), and also for the need to develop reliable ethological methods to assess welfare (Dawkins 2003), to reduce the stress caused by capture and blood-sampling in the individuals. It is generally agreed that direct manipulation and other environmental stressors affect the individual's welfare and can reduce breeding success (Bakken *et al.* 1999), but some researchers are calling for the use of more invasive research tools for captive non-domestic species in captivity, disregarding the findings that do not recommend this approach (Goodrowe 2003). This research, however, found that the impact of research, even non-invasive ones, in the breeding success of captive carnivores can be stronger than previously thought, although a larger sample size would be needed to better support this view.

In this research, there was a significant effect of some aspects of housing in the proportion of infant mortality. Although there are other aspects of the enclosure that should be researched, in this dataset only the number of dens and the available individual area were added to the model, both presenting strong effects on the dependent variable.

Housing conditions are known to affect the welfare and breeding success in many species of carnivores, but different species have different demands in captivity and results vary. For example, clouded leopards are sensitive to husbandry and housing conditions: faecal corticoid measurements were lower in individuals with higher enclosures and those with few keepers that spent more time weekly interacting with them; animals with multiple keepers and those in public exhibition, especially the ones housed in the proximity of potential predators (Wielebnowski *et al.* 2002). A study on captive leopards *Panthera pardus* achieved different results: off-exhibit animals had higher levels of stereotypical behaviour than animals in exhibition, but off-exhibit enclosures were indoors, while exhibition enclosures were larger and mostly outdoors (Mallapur & Chellam 2002).

In this dataset, the number of dens correlated negatively with the proportion of mortality. The type and number of dens had been correlated with levels of cortisol, but again specific preferences may differ. A study with farmed silver foxes *Vulpes vulpes* and blue foxes *Alopex lagopus* determined that these two species have different preferences regarding the design of nest boxes, although urinary cortisol levels, used as a measure of stress, did not vary significantly as long as a nest box was provided (Jeppesen, Pedersen & Heller 2000). Other study showed that cortisol levels were significantly lower in female silver foxes that were provided with a nest box than those that were kept in wire mesh cages with no nest box, suggesting that stress levels can be connected with the presence of a secluded space for nesting (Jeppesen & Pedersen 1991). It would be interesting to research the preferred design of nest boxes in other wild species of carnivores that are not commercially exploited.

Housing conditions also seem to affect leopard cats *Prionailurus bengalensis*, which can be detected through non-invasive monitoring, and the welfare of individuals can be ameliorated through environmental enrichment (Carlstead *et al.* 1993). Simple enrichment techniques, such as the placement of scents and new objects in the enclosure, turning the environment more complex, and feeding devices that increase foraging time, had also very positive results in the behaviour of encaged African lions *Panthera leo* (Powell 1995).

The lack of effect of the number of keepers may be caused by the small variation of this characteristic in the dataset. Further research with larger sample sizes is recommended.

7.6.2. *Individual history.*

This dataset showed a very strong positive correlation of the distance travelled by the dam and the proportion of infant mortality, and this result was confirmed even when the actual distance was not considered, suggesting that any transfer of females can increase infant mortality. Inter-zoo breeding loans are common, especially of species that are under captive breeding programmes, and both males and females can travel distances as far as from Beijing to London (Block & Perkins 1996). There are no further studies on the effect of this practice in breeding success, but this result suggest that transferring females can have an impact in the success of captive breeding programmes and should be researched using a larger sample.

A larger sample would be necessary also to identify the real impact of rearing techniques in infant mortality. The low proportion of infant mortality in this research may reflect the relative facility of keeping these females, once hand-reared carnivores tend to prefer the company of humans to their own species (Read & Meier 1996). On the other side, hand-reared animals can present some behavioural problems. For example, in sloth bears not only the enclosure type and the composition of the captive group affected activity, but also the individual's rearing history: stereotypical behaviour, including self-directed activities, was more common in hand-reared animals than in mother-reared ones (Forthman & Bakeman 1992). Hand-rearing also seems to have an effect on the development of young giant pandas *Ailuropoda melanoleuca*: hand-reared or partially hand-reared cubs grew slower than mother-reared cubs up to 6 months of age, although there was no significant difference after that age (Zhang *et al.* 1996). Response to hand-reared can also have the opposite effect in other species: a study revealed that the use of highly energetic milk replacements in hand-reared brown hyaena pups led to a faster weight gain on those, when compared to mother-reared ones, although the growth rate was equalised between groups after weaning (Volf 1998).

Apart from differences in housing and rearing, individuals can cope differently with levels of stress, as it was shown in a study on beech martens *Martes foina*; according to the type of cortical response, it was suggested that individuals can be classified in high activity individuals (Type A), which are more prone to display stereotypical behaviour and cope poorly in captivity, and low activity individuals (Type B), which would cope better with captive conditions (Hansen & Damgaard 1993).

Unfortunately, the low level of response from the institutions did not allow more robust data analyses. It is possible, however, that husbandry techniques are affecting the breeding success of captive carnivores in a much broader way that it was considerate until now, and further analysis could elucidate which species are more sensitive to hand-rearing and translocations.

7.7. *Conclusion.*

Certain aspects of husbandry and housing conditions of captive carnivores can affect the reproductive output of females. If a species is already prone to higher levels of infant mortality, either by inadequate maternal behaviour or the tendency to stillbirths and exposure to infectious diseases, the conditions in which they are kept can increase the frequency of infant deaths. However, further research is needed to determine safely these factors, once there are many uncontrolled factors in the institutions that have the potential to affect the individuals' welfare and, ultimately, the breeding success of these individuals. Certain common practices of institutions, such as transferring females in breeding loans to other institutions, may have to be reviewed.

We cannot forget that the potential of captive populations is varied. For example, many species are at the verge of extinction, and conservation efforts that last for more than 5 generations of the species have not improved its status. It is possible that some of these species will only be found in captivity, and all the human knowledge will be therefore based on zoo specimens. Important factors come from this possibility: there is not enough research on several species in the wild, and biological parameters are unknown in many. Also, many ethograms are based in captive observations. Unless research in the wild, sometimes of the most basic descriptive nature, is immediately done, many adaptive phenomena will disappear before they can be fitted into the evolutionary chain.

The lack of knowledge in the wild also impairs the correct development of environmental enrichment techniques. Many of them are based on the premise of facilitating natural behaviour. Obviously, if the natural behaviour of the species is unknown, there is no parameter on which to base the results of the experiments.

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