

Predatory and Foraging Behaviour
of Brown Hyenas (*Parahyaena brunnea* (Thunberg, 1820)) at Cape Fur Seal
(*Arctocephalus pusillus pusillus* Schreber, 1776) Colonies



by

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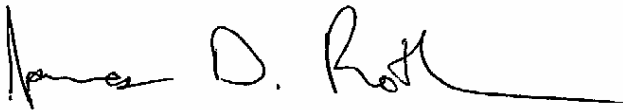
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To Dollar

“When you have assembled what you call your ‘facts’ in logical order, it is like an oil-lamp you have fashioned, filled, and trimmed; but which will shed no illumination unless first you light it.”

(Saint-Exupéry, *The Wisdom of the Sands*)



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Chapter 1

Introduction

Many carnivore studies investigate predator-prey systems mostly within terrestrial or marine ecosystems (Kruuk 1972a, Schaller 1972, David 1987). Within these systems, carnivores usually use a wide variety of prey species with preferences for certain species (Kruuk 1972a, Schaller 1972). Carnivores usually prey on species on a lower trophic level within their ecosystem, but in coastal areas, where the terrestrial and marine ecosystems meet, marine mammalian carnivores may serve as a food source for their terrestrial equivalent (Stirling & McEwan 1975, Smith 1976, Stirling & Archibald 1977, Smith 1980, Andriashek et al. 1985). Such a predator-prey system is unusual and when in existence is usually highly seasonal, as marine mammals spend most of their time at sea or come ashore on islands where terrestrial carnivores do not occur (Burger & Gochfeld 1994).

Exceptions are the Cape fur seal (*Arctocephalus pusillus pusillus*) breeding colonies that are found on the mainland along the Namibian and South African coast. Seals are ashore in these colonies all year round and serve as a permanent and concentrated food source for terrestrial carnivores such as brown hyenas (*Parahyaena brunnea*) and black-backed jackals (*Canis mesomelas*) (Oosthuizen et al. 1997, Wiesel 1998). Studies in these coastal areas have shown that the overall diet of these terrestrial carnivores mainly consists of Cape fur seals (Skinner & van Aarde 1981, Siegfried 1984, Stuart & Shaughnessy 1984, Stuart 1986, Skinner et al. 1995), with no seasonality in the use of this food source. Nevertheless these studies generally conclude that these carnivores rely on seal carcasses (Skinner & van Aarde 1981, Stuart & Shaughnessy 1984, Hiscocks & Perrin 1987), which are more seasonally available (De Villiers & Roux 1992, Skinner et al. 1995), and hence the importance of live prey has only been marginally established (Wiesel 1998).

Eight Cape fur seal breeding colonies are found on the Namibian mainland, including three of the largest in southern Africa (David & Rand 1986, David 1987), at which hundreds of thousands of seals are present during the pupping period. Brown hyenas and black-backed jackals occur along the entire coastal Namib Desert and therefore have access to all of these seal colonies. All



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but one mainland Cape fur seal breeding colonies were established during the past 60 years (Rand 1956, Best 1973, Best & Shaughnessy 1979, David 1987), whereas both terrestrial carnivores historically have occurred along the coast before this time, mainly scavenging carrion (e.g. seals, seabirds, fish and crustaceans) washed up on beaches (Gaerdes 1977). The occurrence of these carnivores might have prevented the settlement of seals in the past, but other, more important factors seems to have influenced the recent establishment of mainland colonies. One explanation is an increasing population size and the lack of space on adjacent islands, which has forced the seals to settle on the mainland opposite such islands (David 1987). Initially mainly non-breeding seals were found in accumulations along the coast and colony growth was possibly subdued due to predation on the few newborn pups (Shaughnessy 1987, Oosthuizen et al. 1997), easily possible due to the lack of anti-predator behaviour. With a further increase in seal population size, the successful establishment of breeding colonies has become possible despite this predation pressure and has led to the present occurrence of large and successful colonies. This development raises questions about how the seals deal with previously unknown terrestrial predators, how these predators use this permanent and concentrated food source and whether these predators influence the population dynamics of the seal colonies.

Therefore, this study investigated the predator-prey system between the brown hyena and the Cape fur seal, also considering black-backed jackals as potential competitors, and examined brown hyena foraging strategies within this unique and relatively recent system. Following descriptions of the study area in the southern Namib Desert and the three studied species in Chapters 2 and 3, Chapter 4 deals with the prey species, the Cape fur seal, and looks at seal attendance patterns during the pupping period. Chapter 5 addresses the resource dispersion hypothesis with regard to allochthonous food subsidies. In Chapter 6, a brief overview of the brown hyenas' foraging behaviour is given, and Chapters 7 and 8 concentrate on the brown hyena's optimal foraging and diet strategies by addressing prey choice and prey use issues. Conclusions are then drawn based on the information gathered.

Chapter 2

Study Areas and Study Period

The southern Namib Desert is distinguished from the central and northern parts of Namibia by its diversity of different landscapes. Rocky mountains and inselbergs with unique succulent flora, vast gravel plains and dune fields, including mobile barchan dunes, are found throughout the area. The coast is predominantly rocky, interspersed with sandy bays and adjacent coastal salt pans.

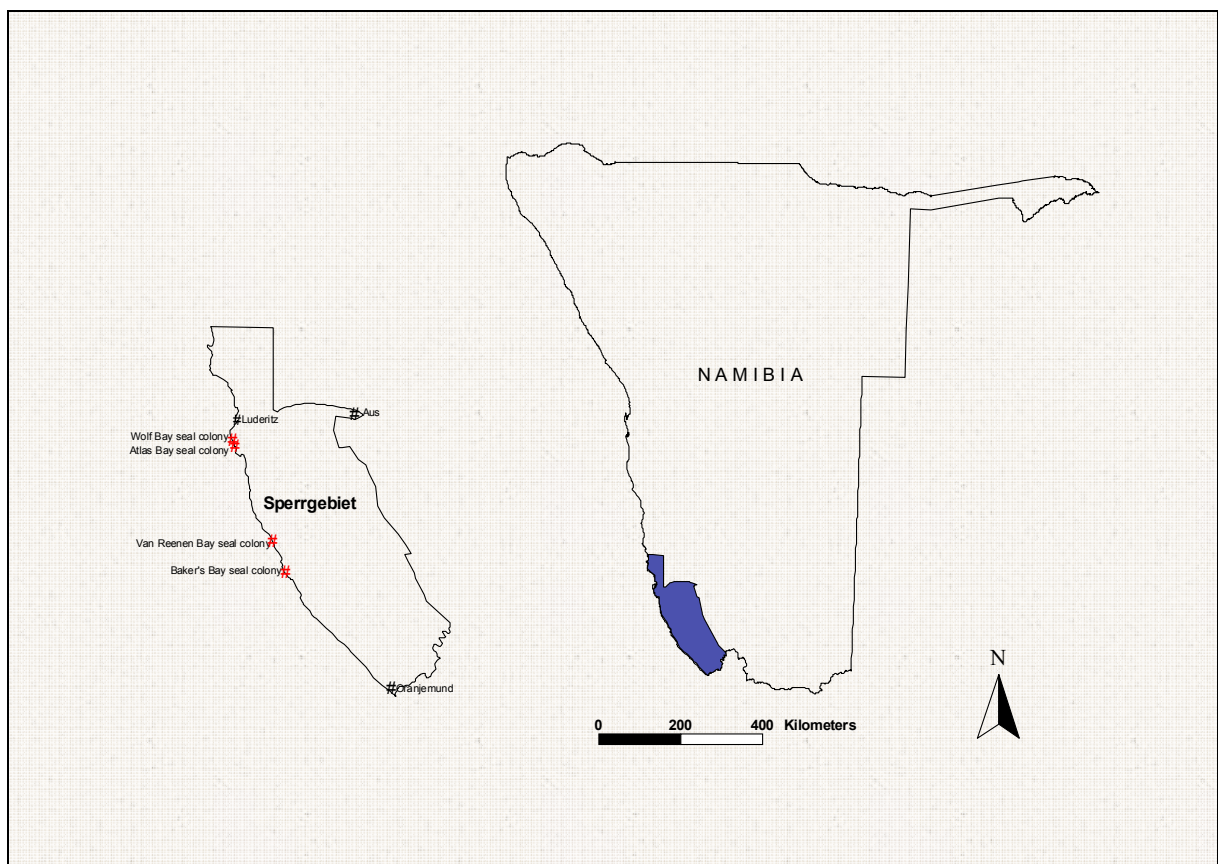


Figure 2.1: The Sperrgebiet's location within Namibia and location of seal colonies.

The southern Namib Desert is also known as the Sperrgebiet (SPG), meaning Restricted Diamond Area (Figure 2.1), and has only recently been declared a National Park. Nevertheless, the entire area is still policed by the diamond company, and human access is strictly controlled and thus minimal.

Precipitation is low and only present in the form of rain and fog. Annual precipitation is less than 100 mm, but varies greatly from year to year. The SPG lies in the transition zone between summer and winter rainfall, so that the



northern areas usually experience rain in summer and the southern areas in winter (Burke et al. 2004).

Along the coast strong south-westerly winds prevail (Stander 1965), with velocities of up to 80 km/h. The high wind velocities and the influence of the cold Benguela ocean current keep air temperatures moderate. The Benguela current is also essential for the sustainability of the productivity of the marine ecosystem (Jarre-Teichmann 1998), which borders the hostile and unproductive desert ecosystem. The marine influence on the terrestrial ecosystem is great and is essential for many fauna. Cape fur seals (*Arctocephalus pusillus pusillus*) breed on offshore islands as well as on the mainland. Four mainland breeding colonies are found in the SPG; the large Wolf Bay and Atlas Bay colonies and the smaller Van Reenen Bay and Baker's Bay colonies (Figure 2.1). Thousands to hundreds of thousands of seals haul out and breed on these mainland colonies and are an abundant, localised food source with all year-round availability for terrestrial carnivores (Oosthuizen et al. 1997).

This study took place at the Wolf Bay and Van Reenen Bay seal colonies and occasionally at the Baker's Bay seal colony, all of which are described in detail below.

2.1 Wolf Bay Seal Colony

This colony (S 26°48'30" E 15°07'10") is one of the largest mainland seal colonies in Namibia. A second, even larger seal colony, the Atlas Bay colony, lies just 2 km south of the Wolf Bay colony separated only by a sandy bay (Wolf Bay) (Figure 2.2). The total size of the Wolf Bay colony is approximately 0.1 km², distributed along a 1.2 km stretch of rocky coastline. Seals haul out at this colony as far as 150 m inland. The surface of the colony is rocky with cliffs of up to 22 m high reaching out into the sea. The rocks are smoothed out by layers of seal hair, faeces, carcasses and bones, which have accumulated over the years.

Human access is restricted to the employees of the Namibian Ministry of Fisheries and Marine Resources, other scientists and the seal concessionaire, which harvests seal pups and bulls between July and November each year.

The Wolf Bay and Atlas Bay seal colonies were the first to be established in the Sperrgebiet. The oldest mainland seal colony in Namibia is at Cape Cross, some 600 km north of Wolf Bay. That colony was established by 1884 (Best &

Shaughnessy 1979), whereas the first reference to seals at Wolf Bay and Atlas Bay was in 1948, mentioning prior congregations of young seals (Rand 1972); breeding was first recorded in 1956 (Rand 1956). Pup production during the last 30 years (1970s – 1990s) has ranged from 10 000 to 40 000, with large annual fluctuations (Butterworth et al. 1987, David 1987, Ministry of Fisheries and Marine Resources).

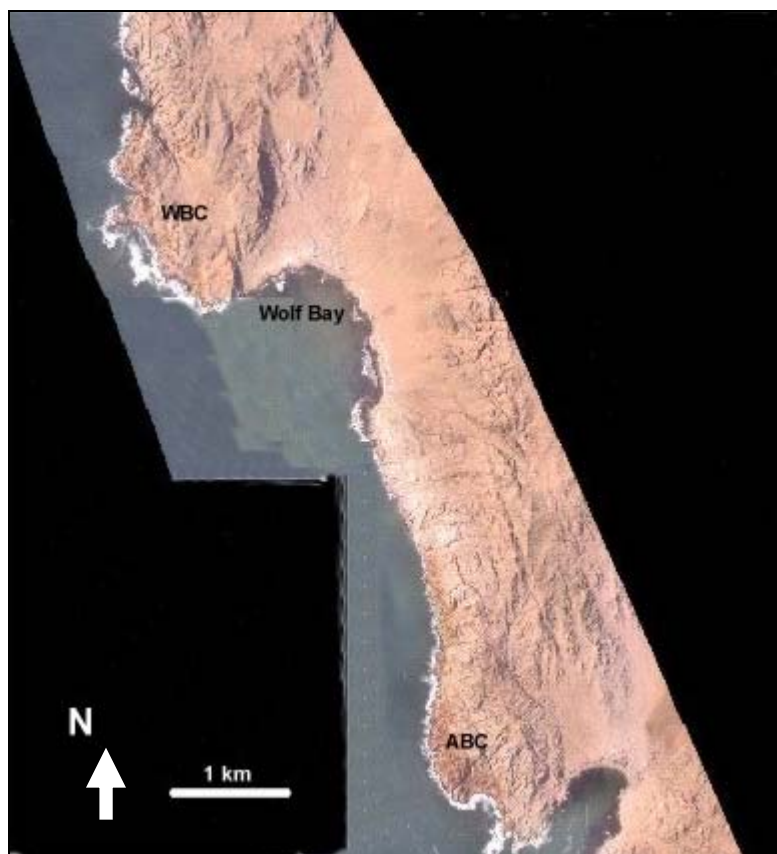


Figure 2.2: Aerial Laser Survey image of the Wolf Bay (WBC) and Atlas Bay (ABC) seal colonies. Courtesy of NAMDEB.

2.2 Van Reenen Bay Seal Colony

The Van Reenen Bay seal colony (S 27°23'50" E 15°21'20") lies approximately 80 km south of the Wolf Bay seal colony (Figure 2.1). These seals haul out on a 2 km stretch of beach, which is surrounded by high cliffs. There is an observation hut on the northern cliff, 17 metres high, which overlooks most of the seal colony. Adjacent to the beach is a flat sandy area, reaching a few hundred metres inland, ending at hummock dune fields or the surrounding cliffs (Chapter 6: figure 6.1). This seal colony has never been harvested (David & Rand 1986).

It is recorded that no seals were found at Van Reenen Bay in 1953 (Best 1973) and breeding was only observed for the first time in 1956 (Rand 1956). Pup



production ranges from 3 000 to 6 000 pups with little change between years (Butterworth et al. 1987, David 1987, Shaughnessy 1987, Ministry of Fisheries and Marine Resources).

2.3 Baker's Bay Seal Colony

The Baker's Bay seal colony (S 27°40'14", E 15°31'28") is found approximately 35 km south of the Van Reenen Bay seal colony (Figure 2.1). It is similar in structure, is 1.7 km long, but stretches over two sandy beaches separated by a rocky area that is also inhabited by seals. The beach is 60 to 100 metres wide and is adjoined by hummock dunes, followed by a large saltpan and mountains further inland.

It is assumed that seals spread to the mainland in the 1950s, as no seals were present in 1947/1948 (Best 1973). Pup production ranges from 3000 to 5000 pups (Butterworth et al. 1987).

2.4 Study Period

Data collection took place at the Wolf Bay seal colony before, during, and after the seal pupping seasons between November and March of 1997-1998, 1999-2000 and 2000-2001. Seal pups are generally born from the middle of November until the first week in January with the peak of pupping taking place in December. Therefore the study period was divided into two phases, representing the different availability and mobility of the pups. The first phase of study began in the middle of November and ended on 7 January the following year in each year of study. This phase represented the time of increasing pup availability from shortage to superabundance, as pups were born throughout this time. Furthermore the pups were relatively immobile and therefore extremely vulnerable to predation and other mortality factors, but large proportions were still guarded by their mothers. The second phase followed directly after the first phase and ended by the middle of March. During this period, there was a superabundance of pups, mostly unguarded, but far more mobile, both on land and at sea.

Data were collected at the Van Reenen Bay seal colony between the beginning of November 2001 and the end of January 2002. The study period was divided into three observation periods. The first period represented the time

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before the peak pupping season between 5 and 23 November. The second period, representing the peak pupping season, started on 2 December and ended on 16 December. The third and last period, representing the time after the peak pupping season, started on 4 January and ended on 23 January.

The periods distinguished themselves through different pup availability. In November pup availability was low, in December pup availability increased and in January all pups had been born and there was a superabundance of food. The period during the peak pupping season, therefore, took an intermediate position between the period of food shortage (November) and the period of superabundance of food (January). Figures 11 to 14 in the appendix highlight the intermediate position of the December period.

Brown hyenas were monitored haphazardly at the Baker's Bay seal colony between June 2002 and March 2005.

Chapter 3

Study Animals

The predator-prey system of the Sperrgebiet comprises two terrestrial carnivores, the brown hyena (*Parahyaena brunnea*) and the black-backed jackal (*Canis mesomelas*), both using mainland seal colonies as their major food source. Other terrestrial animals might profit from the abundance of seals, such as feral dogs (*Canis sp*), porcupines (*Hystrix africaeaustralis*) and African wild cats (*Felis lybica*), but they were not considered for this study.

3.1 Brown Hyena (*Parahyaena brunnea*)

The brown hyena is one of Africa's large carnivores. It is sympatric with the spotted hyena (*Crocuta crocuta*) in the southern African sub-region, but not with its closest relative, the striped hyena (*Hyaena hyaena*) (Eaton 1981). Brown hyenas occur in Angola, Botswana, Lesotho, Malawi, Mozambique, South Africa, Swaziland, Zimbabwe and Namibia. Their total population size is estimated to be 5 000 to 8 000 animals (Hofer & Mills 1998).

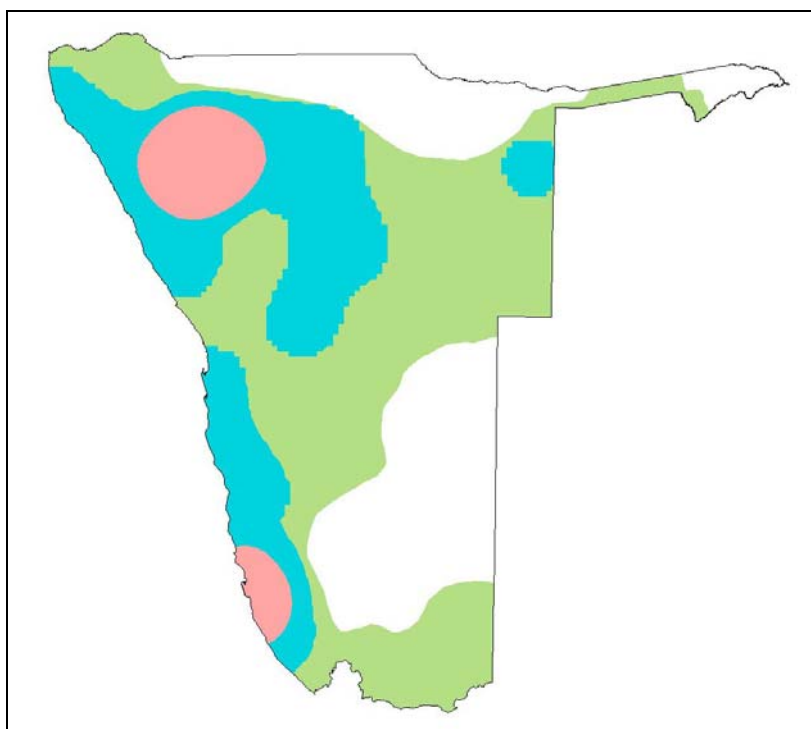


Figure 3.1: Distribution of brown hyenas in Namibia (high density: pink; medium density: blue; low density: green). Courtesy of Predator Conservation Trust.

Within Namibia, they occur in medium (0.1 – 0.15 animals/100 km²) to high (0.15 – 1 animals/100 km²) densities in the central parts of the country up north to the Etosha National Park, west towards the coast and along the entire Namib Desert coast (Figure 3.1). The most recent national population size estimate for Namibia is between 500 and 1 200 animals (Hanssen & Stander 2004).

Brown hyenas have large pointed ears and their body is covered with coarse, brown hair up to 25 cm long (Skinner 1976). The mane around the neck is lighter in colour and their legs are striped (Figure 3.2). There is no apparent sexual dimorphism and the mean body mass for males and females is 40.2 kg and 37.7 kg respectively (Mills 1982b).



Figure 3.2: Adult male brown hyena

Brown hyenas live in clans of up to 10 adult animals (Mills 1990). Their cubs are raised in dens, which are the social meeting point of the clan members. The mean litter size is three cubs, which are weaned after approximately 15 months, and all clan members supplement the cubs' diet by carrying food back to the den (Mills 1983).

Other than at their dens, brown hyenas are usually not seen in clans. They are solitary nocturnal foragers that eat a wide variety of food items (Mills & Mills 1978, Owens & Owens 1978). Their opportunistic diet consists of mammals,

birds, reptiles, insects and fruit, but along the coastal Namib Desert seals form the major part of their diet (Siegfried 1984, Stuart & Shaughnessy 1984, Wiesel 1998).

Sexual maturity is reached within 3 years (Mills 1990). As usually only one female per clan has a litter at a time, young females might start breeding at a later stage. Males often remain in the clan or become nomads, even though they are still believed to reproduce with clan females (Mills 1990). The brown hyena's lifespan in the wild is unknown, but they can reach ages of over 20 years in captivity (Crandall 1964 cited in Mills 1982b).

Brown hyenas are territorial and mark their territories with paste marks that are deposited on grass stalks, bushes or rocks and through defecating in latrines (Figure 3.3). The paste marks consist of two different pastes, a white paste, with a long lasting odour, and a black paste with a less long lasting odour (Mills et al. 1980). Paste marks and latrines are found throughout the brown hyena's territory and are used to communicate with other clan members and to warn off intruders (Mills et al. 1980, Mills 1990).



Figure 3.3: Brown hyena paste mark showing the black and the white paste, and brown hyena latrine.

3.2 Cape Fur Seal (*Arctocephalus pusillus pusillus*)

Cape fur seals only occur and are the only resident otariid seals found along the Namibian and South African coast. They congregate in colonies on offshore islands and on the mainland from Algoa Bay (S 34° E 26°) in South Africa around the Cape Peninsula, up to Cape Frio (S 18°30" E 12°) in Namibia. There are 25

established breeding colonies and nine non-breeding colonies (Oosthuizen & David 1988, Wickens et al. 1992), 23 on islands and 11 on the mainland. Eight of these mainland colonies are situated in Namibia (Figure 3.4).

No recent population size estimates are available. David (1987) gives an estimate of 1.1 million seals in total and the Namibian population is estimated to be at least 700 000 animals (Roux pers. comm.), representing approximately two thirds of the total southern African population.

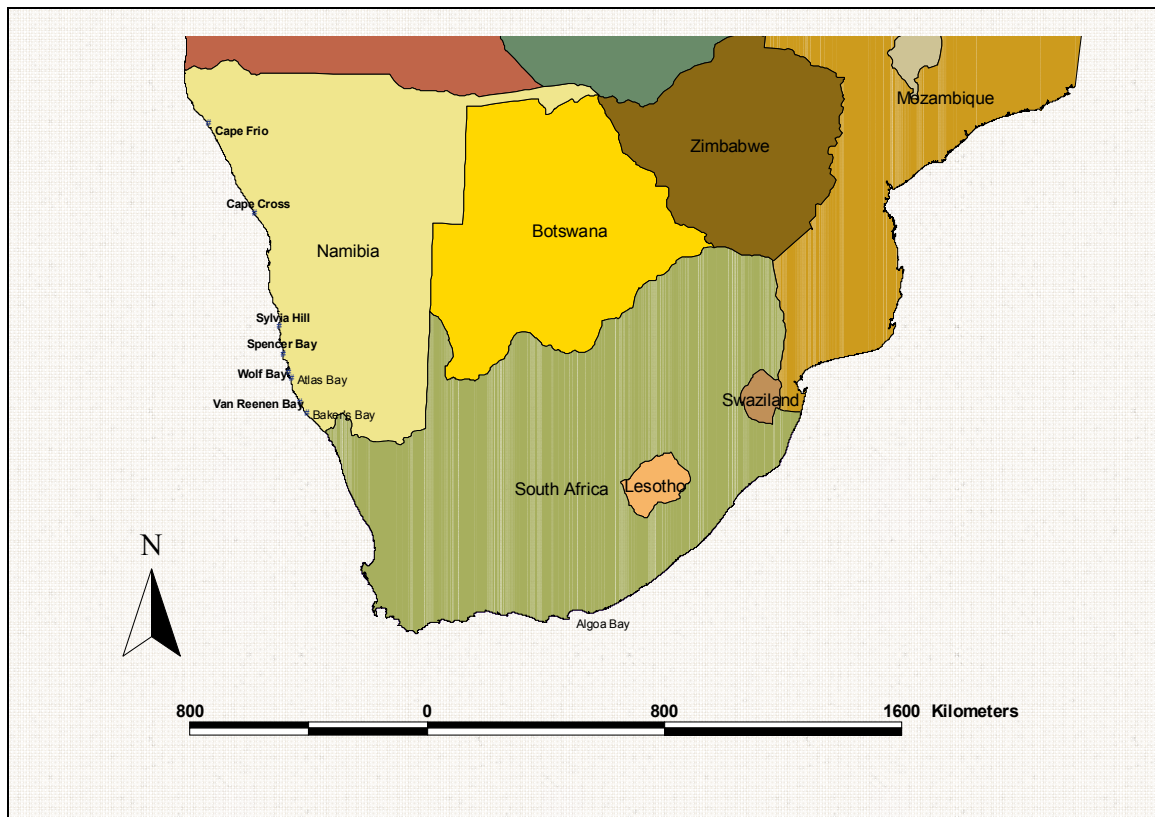


Figure 3.4: Location of mainland seal colonies in Namibia.

There is a distinct sexual dimorphism between male and female Cape fur seals (Figure 3.5). Adult males weigh 247 kg on average and are on average 2.15 m long. Their fur is dark blackish-grey. Females weight 57 kg and reach a mean body length of 1.56 m. Their fur is lighter in colour and brownish-grey (David 1987, Skinner & Smithers 1990). Pups are born in spring, between November and December. Their fur is black at birth and turns silvery-grey after their first moult in autumn (March – May) (Rand 1956).



Figure 3.5: Male Cape fur seal in the centre, an adult female on the left and to the right and black pups in the foreground.

Bulls arrive at the colony to establish territories in the middle of October. The breeding season lasts from November to the beginning of January, with a peak in pupping in December. In late summer adult seals moult. Females predominately moult in February and bulls in February to March (Rand 1956, Rand 1967). Seals go on extensive feeding trips in autumn and winter (March – August), but females visit the colony to raise their pup throughout the year until it is weaned shortly before the birth of the next pup (Rand 1967).

Female seals reach maturity at two years (Rand 1967) but usually breed for the first time at an age of four to five years (Shaughnessy 1982, Butterworth et al. 1987). Although bulls reach maturity at an age of three to four years (Rand 1956, Stewardson et al. 1998), they are usually only able to defend a territory and to successfully breed at an age of 10 to 14 years (David 1989 cited in Stewardson et al. 1998). The total lifespan of seals in the wild is unknown, but female seals have reached ages of up to 23 years in captivity (Wickens 1993).

3.3 Black-Backed Jackal (*Canis mesomelas*)

The black-backed jackal occurs in two distinct areas in Africa, east Africa and southern Africa, which are geographically vastly separated (Skinner & Smithers

1990). The southern African area stretches from south-west Angola and Zimbabwe to the Cape Province in South Africa.

Black-backed jackals are medium-sized carnivores. They have a distinct dark saddle on the back of their body and a dark bushy tail (Figure 3.6). Males weigh on average 7.89 kg, and females average 6.60 kg (Skinner & Smithers 1990).



Figure 3.6: Black-backed jackal

Black-backed jackals form long-term pair bonds, and previous offspring often remain for prolonged periods of time with the parents as helpers (Moehlman 1978). Black-backed jackals give birth to a litter of one to six cubs between July and October each year. Both parents, as well as the helpers, regurgitate food or carry food back to the den (Moehlman 1978), supplementing the cubs' milk diet. The presence of such helpers increases the survival rates of the cubs (Moehlman 1978). Cubs are fully weaned at an age of eight to nine weeks and start foraging with the parents shortly afterwards.

Black-backed jackals are opportunistic feeders and their diet consists of insects, reptiles, carrion and vegetables (Hiscocks & Perrin 1987). Breeding pairs



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are highly territorial, but at large food sources other jackals are tolerated (Skinner & Smithers 1990). Home range sizes vary greatly, but are on average 10.6 km². Sub-adults may disperse to areas more than 135 km away (Ferguson et al. 1983).



Chapter 4

Variability in the Availability of Cape Fur Seal Pups to Foraging Brown Hyenas along the Southern Coastal Namib Desert

4.1 Introduction

The availability of food is one of the most important factors for the occurrence and survival of carnivores in a specific habitat. The distribution and abundance of a potential prey species has to be known and particularly for scavengers it is of importance to know about the mortality factors of those species (Mills 1990). Brown hyenas (*Parahyaena brunnea*) are predominantly scavengers in most ecosystems (Mills & Mills 1978, Owens & Owens 1978), where food is patchily distributed and where other large carnivores occur. A wide variety of food items are opportunistically used.

Along the Namib Desert coast marine carrion is washed ashore and large mainland seal colonies exist. In this ecosystem brown hyenas patrol the beaches to search for food and to forage at the seal colonies. Therefore it is not surprising that seals (*Arctocephalus pusillus pusillus*) form the major part of their diet (Siegfried 1984, Stuart & Shaughnessy 1984). Faeces analysis showed that this food source is used all year round and that seal pups form the major proportion of the food source (Wiesel 1998). If seal pups are of vital importance for brown hyena survival along the Namib Desert coast, fluctuations in pup production due to environmental variability or extensive harvesting could have an influence on brown hyena foraging behaviour. If seal pup availability drops below the requirements of resident brown hyenas, they might have to supplement their diet with other food items washed up along the beaches or found in inland areas of their home range.

Cape fur seals are marine mammals that spend half of their life at sea (Rand 1967). Nevertheless they must come to shore along the southern African coast to breed and to moult, forming large colonies of up to over one hundred thousand animals (Shaughnessy 1982).

Historically, Cape fur seals occurred on islands and islets off the South African and Namibian coast. Their population size was drastically reduced due to extensive harvesting before their first legal protection through the Fish

Proclamation Act of 1893 (Best 1973). Subsequently seal numbers have increased exponentially, resulting in some islands reaching their carrying capacity (Peters et al. 2000), which has possibly directly led to the formation of colonies on the mainland (David 1987). Most mainland colonies did not exist before 1940, but now constitute more than half of the population.

Nevertheless, environmental conditions, such as anomalous warm water events, that affect the productivity of the Benguela system and consequently the abundance and distribution of the seals' food cause large-scale mortality in adult and young seals (Roux 1998). Such events result in years with extremely low pup production, poor pup growth, low pregnancy rate and poor body condition of adult seals.

Cape fur seals, as marine mammals that historically did not occur on the mainland, only have sharks (*Carcharodon* spp) and killer whales (*Orcinus orca*) as natural marine enemies (Rand 1956) and might show anti-predator behaviour towards those. On land they face novel terrestrial carnivores such as black-backed jackals (*Canis mesomelas*) and brown hyenas (Shaughnessy 1987). Nevertheless those carnivores did not prevent the settlement of seals on the mainland and the establishment of successful breeding colonies (Rand 1956), even though they are known to feed on seal pups. Only pups and yearlings are potential prey for brown hyenas. The average mass for seal pups at birth is 5 kg for females and 6 kg for males, and mass at weaning averages 25 kg for males and 20 kg for females (David 1987). Male yearlings weigh 30 kg at the same time, but size and mass increases up to 60 kg in the following year (Rand 1956).

These seal colonies are a permanent, localised food source for terrestrial carnivores, but the seasonally changing structure of the colony and attendance of different seal classes might have an influence on the carnivores' foraging behaviour and success. The three main factors in the brown hyena – Cape fur seal predator-prey system are the availability, the condition and the accessibility of the prey.

These factors formed the scope of this study and regarding the availability of prey it was investigated

- (1) whether pup production fluctuates between years and different colonies and



- (2) whether there is a difference in the availability of sex classes.

Regarding the condition of the prey it was determined

- (1) whether female and male pups differ in mass,
- (2) whether pup growth differs between years,
- (3) how high the rate of non-violent mortality (mortality other than predation) of first-year pups is,
- (4) whether there are differences in the non-violent mortality rate between years,
- (5) whether there are differences in the cause of death during and after the pupping season,
- (6) whether there are differences in mortality between sexes and
- (7) how the value of non-violent mortalities, determined by mass, differs.

Lastly the influence of the seals' anti-predator behaviour on brown hyena behaviour was investigated.

4.2 Material and Methods

4.2.1 Biology of the Study Animal

The structure of Cape fur seal colonies changes seasonally. Breeding takes place in spring, moulting in summer and extensive feeding in autumn and winter (Rand 1967).

Mature bulls arrive at the colonies in the middle of October (beginning of spring) to establish territories. These territories are formed before the females arrive and eventually lead to the grouping of females into harems (Rand 1967). Most females are pregnant at this time. Bulls defend these territories and do not leave them voluntarily until they have mated with all the females, after these have given birth. The rut lasts for approximately two months until the middle of December, after which the bulls' aggression decreases and they mix freely with other age and sex classes. Bulls behave indifferently towards new-born pups and might even accidentally crush them during territorial and reproductive activities (Rand 1967, De Villiers & Roux 1992, Boveng et al. 1998). Moulting then occurs and is a gradual process that takes place from January to April (Rand 1956). After this time bulls are rarely seen at the colonies, spending most of their time at sea.



Adult females give birth to a single pup during the pupping season sometime in November, December or January (Rand 1956). They come into oestrus approximately six days after giving birth, immediately mate with a bull and then leave the new-born pup for their first feeding trip to sea (David & Rand 1986). The duration of these feeding trips increases gradually with the increasing age of the pup. The pups are fully weaned at eight to 11 months of age on average, but sometimes only by the time the next pup is born (Rand 1955, David & Rand 1986, David 1987).

Females are highly gregarious and often lie touching each other (David 1987). The exceptions are females that are close to giving birth or have very young pups. Then they are highly aggressive and will fight vigorously over their pup, especially from the time of birth to their first feeding trip to sea (Rand 1967). Females do not foster or nurse pups other than their own and are aggressive towards milk thieves.

Females are not tied to a particular territory and can leave and enter the pupping place relatively freely (Wickens et al. 1992). Very young pups remain in close vicinity to the original pupping place as the mother will search that area for her pup after returning from her feeding trips (Rand 1967).

Females return to the colonies all year round to nurse the growing pup (David & Rand 1986), and from February onwards the majority of seals found at the colony are first-year pups (pers. observ.)

Pups are born from approximately the middle of November until the first week of January, with a median date of birth at the beginning of December (David 1987). Very young pups are relatively immobile and rely on meeting the mother at the original pupping place. Their movements are therefore restricted, but pups often congregate in “pup pods” while their mothers are at sea, for companionship and mutual protection while sleeping (Rand 1967). It can take up to six weeks before they move farther away from the pupping place often towards the sea, then learning how to swim. By July first-year pups spend a lot of time in the sea close to the colony, also starting to look for additional food (Rand 1967, Roux pers. comm.). Environmental factors play an important role in seal pup mortality, either directly or indirectly by influencing the mother’s attendance behaviour. Factors such as heat stress and starvation are therefore the main causes of seal



pup mortality during the first month of their lives (De Villiers & Roux 1992, Roux 1998).

4.2.2 Study Area and Study Period

Data were collected during the Cape fur seal pupping season at the Wolf Bay seal colony between November and March 1997-1998, 1999-2000 and 2000-2001. The entire seal colony was divided into 24 sample areas of different sizes and habitat and the area for each of these was calculated using a range finder (Sokkisha Tokyo 6656 – 7.5 m - ∞ m) (Wiesel 1998).

4.2.3 Determination of Pup Production

The Ministry of Fisheries and Marine Resources (MFMR) in Namibia took aerial photographs of the Namibian seal colonies during the time when the maximum number of live pups is present in 1997-1998 (18.12.1997) and 2000-2001 (January 2001). Black newborn pups were counted on these photographs to determine pup production (Rand 1955, Shaughnessy 1982, Butterworth et al. 1987, Wickens & Shelton 1992). No aerial photographs were available for the pupping season in 1999-2000. To obtain an estimate of pup production at Wolf Bay for this pupping season, the number of pups in test areas with low, medium and high density of seals was determined, using the following density definition:

- (1) low: hardly any body contact between adult seals, single pups in the area
- (2) medium: body contact between adult seals, single pups in the area, and
- (3) high: body contact between adult seals and presence of pup pods.

Eleven counts were carried out in low-density test areas, 14 in medium-density test areas and 16 in high-density test areas and the ratio pups/m² for the 1999-2000 study period was determined. Each of the 24 sample areas was placed in one of the three density categories, the total area (m²) per density category was calculated and the total number of pups was determined using the following equation:

$$Y = \sum (X_n * (N_n / A_n))$$

with Y being the pup production in absolute numbers, n representing low, medium and high density areas, X being the total size of the sample areas of category n in



m^2 , N being the mean number of pups counted in low, medium or high density test areas and A being the size of the low, medium or high density test area in m^2 .

4.2.4 Seal Pup Growth, Sex Ratio and Pup Availability

The mass of live seal pups was measured in collaboration with the MFMR in Lüderitz for each pupping season on five to seven days between the middle of December and mid-March. On average, 130 pups were weighed in each sample and the sex ratio of pups for each sample was determined.

For the pupping season 1999-2000 and 2000-2001 data sets of the MFMR's study site at the Atlas Bay seal colony were available for analysis. These data sets included date of birth, mass at birth, sex, standard length and girth measurements of all newborn pups in their sample area.

From these data sets, the mean day of birth and average mass at birth for each sex and the overall sex ratio of newborn pups could be determined.

Seal pups are guarded by their mothers for the first six days of their life (David & Rand 1986) and are more vulnerable to mortality as soon as their mothers leave the colony for their first feeding trip to sea. Therefore the cumulative number of guarded and unguarded pups for each day of each pupping season was determined. The number of guarded pups G on Julian day n was

$$G_n = \sum_{i=n-6}^n B_i$$

with B being the number of pups born on Julian day i . The number of unguarded pups U on Julian day n , assuming a closed population, was $U_n = U_{n-1} + B_{n-6}$.

The Julian day number 1 was 1 January; 31 December represented Julian day number 0, counting backwards until the beginning of the study period in November.

4.2.5 Non-Violent Mortality

Any source of pup mortality other than predation was considered non-violent. To determine non-violent mortality of newborn pups, 10 representative sample areas out of the 24 were chosen for data collection in 1997-1998 and 1999-2000, and 14 in 2000-2001. Between the birth of the first pup in November each year and 15 or 16 March (Julian day no. 75) of the following year all dead pups in these

sample areas, which were dead for less than 24 hours, were recorded and marked with a numbered plastic or metal tag to avoid double counts. Dead pups that were not marked and already bloated or rotten and therefore had been dead for more than 24 hours (compare with Trillmich et al. 1986 and Geraci & Lounsbury 1993) were noted, their flippers clipped, and were included into the mortality rate estimates for days where no data collection took place.

During the seal pupping season (November until 7 January) the colony was visited every week for 3 to 4 days in 1997-1998, 4 to 5 days in 1999-2000 and 5 to 6 days in 2000-2001. After 7 January the colony was only visited on 2 (1997-1998), 2 to 3 (1999-2000) and 3 to 4 days every week (2000-2001). Not every sample area could be visited on each day, as the disturbance of seals had to be minimised and accessing the dead pups was not always possible. Therefore the haphazard sampling method was used (Martin & Bateson 1993). Criteria such as weather conditions and the number of adult seals in the sample areas influenced the decision on a daily basis.

On average, each of the original 10 sample areas was checked 25 times in 1997-1998, 41 times in 1999-2000 and 74 times in 2000-2001. The 4 additional sample areas in 2000-2001 were checked 31 times.

For all dead pups the cause of death was determined as either stillbirth, starvation, heat stress or unknown causes. For days where no data collection took place, either the median number of dead pups of the three previous visits and three consecutive visits was calculated or in case of one missed day between data collection the number of bloated pups was used. In the case of a hot day during the pupping season, with low wind speeds and northern or easterly winds, the mean number of dead pups on previous and consecutive hot days was calculated, because heat stress as a cause of death is extremely weather dependent (Rand 1967, De Villiers & Roux 1992, Wiesel 1998) and has also been recorded for other seal species (Francis & Heath 1991).

Mortality caused by hyena predation differed from non-violent mortalities by the pups having a crushed skull (compare with Chapter 6) and were not included in the non-violent mortality estimates.

Non-violent mortality was calculated in a life table described by Caughley (1977). The daily mortality frequency (f_m) (number of dead seal pups) and the



daily number of pups that were exposed to the risk of dying (F_m) were determined. The daily survival rate was calculated as $(1 - (f_m / F_m))$ and the total annual mortality was $(1 - (\prod 1 - (f_m / F_m)))$. The number of pups exposed to the risk of dying on day 1 was the number of pups counted on aerial photographs or calculated with the density index in all sample areas together, added to the number of pups that had already died before the aerial photographs were taken or before the density estimate was done. The daily number of pups exposed to the risk of dying was calculated from the number of live ones on the previous day (F_m) minus the number of pups that died of non-violent mortality and predation.

4.2.6 Seal Pup Carcass Availability along Beaches

Freshly washed up seal pup carcasses, which possibly drowned, especially during storms (Rand 1967), were counted at irregular intervals during the study period at Wolf Bay beach (compare with Skinner et al. 1995). The 1 km long beach, which separates the Atlas Bay and Wolf Bay seal colonies, lies just northeast of the Long Islands seal colonies and faces southwest, and is therefore favourably positioned for washed up carrion due to direct input from the prevailing current. Carcasses, which appeared fresh, judged by the degree of decomposition (not bloated or rotten and fur still attached) (Rand 1967, Trillmich et al. 1986, Geraci & Lounsbury 1993), were counted with a counter at the high water mark. Three time periods were distinguished:

- (1) before the peak of the pupping season (before 50% of the pups were born),
- (2) from the peak pupping period to the end of highest risk for non-violent mortality in Cape fur seal pups (end of January, compare with David 1987 and De Villiers & Roux 1992) and
- (3) after the highest risk for seal pup mortality (February to March).

4.2.7 Mortality Factors

Dead pups were examined thoroughly and their age, sex and condition was recorded. Age determination could only take place for the first three days after birth. The umbilical cord of newborn pups (day one) is still visible and moist. On day two, the outside of the umbilical cord is already dry. On day three, it is

completely dry. Pups older than three days have lost their umbilical cord altogether (Boness et al. 1991), which makes further age determination impossible. To determine the condition of the dead pups the following measurements were taken:

- (1) their mass up to 10 kg with an accuracy of 50 g and from 10 kg to 25 kg with an accuracy of 100 g;
- (2) their standard length, measured in cm in a straight line from the tip of the nose to the last vertebra in the tail with a precision of 0.5 cm;
- (3) their girth, measured in cm, behind the front flippers, with a precision of 0.5 cm; and
- (4) their blubber thickness in mm, by making a 1 cm ventral incision on the sternum.

Stillborn pups were identified according to the following: They are born with their eyes closed, and the umbilical cord is either moist or the placenta is still attached. Some stillborn pups were found still in their amniotic sac. Pups that have died of starvation are visibly thin (Trillmich et al. 1986), weigh less than the average birth mass for that season, and have no blubber (compare with Steiger et al. 1989). Starvation is unlikely to happen in very young pups. However, due to the definition used in this study, some young pups were included in the starvation category. Heat stress as a mortality factor was only recorded after hot days. Pups observed in heat stress experience extreme convulsions. Dead heat-stress pups are identified by having the typical body position of an outstretched body with the head bend backwards and with front flippers stretched away from the body at an angle of approximately 90°. They have often also vomited before dying. Whenever the cause of death was not clear it was recorded as unknown.

The sex ratio of non-violent mortalities was determined for each study period in total, for the seal pupping season (middle of November until 7 January), and for the time after the seal pupping season (8 January until Julian day 75 – middle of March).

4.2.8 Anti-Predator Behaviour of Seals

Focal-animal sampling (Altmann 1974) was used to quantify the response of seals to foraging brown hyenas at the Van Reenen Bay seal colony (see Chapter



6). During the observations the behaviour of the seals with regard to changes in brown hyena behaviour, was noted, as well as the reaction of the brown hyena to changes in seal behaviour.

Seal reactions were classified as

- (1) seals running towards the sea, one initial seal often causing a stampede,
- (2) seals being alert (not sleeping) and moving slightly and
- (3) seals attacking the hyena by moving towards them with open mouths and their heads and necks stretched forward, or by actually aggressively threatening the hyena by moving their heads with open mouths towards the hyena, possibly also vocalising.

The hyena was regarded as present within the detection capabilities of the seals when it was walking between the seals, alongside the colony or away from the colony (leaving the immediate area of the colony), or when it was standing, creeping, hunting or performing other activities in the area of the colony, such as urinating, paste marking or resting. Walking and leaving were regarded as behaviours less threatening to seals than standing while orientating or staring at the seals, approaching and hunting.

4.2.9 Data Collection and Statistics

Data were recorded in a field diary and entered into Microsoft Office Excel spreadsheets. Statistical tests (Sokal & Rohlf 1981, Zar 1984) were conducted using GraphPad Prism 4 and Minitab 14. Figures were drawn in GraphPad Prism 4 and Excel. In case of normally distributed data (Kolmogorov-Smirnov Test), parametric tests (t-test, One-way ANOVA, Pearson Product Moment) were used; otherwise, non-parametric tests (Mann-Whitney U-Test, Kruskal Wallis Test, Spearman Rank Correlation) were used. Post-hoc tests were used in case of multiple comparisons to test for differences between the variables. Contingency tables were analysed to determine differences between rates and proportions (Chi² Test, Fisher Exact Test). Proportions were arcsine square root transformed before analysis. Linear regression equations were compared by testing the two regression lines for differences in their slopes (Sokal & Rohlf 1981, Zar 1984). Parallel slopes were then tested for differences in their elevation, and all lines were tested for differences in the intercepts.

Unless otherwise stated the same data collection methods and statistical tests have been used in all subsequent chapters.

4.3 Results

4.3.1 Pup Production at Mainland Cape Fur Seal Colonies

Pup production varied between years and decreased continuously during the course of the study. Pup production in 2000-2001 was 42% lower than at the beginning of the study in 1997-1998 (Figure 4.1). The total number of pups born in the sample areas was 8 950 in 1997-1998, 5 450 in 1999-2000 and 2 900 in 2000-2001.

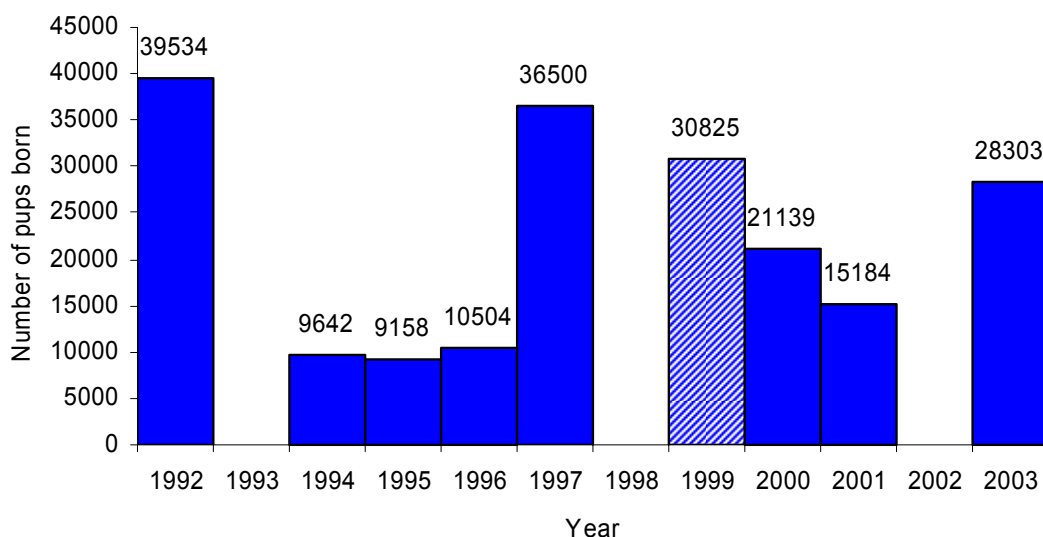


Figure 4.1: Pup production at the Wolf Bay seal colony between 1992 and 2003. Blue bars show pup numbers resulting from the count on aerial photographs (Ministry of Fisheries and Marine Resources, Namibia) and the shaded bar for 1999 the results from the density estimate.

To determine whether the variation in pup production at the Wolf Bay seal colony, which was harvested for pups and bulls in the winter of each year, was affected by the harvest, these numbers were compared with the pup production at the Van Reenen Bay seal colony, which was not harvested. Pup productions at these two colonies were significantly correlated (Pearson Product Moment $r = 0.88$, $p = 0.009$), which indicated that other factors besides harvest were responsible for these fluctuations (Figure 4.2).

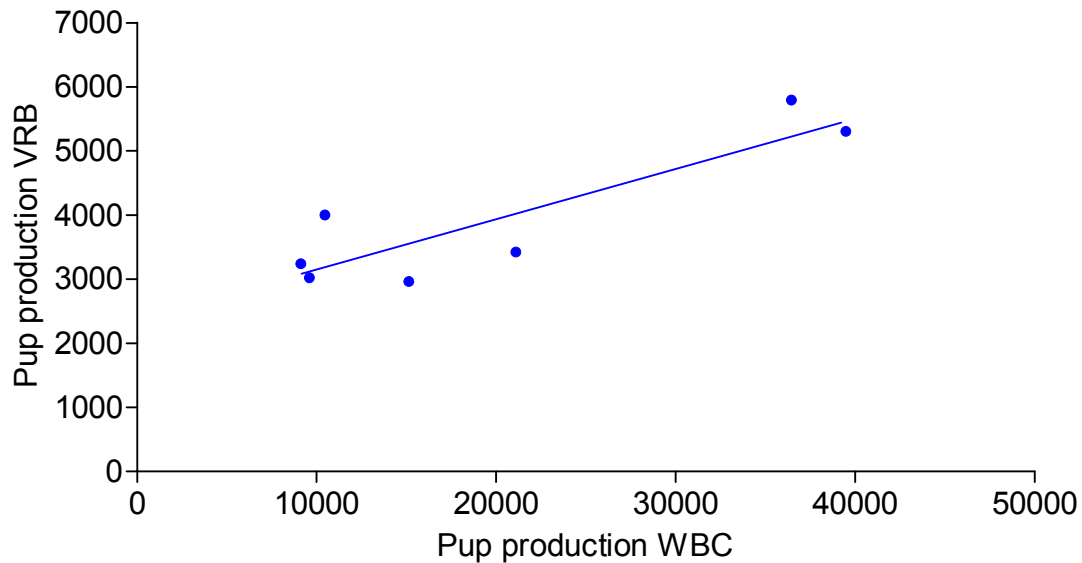


Figure 4.2: Correlation between the pup production at the Van Reenen Bay (VRB) and Wolf Bay (WBC) seal colony for the years 1992, 1994-1997, 2000 and 2001. Counts were made from aerial photographs (MFMR).

4.3.2 Seal Pup Growth

The mass of male pups was significantly higher than the mass of female pups during all pupping seasons (Table 4.1).

The growth curves for males and females each year differed significantly for elevations (1997-1998 $F_{1,9} = 18.3$, $p = 0.002$; 1999-2000 $F_{1,11} = 39.8$, $p < 0.0001$; 2000-2001 $F_{1,9} = 20.7$, $p = 0.0014$) but not slopes (1997-1998 $F_{1,8} = 0.988$, $p = 0.35$; 1999-2000 $F_{1,10} = 0.515$, $p = 0.49$; 2000-2001 $F_{1,8} = 0.323$, $p = 0.59$). Therefore growth rates of male and female pups were equal, but mass at birth differed (Figure 4.3). The difference in birth weight between males and females could be tested for the years 1999-2000 and 2000-2001. The mean mass (\pm SD) of male pups at birth in 1999 (6.2 kg \pm 0.7) was significantly higher than that of female pups at birth (5.4 kg \pm 0.6) (Mann-Whitney U-Test $U = 11200$, $p < 0.0001$). Male pups in 2000 were also significantly heavier at birth (5.7 kg \pm 0.8) than female pups (4.8 kg \pm 0.7) (t-test $t = 5.373$, $df = 84$, $p < 0.0001$).



Table 4.1: Mean mass (kg) of male and female seal pups during different periods from cross samples.

Period	Month	Julian day	Mean Mass \pm SD		Test	t / U	p	N
			Males	Females				
1997/1998	December	-18	6.7 \pm 1.1	5.8 \pm 0.9	t-test	5.664	< 0.0001	158
	January	9	7.3 \pm 1.5	6.4 \pm 1.2	t-test	3.023	0.0033	92
	January	20	8.7 \pm 1.4	7.5 \pm 1.2	Mann-Whitney U-test	8054	< 0.0001	373
	February	48	7.0 \pm 1.4	6.0 \pm 1.2	t-test	5.005	< 0.0001	172
	March	66	12.0 \pm 1.9	10.5 \pm 1.2	t-test	4.445	< 0.0001	92
	March	76	12.3 \pm 1.6	11.0 \pm 1.5	t-test	3.159	0.0024	68
1999/2000	December	-15	6.5 \pm 1.1	5.5 \pm 0.8	t-test	8.317	< 0.0001	236
	January	6	6.7 \pm 1.2	5.6 \pm 0.8	t-test	5.265	< 0.0001	120
	January	20	7.0 \pm 1.4	6.0 \pm 1.2	t-test	5.005	< 0.0001	172
	February	41	7.8 \pm 1.5	6.2 \pm 1.3	Mann-Whitney U-test	774	< 0.0001	133
	February	59	8.1 \pm 1.7	7.1 \pm 1.8	t-test	2.950	0.0039	113
	March	83	9.5 \pm 2.0	7.7 \pm 1.4	t-test	5.331	< 0.0001	108
2000/2001	January	6	7.4 \pm 1.5	6.4 \pm 1.3	t-test	4.343	< 0.0001	151
	January	20	8.2 \pm 2.0	6.8 \pm 1.5	t-test	3.960	0.0001	99
	February	54	10.5 \pm 2.1	9.2 \pm 1.3	t-test	3.676	0.0004	103
	March	78	13.5 \pm 2.4	11.6 \pm 1.5	t-test	4.825	< 0.0001	101

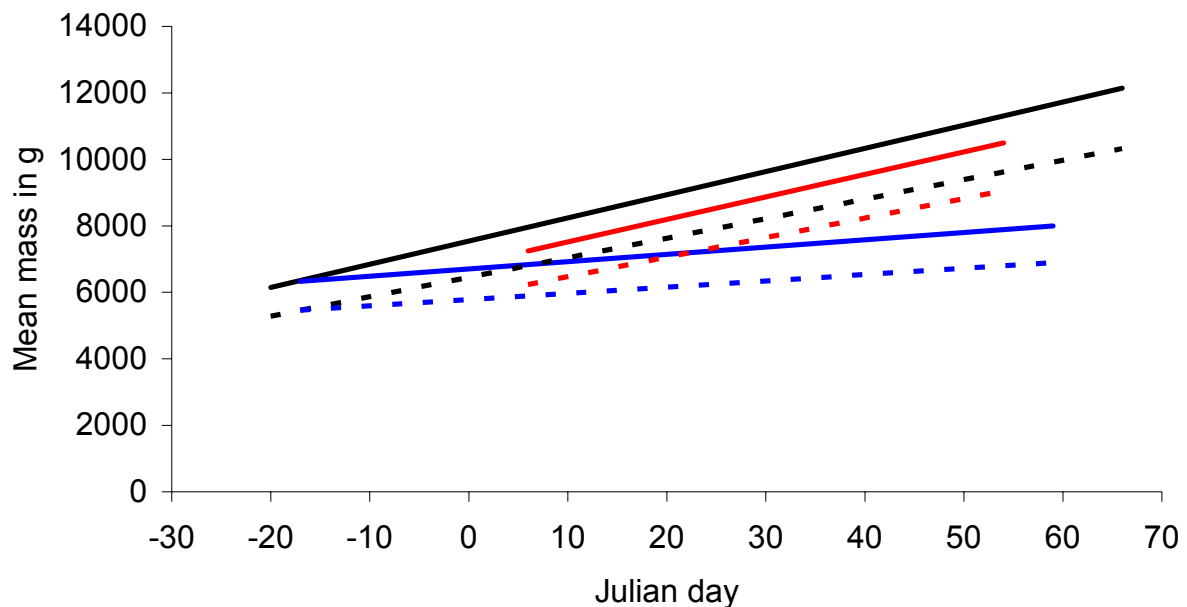


Figure 4.3: Linear growth curves for male (solid lines) and female (dashed lines) pups in 1997-1998 (black), 1999-2000 (blue) and 2000-2001 (red).

The growth curves of seal pups were different between years (Figure 4.4). The slope of the regression for the year 1999-2000 was significantly different and

less steep than the slopes in 1997-1998 ($F_{1,24} = 17.1$, $p = 0.0004$) and 2000-2001 ($F_{1,24} = 10.2$, $p = 0.004$).

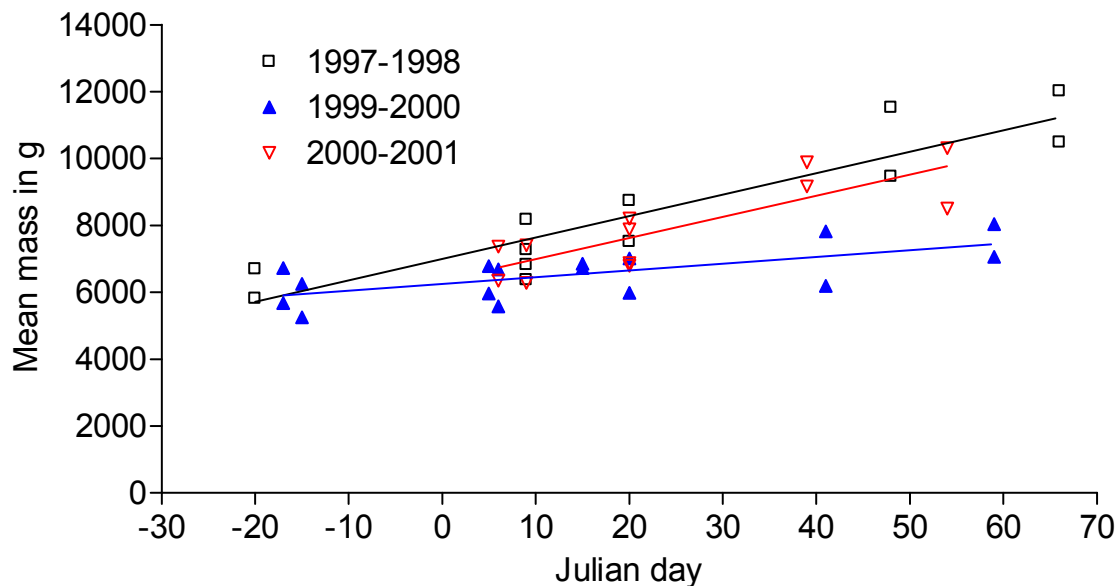


Figure 4.4: Growth curves of seal pups in 1997-1998 (black line), 1999-2000 (blue line) and 2000-2001 (red line).

There was no significant difference between the slopes, elevations and intercepts between 1997-1998 and 2000-2001.

4.3.3 Pup Availability and Sex Ratio

The sex ratio of pups at birth was 47% males to 53% females in 1999-2000 and 54% males to 46% females in 2000-2001. The difference between years did not differ statistically (Fisher Exact Test $p = 0.40$). The overall sex ratio calculated from all cross samples later in the season was 68% males to 32% females (1997-1998), 54% males to 46% females (1999-2000), and 53% males to 47% females (2000-2001).

The mean date of birth for male and female pups was one day apart. In 1999 50% of all females had been born by 13 December and 50% of all males a day later. In 2000 males reached the mean date of birth one day earlier than females, on 10 December. The differences in birth date did not differ significantly (Mann-Whitney U-test: 1999-2000 $U = 49220$, $p = 0.31$; 2000-2001 $U = 31870$, $p = 0.29$).

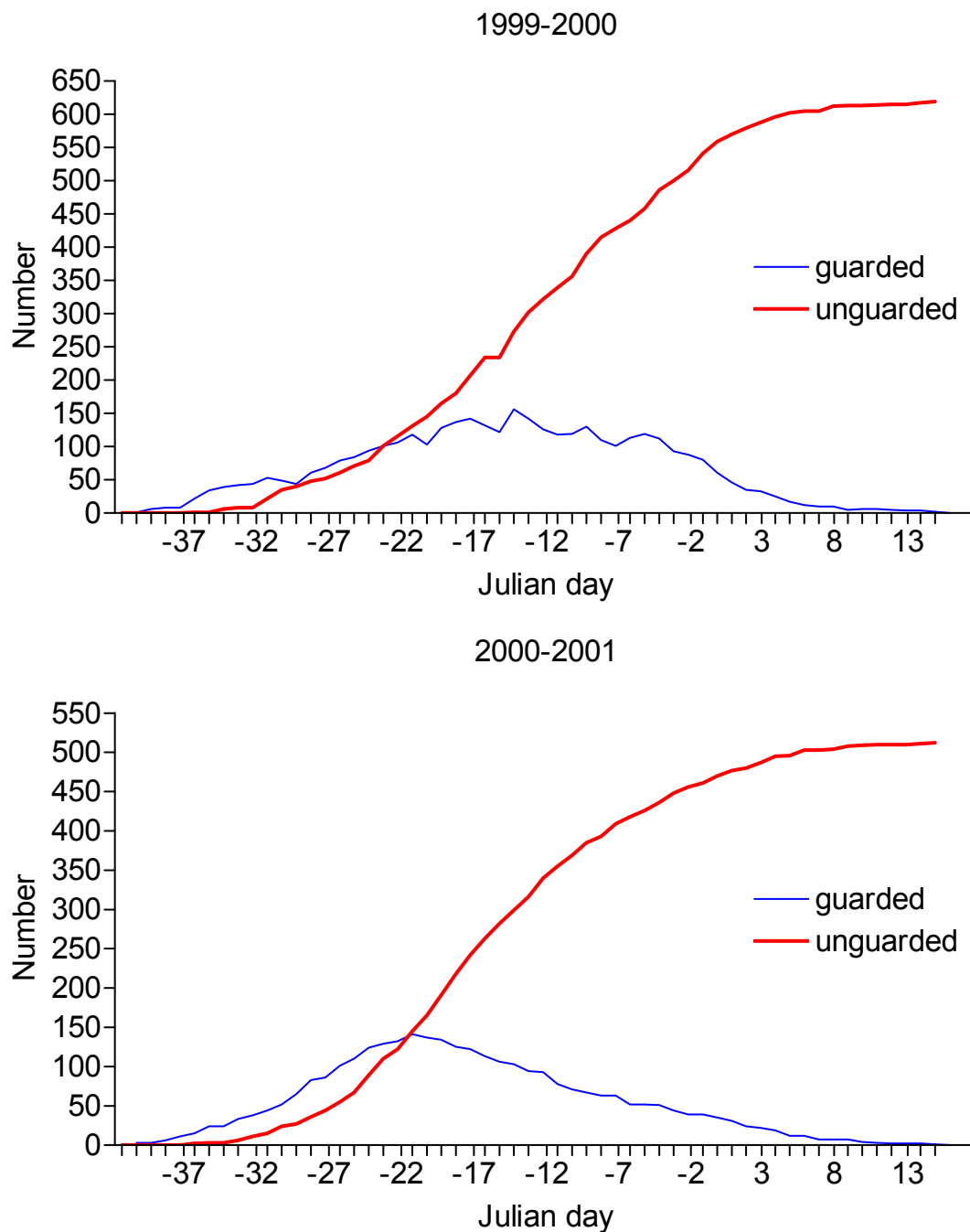


Figure 4.5: Cumulative number of guarded (blue) and unguarded (red) pups during the pupping season in 1999-2000 and 2000-2001.

The switch from predominately guarded to unguarded pups took place on 10 December in both pupping seasons (Figure 4.5). In 1999-2000 most of the female pups were unguarded two days earlier than the male pups, but there was no difference in date in 2000-2001.

4.3.4 Non-Violent Mortality

Non-violent mortality of seal pups from the beginning of the pupping season in November until 15 or 16 March (Julian day 75) of the following year was 22% in 1997-1998, 61% in 1999-2000 and 18% in 2000-2001 (Figure 4.6) of all pups born.

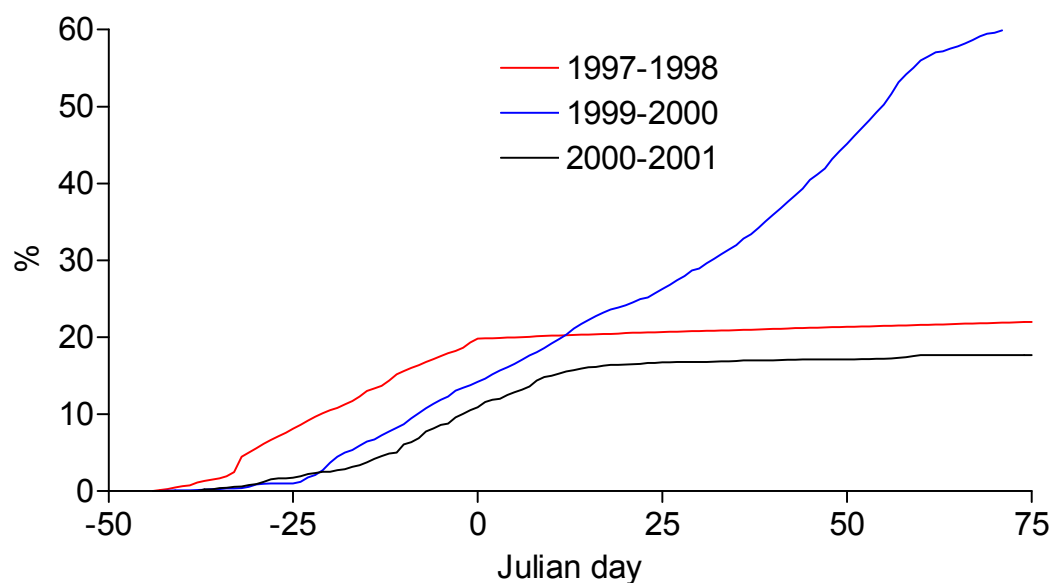


Figure 4.6: Cumulative non-violent mortality rate for three pupping seasons from the beginning of the seal pupping season in November until March of the following year (note: 1997-1998 curve appears flat, although slightly increasing, due to the scaling of the y-axis).

The difference in daily non-violent mortality rates between all years was highly significant (Arcsine square root transformed data: Kruskal Wallis Test $H = 114.2$, $p < 0.0001$). Daily non-violent mortality was significantly higher in 1999-2000 than in the other two years (Dunn's Multiple Comparison Test: 1997-1998 vs 1999-2000 $p < 0.001$; 1999-2000 vs 2000-2001 $p < 0.001$).

Counts at the southwest-facing beach at Wolf Bay increased during the peak pupping season compared to the time before and after the peak in both years (Figure 4.7).

Counts of both years were combined to test for differences between periods as the individual sample sizes were too low, and the counts showed a similar pattern (Figure 4.7). A significantly larger number of carcasses washed up on the beach from the beginning of the peak pupping season from 2 December until the 31 January than before that time (Kruskal Wallis Test $H = 14.10$, $p =$



0.0009; Dunn's Multiple Comparison Test: before vs during $p < 0.001$ – no comparison for “after” due to small sample size) (Figure 4.8).

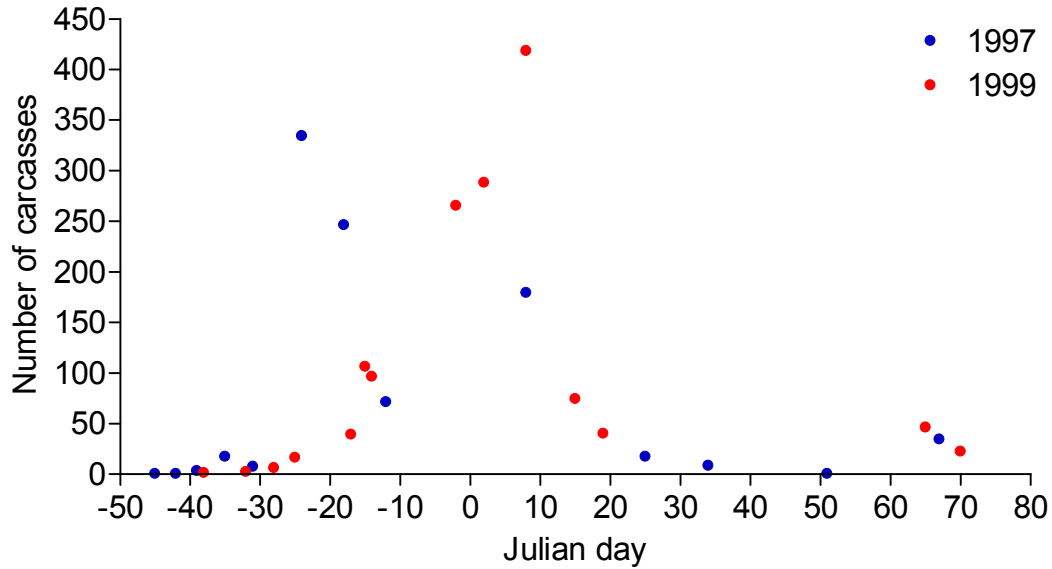


Figure 4.7: Number of washed up seal pup carcasses at the Wolf bay beach.

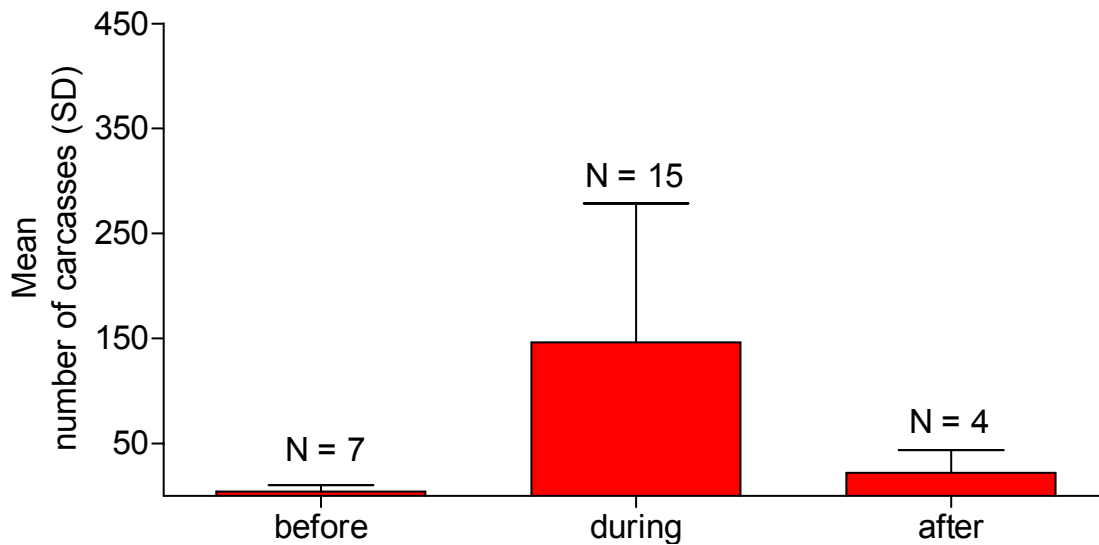


Figure 4.8: Mean number of seal pup carcasses per day washed up at Wolf Bay beach before the peak pupping season, during the time of highest non-violent mortality risk, and after the highest mortality risk.

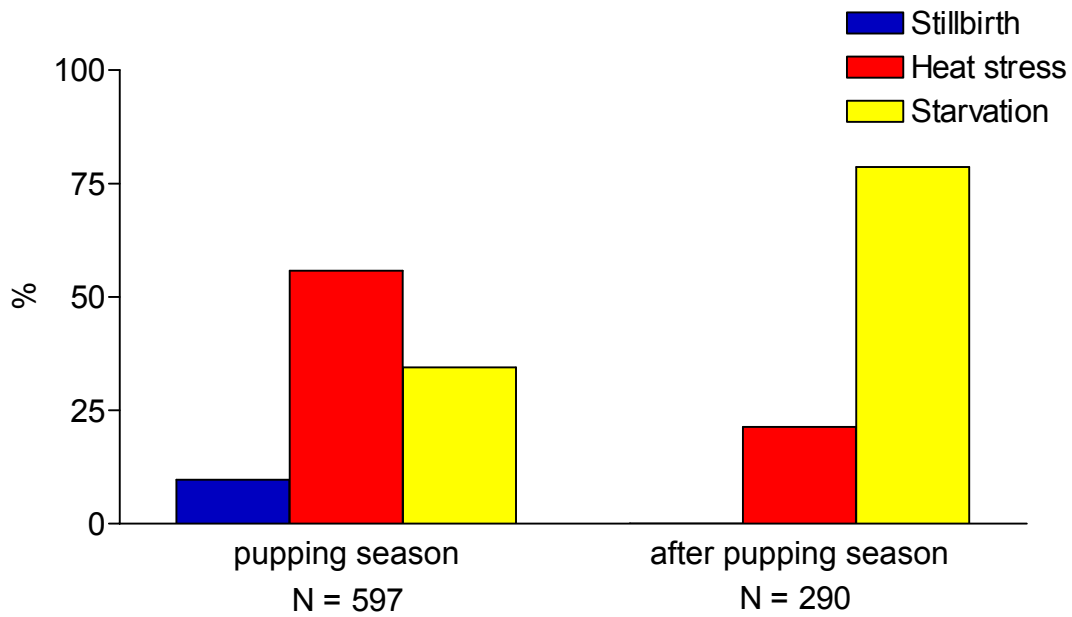


Figure 4.9: Causes of death (stillbirth, heat stress and starvation) of seal pups during and after the pupping season.

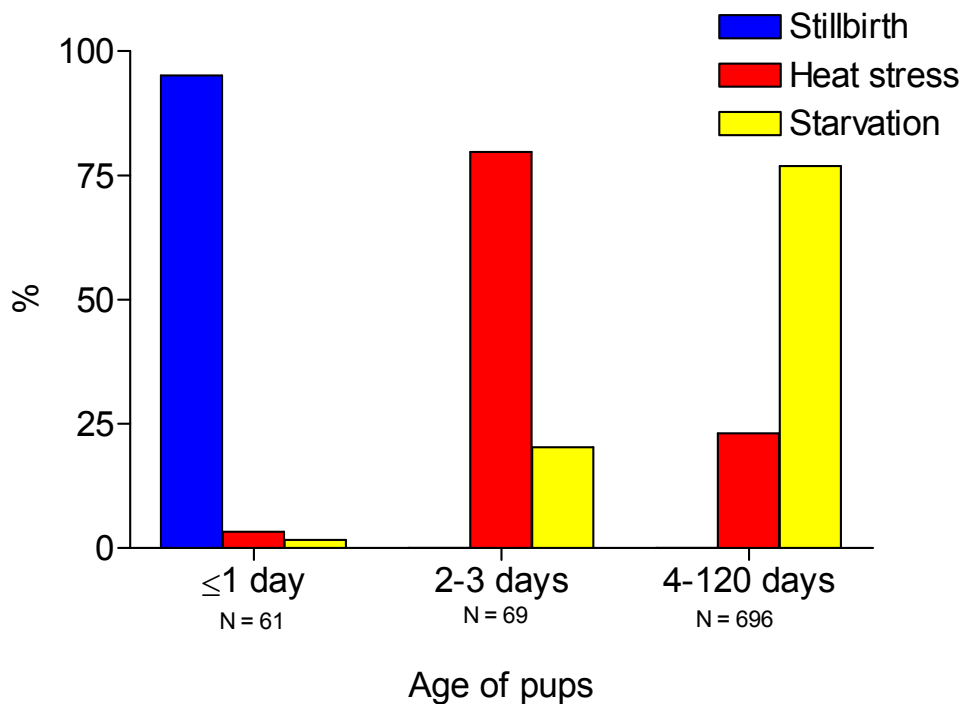


Figure 4.10: Age related causes of death of seal pups.

Three mortality factors could be determined: stillbirth, heat stress and starvation. The causes of death of seal pups during the pupping season (November until 7 January the following year) and after the pupping season differed (Chi² Test $\chi^2 = 157.7$, df = 2, p < 0.0001). The main cause of death during

the pupping season was heat stress, whereas the main mortality factor after the pupping season was starvation (Figure 4.9).

Furthermore, the cause of death was significantly age dependent (χ^2 Test $\chi^2 = 888.8$, $df = 4$, $p < 0.0001$). Initially most dead pups were stillborn, but less than four-day-old pups died predominantly of heat stress and older pups of starvation (Fig. 4.10).

The sex ratio of non-violent mortalities was biased towards males during the 1997-1998 study period (Table 4.2). However, significantly more male pups died of non-violent causes during the pupping season in 1997-1998 and 1999-2000, but the difference in sex ratio after the pupping season was not significantly different from 1:1. The sex ratio in 2000-2001 did not show any significant difference between sexes. The pooled data set of all study periods showed a highly significant bias towards male pups only during the pupping season but not after the pupping season.

Table 4.2: Number of dead pups of each sex during the study periods.

Pupping season	Period	Number of dead males	Number of dead females	% males	χ^2	p
1997/1998	<i>Nov - March</i>	173	122	58.64	8.82	0.003
	<i>pupping season</i>	164	108	60.29	11.53	0.001
	<i>after pupping season</i>	9	14	39.13	1.09	0.297
1999/2000	<i>Nov - March</i>	383	347	52.47	1.78	0.183
	<i>pupping season</i>	211	165	56.27	5.89	0.015
	<i>after pupping season</i>	172	182	48.59	0.28	0.595
2000/2001	<i>Nov - March</i>	234	204	53.42	2.05	0.152
	<i>pupping season</i>	184	165	52.72	1.03	0.309
	<i>after pupping season</i>	50	39	56.18	1.36	0.244
all seasons	<i>Nov - March</i>	790	673	54.00	9.36	0.002
	<i>pupping season</i>	559	438	56.07	14.68	0.0001
	<i>after pupping season</i>	231	235	49.57	0.03	0.853

The changes in mass of dead pups differed significantly from the growth curves of live pups (Figure 4.11). During the 1997-1998 study period the graph slope and therefore growth of live pups was significantly steeper ($F_{1,296} = 7.01$, $p = 0.009$). In 1999-2000 the graph slopes did not differ ($F_{1,694} = 1.48$, $p = 0.22$) but the elevation of the regression line of dead pups was significantly lower ($F_{1,695} =$

40.6, $p < 0.0001$). In 2000-2001 the graph slope of non-violent mortalities was again significantly less steep than that of live pups ($F_{1,377} = 17.9$, $p < 0.0001$).

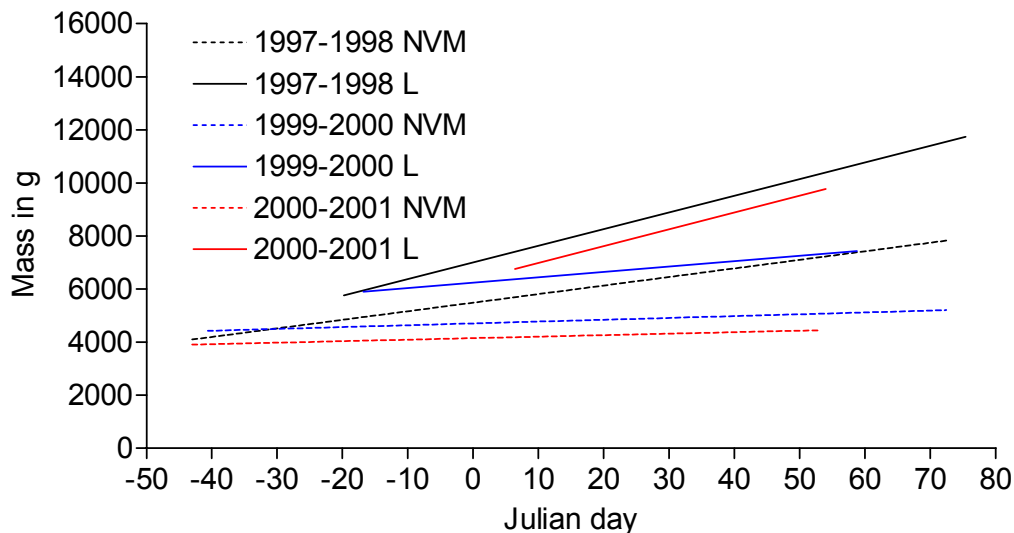


Figure 4.11: Change of mass of non-violent mortalities (NVM) and growth curves of live (L) seal pups during different seasons.

The differences in the changes of mass of non-violent mortalities between years were also significantly different (Figure 4.11). The slopes between 1997-1998 and the other two years were significantly different, but the difference between 1999-2000 and 2000-2001 was only significant for the elevations (1997-1998 vs 1999-2000: $F_{1,964} = 53.6$, $p < 0.0001$; 1997-1998 vs 2000-2001: $F_{1,651} = 34.9$, $p < 0.0001$; 1999-2000 vs 2000-2001: slopes $F_{1,1047} = 0.12$, $p = 0.73$, elevations $F_{1,1048} = 67.0$, $p < 0.0001$).

The mass of male non-violent mortalities in 1997-1998 was significantly different to the mass of female mortalities. Males were less heavy at the beginning of the pupping season, but heavier later in the season and the slopes of the linear regression equations were significantly different ($F_{1,282} = 9.42$, $p = 0.002$). The slopes of the regression lines in 1999-2000 and 2000-2001 were parallel and males were heavier than females (1999-2000: slopes $F_{1,677} = 0.01$, $p = 0.91$, elevations $F_{1,678} = 119.8$, $p < 0.0001$; 2000-2001: slopes $F_{1,365} = 3.21$, $p = 0.07$, elevations $F_{1,366} = 81.8$, $p < 0.0001$). The summary of these results is compiled in Table 4.3.

Chapter 4

Table 4.3: Comparison of the linear regression lines of the growth curves of live pups and the change of mass of dead pups of both sexes (ns = no significant difference).

Compared to	Period	Parameter	Mass of dead pups
Mass of live pups	1997-1998	growth	slower
		mass at birth	ns
	1999-2000	growth	ns
		mass at birth	lower
	2000-2001	growth	slower
		mass at birth	ns
Mass of dead pups during different years	1997-1998 vs 1999-2000	growth	steeper
		mass at birth	ns
	1997-1998 vs 2000-2001	growth	steeper
		mass at birth	ns
	1999-2000 vs 2000-2001	growth	same
		mass at birth	lower
Compared to	Period	Parameter	Mass of dead males
Mass of dead females	1997-1998	growth	different
		mass	lighter to heavier
	1999-2000	growth	same
		mass	heavier
	2000-2001	growth	same
		mass	heavier

4.3.5 Anti-Predator Behaviour of Seals

The data set included 2 550 observations of changes in brown hyena behaviour and the subsequent seal reactions. Adult seals did not show any reaction towards the presence of brown hyenas in their immediate area in 89% of the cases. Seals ran towards the sea, moved and attacked or threatened the hyena in 5%, 5% and 1% of the cases respectively. Seals reacted significantly more often when hyenas approached them or hunted, as opposed to when hyenas walked between, alongside or away from them (Chi² Test $\chi^2 = 123.2$, df = 1, p < 0.0001).

Seals only attacked or threatened brown hyenas when the hyena was approaching them or was hunting (Table 4.4). Four bulls, four adult females without pups and six females with pups were observed attacking hyenas. The hyena retreated in four, two and four of the cases respectively.

Seal attacks or threatening behaviour was the most successful anti-predator strategy and led to the retreat of the hyena in 74% of the cases (Table 4.5).

Table 4.4: Percentage of seal reaction towards brown hyena behaviour

seal behaviour	hyena behaviour		
	walking	leaving	approaching & hunting
no reaction	97	95	85
running towards sea	2	2	7
moving	1	3	7
attack or threat	0	0	1

Table 4.5: Percentage in change in brown hyena behaviour following different reactions of seals

Preceding seal behaviour	Change in hyena behaviour				
	walking: change of direction	approaching	hunting	fleeing/walking away	no reaction
seals run towards sea	31.5	45.7	6.3	10.2	6.3
seals move	37.4	34.2	5.7	15.4	7.3
seals attack or threaten	0	10.5	10.5	73.7	5.3

Brown hyenas reacted significantly differently to attacking or threatening seals than to seals that retreated by moving or running towards the sea (Chi² Test $\chi^2 = 63.77$, $df = 5$, $p < 0.0001$).

Nevertheless, when the hyena was approaching or hunting seals it reacted significantly less to a change in seal behaviour than when it was walking between seals, alongside the colony or away from the seals (Chi² Test $\chi^2 = 161.3$, $df = 3$, $p < 0.0001$).

4.4 Discussion

4.4.1 Prey Availability

Brown hyenas along the southern coastal Namib Desert predominantly feed on seal pups (Siegfried 1984, Stuart & Shaughnessy 1984). Their availability changes between years or within one season due to changes in seal attendance patterns, and is also different between colonies.

Seal numbers at the Wolf Bay seal colony had gradually been increasing in the 1970s whereas numbers at Van Reenen Bay showed hardly any change (Shaughnessy 1987). Numbers slightly increased until a drastic drop in pup production at the Wolf Bay seal colony between the 1993 and 1994 cohort



caused by an anomalous warm water event in late 1993 that had an impact on the migrating pattern and spawning success of fish as well as on their mortality (Roux 1998). Consequently seal pup survival was low and starved adult seals washed up along the entire Namibian coastline, which reduced the Namibian seal population by approximately one third to one half. Similar impacts of environmental anomalies, such as El Niño events, have also been known to influence other seal species populations (Francis & Heath 1991). Nevertheless, successive years showed hardly any increase in pup production until the cohort in 1997 had a similar strength to the one in 1992.

This study only commenced in 1997, but prior to that year's pupping season in September, one emaciated adult brown hyena of age class III (4 to 6 years) was found dying close to the Wolf Bay seal colony. It is unclear whether the cause of death was starvation, but it might be an indication that brown hyenas heavily rely on a certain abundance of seals for their survival.

As the Wolf Bay and Van Reenen Bay seal colonies historically have not shown the same rate of increase, the decreasing trend in pup production during the course of this study, especially at the Wolf Bay seal colony, was investigated. The results show that the variation in pup numbers is possibly the result of environmental fluctuations and not the result of extensive harvesting at the Wolf Bay seal colony, because the rate of decline of both seal colonies was positively correlated.

The sex ratio of Cape fur seal pups at birth did not show any significant differences from 1:1, possibly due to the low sample size. Studies of other seal species describe a male-biased sex ratio at birth, which stays stable between years (Ono & Boness 1991, Bradshaw et al. 2003) but becomes less significant in years with strong environmental fluctuations (Francis & Heath 1991, Bradshaw et al. 2003). The sex ratio of Cape fur seal pups is described as male-biased (Rand 1956) although foetus sex ratios of only 49.7% males were found (Oosthuizen 1991). Nevertheless the sex ratio at six weeks of age shows a bias towards males (Shaughnessy 1982, Oosthuizen 1991), which conforms with patterns shown in this study, where the overall sex ratio from cross samples done between January and March each year was in favour of males.



The mean date of birth between male and female pups was a maximum of one day apart. It is therefore unclear whether there was a difference in availability of sex classes for brown hyenas during the pupping season, although more male pups seem to be available later in the season. Nevertheless it has to be noted that cross samples were done during the day and the sex- and age-related mobility and behaviour of pups could have an influence on capture success during the sample. Kirkman et al. (2002a) found that female pups are less likely to be seen during re-sight sessions of tagged pups or caught during cross samples. For these reasons, the true availability of sex classes during different times of the study period is unclear.

As mentioned above, seal pups form the major proportion of the brown hyena's diet (Wiesel 1998). Adult female seals weigh on average 57.4 kg and the mean weight of adult bulls is 247 kg (David 1987). Both sexes of adult seals are therefore heavier than brown hyenas, which weigh on average 37 to 40 kg (Chapter 3) and due to this unfavourable size relationship seal pups and possibly yearlings fit best into the food spectrum of these solitary foraging predators. Not only the general availability of seal pups in total numbers is of importance but also the degree of protection against predation that they receive from their conspecifics. Many factors influencing protection can play a role such as habitat structure, density of seals and the location within the colony. The Wolf Bay seal colony is large and reaches up to 150 metres inland. Pups might be better protected when they are born close to the sea or in the centre of the colony where they are surrounded by adult seals than when they are born at the border of the colony. It has already been hypothesized that one strategy of female gregariousness (for other strategies: see below) in fur seals, termed the "ecological marginal male effect" (Trillmich 1987) reduces intraspecific mortality through a decrease in the intensity and frequency of between sex interactions, which reduces the danger of attacks on pups by subadult males through their exclusion by territorial bulls. These factors require further investigation but the factor of female attendance and protection of the pup was investigated during the course of this study. Adult females shortly before and after parturition become highly territorial by claiming space within the bulls' territory. They do not tolerate other seals in the immediate vicinity (Rand 1967). After parturition the female seal



protects her offspring for about five days before leaving for the first feeding trip to sea, which coincides with her coming into oestrus and mating with the bull (Rand 1967, David & Rand 1986). Before that time they fight vigorously over their pup and will carry it away from danger. Other pups are also not tolerated. Nevertheless some females appear indifferent to the whereabouts of their pup when they return from sea and the mother-pup bond is usually strongly maintained by the pup rather than the mother (Rand 1967). Pups seldom leave their birthplace as they depend on meeting and finding their mother there. Nevertheless they often congregate in “pup pods” to escape danger, to find security while they are sleeping and for companionship.

The pupping season of the Cape fur seal starts in the middle of November and the majority of pups are born by 17 to 22 December (Butterworth et al. 1987). The crucial time for predators is the switch from the majority of pups being strongly guarded by their mothers to the time when most of the pups are increasingly unguarded. This switch took place at the Wolf Bay seal colony on 10 December in both pupping seasons without differences in sex in 2000-2001 but with female pups being unguarded two days earlier than male pups in 1999-2000. This switch coincides with the mean birth date of pups, which was between 9 and 12 December at the Wolf Bay seal colony. 50% of the pups were available and the majority were unguarded from that time on and therefore food availability in the form of defenceless pups for predators was high. Although females usually return after a few days from their first feeding trip to sea (Rand 1956, David & Rand 1986), the duration of shore visits are shorter than the duration of feeding trips and attendance onshore decreases in the progressing pupping and nursing season (Carnio 1982, David & Rand 1986). Females generally forage until their fat reserves are replenished (Trillmich 1987).

Other factors influencing the foraging behaviour of predators could be the daily and monthly fluctuation in seal abundance at the seal colony. In general most females arrive at the seal colony in November with a peak in the first week of December and a decline in numbers from then on (David & Rand 1986).

In addition the moon phase also seems to have an influence on the general attendance pattern of seals as a larger number of seals seem to forage at sea during new moon phases when it is darker. Seals usually dive at night or

around dusk and dawn, when their prey is closer to the surface and less energy is used during shallow dives (Kooyman & Gentry 1986). During full moon phases dives have to be deeper than during new moon phases and the energy balance could be unfavourable. This influence could confirm the subjective observations at the Wolf Bay seal colony that apparently showed more females onshore during full moon phases (compare with Trillmich & Mohren 1981).

Furthermore the daily attendance pattern of females differs between seasons and can influence the daytime foraging activity or even the overall foraging activity of predators. In summer, attendance is high in the cool morning hours and late in the afternoon, but in winter the flow of females to the sea is more variable and a minimum number of female seals is recorded in the early evening (David & Rand 1986). Similar attendance patterns have been recorded for other seal species. Nevertheless unfavourable environmental conditions influence the normal attendance pattern significantly (Francis & Heath 1991, Heath et al. 1991, Ono & Boness 1991) and annual fluctuations can occur. Weather conditions also play a role as seals often remain on land during gales or heavy swells (Rand 1967).

The attendance pattern of adult seals, in particular females, can therefore have a large impact on predators' foraging behaviour and daily activity pattern and further investigation of these matters is required.

The activity of the pup is largely dependent on the mother's presence at the seal colony. During the female's shore visit, the pup will spend most of its time suckling, to maximise energy intake. During the mother's absence, pups can afford to engage in other activities, but these are largely dependent on their age.

Pups of different seal species are poor swimmers at birth (Ono & Boness 1991) and some Cape fur seal pups only learn how to swim at six weeks of age (Rand 1967). In other words young lactating pups seldom leave their birth place and hardly show any signs of activity (Rand 1956). This helps to conserve valuable energy during the time when their mothers are at sea (Ono & Boness 1991).

Weaning is a gradual process and often only ends at the time the next pup is born (1 year later). Nursing pups start exploring edible matter from March onwards when they have their permanent dentition (approximately four months



old) even though weaning has not taken place. Nevertheless the switchover from milk to solid food is visible by a decline in weight increase from about nine months of age onwards (David & Rand 1986) and by the occurrence of pups often staying away for several days to forage (Rand 1967).

The increase in the Cape fur seal pups' activity and mobility becomes apparent at the colony from January onwards, when most of the pups have learned how to swim in protected pools and often move towards the sea during their mothers' absences.

In summary pup production at seal colonies, the attendance pattern of female seals and the mobility and activity of seal pups and resulting attendance pattern could influence the foraging behaviour and success of predators and will be further discussed in the following chapters.

4.4.2 Condition of Prey

As mentioned above, for predators especially scavengers and opportunistic foragers, such as the brown hyena, it is important to know about the mortality of their prey species (Mills 1990). Knowledge about mortality of different age and sex classes and their mortality factors is essential to evaluate the value of certain prey items. Furthermore predators are likely to choose the easiest and safest way of obtaining food and a sufficient amount of carrion or other predator's kill remains is likely to inhibit extensive hunting in predominately scavenging species (Estes 1967). For this review and assessment, brown hyenas are regarded as scavengers and mortality factors are discussed with regard to this aspect. The question of differences in the value of different prey categories will be discussed in a later chapter. For simplification, the mass of the seal pup is considered to reflect its value to a consumer.

Male Cape fur seal pups were significantly heavier at birth and throughout the study period, which conforms to studies of other fur seal species (Boltnev et al. 1998). Nevertheless the proportional increase in mass over time was the same for males and for females in all years in this study. These results differ from other studies on Cape fur seals and other fur seal species where the changes in mass were greater in males (Rand 1956, Kerley 1985, Bradshaw et al. 2003). Similar or lower growth rates for males and females are only described for resource-poor



years (Francis & Heath 1991, Iverson et al. 1991, Bradshaw et al. 2003). Nevertheless this study's observation periods were short and only reflected the linear initial growth of pups and growth up to the time of weaning is therefore unknown. Increased growth of male pups might therefore only be visible later in the season. The study period in 1999-2000 reflected a resource poor year. Adult females were in a visibly poor condition, the growth curve of pups was significantly lower than during the other two study periods, and non-violent mortality was higher (see below). Apart from this, male and female pups showed the same proportional increase in mass over time in contrast to the findings of other studies. The value (expressed as mass) to predators of male pups compared to female pups is therefore constant and not increasingly higher.

Mortality estimates for pups of different seal species and within species vary greatly from 1% to 4% in harp seals (*Pagophilus groenlandicus*) (Kovacs et al. 1985), 5% to 20% in Northern fur seals (*Callorhinus ursinus*) (York 1991), 12% to 26% in harbor seals (*Phoca vitulina*) (Steiger et al. 1989), 16% to 29% in Antarctic fur seals (*Arctocephalus gazella*) (Boveng et al. 1998) and 20% to 35% in Cape fur seals (David 1987, De Villiers & Roux 1992). This study's non-violent mortality estimates are 22% for 1997-1998, 61% for 1999-2000 and 18% for 2000-2001. The first estimate is similar to the ones found for Cape fur seals by David (1987) and De Villiers & Roux (1992). The estimate for the year 2000-2001 is conservative, as the decrease in pup production over years resulted in empty sample areas and additional sample areas were only included in the data collection later in the pupping season. Nevertheless, the daily mortality rates and overall mortality estimate for the year 1999-2000 were significantly higher than the estimates of the other two years and did not decline towards the end of the study period. Mortality is usually highest shortly after birth and up to 50 days after the peak in pupping (David 1987, De Villiers & Roux 1992).

In general mortality can be density dependent (Trillmich 1987), which seems unlikely in this case as pup production was lower in 1999-2000 than in 1997-1998. Density dependent mortality was also not regarded as a plausible cause of non-violent mortality by Francis & Heath (1991) for California sea lion pups (*Zalophus californianus*) during an El Niño year, as attendance decreased. Unfavourable environmental conditions resulting in the lack of food for adult

female seals can also cause large scale mortality later in the season (Roux 1998) and is regarded to have caused the high non-violent mortality rates in 1999-2000.

One of the most common causes of non-violent mortality is starvation (Kovacs et al. 1985, McCann 1987, Heath et al. 1991, Boltnev et al. 1998, Boveng et al. 1998), although Cape fur seal pups are known to be able to survive without milk for a period of 2 weeks (Rand 1956). This is similar to California sea lions where pups can survive without milk for up to nine days (Heath et al. 1991). Nevertheless in periods of extreme food shortage, New Zealand fur seals (*Arctocephalus forsteri*) have been found to abandon their pups (Bradshaw et al. 2003) and adult California sea lions showed greater foraging effort by spending prolonged periods of time at sea during El Niño years (Heath et al. 1991). A delay in the replenishment of the female seals' fat reserves can therefore lead to the starvation of the pup on land.

The two representative study periods in 1997-1998 and 2000-2001 showed increasing pup mortality during the first months of the pups' life, as described by De Villiers & Roux (1992) and carcass counts at the Wolf Bay beach also confirm this pattern. Most carcasses were washed up in December and January, which coincides with the peak pupping period until approximately 30 to 50 days later.

Other causes of non-violent mortality are premature birth or stillbirth (Steiger et al. 1989), failure of establishment of mother-pup bond (McCann 1987), diseases (Steiger et al. 1989), exposure to tides and surf and subsequent drowning especially during the period when pups are poor swimmers (Rand 1967, Shaughnessy 1982, Shaughnessy 1984, Heath et al. 1991) and heat stress (Rand 1967, Francis & Heath 1991, De Villiers & Roux 1992). Large daily fluctuations in non-violent mortality are therefore possible due to environmental factors such as heat and swell. Carcass counts on the south-west facing beach at Wolf Bay showed a high number of washed up seals after storms and extremely high swells and the majority of pups during the pupping season in fact died of heat stress, although it has to be mentioned that the number of pups from the sample areas that drowned at sea could not be determined and this factor might therefore be underestimated. Nevertheless, the only way of avoiding heat stress for young and immobile pups is to lie motionless and to increase thermoregulation

through outstretching their fore flippers. Adult seals and older pups can escape heat stress by escaping into the sea and by finding shelter under rocks (Rand 1967).

After the peak of the pupping season the main mortality factor was starvation. Heat stress occurred less often as older pups are more mobile and have learned how to swim (Rand 1967).

In summary, a large amount of seal carcasses is available for predators particularly during the time of highest seal pup mortality. Due to environmental factors not only starved pups of possibly less value, but also dead pups in a good condition are occasionally available, but in greater numbers during the peak of the pupping season.

The sex ratio of non-violent mortalities was biased towards males during the peak of the pupping season in 1997-1998 and 1999-2000, which is in contrast to the findings of Oosthuizen (1991) and De Villiers & Roux (1992), who found higher initial female pup mortality. Nevertheless there was no significant difference in sex-related mortality after the peak of the pupping season, but a trend towards higher female pup mortality was apparent for two of the three study periods. However in other fur seal species such as the Northern fur seal no differences in mortalities of different sexes are found (Boltnev et al. 1998). The lack of a significant sex related difference in mortalities after the peak of the pupping season and the trend towards a sex ratio in favour of males of live pups during that time indicates that female pup mortality in relative numbers to their overall availability might be higher than male pup mortality, but a larger sample size is necessary to detect such a pattern.

Therefore carcass availability regarding sex classes was equal in absolute numbers, but the value of carcasses of different sex classes might differ regarding their mass and is discussed in the following section.

Live male Cape fur seal pups are heavier than live female pups. Pups that died of non-violent causes were significantly lighter than live pups during all study periods. Nevertheless there were differences between years. Mass at birth was not significantly related to mortality in 1997-1998 and 2000-2001, but during the year of unfavourable environmental conditions in 1999-2000 mass at birth of live and non-violent mortalities differed. Lower mass at birth increased the mortality



risk. However, the growth rates of live pups and the change of mass of dead pups were the same, indicating that pups were generally in a poor condition. This also resulted in the constant mortality rate until the end of the study period. Boltnev et al. (1998) and Kirkman et al. (2002b) found that pup survival increased with birth weight and this relationship could explain our findings for the resource poor study period.

The difference in mass between male and female mortalities was significantly different during all study periods. Male mortalities were generally heavier than females. Nevertheless, there were differences in the growth pattern between years. In 1997-1998 male mortalities at the beginning of the pupping season were lighter than females, but their change of mass increased to heavier weights from January onwards. During the 1999-2000 and 2000-2001 study period male mortality weights were significantly lower than in 1997-1998 during the entire time, which indicates again that mass at birth could be a mortality-determining factor in resource-poor years and the after effects could influence pup mortality in successive years, as it has been shown in California sea lion populations after El Niño events, where a decrease in copulation rate, decrease in fecundity and an increase in abortions during that time influenced adult seal attendance and pup production in following years (Francis & Heath 1991).

4.4.3 Anti-Predator Strategies of Cape Fur Seals

Many species form aggregations for the benefit of reproduction and survival (Begon et al. 1996). Social relationships are not essential for the formation of these aggregations and therefore are usually missing and animals often only engage in aggressive behaviours (Franck 1985). The selective advantage of the principle of such a “selfish herd” (Hamilton 1971) seems to favour the survival of individuals within an aggregation as the predation or mortality risk per individual decreases by reducing its “Domain of Danger” through moving towards multiple neighbours (Morton et al. 1994) independent of a predator attack occurring from the outside or from within the group (Viscido et al. 2001). For prey animals their perception of being at risk of attack by a predator is the basis on which anti-predator strategies are implemented (Hill & Dunbar 1997). This perception depends on the prey’s ability to detect a predator and to escape from an attack



(Roberts 1996). The actual predation rate is the level of successful predator attacks that the prey is unable to control after implementation of anti-predator strategies (Hill & Dunbar 1997) and depends on prey encounter rate, attack probability and hunting success of the predator (Janson 1998). In order to keep the predation rate low, prey animals seek to reduce their predation risk. The formation of groups is one such strategy and can lead to a “confusion effect” for the predator, as it becomes more difficult for the predator to capture prey that is surrounded by conspecifics as cognitive constraints can cause a lack of concentration and hence reduce killing efficiency (Krakauer 1995, Schradin 2000). The per capita attack rate and kill/attack ratio is reduced (Landeau & Terborgh 1986) and hence the predation rate decreases. A second advantage of group living is an increase in predator detection through shared vigilance (Roberts 1996). Nevertheless anti-predator strategies involve costs and although the prey species should seek to interrupt predation sequences as early as possible (Endler 1991), the population can sustain higher levels of predation depending on habitat characteristics and reproductive rate, if the reproductive rate can compensate for losses, especially if only immature animals are lost (Hill & Dunbar 1997).

Breeding activity often increases the predation risk for animals (Quinn & Kinnison 1999), especially for across-habitat species with poorly developed anti-predator strategies towards uncommon carnivores, as in the case of many seabirds and marine mammals (Kruuk 1964, Burger & Gochfeld 1994). The most common anti-predator strategies for these species are choosing inaccessible breeding habitat for colony establishment, for example on remote islands, or the avoidance of grouping to reduce detection (David 1987, Hammill & Smith 1991).

Fur seals, for instance, form large colonies due to the lack of adequate breeding sites. Furthermore, being on land always involves high costs for fur seals, as they cannot spend time foraging at sea. Hence, the fur seals’ strategy to breed effectively is to maximise their density in time and space by forming large aggregations (Roux 1986).

The predator-prey relationship between Cape fur seal and brown hyena is a recent one judged in historical terms (Chapter 2). The only exception in southern Africa is the Cape Cross seal colony approximately 600 km to the north



of the Wolf Bay seal colony, which was probably established between 1848 and 1884 (Best & Shaughnessy 1979). Establishment on the mainland was made possible due to the absence of space restrictions, the absence of human disturbance and the past elimination of large carnivores (David 1987), although brown hyenas were reported to occur around Cape Cross (Best & Shaughnessy 1979) and other parts of the Namibian coast (Gaerdes 1977).

The majority of seal species only experiences predation from marine predators, which can cause high mortality rates. Up to 38% of Antarctic fur seal pups are preyed on by leopard seals (*Hydrurga leptonyx*) (Boveng et al. 1998), 8% of South American fur seals (*Arctocephalus australis*) are taken by Southern sea lions (*Otaria byronia*) (Harcourt 1992 cited in Boveng et al. 1998) and 25% of elephant seals (*Mirounga leonina*) are killed by killer whales (Guinet & Jouventin 1990 cited in Boveng et al. 1998). Cape fur seals are also known to be killed by killer whales and sharks, but the extent is unknown (Rand 1956). Terrestrial predation is less common, but the predator-prey relationship between ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) is well studied (Hammill & Smith 1991, Stirling & Øritsland 1995) and mortality estimates lie around 21%. The anti-predator strategy that possibly evolved as a response to polar bear predation is the use of subnivean lairs to reduce pup mortality (Smith 1976). Other Arctic pinnipeds are larger in body size than ringed seals, which might already serve as a protection against predation (Hammill & Smith 1991). Arctic foxes (*Alopex lagopus*) are also known to prey on ringed seal pups (Hammill & Smith 1991) and coyotes (*Canis latrans*) occasionally prey on harbour seal pups (Steiger et al. 1989). The extent of terrestrial predation on Cape fur seal pups is largely unknown (Rand 1967), but was not expected to have a large impact (De Villiers & Roux 1992). Predation by brown hyenas was first investigated by Wiesel (1998), but the reaction of seals to terrestrial predators is unknown and despite the lack of social cohesion between seals, pups do not seem to be exposed to large scale predation (Rand 1967). However, large terrestrial carnivores are a novelty to Cape fur seals and specific anti-predator strategies are therefore likely to be poorly developed.

In this study, seals did not react to the presence of a brown hyena 89% of the time. Attack and threatening behaviour towards the hyena only occurred in

1% of the cases and otherwise seals usually ran towards the sea or moved and were alert. Nevertheless the behaviour of the brown hyena played an important role in the seals showing these possible anti-predator behaviours. The approach and hunting of hyenas triggered significantly more reaction in the seals than simply moving in or alongside the colony. Attack and threatening behaviour was only shown when the hyena approached the seals or actively hunted.

In the majority of the cases brown hyenas reacted to the seals' change in behaviour. From the slightest movement of seals, to running towards the sea resulted in the approach and hunting of the hyena in 40% and 52% of the cases respectively. These possible anti-predator strategies therefore seem to be unfavourable for the seals. The only positive and successful anti-predator strategy seems to be the attack and threat, as the hyena walked away from the seals in 74% of these cases. Although the data set is small, it showed that bull attacks and threats were always successful and that 67% of attacks of females with pups and 50% of females without pups were successful. The anti-predator behaviour of female seals with pups might therefore be more intense than of pup-less females. Nevertheless, approaching and hunting hyenas showed significantly less reaction to anti-predator behaviours than walking ones.

These possible anti-predator strategies did not seem to be special adaptations to avoid brown hyena predation. Seals reacted in similar ways to the presence of jackals and humans. Cape fur seals are easily disturbed by movements or wind-born odours, which often cause a stampede (Rand 1967). Bulls are highly territorial and defend their territory boundaries irrespective of intruding bulls, humans and possibly other species (Roux, pers. comm.). Females vigorously defend their pups against conspecifics, especially shortly after giving birth (see above), but show similar behaviour towards human intruders (pers. observ.). Stampedes are a regular occurrence, but the strong gregariousness on land and the mother-pup bond, also on a spatial basis, lead to the quick re-organisation of the herd (Rand 1967).

In summary, anti-predator strategies towards terrestrial carnivores do not seem to be well developed, but under some circumstances these strategies are successful. Nevertheless, anti-predator behaviours usually carry fitness costs (Janson 1998). Endler (1991) describes the predation sequence that the prey

should try to interrupt as soon as possible as follows: detection followed by identification of prey, the approach, subjugation and consumption. The predation risk and energy used for defences increase with every stage.

Possible anti-predator strategies for Cape fur seals include: (1) choice of breeding habitat, (2) general behaviour on land, (3) flight or fight and (4) past experience. The most successful way for Cape fur seals to avoid encounter with terrestrial carnivores is to choose inaccessible breeding habitat. Originally Cape fur seals exclusively bred on off-shore islands and the same strategy is sought by many colony breeding sea birds (Burger & Gochfeld 1994). Nevertheless Cape fur seals started to breed on the mainland and hence have to face novel predators which might encounter them. As they are a gregarious species the second stage of the predation sequence can be interrupted through the confusion effect, so that the per capita attack rate and kill/attack ratio decreases (Landeau & Terborgh 1986). Nevertheless, Cape fur seals are not very vigilant as they mostly sleep while on land. Sleeping animals are relatively unresponsive and unaware of their surroundings and therefore extremely vulnerable to attacks from predators (Lima et al. 2005). However, Cape fur seal aggregations at breeding colonies are large and not all animals sleep simultaneously. Wind-born odours disturb seals more than movements do (Rand 1967), and the disturbance of a single seal can cause a stampede, possibly as individuals of a group tend to conform to their neighbours' activities (compare with Khan & Ghaleb 2003). No information about the flight distance of seals to different kinds of disturbance is available and it therefore cannot be established whether flight distance in seals is correlated with the representation of danger of a certain predator, as seen with many herbivore species in the Serengeti (Schaller 1972). Flight in Cape fur seals makes most sense when all animals can flee, irrespective of age class. Female seals would have to leave their newborn pups behind while running into the sea, which is counterproductive and therefore an unsuccessful anti-predator strategy. Nevertheless the most common strategy of seals to escape danger and therefore interrupt the predation sequence for themselves is the flight behaviour during the approach stage.

Another method at this stage is to fight the predator off. The critical factor for the decision to defend offspring is the size relation between the predator and

the prey. Attacks and fights usually only occur when the prey outweighs the predator three times (Schaller 1972). It is suggested for Arctic pinnipeds that their generally large body size developed as an anti-predator strategy (Hammill & Smith 1991), but in the case of Cape fur seals, adult female seals only outweigh brown hyenas by one and a half times and therefore protecting the pups seems unfavourable. Furthermore, although attack and threat seemed to be the most successful strategy in forcing the hyena to retreat, it was the least common strategy and once the brown hyena reached the approach stage of the predator sequence, it was less disturbed by seal attacks or threats than before.

Lastly the experience of seals with predators most definitely plays an important role in the development of anti-predator strategies. In Weddell seals (*Leptonychotes weddellii*), pups of multiparous mothers show a higher rate of survival (Hastings & Testa 1998). Nevertheless female seals can only learn from experience if they (1) survived an attack as a pup, which is highly unlikely considering the hunting success of brown hyenas (see chapter 6) or (2) observed neighbouring pups being killed, but the impulse for learning might be low due to the lack of social bond between conspecifics and (3) gain knowledge of the cause of death of their seal pup. Non-violent seal pup mortality is high (see above) and many females lose their pups while they are at sea. Unless the female observes her pup being killed by a predator, she would not be able to gain knowledge about the cause of its mortality. No long-term data about the experienced pup mortality of individual female seals over time is available, but it is assumed that the probability of the same female observing the loss of her pup to predation in successive years is small.

Cape fur seals to date, therefore, show a relative lack of anti-predator behaviour, similar to seabirds and other prey species exposed to novel or non-indigenous predators introduced to islands or continents (Burger & Gochfeld 1994, Short et al. 2002) or the non-existing adaptive behaviour of domestic stock in enclosures (Stuart 1986). The effect of the Cape fur seal's existing anti-predator behaviour defined as the reduction of predation through the occurrence of such behaviours (Kruuk 1964) seems to be low.



4.5 Summary

The review and assessment of factors that could influence brown hyena foraging activity and hunting success at mainland Cape fur seal colonies showed a variety of different influences. Prey availability as total pup production shows annual fluctuations, often following larger scale environmental anomalies. The true sex ratio of Cape fur seal pups is not known, but is possibly male biased, but sexes of non-violent mortalities are equally available.

The attendance of the female seals and the increased mobility and activity of pups might influence brown hyena foraging activity during different times of the year. Male pups are in general heavier than female pups and non-violent mortality pups weigh less than live ones. Cape fur seals show poorly developed anti-predator strategies, although some behaviours do influence the foraging behaviour of brown hyenas.

Nevertheless, it is apparent that many dead pups of varying conditions are easily available for scavengers during the seal pupping season and the use of this food source is likely to represent the easiest and safest way of obtaining food.



Chapter 5

The Importance of Coastal Resource Availability and Resource Distribution for Brown Hyena Abundance, Activity, Movement and Energy Budget

5.1 Introduction

Coastal ecotones are influenced by allochthonous food resources and the movement of prey from water to land can be important for local terrestrial carnivore abundance, and can influence their territorial behaviour, feeding behaviour and reproductive success (Polis et al. 1997). The inclusion of marine food resources generally leads to the expansion of the carnivore's diet (e.g., coyotes (*Canis latrans*): Rose & Polis 1998, wolves (*Canis lupus*): Szepanski et al. 1999). This expansion is not only a result of unusual food availability but also occurs when other regular food sources become scarce and predators have to switch to other prey species within their home range (Szepanski et al. 1999).

Many coastal areas show a great abundance of carnivores, such as in the case of coyotes (Rose & Polis 1998), or when the use of marine resources results in higher productivity in a carnivore species, such as in salmon-feeding brown bears (*Ursus arctos*) (Hilderbrand et al. 1999). The amount of marine carrion can be significant, especially around sea bird or marine mammal colonies (Polis & Hurd 1996). Coastal carnivores benefit from these food resources, which are often donor-controlled, as the resource renewal rate is not affected by increased carnivore activity and cannot be overexploited (Polis et al. 1997). Therefore, the local increase in abundance of carnivores whose success is linked to marine subsidies is independent of local terrestrial food abundance and increased carnivore density due to subsidies can depress local food resources (Polis et al. 1997). The influence of marine subsidies and its effects on carnivores and local food resources should be seen in times when marine input fluctuates greatly or decreases to amounts that cannot support a high abundance of carnivores so that individual energy requirements cannot be met. Generally energy requirements of carnivores can be used to infer their impact on prey populations (Laundré & Hernández 2003), not only on local typical prey, but also on marine prey.

Group structure, size of group and territory size are also influenced by allochthonous food subsidies as they are determined by the dispersion and

abundance of resources according to the resource dispersion hypothesis (Macdonald 1983). Such resources are usually food but other crucial resources such as breeding den site availability and location can also determine territory shape and size, as has been shown in badgers (*Meles meles*) (Doncaster & Woodroffe 1993). Macdonald (1983) introduces the term “minimum sized territory”, which is the minimum size that is required to sustain a pair of animals and contains a minimum of the total area of all key habitats. Its size and configuration are determined by the dispersion of transient patches of available food resources and it is expected to be larger when patches are more dispersed. In cases where a territory provides food security for other than the original occupants, groups can form, even if group members do not forage communally or only develop infrequent social ties (Macdonald 1983, Carr & Macdonald 1986). Such group members often rather form “spatial groups”, with greatly overlapping individual home ranges (Macdonald 1983).

Localised marine subsidies, such as mainland Cape fur seal (*Arctocephalus pusillus pusillus*) colonies, therefore, could influence the group size and structure and home range or territory size of terrestrial carnivores such as black-backed jackals (*Canis mesomelas*) and brown hyenas (*Parahyaena brunnea*).

Brown hyenas are well adapted to live in arid regions where herbivore abundance is low (Mills & Mills 1978). They have a catholic diet comprising of predominantly vertebrate remains, especially of mammals, but insects, wild fruits and bird eggs are also consumed. Hunting plays a minor role and most of their food is scavenged (Mills & Mills 1978), often from kills left by other predators (Owens & Owens 1978).

The coastal areas of the Namib Desert distinguish themselves through the juxtaposition of an unproductive land habitat and a productive marine habitat (Polis & Hurd 1996), where the input of marine resources subsidises terrestrial carnivores (Polis et al. 1997, Rose & Polis 1998, Roth 2002). Cape fur seals were found to be the most important food item to brown hyenas, regardless of being determined through scat analysis (Siegfried 1984, Stuart & Shaughnessy 1984, Wiesel 1998) or from bone assemblages at brown hyena dens (Skinner & van Aarde 1991, Skinner et al. 1998). Brown hyenas seem to be closely associated

with the occurrence of mainland seal colonies (Skinner & van Aarde 1981), which results in the expansion of their diet breadth by not exclusively using terrestrial food resources, whose density and diversity in these areas is generally very low (Skinner et al. 1995).

Hence, marine prey can be influenced on a spatial and population basis in the case of the predator-prey relationship between terrestrial carnivores and Cape fur seals (Oosthuizen et al. 1997).

Brown hyenas are territorial (Mills 1982a) and home ranges of individual clan members (Owens & Owens 1978) or between clans (Skinner et al. 1995) can overlap. In the southern Kalahari, the movement patterns of brown hyenas of different clans vary, depending on the habitat composition and the dispersion pattern of food. Mills (1982a) concluded that territory size in brown hyenas is determined by the distribution of food, whereas the clan size is affected by the quality of food, and that animals living in smaller territories usually travel shorter distances between feeding sites. Nevertheless, Skinner et al. (1995) found that coastal brown hyenas maintained home ranges of sizes up to 220 km² despite concentrated food availability along the coast, and that clan size might rather be limited by the dispersion and not the availability of food.

This chapter evaluates the importance of the coastal area for brown hyenas by investigating how the amount of marine food subsidies affects brown hyena abundance, by determining their home range size, specific habitat use and activity in relation to the distribution of food and by relating energy requirements to habitat use, activity and movement patterns. It is predicted that

- (1) brown hyena abundance and density is related to the availability of food,
- (2) home range size is only partly affected by the dispersion of food and that other key resources exist and
- (3) the energy requirements of brown hyenas depend on the availability and distribution of food and hence have an impact on movement and activity pattern.



5.2 Material and Methods

5.2.1 Immobilisation of Hyenas

Brown hyenas were immobilised under veterinary supervision to fit them with visual, VHF or GPS collars. Hyenas were attracted to bait and darted with a Pseudart charge injection rifle (Model 389) from a distance of 20 to 25 metres. The standard darts contained 250 mg of Zoletil (a combination of 125 mg Tiletamine and 125 mg Zolazepam). Zoletil has been proven to be effective with spotted hyenas at a dose of 250 mg (van Jaarsveld 1988). Body measurements, blood, tissue and hair samples were taken while the hyena's respiration and pulse were monitored regularly. Visual, VHF collars or GPS collars were fitted. Hyenas were transferred into a recovery cage and could usually be released two hours after immobilisation.

5.2.2 Assessment of the Importance of the Coast and the Seal Colonies

One male brown hyena in each of two coastal study sites (Van Reenen Bay, Baker's Bay) and one male brown hyena of an adjoining inland study site were fitted with GPS collars. The collars fitted to coastal hyenas had different positioning schedules to maximise the life of the battery (Table 5.1), were equipped with a drop-off mechanism for retrieval of the collar, and also emitted VHF signals for aerial tracking. The collar of the inland hyena was programmed to record a GPS position every 10 minutes.

All recorded GPS positions were used to evaluate the importance of the coast and the seal colonies with regard to brown hyena movement and activity. Adaptive Kernel densities (AK Density) were calculated with the home range extension for ArcView GIS 3.3. The associated volume percentages contain x% of the points that were used to calculate the kernel density estimate.

Furthermore, the intervals between visits to the coast were determined by analysing GPS positions taken from the coastline up to 1 km inland, which provided a conservative estimate of the interval of foraging trips to the coast as a further indicator of its importance as a food source (compare with Goss 1986).

The estimation of brown hyena home range sizes required independence of data. Therefore a random sample of one third of the recorded GPS positions of each hyena was generated with MINITAB 14 to obtain a Schoener's Index close



to 2.0 (Schoener 1981) and a Swihart & Slade Index of < 0.6 (Swihart & Slade 1985). Deviations from the Schoener index indicate a correlation between distance and time, and high values of the Swihart & Slade index indicate autocorrelation. The Adaptive Kernel Volume (AK Volume) and Minimum Convex Polygon (MCP) methods were used to calculate and compare home range sizes.

GPS positions of occasional excursions out of the home range area (not included or separated 95% Kernel volume contours) were regarded as outliers.

Table 5.1: GPS positioning schedule of two GPS collars in different study areas. The filled rectangles indicate that a GPS position was programmed to be taken on that hour of the 24 hour period.

Hyena ID	VRBhb1m	BBhb9m
Hyena alias	Django Van Reenen Bay	Halenge Baker's Bay
Study area	Van Reenen Bay	Baker's Bay
GPS positioning schedule (time of day)	0	■
	1	■
	2	■
	3	■
	4	■
	5	■
	6	■
	7	■
	8	■
	9	■
	10	
	11	
	12	■
	13	
	14	
	15	■
	16	
	17	■
	18	
	19	■
	20	■
	21	■
	22	
	23	■

The coastal brown hyena BBhb9m was fitted with a GPS collar for the duration of 11 months (March to January) and therefore included movement information for the time of superabundance of food during the seal pupping season from November 2004 to January 2005. VRBhb1m was fitted with a GPS



collar from June to October 2005 and data, therefore, did not include the time of the seal pupping season. Animal movement data was plotted in ArcView GIS 3.3 and visually analysed. Three different behaviours were distinguished: (1) walking; when the animal was moving in inland areas of its home range, (2) foraging; when the animal walked in the coastal area (up to 1 km away from the coast) and (3) resting; when the animal was not moving. The daily proportion of these behaviours between different months was compared to obtain information about seasonal changes in brown hyena behaviour.

5.2.3 Brown Hyena Activity Pattern and Field Metabolic Rate

Energy requirements can be expressed as the field metabolic rate (FMR) by including parameters such as the mass of the animal, distance travelled over time and activity periods in the calculation.

The hourly straight distance between successive GPS positions was calculated for each hyena to determine the distance travelled during different times of the 24 hour period (activity pattern). The home ranges of two of the hyenas included coastal areas, whereas the third brown hyena lived in inland areas of the Sperrgebiet and only occasionally visited the coast.

Three calculations were used to determine the FMR of the three hyenas. Depending on the calculation, the following parameters were required: (1) mass of hyena, (2) total distance travelled, (3) total time in hours, (4) number of active hours and (5) number of inactive hours (Table 5.2).

Table 5.2: Daily FMR calculations (M = Mass in kg, t = time in hours, d = distance in km, R = resting, A = active)

Method	Calculation
Laundré & Hernández (2003)	$FMR = 5.8 * M^{0.75} * t + 2.6 * M^{0.60} * d$
Saunders et al. (1993) Kleiber (1961) cited in Stirling & Øritsland (1995) & Nagy (1987)	$FMR = (((0.608 * M^{-0.25} * t_R + 1.7 * (0.608 * M^{-0.25}) * t_A + 0.606 * M^{-0.34} * d) * 20.083) / 4.184) * M$
	$FMR = (70 * M^{0.75}) * 2$

Two of the brown hyenas were weighed after fitting the GPS collars. The mass of the third brown hyena was estimated using (1) the mean mass of all weighed male brown hyenas (N=10) and (2) the mean mass of other male brown hyenas of the same age class (N=2). Although brown hyenas of different age groups are known to differ in mass (Mills 1982b) both mass calculations were



used to determine the third hyena's FMR because of the low sample size of same age class males.

The total distance travelled was the sum of all distances of successive GPS fixes and the total time was the amount of time from the first GPS fix to the last GPS fix taken. The first 24 hours after immobilisation were excluded from the analysis, as the influence of capture and drugging might have affected the animal's movements.

The accuracy of fixes was determined by testing all collars before deployment by leaving them stationary outside for several days to record GPS positions. The error of accuracy of these positions was regarded as the possible error of positions taken when the brown hyena was resting. The maximum error, the mean error and the median error were used to determine the FMR using the method described by Saunders et al. (1993), which required knowledge of activity. All distances and corresponding times in hours that were less than or equal to the calculated maximum, mean or median error were regarded as inactive periods.

5.2.4 Brown Hyena Abundance around Mainland Seal Colonies

Brown hyena abundance was determined in three study areas around mainland seal colonies (Wolf Bay, Van Reenen Bay, Baker's Bay) that differed in size and habitat. The Wolf Bay seal colony is a large colony on rocky ground with rocky hills and slopes of up to 22 metres high reaching into the sea. The other two seal colonies at Van Reenen Bay and Baker's Bay are smaller and situated on sandy beaches with a few rocky areas at the edges of the colony.

Three methods were used to identify brown hyenas:

- (1) artificial ear notches, where triangular shaped notches (maximum of two per ear) were cut into the edges of the ears;
- (2) visual collars made out of machine belting and marked with a numbered plate, and radio collars (Advanced Telemetry Systems) or GPS collars (TVP Positioning) with a unique VHF frequency; and
- (3) photographic identification of natural marks.

To obtain a definite identification of an unmarked animal (method 3), photographs of both ears and forelegs, from the front and side, had to be taken.

In most cases large natural ear notches already provided a clear identification of the individual brown hyena, but as these can change over time, the combination of ear notches and stripe pattern on the forelegs was used. Once the photographic identification was made, identifications of individual brown hyenas could be made visually or from photographs. Similar methods have been used by Pennycuik & Rudnai (1970) for lions (*Panthera leo*) and by Miththapala et al. (1989) for leopards (*Panthera pardus kotiya*).

Population size was estimated using sightings from systematic monitoring of the seal colonies (high effort) and using only incidental sightings (low effort). A modified version of the Peterson estimate (Lincoln Index) was used to calculate $N = ((n_1+1)*(n_2+1)/(m_2+1))-1$ (compare with Minta & Mangel 1989, Arnason et al. 1991). The parameter n_1 was the number of individually identifiable brown hyenas on day 1, m_2 the number of different individuals identified during sightings and n_2 the number of total sightings per total number of identified animals divided by m_2 . The use of individual identification and the Lincoln Index to census brown hyenas has been suggested by Mills (1998). The 95% confidence limits were determined as described in Greenwood (1999).

5.2.5 Brown Hyena Density

The abundance estimates for the two coastal areas and the home range sizes of the corresponding GPS collared brown hyenas were used to determine the density of coastal brown hyenas per 100 km². It was assumed that the abundance of brown hyenas was relatively stable during the time of the study and that home ranges of individual brown hyenas of the same clan were of similar size (compare with Mills 1990).

5.3 Results

5.3.1 Assessment of the Importance of the Coast and the Seal Colonies

Home ranges of individual brown hyenas varied depending on the method used and on the inclusion or exclusion of outliers (Table 5.3). The coastal home range estimates varied from 420 to 980 km² (MCP) and 500 to 1250 km² (AK Volume). The inland hyena had a larger home range than both coastal hyenas.



Chapter 5

The length of coastline that was used by coastal hyenas to forage for food ranged from 16 to 20 km using the MCP perimeter and from 23 to 26 km using the AK Volume perimeter (Table 5.4), representing similar proportions of the total perimeter of each hyena's home range (VRBhb1m: <20%, BBHb9m: >25%, Fisher Exact Test: $p = 0.14$ (MCP); $p = 0.33$ (AK Volume)).

Table 5.3: Home ranges of two coastal brown hyenas and one inland brown hyena. (AK = Adaptive Kernel, MCP = Minimum Convex Polygon).

Hyena ID	Time period	Outliers	Number of fixes (of total no of fixes)	Schoener's Index	Swihart & Slade Index	AK Volume (95%) in km ²	MCP (100%) in km ²
VRBhb1m "Django"	June 05 - Oct 05	yes	470 (1415)	1.99	0.064	1250	980
		no	461 (1415)	1.99	0.003	1070	820
BBHb9m "Halenge"	March 04 - Feb 05		840 (2526)	1.99	0.099	500	420
KHb2m "Alfie"	March 05 - Aug 05	yes	5000 (15674)	2.00	0.035	2670	4370
		no	4444 (15674)	2.00	0.028	1530	1460

Table 5.4: Perimeter of home ranges for coastal brown hyenas and length and proportion of coastline within the home range.

Hyena ID	Outliers	MCP (100%) perimeter (km)	AK Volume (95%) perimeter (km)	MCP (100%) length of coast (km)	AK Volume (95%) length of coast (km)	% MCP perimeter	% AK Volume perimeter
VRBhb1m	yes	120	138	16	26	13	19
	no	111	131	16	25	14	19
BBHb9m		78	85	20	23	26	27

The AK Density contours (Figure 5.1) show six regions of the two coastal home ranges of low to highest constant probability density expressed as volume in percent. It clearly highlights the importance of the coastal area within the brown hyena's total home range.

The interval between visits to the coast for both brown hyenas ranged from zero to six days (Figure 5.2). There was no difference between the interval for either hyena (Mann-Whitney U-Test $U = 15440$, $p = 0.28$). VRBhb1m visited the coast on successive days 78% of the time and BBHb9m 86% of the time.

BBHb9m spent 23% of the total time in coastal areas (up to 1km inland) and VRBhb1m spent 40% of the total time near the coast. The distances walked in those areas represented 25.2% and 31.6% respectively of the total distance walked by each hyena.

The time spent at the coast increased slightly after the onset of the seal pupping season on 15 November for BBHb9m. He spent 26% of the entire time in the coastal area as opposed to 22% before the onset of the pupping season. The remaining time was spent in inland areas of his home range with only 9.4 % of his time spent close to the home range boundary.

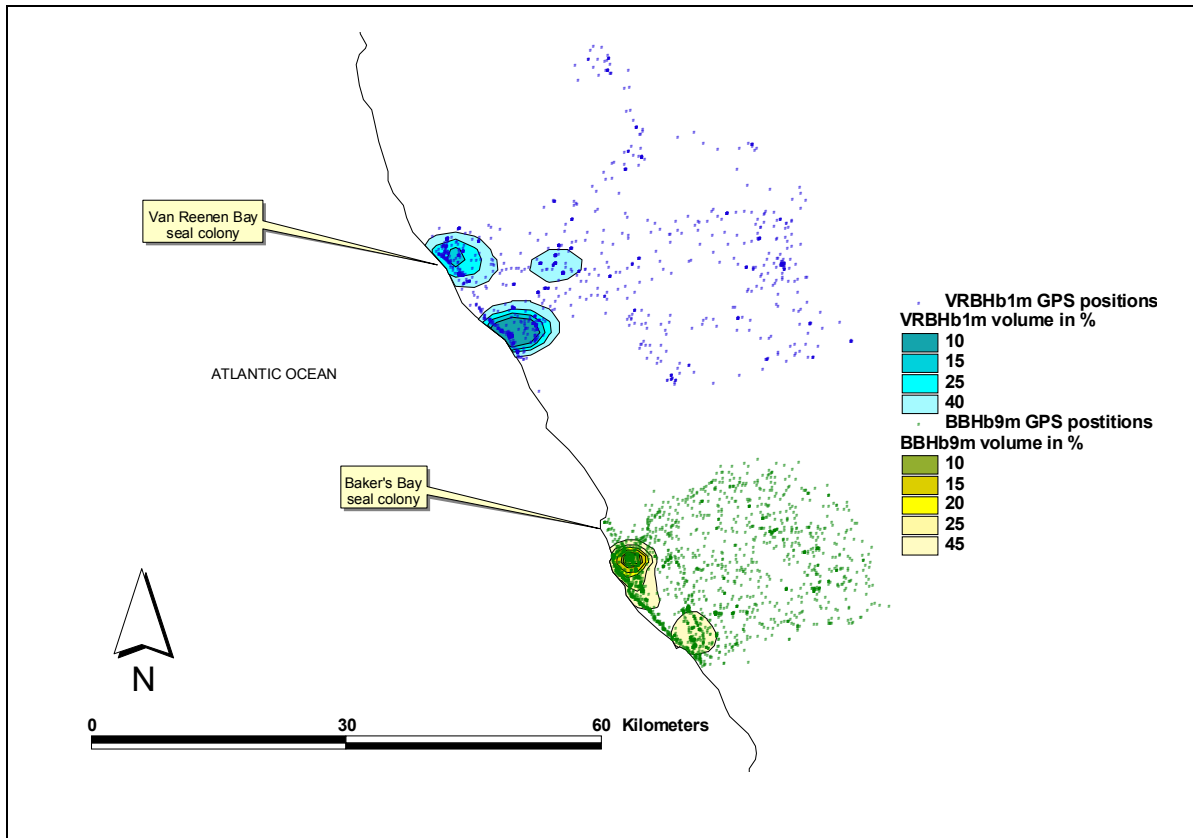


Figure 5.1: Constant probability density contours and percent volume calculated through the Adaptive Kernel Density method, highlighting areas from low to high constant probability density with associated volume percentages and showing the location of the mainland Cape fur seal colonies. Points represent all GPS locations recorded for VRBhb1m (1415) and BBHb9m (2526).

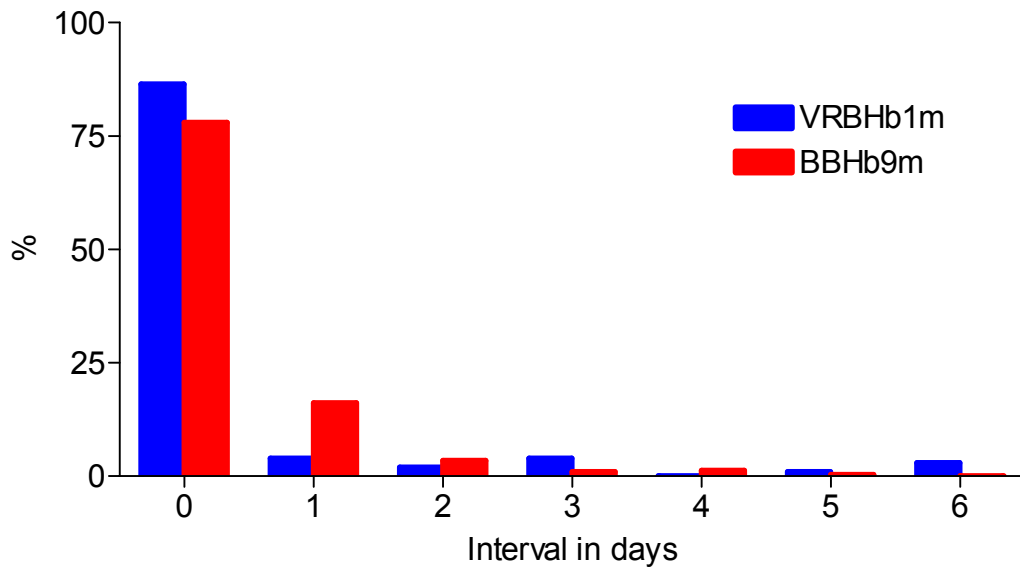


Figure 5.2: Percentage of interval of visits to the coast for two coastal brown hyenas.

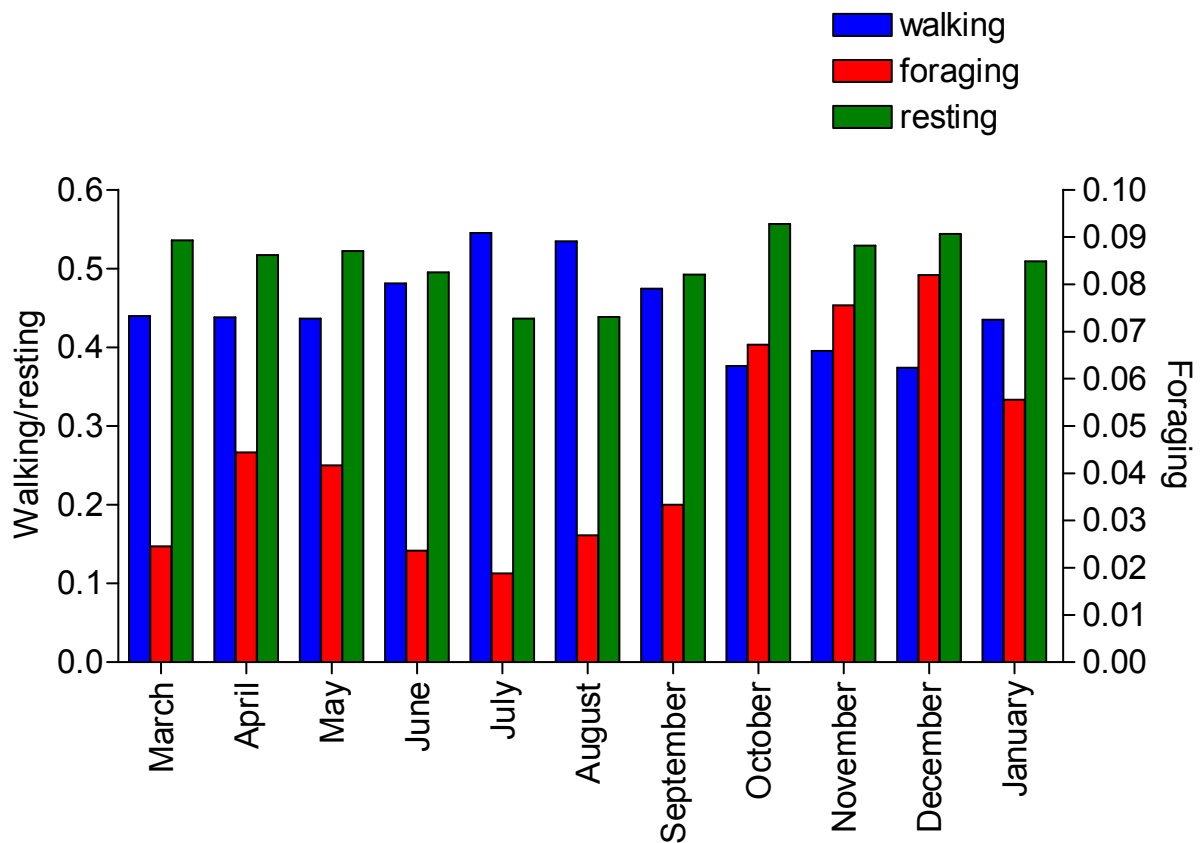


Figure 5.3: BBHb9m's average proportion of time spent walking, resting and foraging.

The hyena at Baker's Bay (BBHb9m) increased foraging activity along the coast shortly before the start of the pupping season (Figure 5.3) in October. Monthly foraging activity differed (Kruskal Wallis Test $H = 28.04$, $p = 0.0018$), with

decreased foraging in July compared to November (Dunn’s Multiple Comparison Test $p < 0.05$; no other pairwise comparisons were significant). BBHb9m spent significantly less time walking in October, November and December as compared to July and August (One-Way ANOVA $F_{10,320} = 3.60$, $p = 0.0002$; Tukey’s Multiple Comparison Test $p < 0.05$). There was no difference in the time BBHb9m spent resting between months (One-Way ANOVA $F_{10,320} = 1.79$, $p = 0.063$).

5.3.2 Brown Hyena Activity Pattern and Field Metabolic Rate

The two coastal brown hyenas VRBhb1m and BBHb9m travelled $15.46 \text{ km} \pm 0.95$ (SE) and $26.44 \text{ km} \pm 0.82$ (SE) per day respectively, and the daily distance travelled by KHb2m in inland areas of the Sperrgebiet was $46.84 \text{ km} \pm 1.58$ (SE) (Table 5.5). The difference between the daily movement of all three brown hyenas was statistically significant (Kruskal Wallis Test $H = 167.3$, $p < 0.0001$). Maximum daily distances travelled ranged from 48.4 to 91.4 km.

Table 5.5: Daily distance travelled by brown hyenas in km

Hyena ID	Hyena alias	Distance in km			
		Mean	Median	Minimum	Maximum
VRBhb1m	Django	15.46	15.03	0.07	48.37
BBHb9m	Halenge	26.44	24.87	0.96	73.40
KHb2m	Alfie	46.84	48.50	8.18	91.38

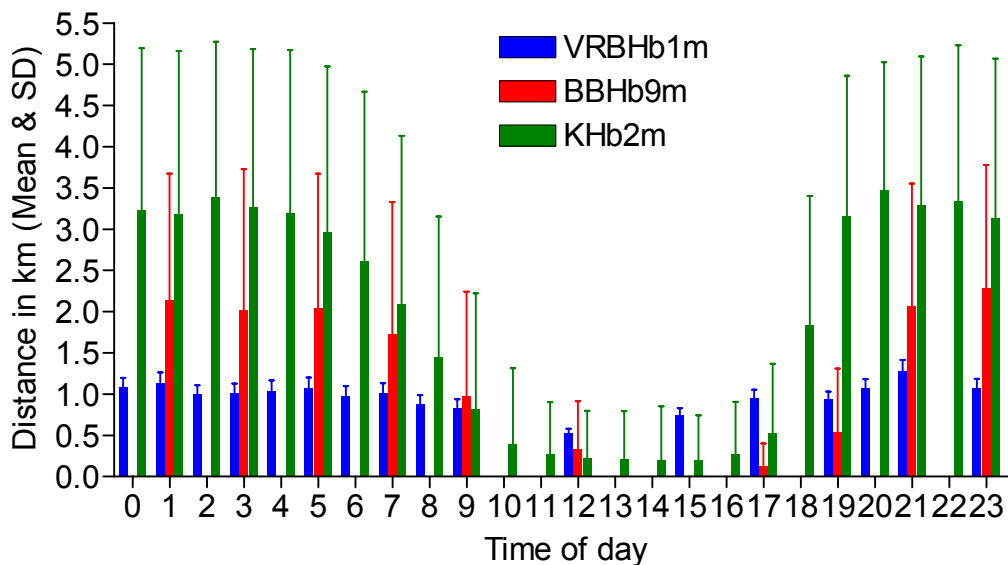


Figure 5.4: Mean distance (km) moved by three brown hyenas at different times of the day.



Activity for all brown hyenas decreased during daylight hours compared to activity at night (Fig. 5.4). In general, hourly distances ranged from close to zero to 7.80 km, 7.13 km and 4.65 km for KHb2m, BBHb9m and VRBHb1m respectively.

VRBHb1m spent 39.7%, BBHb9m 27.7% and KHb2m 42.9% of the 24 hour period inactive.

Field metabolic rate (FMR) calculations showed mean values of 2 265 kcal/day \pm 66.16 (SE) for VRBHb1m, 2 512 kcal/day \pm 101.00 (SE) for BBHb9m and 2 861 kcal/day \pm 186.40 for KHb2m (Table 5.6). The inland hyena KHb2m had a significantly higher FMR than the coastal brown hyena VRBHb1m but the difference with BBHb9m and between the coastal brown hyenas was not significant (Friedman Test $H = 7.84$, $p = 0.030$; KHb2m vs VRBHb1m: Dunn's Multiple Comparison Test $p < 0.05$).

Table 5.6: Calculation of field metabolic rates (FMR) for three brown hyenas, using different methods.

Hyena ID	Method	Inactivity value	Mass (kg)	Total distance (km)	Total hours	Hours/day inactive	Hours/day active	FMR (kcal/day)
VRBHb1m "Django"	Laundré & Hernández (2003)		40.0	1593	2474			2582
	Sauders et al. (1993)	Maximum				13.0	11.0	1984
		Mean	40.0	1593	2474	9.5	14.5	2098
		Median				7.9	16.1	2150
Kleiber (1961) & Nagy (1987)		40.0	1593	2474			2227	
VRBHb1m "Django"	Laundré & Hernández (2003)		41.7	1593	2474			2663
	Sauders et al. (1993)	Maximum				13.0	11.0	2266
		Mean	41.7	1593	2474	9.5	14.5	2164
		Median				7.9	16.1	2218
Kleiber (1961) & Nagy (1987)		41.7	1593	2474			2299	
BBHb9m "Halenge"	Laundré & Hernández (2003)		39.3	8377	7450			2820
	Sauders et al. (1993)	Maximum				10.0	14.0	2434
		Mean	39.3	8377	7450	6.7	17.3	2540
		Median				5.8	18.2	2568
Kleiber (1961) & Nagy (1987)		39.3	8377	7450			2197	
KHb2m "Alfie"	Laundré & Hernández (2003)		38.0	5340	2744			3207
	Sauders et al. (1993)	Maximum				13.5	10.5	2899
		Mean	38.0	5340	2744	10.3	13.7	2999
		Median				8.4	15.6	3059
Kleiber (1961) & Nagy (1987)		38.0	5340	2744			2143	



5.3.3 Brown Hyena Abundance

Brown hyena abundance was calculated for the areas around three mainland seal colonies, which differ in size and habitat (Table 5.7). The 95% confidence intervals were large for years and areas, where sampling effort was low (Wolf Bay 1999-2000 and 2000-2001).

The abundance estimate was similar in all areas around mainland seal colonies, but due to the low sample size, the influence of pup production on the number of brown hyenas could not be determined.

Table 5.7: Abundance estimate (N) of brown hyenas around three mainland seal colonies in different years and pup production at these seal colonies (* = count from 2001; ¹ = low effort)

Seal colony	Period	95% min	95% max	N	Pup production at seal colony
Wolf Bay	Nov 97 - Oct 98	8.89	11.43	10.00	36500
	Nov 99 - Oct 00 ¹	8.87	33.13	13.46	30825
	Nov 00 - Oct 01 ¹	10.80	32.80	15.80	21139
Van Reenen Bay	Nov 01 - Jan 02	12.56	14.50	13.46	2953
	Nov 03 - Feb 04	11.08	13.09	12.00	2953*
Baker's Bay	Aug 02 - April 04	11.37	12.71	12.00	6163*

5.3.4 Brown Hyena Density

Brown hyena density in the Van Reenen Bay area ranged from 1.0 to 1.6 brown hyenas per 100 km² depending on the home range estimate method used and whether outliers were included (Table 5.8). The density of brown hyenas in the Baker's Bay area was higher with values of 2.4 hyenas to 2.9 hyenas per 100 km². The sample size was too low to relate density estimates to pup production.

Table 5.8: Density of brown hyenas in two study areas

Hyena ID	Study area	Outliers	Home range size (km ²)	Clan size	Density/100 km ²	
BBHb9m "Halenge"	Baker's Bay		MCP	420	12	2.9
			AK Volume	500	12	2.4
VRBb1m "Django"	Van Reenen Bay	yes	MCP	980	12	1.2
		yes	AK Volume	1250	12	1.0
		yes	MCP	980	13.46	1.4
		yes	AK Volume	1250	13.46	1.1
		no	MCP	820	12	1.5
		no	AK Volume	1070	12	1.1
		no	MCP	820	13.46	1.6
		no	AK Volume	1070	13.46	1.3



5.4 Discussion

5.4.1 Brown Hyena Abundance and Density

Based on other studies of predator-prey relationships in coastal ecotones, brown hyena densities along the coastal Namib Desert were expected to be high, as they are subsidised through allochthonous food resources from the Atlantic Ocean. Cape fur seals are abundant, not only at mainland colonies, but also in the form of carcasses from these colonies and off-shore islands that wash up on the beaches along the coast (Chapter 4). Other marine subsidies include carcasses of sea birds, whales, dolphins, turtles and many invertebrates, especially crustaceans, but judging by their contribution to the overall prey biomass, they possibly play a minor role in the brown hyena's diet.

Brown hyena abundance seemed to be independent of annual pup production at the mainland seal colonies. Estimates ranged from 10 to 16 animals foraging at each of the seal colonies, and their density was estimated to be between one and three brown hyenas per 100 km². The Namibia Large Carnivore ATLAS (Hanssen & Stander 2004) describes most of the parts of the coastal Namib Desert as a medium density area for brown hyenas and the coastal areas of the Sperrgebiet as a high density area, with values of 0.15 to 1 animal per 100 km² calculated from incidental sightings. The use of incidental sightings for abundance estimates can be problematic, however. Although abundance estimates obtained from using incidental sighting data around the Wolf Bay seal colony during this study gave similar abundance estimates compared to high effort years, the confidence intervals were much larger and therefore the estimates were less reliable. However, the data still indicate that abundance remained relatively constant throughout the duration of the study (compare with Mills 1990), and densities were higher than the ATLAS estimates (Hanssen & Stander 2004). The density estimates in this study correspond to brown hyena density in the Southern Kalahari, which is estimated to be 1.8 animals per 100 km² (Mills 1987), ranging from 0.4 to 4.4 per 100 km² (Mills 1990).

The estimates obtained in this study might be conservative, as monitoring only took place during daylight. After two years of intensive monitoring at the Baker's Bay seal colony, 12 brown hyenas were estimated to forage at this seal colony. All 12 animals were well-known and re-sighted regularly by then. The first

capture took place in 2004 and a well-known animal was caught during the day, but at night an unknown animal was darted and an additional unknown animal was seen. These observations might indicate that some brown hyenas are strictly nocturnal and that this study's estimates therefore are low. Assuming the same number of animals forage at night as during the day, the density of brown hyenas at the Namib Desert coast may be two to six animals per 100 km², higher than in the Southern Kalahari. In an earlier study, Goss (1986) observed a group of nine brown hyenas (five adults and four sub-adults) at the Namib Desert coast near the town of Lüderitz. The group's home range size was estimated as 220 km². The density of adult brown hyenas therefore was 2.3 animals per 100 km² and by including sub-adult clan members increased to 4 animals per 100 km², which corresponds to this study's extrapolated results regarding coastal brown hyena density.

The density estimates differed between the Van Reenen Bay seal colony and the Baker's Bay seal colony areas. Densities around Van Reenen Bay were estimated to be between 1.0 and 1.6 animals per 100 km², whereas the density at Baker's Bay was estimated to be higher, with values ranging from 2.4 to 2.9 animals per 100 km². Both seal colonies are similar in size and habitat structure, but the Van Reenen Bay seal colony lies within the home range of VRBhb1m whereas the Baker's Bay seal colony is situated at the north-western edge of BBhb9m's home range. Therefore animals of more than one clan might use the latter seal colony as a food source, while the Van Reenen Bay seal colony only seems to be used by the members of one brown hyena clan. By taking the position of the seal colonies within the home range of the hyenas into consideration there would be no differences in brown hyena density between the areas around both seal colonies.

The results of this study (1.0 to 2.9 hyenas/100 km²) suggest that brown hyena density is within the normal range and not disproportionately high compared to Southern Kalahari density estimates (0.4 to 4.4 hyenas/100 km²). Therefore other factors besides food availability must limit brown hyena abundance in coastal areas of the Sperrgebiet. One possible explanation is intraspecific competition, which could limit population growth. Brown hyenas foraging at seal colonies seldom encounter each other, and the few observations

of two simultaneously foraging hyenas did not result in physical interaction. Nevertheless, coastal brown hyenas in the Sperrgebiet show signs of intense fighting, such as extensive scarring around the neck. Most captured animals had fresh bite wounds, mostly around the neck, but also in the ears and face. Mills (1990) describes similar wounds resulting from intraspecific agonistic encounters and two brown hyenas even died of severe neck injuries, possibly inflicted by conspecifics. Goss (1986) captured a very old animal during his study and described a hairless neck with abscesses and septic sores. Such intraspecific encounters are usually between single animals, but strange animals seldom meet in the Southern Kalahari and it seems as if brown hyenas from neighbouring clans prefer to avoid each other (Mills 1990).

A more obvious explanation for limited population growth is the existence of times of food shortage. In general, seal availability is guaranteed during the entire year but there are seasonal differences. Seal pup availability is extremely high during the pupping season, from late November until the beginning of January each year. New born seals are vulnerable, as they are relatively immobile and mostly unattended (Chapter 4). Furthermore, non-violent seal pup mortality is highest during the first 30 days of their life (De Villiers & Roux 1992), providing scavengers with large amounts of fresh carcasses, as hundreds of dead pups are washed up along the beaches (Skinner et al. 1995) or found at the seal colony (Wiesel 1998). From January onwards seal pups are more mobile and start spending time at sea. Non-violent mortality drops to close to zero by the beginning of February and hardly any seal pups are found washed up along the beaches later than May. Additionally some seal colonies are harvested for pups and bulls from July to the beginning of the next pupping season in the middle of November, which could considerably reduce the number of available pups for carnivores. At the same time seal pups are gradually weaned, which results in increasing mobility and increased time spent away from land at sea to start their own foraging. This time of relative food shortage might have an influence on large carnivore density and brown hyenas might have to switch to other available and more typical food resources that are found further inland.

Thirdly, it is possible, that the time scale required for a numerical response of the carnivores to an increased and predictable food supply has not been long



enough and that the impact of marine food subsidies will only show in future generations. Under some circumstances (e. g. territoriality) carnivores have shown weak numerical responses even over a long time scale (Holt & Lawton 1994). Reproduction in brown hyenas is slow and occurs at irregular intervals. Only one female brown hyena in a clan usually gives birth to a litter of one to four cubs, although age of first parturition is 35 months (Mills 1990). The cubs are weaned within 15 months and by then have to forage on their own. There is no information available about sub-adult mortality, but many sub-adults disappear, possibly through migration or death. This study only shows a trend towards an influence of the marine input on the population dynamics of this higher trophic level carnivore in comparison to descriptions of other authors (Polis & Hurd 1996, Hilderbrand et al. 1999). Coyotes inhabiting coastal areas show 2.4 to 13.7 times higher densities than adjacent inland areas (Rose & Polis 1998), which also results in negative impacts on their typical prey species. Polar bear (*Ursus maritimus*) density and population size is significantly positively correlated to ringed seal (*Phoca hispida*) density and abundance between and within strata (Stirling & Øritsland 1995). Historical data about coastal brown hyena density is not available. Whether future generations of brown hyenas show a similar numerical response or whether their social organization suppresses such a response requires further investigation, as does the possibility of subsequently suppressed local typical prey abundance.

In summary, brown hyena abundance along the coastal Sperrgebiet is high compared to the Namibian ATLAS information and corresponds to estimates from the Southern Kalahari, but might be even be higher due to constraints in this study's monitoring techniques. Therefore the quality of food seems to influence brown hyena abundance but seasonality in food availability might limit growth. If this proves true, home range sizes should be similar to other areas without highly predictable and concentrated food resources.

5.4.2 Brown Hyena Home Range Size, Activity and Habitat Use

Home ranges of coastal brown hyenas with access to mainland seal colonies and hence a localised food supply should be smaller than home ranges of inland hyenas with widely dispersed food resources. Furthermore territorial animals

should minimize the ratio of perimeter to area of their home range in order to maximize its defendability (Kruuk 1978 cited in Mills 1982a) and minimise the chance of strange animals of the same species discovering key resources.

Home range sizes of brown hyenas in the Southern Kalahari and in the Central Kalahari vary between 235 and 481 km² (Mills 1984) and between 170 and 400 km² (Owens & Owens 1996) respectively. The only home range estimate available for coastal areas of the Namib Desert is for individual home ranges is calculated at between 31.9 and 220 km² (Skinner et al. 1995). The latter clan's home range perimeter comprised 50% coastline (Goss 1986), hence a greater portion of localised food source than described in this study but without a mainland seal colony in that area. The home ranges of coastal brown hyenas estimated in this study are considerably larger ranging between 420 and 1250 km² (depending on the method used) and were therefore of similar size or larger than in the Kalahari. Smaller home range sizes for brown hyenas in coastal areas are predicted according to the resource dispersion hypothesis, but the data suggest otherwise. Skinner et al. (1995) hypothesised that coastal brown hyenas might maintain larger than necessary territories due to the acquisition of territories from predecessors, the excess amount of time available to spend on territorial activity due to short foraging times, or the advantage of keeping intruders away from the rich food supply. Although this study's coastal home range estimates are actually small compared to the adjacent inland home range estimate of between 1460 and 4370 km², they still seem too large to represent the minimum-sized territory predicted in the resource dispersion model, if food availability and distribution were the key resource.

The acquisition of territories from predecessors does not seem to be a plausible explanation for the large home range size in the two coastal areas that were studied. Brown hyenas react to changes in their environment contrary to the suggestion of Skinner et al. (1995). The home range of the brown hyena clan that was studied by Goss (1986) included areas to the north and east of the coastal town of Lüderitz. Some years after the completion of that study the gravel road leading from inland to the town was upgraded and tarred, which subsequently led to an increase in vehicle traffic. The territory boundary of the brown hyena clan shifted to south of the tar road and a large proportion of their previous home

range was thus excluded (Wiesel, unpublished data). If brown hyenas respond relatively quickly to such changes it would be more than probable that they would optimise the boundaries of their territory in relation to concentrated and predictable food availability and distribution.

It also seems unlikely that coastal brown hyenas spend the excess time available in territorial maintenance to try to keep intruders away from the rich food source. Between 28% and 40% of their time was spent in coastal areas and BBHb9m only spent 9.4% of the total time in areas close to the inland home range boundary. The easiest access for intruders from neighbouring clans to the coast is found at the north-western and south-western edges of the home ranges. The constant probability density and associated volume percentages of both coastal brown hyenas was high in these areas, which indicates a territorial function, but could also be a result of topographical features. However, density is localised in the coastal area and does not explain the inland expansion of the home range.

Goss (1986) discussed the possibility of the importance of other food resources in times of food scarcity or other key resources such as water in relation to the inland expansion of coastal brown hyenas, but rejected this point. The total duration of his study is unknown, but the main data collection took place between May and September before the onset of the seal pupping season. He did not detect any changes in the foraging behaviour of brown hyenas during the course of his study. This study shows different results although the data set is small, as only one brown hyena, BBHb9m, was fitted with a GPS collar for nearly an entire year and data thus included times of food scarcity and overabundance. BBHb9m spent more time foraging along the coast between October and January compared to July and August, when the decreased amount of foraging time was compensated by increased time spent walking in inland areas of the home range. It is possible that the brown hyena searched for food further inland and re-allocated overall activity to compensate for the increased difficulty in finding marine food (compare with Ebensperger & Hurtado 2005). The time spent resting was not influenced by the change in food availability.

Large home ranges could therefore be maintained due to the necessity to compensate for periods of food shortage (compare with Lindstedt et al. 1986).

Brown hyenas spend more time in inland areas of the home range when food is scarce, possibly to look for alternative food (Skinner et al. 1995), which coincides with the pattern seen in this study. Nevertheless, overall activity was not influenced by change in food availability.

Lastly key resources other than food can also play a role in determining territory size and structure. For European badgers the den site is the key resource and territory boundaries are placed as far away as possible from the den (Doncaster & Woodroffe 1993). Therefore the location of the den site determines the quantity and quality of other resources. In this study, the location of active den sites was unknown. Although some dens were discovered in the vicinity of the coast, they were not used during the study period. The inland hyena's active den site was situated in the centre of the home range and KHb2m visited the site regularly. Most dens are found in mountains and the availability of this habitat has to be ensured within the home range. Mills (1990) also found that the location of dens was not random and that they were situated in areas that attract few competitors. Both factors might play a role in coastal brown hyena choice of den site habitat and could therefore have an influence on home range size and structure. Open fresh water, another key resource, is thought to play a minor role for brown hyenas (Owens & Owens 1978, Skinner & van Aarde 1981, Mills 1987). In coastal areas of the Sperrgebiet artificial and natural fresh water sources are present. Inland areas however have the lowest rainfall between October and March and summer rain becomes increasingly important from south to north (Burke et al. 2004). The inland hyena KHb2m visited a natural fountain 40 km to the north of his home range in March, before the onset of rain, which suggests that water may be more important than previously thought. For instance the diet of brown hyenas in the Southern Kalahari contains fruit and might serve as a source of moisture (Mills & Mills 1978) and activity is mostly restricted to night-time, which reduces loss of water (Mills 1987).

In general most home ranges are to some degree heterogeneous and hence disproportionally used. Homogeneous dune habitat territories in the Southern Kalahari show uniform use of the entire area, as food sources are evenly distributed (Mills & Mills 1982). However more heterogeneous habitats show a higher use of food-rich habitat where prey abundance is higher (Mills &

Mills 1982). Southern Kalahari brown hyenas travelled 45.2% of the total distance in those areas. Nevertheless, a small perimeter to area ratio is kept as a too elongated home range increases the travelling distance to the den, makes it too difficult to defend and would result in a negative energy balance while foraging (Mills 1990).

In coastal ecotones a large number of carcasses wash ashore and marine mammal and seabird colonies provide significant biomass for coastal carnivores (Polis & Hurd 1996). Coyotes, for instance, seem to make disproportional use of the coastal area (Rose & Polis 1998). Along the Namib Desert coast a large number of seal carcasses are washed up, but there are seasonal differences, with a period of food abundance between December and May and a period of food shortage between July and November (Skinner et al. 1995). Brown hyenas spend a considerable amount of time in the coastal area, as they find 91% of their food within 1 km off the coast and use mountainous hills and cliffs in the coastal and sub-coastal area as resting sites (Goss 1986), indicating that they tend to rest close to their food source (Mills 1977 cited in Goss 1986).

Brown hyenas in this study spent 23% to 40% of the total time near the coast, with small seasonal differences (22% before the start of the pupping season and 26% afterwards). The total distance travelled in the food-rich coastal habitat was between 25.2% and 31.6%, which is less than described for food-rich habitats in the Southern Kalahari. Cape fur seals aggregate in large colonies and the distribution of food in the study areas is therefore extremely clumped, more so than in the Southern Kalahari. Thus, brown hyenas seldom need to travel to other food sites, which is reflected in the short travelling distances in that part of the home range. The hyenas were found close to the coast on successive days 78% to 86% of the time, and the longest interval between visits was six days.

Home ranges excluding outliers were clearly defined in this study and despite different sizes included a similar proportion of coastline. The same is found in arctic foxes that find most of their food in current favoured productive bays. Each arctic fox territory contained a constant length of productive coastline (Macdonald 1983).

Therefore, the time brown hyenas spend in coastal areas, as well as the short interval between visits to the coast and the inclusion of a constant portion of



food-rich habitat, highlights the importance of the coastal area for brown hyenas. Nevertheless home range size is influenced by other factors such as the perimeter to area ratio, predictable periods of food shortage, and other key resources, e.g. suitable den site habitat.

5.4.3 Brown Hyena Movement and Field Metabolic Rate

The inland brown hyena of this study, KHb2m, showed similar activity to Southern Kalahari brown hyenas. He spent 42.9% of his time inactive, which corresponds to 42.6% in Kalahari hyenas (Mills 1984). Temperatures in inland areas of the Sperrgebiet are high during the day and brown hyenas need to rest for thermoregulatory purposes. In contrast temperatures in coastal areas are moderate as the prevailing south-westerly wind in summer prevents extremely high air temperatures. Coastal brown hyenas were inactive for only 27.7% and 29.7% of the total time in contrast to the findings of Goss (1986) for brown hyenas in the vicinity of the town Lüderitz. His study animals were inactive for 33.6% and 68.6% of the night and he extrapolated the data for the entire 24 hour period to obtain inactivity values of 62.7% and 81.7%, but he regards the first estimate as more representative. It is possible that brown hyenas in areas with human disturbance are strictly nocturnal (Skinner 1976). Nevertheless he only followed brown hyenas from dusk to dawn and could not find the representative brown hyena one third of the time and therefore might have missed daytime activity. In general brown hyenas are more active at night (Mills 1984), which was also seen in this study irrespective of the study area.

Coastal brown hyenas travelled significantly less during the 24 hour period than the inland brown hyena, but the daily distance also differed between the coastal animals. This study's sample size of three brown hyenas is low and the differences could therefore be explained on an individual basis. Nevertheless it is assumed that inland and coastal hyenas differ in their movement and activity, mainly related to thermoregulatory purposes and the distribution of high quality food. Southern Kalahari brown hyenas move on average 32 km per night, ranging from 1.5 to 54.4 km (Mills 1978). Coastal brown hyenas around Lüderitz (Goss 1986) moved between 12.3 and 21.9 km per night, similar to the distance moved by coastal brown hyenas in this study (15.5 to 26.4 km). The inland hyena of this



study covered a greater distance of 46.8 km, ranging from 8.2 to 91.4 km, as compared to Southern Kalahari brown hyenas, but only night-time movements were included in that study. Nevertheless ungulate density in inland areas of the Sperrgebiet is much lower than in the Southern Kalahari and brown hyenas therefore have to travel greater distances to find food.

The energy that animals require to survive is directly related to the individual body mass, the time spent active and the distance travelled (Saunders et al. 1993, Laundré & Hernández 2003). The mean field metabolic rate (FMR) calculations for coastal brown hyenas were 2265 kcal/day and 2512 kcal/day, whereas the inland brown hyena had a FMR of 2861 kcal/day. The difference was only statistically significant between the extreme values of VRBhb1m and KHb2m. Nevertheless a trend towards higher energy expenditure can be seen between coastal and inland brown hyenas, and the distance travelled and hence the time spent foraging seems to be the most determining factor: the mass of the three male brown hyenas was similar and a similar range of time was spent inactive, although the inland hyena's average resting time was higher. Nevertheless coastal brown hyenas travelled less during the 24 hour period. Therefore differences in thermoregulatory costs do not seem to influence the FMR between hyenas living in cooler coastal areas as opposed to hyenas living in hot inland areas. The metabolic rate of coyotes was also independent of a change in air temperature, and thus the costs were considered minimal (Shield 1972 cited in Laundré & Hernández 2003). The use of body mass as the only parameter to calculate the FMR gave similar estimates to the calculations that included distance and time for the least active coastal brown hyena (judged by the distance travelled). The other two hyenas were more active and the difference between the method only including body mass and the other two methods was greater. This difference again shows that the distance travelled seems to be the most influencing factor to calculate FMR and animals that travel more have higher energy expenditures (Laundré & Hernández 2003).

Once again, the sample size in this study was low and several other considerations must be taken into account to obtain reliable information about energy requirements of brown hyenas inhabiting different habitats. The FMR might differ between sexes or seasons and could vary with reproductive effort.

The energy required to capture prey can also influence the FMR, and the time interval between successive GPS fixes should be short to obtain reasonable movement estimates (Laundré & Hernández 2003). The diet of animals influences home range size, and meat eaters generally have large home ranges, which increase in size with metabolic needs (McNab 1963, Gittleman & Harvey 1982, Lindstedt et al. 1986). Inland hyenas of the Sperrgebiet inhabiting larger home ranges, therefore, should have higher FMR than coastal ones.

The only estimate of consumption rate for brown hyenas is from the Southern Kalahari, where an average of 2.8 kg of meat is consumed daily (Mills 1978). Using the estimate of Schaller (1972) this amount of meat consumption would correspond to a caloric value of 4200 kcal, which is higher than the FMR calculated in this study. Nevertheless, the FMR estimates are valuable for the further investigation of the brown hyena's energy requirements and their impact on typical and allochthonous prey populations.

5.5 Summary

Brown hyena abundance and density in coastal areas of the Sperrgebiet is related to seasonality in food availability, which might limit growth. This seasonality contributes to the maintenance of large home range sizes despite localised food resources. Compared to home ranges in inland areas of the Sperrgebiet, coastal home ranges are small and coastal brown hyenas travel shorter distances, which results in a lower field metabolic rate and hence lower consumption rate.



Chapter 6

Brown Hyena Foraging and Hunting Behaviour at Mainland Cape Fur Seal Breeding Colonies

6.1 Introduction

Foraging behaviour is influenced by instincts and learned behaviours, triggered by a variety of stimuli (Eaton 1970, Kossak 1989). Animals need to optimize their rate of energy intake during foraging bouts (Charnov 1976 cited in Hills & Adler 2002), trading-off the time spent foraging with the time lost for other critical activities (Cook & Cockrell 1978, Ebersperger & Hurtado 2005). Time is often a good indicator of effort (Gende & Quinn 2004) and foraging-related behaviours can be valued by this currency. According to optimization models, the time spent on certain behaviours should be enlarged as long as it results in a positive energy balance (MacArthur & Pianka 1966). However, in order to evaluate optimal strategies it is important to determine what is to be maximized or minimized (Schoener 1971). Considerations such as the foraging space, foraging period and foraging group size as well as the optimal diet play important roles in optimizing the energy yield of a foraging strategy (Schoener 1971) for different predator guilds. A predators' foraging expenses, for example, may include the search for prey (Schoener 1969), although this cost may be reduced in some foraging strategies (e.g. "sit-and-wait" predators), and the combination of all expenses influences the decision whether time or energy need to be maximized. Nevertheless, different optimal diet strategies do not necessarily have to be exclusive, and switching can take place with changes in prey availability (MacArthur & Pianka 1966, Rapport 1971).

A predator's foraging and hunting techniques can vary according to the prey species and the environment (Kruuk 1975). Predators can, for example, increase their encounter rate with prey by spending prolonged time in patches (optimal search rate hypothesis) or increase their detection of prey by spending more time viewing a particular part of the patch (stare duration hypothesis) (Endler 1991). Furthermore, the orientation of the killing bite could depend on the defensive capabilities of the prey, and different stimuli can act to modify the bite accordingly (Kruuk 1975, Ben-David et al. 1991). In this regard, learning from

conspecifics or through experience can play an important role (compare with Fox 1969).

Most predators show optimal strategies to a certain degree and many models have been modified to fit individual species' strategies, especially with regard to partial preferences in their diet (Emlen 1966, Pyke et al. 1977, Sih 1980, Temple 1987). However, some foraging strategies seem to oppose optimization models, such as mass kill events and surplus kills, a phenomenon which plays a role in this study.

The definition of a surplus kill by Short et al. (2002) is "the killing of prey by a predator at a rate far beyond that necessary to supply its immediate needs for food or food storage, and is characterized by an absence of, or low level of, utilization of the prey carcass by the predator". This definition excludes one factor mentioned in Kruuk (1972b), this being the use of the accessible carcass (with no dominant competitors in the area) by members of the same social unit or the predator's offspring. The occurrence of surplus kills or mass kill events seems to contravene optimal foraging theories and rather seems a waste of energy and effort by the predator (Kruuk 1972b). However, these killing events often happen during unusual environmental conditions such as new moon nights, heavy rain or snow (Goethe 1956, Kruuk 1972b, DelGiudice 1998), when the prey species show a lack of anti-predator behaviour, (Kruuk 1964, Kruuk 1972b, Quinlan & Lehnhausen 1982). Surplus kills also may serve as a method of storing food for times of food shortage (MacDonald 1976, Oksanen et al. 1985, Jedrzejewska & Jedrzejewski 1989), which can, under these circumstances, be an optimal strategy. Mass kill events and surplus kills only occasionally happen on a regular basis, usually when predators and prey did not co-evolve (Short et al. 2002).

In many cases, extra energy may be spent on further killing (MacDonald 1976, Oksanen et al. 1985), but the killing definitely seems to be independent of the satiation of the predator. Therefore, the regular stimuli that inhibit further killing are suppressed, and killing and consumption of prey do not seem to be linked (Kruuk 1972b). Such surplus killing can be triggered through unusual behaviour of the prey (Goethe 1956, Kruuk 1972a) or a superabundance of food (Oksanen et al. 1985, Kossak 1989), but can also be a method of gaining more hunting experience (Kruuk 1972b).



Brown hyenas (*Parahyaena brunnea*) are described as being predominately scavengers, using food opportunistically (Mills & Mills 1978). They usually forage alone at a quick pace, mainly relying on the olfactory detection of carcasses (Mills 1978) while using a zigzag mode of travelling (Owens & Owens 1978). Hunting is poorly developed and a rather “primitive chase and grab affair” (Kruuk 1976). Nevertheless they can become specialists in hunting certain prey species (Mills 1978) with good success.

Long-term studies describing the foraging and hunting behaviour of brown hyenas have been done in areas with patchily distributed food sources and the occurrence of other large carnivore species (Owens & Owens 1978, Mills 1990). Apart from the spotted hyena (*Crocuta crocuta*), these species are not in direct competition with brown hyenas, as they are largely true predators and brown hyenas fill the niche of the scavenger. Along the southern Namib Desert coast, however, no other large carnivores exist and black-backed jackals (*Canis mesomelas*) are the only competitors. There is a localized, year-round availability of seals (*Arctocephalus pusillus pusillus*) at mainland breeding colonies. Brown hyenas have been observed killing and scavenging seal pups (Goss 1986, Skinner et al. 1995, Wiesel 1998), but their specific foraging behaviour at these seal colonies has not yet been described.

The objective of this chapter is to describe their foraging behaviour in this food-rich area in the context of foraging behaviour of brown hyenas in other environments and by other species. Furthermore, the factors influencing the foraging-related time budget, such as hunger state and density of seals, were investigated by looking specifically at the brown hyena’s prey encounter rate and hunting efficiency. Finally, the factors influencing the predation rate and occurrence of mass kill events were analysed. It was expected that

- (1) the density of seals influences brown hyena time budget, hunting efficiency and predation rate and that
- (2) satiation plays a role in the brown hyena’s foraging behaviour. Also,
- (3) possible stimuli leading to mass kill events and surplus kills are discussed.



6.2 Material and Methods

6.2.1 Study Area and Study Period

Behavioural data were collected at the Van Reenen Bay seal colony between November 2001 and January 2002 during three observation periods: before (5 – 23 November), during (2 – 21 December), and after (4 – 23 January) the peak pupping season. The seal colony was observed daily between 06:00 and 19:00 or 20:00 from an observation hut on the northern cliff, 17 meters high, that overlooks most of the colony (Figure 6.1).

Additional data were collected during the Cape fur seal pupping season at the Wolf Bay seal colony between November and March 1997-1998, 1999-2000 and 2000-2001. The entire seal colony was divided into 24 sample areas of different sizes and habitat (Chapter 4) to collect data regarding brown hyena predation.

6.2.2 Brown Hyena Attendance at the Van Reenen Bay Seal Colony

Arrivals and departures of all brown hyenas visiting the seal colony were recorded. Brown hyenas could disappear out of sight only in the area directly underneath the observation hut and behind one of the three large rocks, whose surrounding areas were used as a feeding site (Figure 6.1). Occasionally brown hyena arrival or departure could not be recorded due to unfavourable weather conditions (twilight or fog), and such observations were excluded from the data analysis. Brown hyenas that arrived in the visible area (Figure 6.1, blue line), but did not go foraging at the colony itself (the area between the yellow line and the sea), were regarded as present, but also not included in the analysis.

Brown hyena attendance time at the seal colony started when the animal reached the yellow outlined area and ended when this area was left on its final departure. Therefore out-of-sight observations outside the seal colony area and the time spent in the visible area, but not at the colony itself, were excluded.

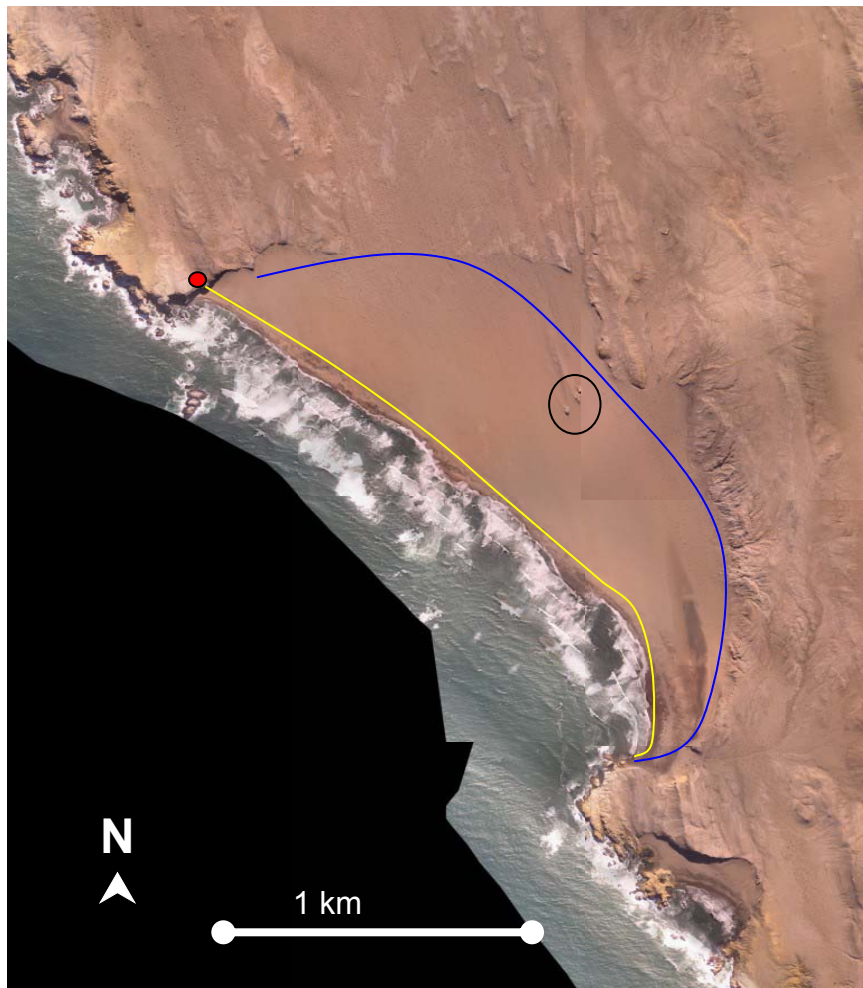


Figure 6.1: Aerial Laser Survey image of the Van Reenen Bay seal colony (red dot: observation hut overlooking the seal colony, oval: large feeding site, blue line: eastern boundary of visible area from the observation hut, yellow line: approximate outline of seal colony). Courtesy of NAMDEB.

6.2.3 Brown Hyena Foraging Behaviour

Brown hyena behaviour at the seal colony was recorded continuously on a dictation phone (Precision VCO) from its arrival until its departure, using focal animal sampling (Altmann 1974). Observations were made with binoculars (Kamakura 8 x 32) and a telescope (Kamakura 20-45x). The choice for the daily focal animals was the first animal to arrive until its departure, the next animal arriving after the previous focus animal's departure and so forth. A second observer recorded arrivals and departures of other brown hyenas during the focal observations. A transcript of the recorded material was made, adding the time and duration of the observed behaviours from a stopwatch, using an ethogram developed for this study (Table 6.1).



Table 6.1: Ethogram of recorded brown hyena behaviours at the Van Reenen Bay seal colony.

Behavioural Group	Behaviour	Sub-behaviour	Unit	Description
walking	walking	in area	state	walking parallel or randomly outside the colony area
		towards colony	state	walking straight towards the seal colony
		alongside colony	state	walking next to the seals parallel to the seal colony
		in colony	state	walking between the seals
		away from colony	state	walking straight away from the seal colony
		away from seals	state	walking away from the seals to continue walking along or away from colony
standing	stop	orientating	state	looking to the sides and/or ahead/backwards while standing
		staring	state	looking straight forward, head stretched slightly forwards
Hunting and creep	creep	upright	event	walking slowly towards seals, body in upright position
		crouched	event	walking slowly towards seals, body position crouched, head low
	hunting	kill	event	bite into seal pup, resulting in its death
		attempt	event	attempt to bite seal pup without touching the pup
		contact attempt	event	bite into seal pup and release, pup still alive
Handling	carrying	dragging	state	carrying pup a few metres back- or forward after the kill, pup touches ground
		feeding related	state	carrying pup to a feeding site or away from colony
	dropping	hunting related	event	drop off after kill
		feeding related	event	drop off to feed
		competition related	event	drop off to compete with jackals
		change of grip	event	drop off to change the grip from skull to back or vice versa
	holding	hunting related	state	holding pup after kill
		feeding related	state	holding pup between feeding bouts
competition related		state	holding pup while attacked by jackals	
Feeding	feeding	kill	state	feeding on kill
		carrion	state	feeding on carrion
		return kill	state	feeding on a previous kill
		return carrion	state	feeding on a previously scavenged pup
Others	others	resting	state	lying down away from seals
		defecating/urinating	event	squatting and defecating or urinating
		pasting	event	extruding anal gland and pasting
		shamming	state	lying down in between seals
		death shake	event	holding kill or carrion while shaking the head vigorously
Intraspecific competition	intraspecific	dominant	event	see Mills (1990)
		submissive	event	see Mills (1990)
		staring	event	staring at other hyena while walking or standing at 5 to 10 m distance
Interspecific competition	competing	chasing	state	running after jackals
		attacking	state	attacking jackals by biting
		protecting prey	state	holding onto prey while jackal pulls
		reclaiming prey	event	reclaiming prey that was briefly grabbed by jackals
Anti-predator behaviour	fleeing	retreat from seals	event	fleeing from seal attack



To compare the influence of food availability on foraging behaviour, the duration of states and the occurrences of events per time unit were compared for differences before and after the peak of the pupping season in December for each individual identifiable brown hyena and in total. Hyenas were identified through their unique stripe pattern on their forelegs and natural ear notches (Chapter 5). For each continuous observation of a focus animal, the proportion of time spent in each behavioural group was determined. To test for independence between the observations, the proportions of each behavioural group were compared between individual hyenas and within different observations of the same focus animal by using the paired t-test, and in case of not normally distributed data the Wilcoxon Signed Rank Test. Whenever necessary the data were arcsine square root transformed before analysis, which did not always result in parametric data (compare with Ebensperger & Hurtado 2005).

6.2.4 Foraging and Hunting Behaviour

The sequence of different behaviours of each focus animal was recorded from its arrival at the seal colony until its departure. The study distinguished between (1) kill, (2) carrion, (3) return kills, when the focus animal returned to one of its previously killed pups, and (4) return carrion, when the animal returned to carrion that it had previously been feeding on. A transition matrix expressing the conditional probability of the occurrence of the behaviour at time t given the occurrence of the behaviour at time $t - 1$ was constructed using the Markov Chain Method (Suen & Ary 1989), and a transition diagram was created from the matrix. The required sample size necessary was calculated in order to evaluate whether χ^2 statistics could be used to test whether the transition matrix model showed serial dependency or represented a random walk process (Gottman & Notarius 1978, Lehner 1996). It was also tested whether the matrix of an individual brown hyena differed significantly from the matrix that combined all focus animal observations by comparing the arcsine square root transformed proportions in corresponding matrix rows.



6.2.5 Prey Encounter Times

Brown hyenas mostly walked alongside and between the seals, and continuously encountered possible prey items. Therefore, the prey encounter time was defined as the time between the arrival (see Chapter 6) at the seal colony to the first contact with a prey item and between successive contacts with prey items. Prey encounter included contact (feeding, holding, licking) with dead pups (carrion) and actual kills. All prey encounter times and the interval between kills were compared for the times before and after the peak pupping season (November and January). The time during the peak pupping season was excluded for data analysis, as it represents an intermediate position between low availability of pups and superabundance of pups (see Figures 11 to 14: Appendix, and compare with Chapters 4 and 5).

6.2.6 Efficiency and Capture Rate

Hunting efficiency was the number of kills per attempt (Darimont et al. 2003). An attempt was a determined movement towards the prey, which included the “creep” behaviour. The capture rate was expressed as the number of seal pups killed per unit of time. Efficiency and capture rate were also compared for differences between the time before and after the peak pupping season.

6.2.7 Predation Rate at Seal Colonies

Data on predation of Cape fur seal pups were collected at the Wolf Bay seal colony. To determine the predation rate on newborn pups, 10 representative sample areas out of the 24 were chosen for data collection in 1997-1998 and 1999-2000, and 14 in 2000-2001. Between the birth of the first pup in November each year and 15 or 16 March (Julian day no. 75) of the following year all predations in these sample areas, which had been dead for less than 24 hours, were recorded and marked with a numbered plastic or metal tag to avoid double counts. Predations that were not marked and already bloated or rotten and therefore dead for more than 24 hours (compare with Trillmich et al. 1986, Geraci & Lounsbury 1993) were noted, their flippers clipped, and were included in the mortality rate estimates for days where no data collection took place (Chapter 4). Brown hyenas always killed seal pups with a single bite into the skull, which



crushed the fragile cranium that still has open sutures (Rand 1956). The study distinguished between

- (1) surplus kills; where the skull was crushed but the pup was not eaten;
- (2) excessive kills; where only the brain and parts of the skull were eaten;
- (3) completely consumed kills; where usually only fur and the jaw bone remained; and
- (4) cached excessive kills; where only skull bone remains were found at the colony

(Figures 5 to 9; Appendix). The skinned skull of surplus kills showed the predator-specific injury pattern of bite marks, and haemorrhaging indicated that the injuries were inflicted on a live pup (compare with Miller et al. 1985, Husseman et al. 2003). The feeding site around partly and completely consumed pups, as well as cache remains, was covered with blood, and blood trails could be found in the direction the cache was carried, indicating that the pup was killed by the brown hyena. The crushed skulls of surplus kills could easily be felt, and no other sources of mortality could have caused such injuries.

Predation mortality was calculated using life tables (Caughley 1977, Chapter 4). Hot weather was excluded as a factor influencing mortality in the estimate of the predation rate on days without data collection (Chapter 4).

6.2.8 Mass Kill Events

Data on mass kills were also collected at the Wolf Bay seal colony. Multiple killings, where two or more killed seal pups were found not more than 20 metres away from each other and/or where it was obvious that the brown hyena had killed along a passage to reach other parts of the colony (Figure 6.2), were recorded as mass kill events (compare with Kruuk 1964). A total of 84 mass kill events were recorded at the Wolf Bay seal colony during all three study periods and compared for differences between months, years and between pup categories (guarded vs unguarded pups; Chapter 4).



Figure 6.2: Mass kill event along a passage towards sample area no. 5. Note that all pups were killed in surplus.

6.3 Results

6.3.1 Attendance of Brown Hyenas at the Van Reenen Bay Seal Colony

A total of 40 brown hyena sightings were included into the dataset, representing a minimum of six individuals. The time brown hyenas spent at the colony ranged from 26 to 221 minutes in November, 12 to 107 minutes in December and 2 to 69 minutes in January, and differed significantly between the periods (One-way ANOVA $F_{2,39} = 6.35$, $p = 0.004$). Therefore, brown hyenas spent on average 6.1% of the day foraging at the seal colony, ranging from 0.3% to 23.8%. Brown hyenas spent significantly more time at the colony in November, before the peak pupping season, than in December and January (Tukey's Multiple Comparison Test: during $q = 4.19$, $p < 0.05$; after $q = 4.54$, $p < 0.01$) (Figure 6.3). Nevertheless, the number of brown hyena sightings per hour of observation did differ significantly among the periods (Kruskal Wallis Test $H = 0.34$, $p = 0.84$). Brown hyenas arrived at and left the colony significantly earlier in January than in November (t-test: arrival $t = 3.52$, $p = 0.001$; departure $t = 4.37$, $p = 0.0001$) (Figure 6.4).

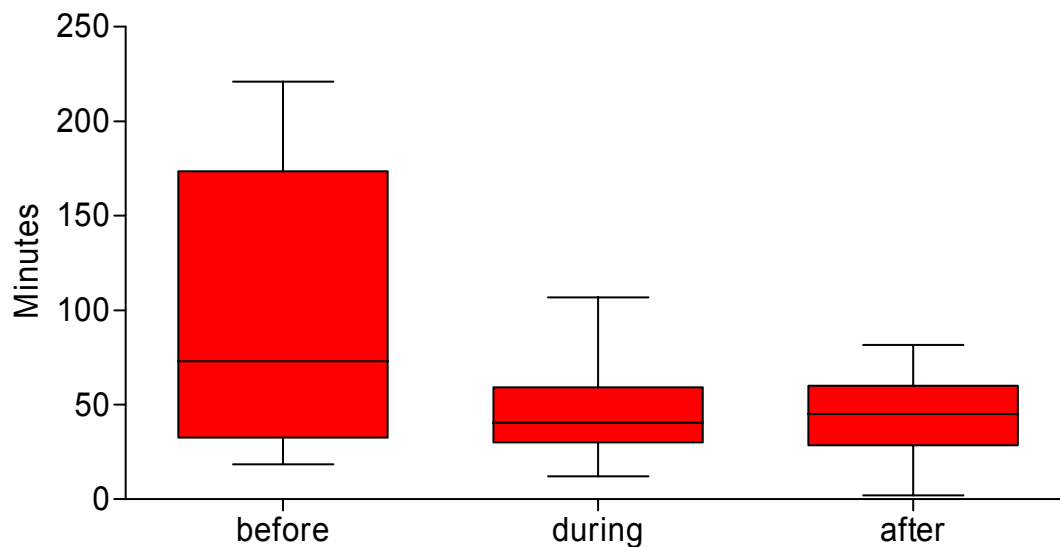


Figure 6.3: Time spent by brown hyenas at the Van Reenen Bay seal colony before, during and after the peak pupping season in December.

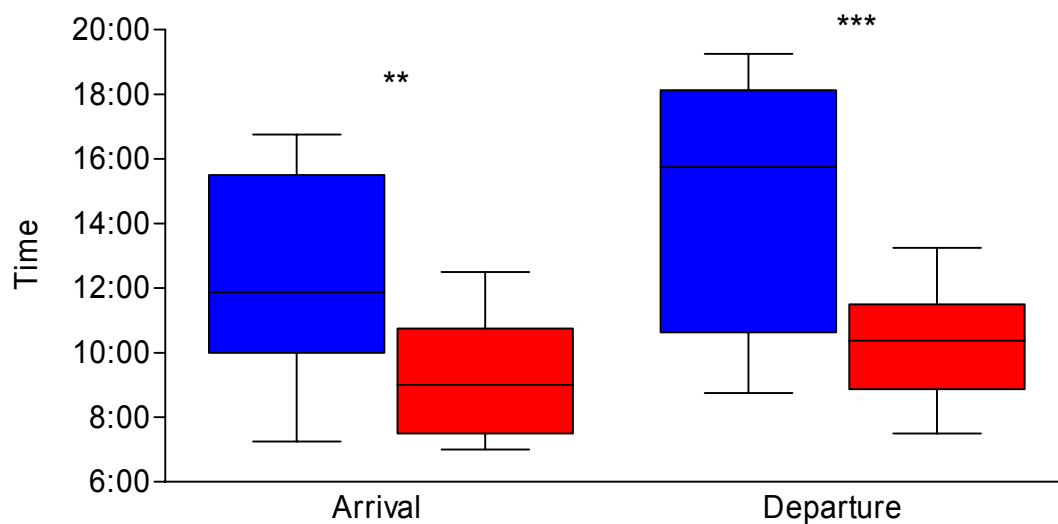


Figure 6.4: Time of arrival and departure of brown hyenas at the Van Reenen Bay seal colony (blue = November, red = January).

6.3.2 Brown Hyena Foraging Behaviours

Only two individuals (HbK and HbT) were recorded frequently enough to compare the proportion of time individual brown hyenas spent engaged in different behaviours (walking, standing, handling, feeding and competing). The time budgets of these individuals while at the seal colony did not differ significantly (HbK vs HbT t-test: walking $t = 0.45$, $p = 0.66$; handling $t = 1.09$, $p = 0.29$; arcsine square root transformed data: standing $t = 0.91$, $p = 0.38$; feeding $t = 1.39$, $p = 0.19$; Mann-Whitney U-Test: competing $U = 25$, $p = 0.64$) (Figure 6.5), nor did repeated observations of the same individual (Repeated Measures ANOVA: HbK

$F_{9,59} = 0.039, p = 1.00$; HbT $F_{5,29} = 0.069, p = 0.10$). The proportions of time spent on various behaviours by these two individuals also did not differ from all other sighted brown hyenas combined (HbK: t-test walking $t = 1.10, p = 0.28$; arcsine square root transformed data: standing $t = 1.33, p = 0.19$; handling $t = 1.33, p = 0.19$; Mann-Whitney U-Test arcsine square root transformed data: feeding $U = 150, p = 0.99$, competing $U = 96, p = 0.094$; HbT: t-test walking $t = 0.39, p = 0.70$; arcsine square root transformed data: standing $t = 0.023, p = 0.98$; handling $t = 0.50, p = 0.62$; feeding $t = 1.52, p = 0.14$; Mann-Whitney U-Test arcsine square root transformed data: competing $U = 88, p = 0.61$). Therefore the data were combined for all subsequent analyses.

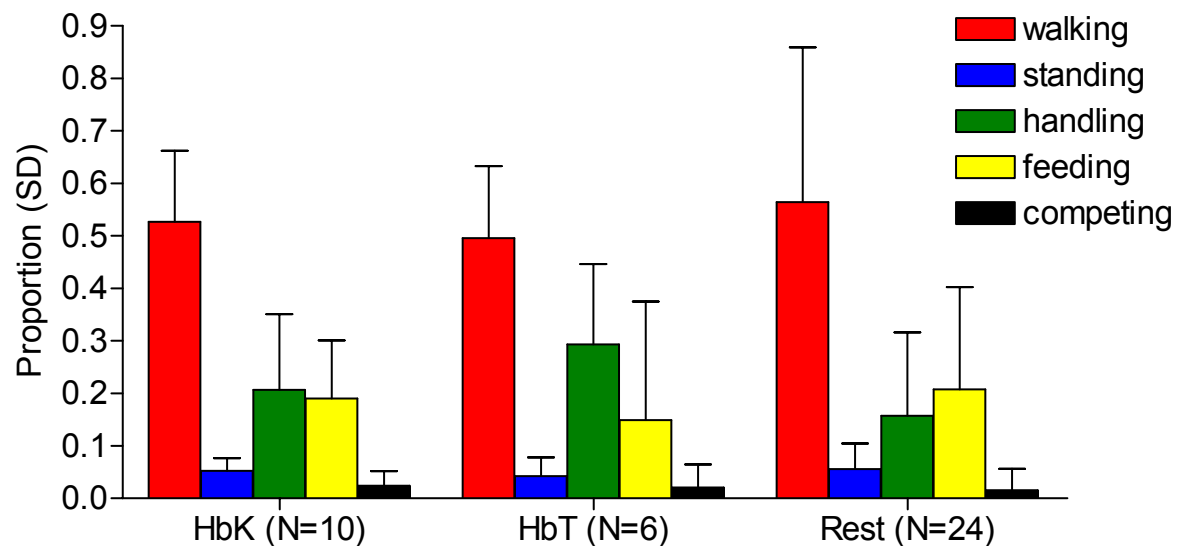


Figure 6.5: Proportion of time spent on different behaviours of brown hyena HbK, HbT and all remaining observations.

The time spent engaged in various behaviours differed significantly between the period before and after the peak pupping season (Figure 6.6). Brown hyenas spent significantly less time walking (t-test $t = 3.40, p = 0.002$) and competing (arcsine square root transformation: Mann-Whitney U-test $U = 39, p = 0.007$) during a foraging bout in January than in November, while feeding time and handling time increased significantly (feeding: t-test $t = 3.17, p = 0.004$; handling: arcsine square root transformed data: t-test $t = 2.56, p = 0.017$). The occurrence of creeping and hunting did not differ significantly between the two periods (Mann-Whitney U-Test creep $U = 63, p = 0.12$; hunt $U = 79.5, p = 0.42$), but these two events were significantly correlated (Spearman Rank Correlation $r = 0.62, p < 0.0001$) (Figure 6.7).

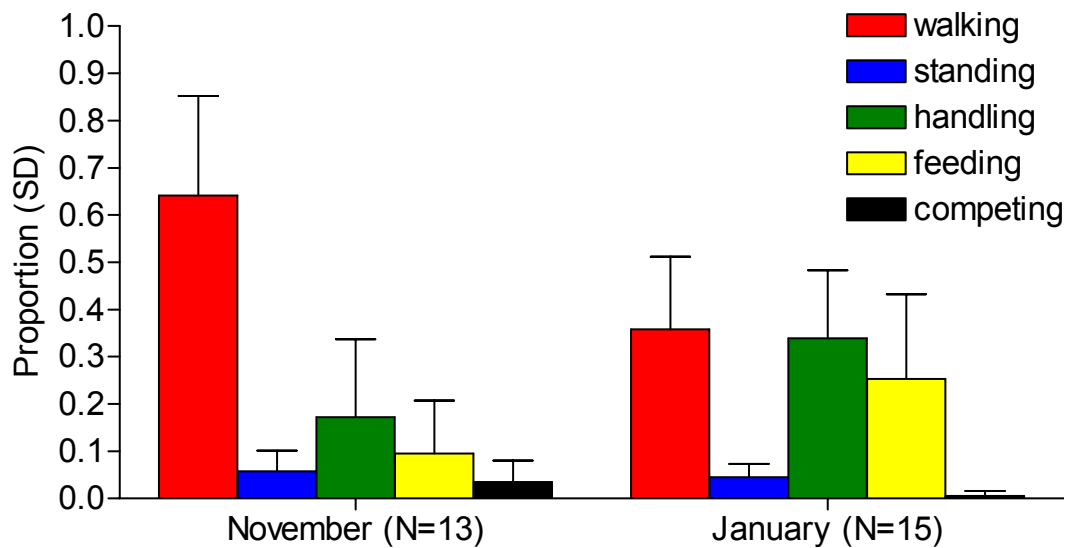


Figure 6.6: Changes in the proportion of time spent for various behaviours between November and January.

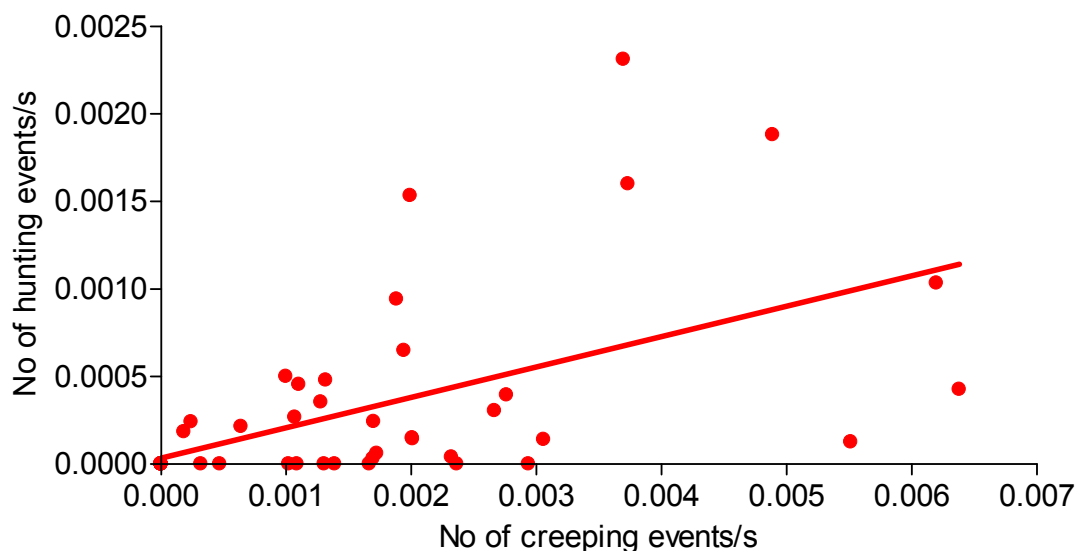


Figure 6.7: Correlation between the occurrence of hunting events and creeping events per second of observation.

6.3.3 Brown Hyena Foraging Behaviour at the Van Reenen Bay Seal Colony

The combined matrix (Table 6.2) included observations of 36 focus animals (four observations had to be excluded due to problems with the recording of the dictation phone). An individual matrix was also constructed for HbK, which included nine observations. The transformed proportions of corresponding rows of both matrices did not differ significantly (paired t-test or Wilcoxon Signed Rank Test (incl. Spearman Rank Correlation): e.g. walking $W = 15.0$, $p = 0.43$, $r = 0.99$, $p < 0.0001$; stop $W = 29.0$, $p = 0.16$, $r = 0.95$, $p < 0.0001$; creep $W = 13.0$, $p =$

Chapter 6

0.49, $r = 0.78$, $p = 0.0005$), suggesting that the combined matrix represents a description of brown hyena foraging behaviour at the Van Reenen Bay seal colony in general.

Table 6.2: Transition matrix of 36 focus animal observations at Van Reenen Bay showing the percentage of the sequential occurrence of a behaviour at time t .

t-1	t													
	Leaving	Walking	stop	creep	kill	attempt	grab & carry	drop	Compete	others	feeding on kill	feeding on carrion	cache	out of sight
Arrival	0	100	0	0	0	0	0	0	0	0	0	0	0	0
walking	1	0	63	20	0	0	3	0	2	2	1	2	0	6
stop	0	72	0	18	0	0	2	0	1	1	0	4	0	1
creep	0	26	56	0	13	3	1	0	0	1	0	0	0	1
kill	0	0	0	0	0	0	83	17	0	0	0	0	0	0
attempt	0	38	19	13	6	0	6	19	0	0	0	0	0	0
grab & carry	0	1	2	0	0	0	14	57	2	0	2	2	14	7
drop	0	12	8	10	2	0	42	0	9	0	15	1	0	1
compete	0	22	9	0	0	0	28	1	0	0	25	9	0	5
feeding on kill	0	36	5	8	0	0	5	2	42	0	0	0	0	2
feeding on carrion	0	60	7	1	0	0	15	0	13	2	0	0	0	2
others	0	68	18	10	0	0	0	0	0	0	0	0	0	5
cache	86	14	0	0	0	0	0	0	0	0	0	0	0	0
out of sight	0	71	5	0	0	1	14	0	4	1	2	1	0	0

Brown hyenas generally walked alongside the seal colony, interrupted by phases of stopping and standing while orientating or staring at the seals, which in the majority of the cases lead to a kill (Figure 6.8). The killing bite was always directed towards the skull of the seal pups. Only one already dead pup, a return kill, was bitten in the head, but dropped immediately to change the grip to the back to be carried away.

After killing the pup, the hyena remained at the kill site while holding the pup in its mouth in 41% of the cases. Otherwise it turned around and carried the pup for a few meters (22%) or dragged it backwards a few metres (12%). The hyena only occasionally performed the death shake (8%) after biting and holding onto the pup, twice due to the fact that the pup was still alive. The death shake also occurred in feeding-related circumstances, twice on carrion and three times on return kills.

Killed seal pups were carried away from the kill site more frequently than immediately consumed. While feeding on a kill, brown hyenas often engaged in competitive behaviours with jackals. Other than that, a kill was dropped to change



the grip from holding the skull to holding it on its back (75%) and then carried away from the seal colony.

Brown hyenas also scavenged seal pups. Feeding on carrion was generally followed by continuing to walk along the seal colony or by carrying the prey item away from the seal colony. Feeding on a scavenged pup only succeeded walking or standing at the colony in less than 10% of the sequences (Figure 6.8).

The combined matrix could not be tested with χ^2 statistics for serial independence due to the low sample size of 3 126 sequences (346 163 sequences were required), but the test showed that the expected frequencies differed from the observed frequencies (Chi² Test $\chi^2 = 8320$, $df = 169$, $p < 0.0001$). Therefore, it was assumed that the behaviours do not follow a random walk process and therefore show serial dependence, meaning that the preceding behaviour determines the following one.

After arrival at the seal colony, brown hyenas only left the colony without contact with prey in 10% of the sequences (Figure 6.9). In 65% of the sequences, the brown hyena fed on carrion first and only killed a seal pup first in 25% of the sequences. Feeding on a scavenged pup was followed in declining frequencies by feeding on another scavenged one, killing a seal pup or caching the scavenged pup. On the other hand, once the brown hyena had killed a seal pup, it continued killing, returned to feed on a previous kill or cached one of its kills, but did not return to a scavenged pup.

The expected values differed from the observed values (Chi² Test $\chi^2 = 143.2$, $df = 30$, $p < 0.0001$) and serial dependency was therefore assumed.

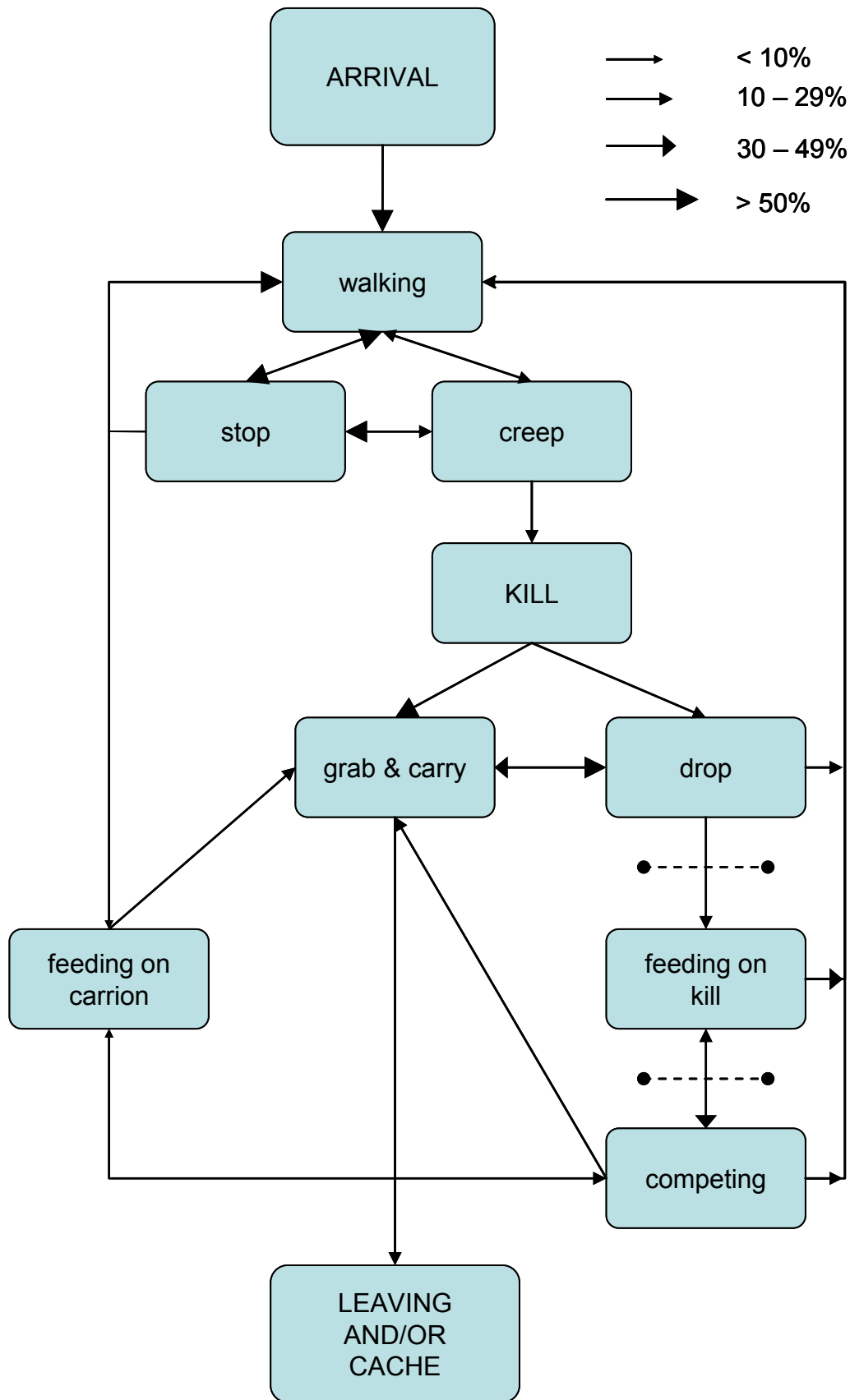


Figure 6.8: Transition diagram of the foraging behaviour of brown hyenas at the Van Reenen Bay seal colony. Dashed bars indicate impossible sequences for the scavenging part of the matrix.

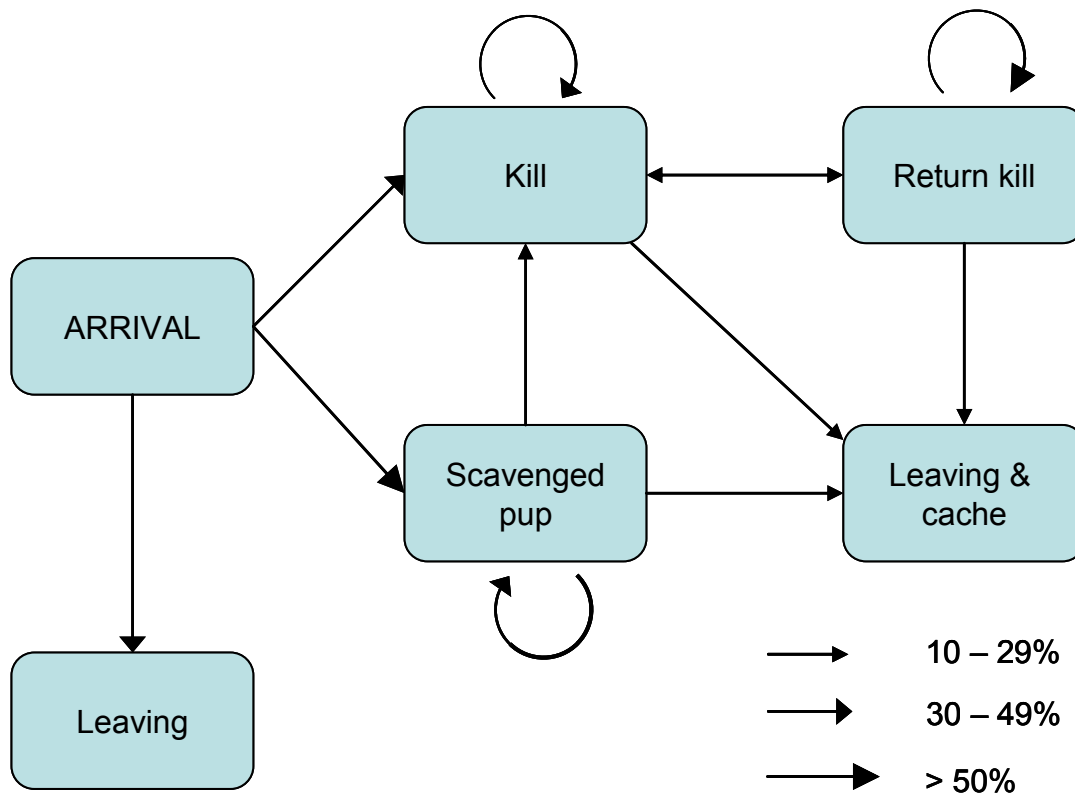


Figure 6.9: Transition diagram showing the sequence of handling of different prey categories.

Feeding on the first encountered and handled pup (kill or carrion) took place in 70% of the observations and in 15% of the observations a successively encountered and handled pup was the first feed. In 15% of the observations no pup was fed on at the colony, but 10% of the time a pup was carried away. Brown hyenas left the colony without killing a pup in 42.5% of the observations.

Brown hyenas approached seal pups either in an upright body posture or crouched. Both behaviours led to kills without significant differences in capture success (Fisher Exact Test $p = 0.22$), but seals were approached less frequently in a crouched position (Figure 6.10). The transition matrix could not be tested for serial dependency due to too many zero values. Nevertheless, the transition diagram shows that creeping in an upright position mainly followed walking, and creeping in a crouched position usually happened after the brown hyena had stopped.

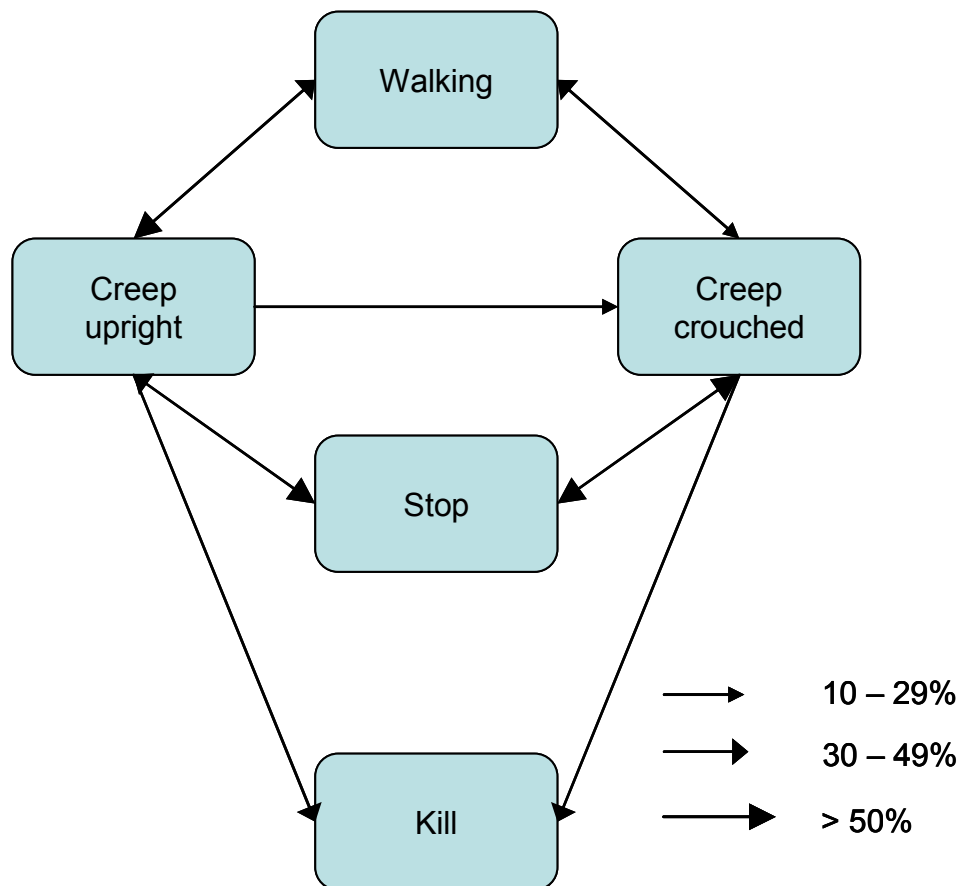


Figure 6.10: Transition diagram showing the sequences leading to the kill of a seal pup.

6.3.4 Prey Encounter Times, Hunting Efficiency, and Capture Rate

The prey encounter times before and after the peak pupping season were significantly different (Mann-Whitney U-Test $U = 378$, $p < 0.0001$). The interval between prey items was longest in November, averaging 47 minutes between prey encounters, and declined towards January with an average of 6 minutes between prey encounters (Figure 6.11).

Similarly, the interval between kills was significantly lower in January, after the peak pupping season, than in November, before the start of the peak pupping season (Figure 6.12) (Mann-Whitney U-Test $U = 84$, $p = 0.003$). A seal pup was killed on average every 64 minutes in November as opposed to every 10 minutes in January.

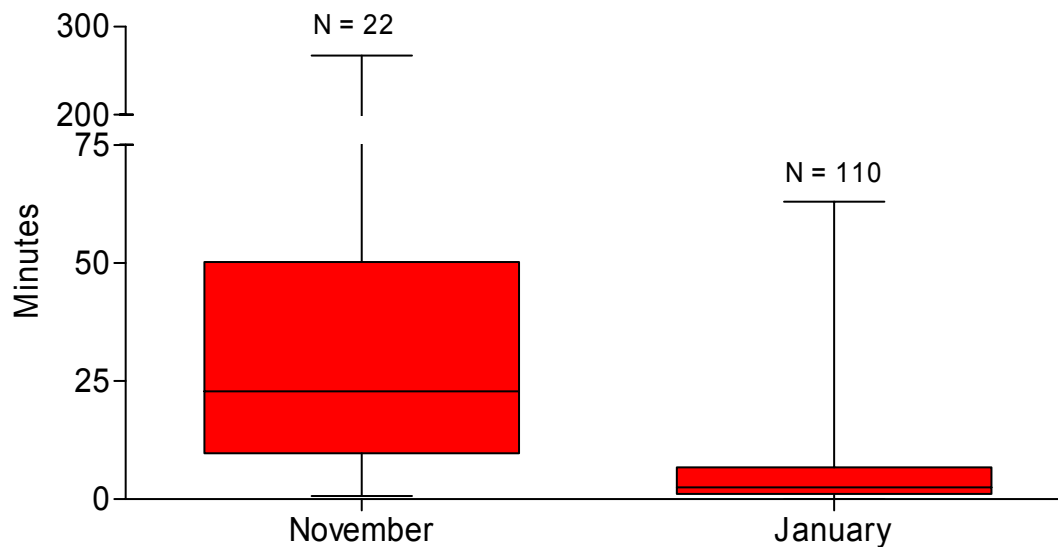


Figure 6.11: Interval between prey encounters (in minutes) before and after the peak pupping season.

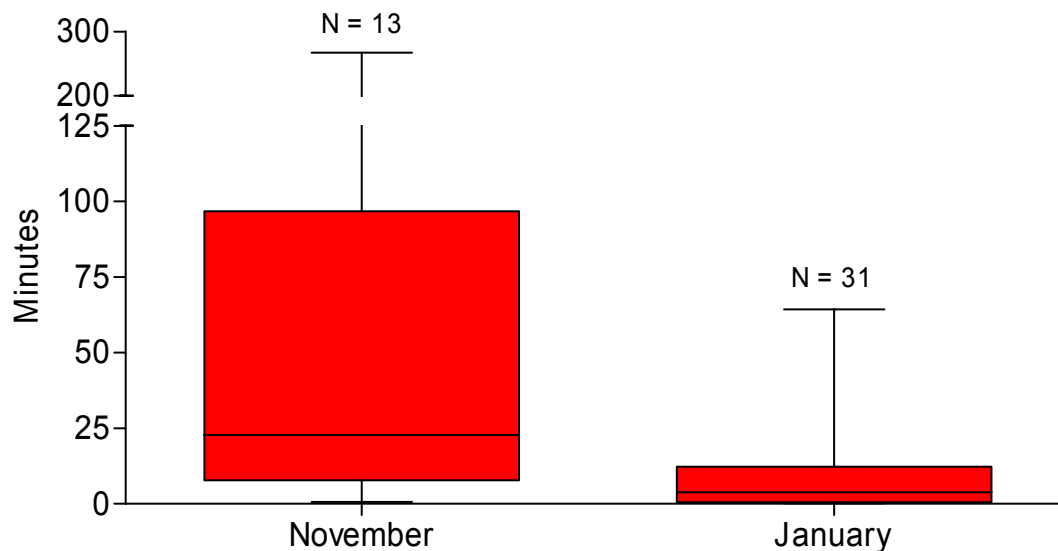


Figure 6.12: Interval between kills (in minutes) before and after the peak pupping season.

Hunting efficiency was significantly higher in January than in November (arcsine square root transformed proportions, Mann-Whitney U-Test $U = 21.5$ $p = 0.015$) (Figure 6.13). Hunting efficiency averaged 14% (± 0.27 SD) in November and 47% in January (± 0.33 SD). The mean capture rate in January was 2.71 ± 2.87 (SD) pups per hour and was significantly higher than the capture rate in November, where a mean of 0.51 ± 0.63 (SD) pups were killed per hour (Figure 6.14) (Mann-Whitney U-Test $U = 58$, $p = 0.045$).

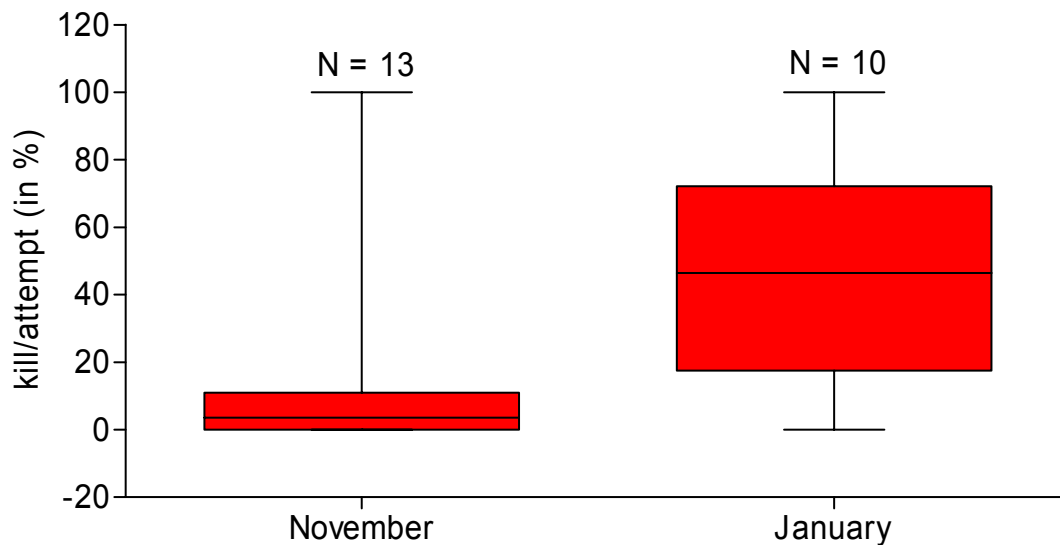


Figure 6.13: Hunting efficiency (in %) of brown hyenas before, during and after the peak pupping season.

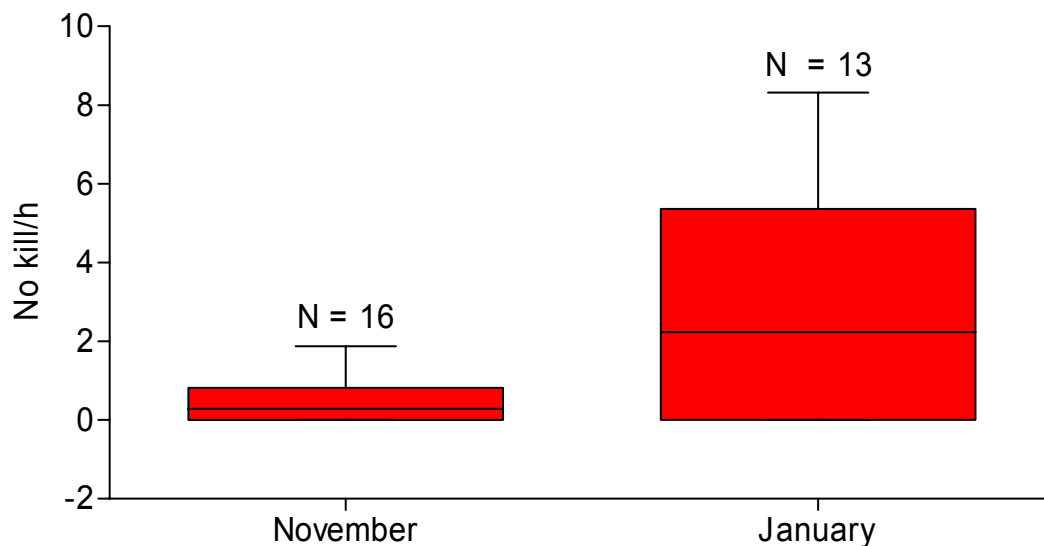


Figure 6.14: Capture rate (Number of kills per hour) of seal pups before and after the peak pupping season.

6.3.5 Seal Pup Predation

Brown hyenas killed seal pups throughout the study periods (November until March for three years). The predation rate of seal pups was 9.4% in 1997-1998, 9.6% in 1999-2000 and 5.1% in 2000-2001 (Figure 6.15). The daily predation rates differed significantly between years (Arcsine square root transformed data: Kruskal Wallis Test $H = 34.95$, $p < 0.0001$), with rates in 2000-2001 significantly lower than the previous two years (Dunn's Multiple Comparison Test $p < 0.001$).

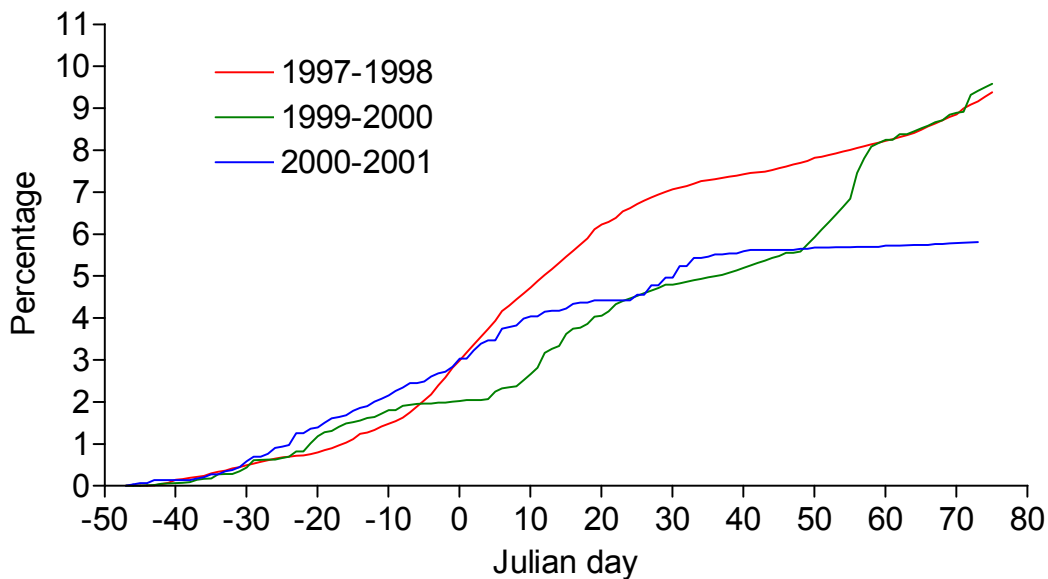


Figure 6.15: Cumulative predation rates (% of pups killed by hyenas) at the Wolf Bay seal colony between the beginning of the pupping season in November and 15 or 16 of March (Julian day 75) of the following year.

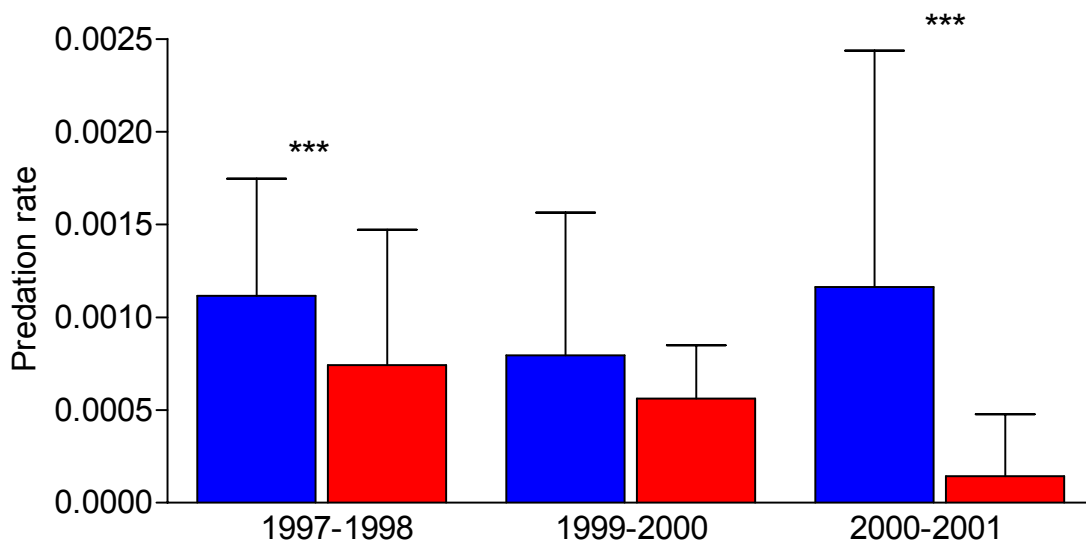


Figure 6.16: Daily predation rates (kills per available pups) in December and January (blue) and in February and March (red).

The predation rate in December and January, during the time when most non-violent mortalities were available and seal pups were abundant and relatively immobile, was significantly higher than in February and March during the 1997-1998 (Mann-Whitney U-Test $U = 691$, $p < 0.0001$) and 2000-2001 study period (Mann-Whitney U-Test $U = 606$, $p < 0.0001$). The predation rates in 1999-2000 did not differ between periods (Mann-Whitney U-Test $U = 1059$, $p = 0.051$) (Figure 6.16).

The absolute number of pups killed in the sample areas per day was significantly different in all years (Kruskal Wallis Test $H = 118.8$, $p < 0.0001$, Dunn's Multiple Comparison Test $p < 0.001$) (Figure 6.17). Within years, significantly more pups were killed in December and January than in February and March (1997-1998: Mann-Whitney U-Test $U = 502.5$, $p < 0.0001$; 2000-2001: Mann-Whitney U-Test $U = 659$, $p < 0.0001$), except in 1999-2000 (Mann-Whitney U-Test $U = 1305$, $p = 0.97$) (Figure 6.18).

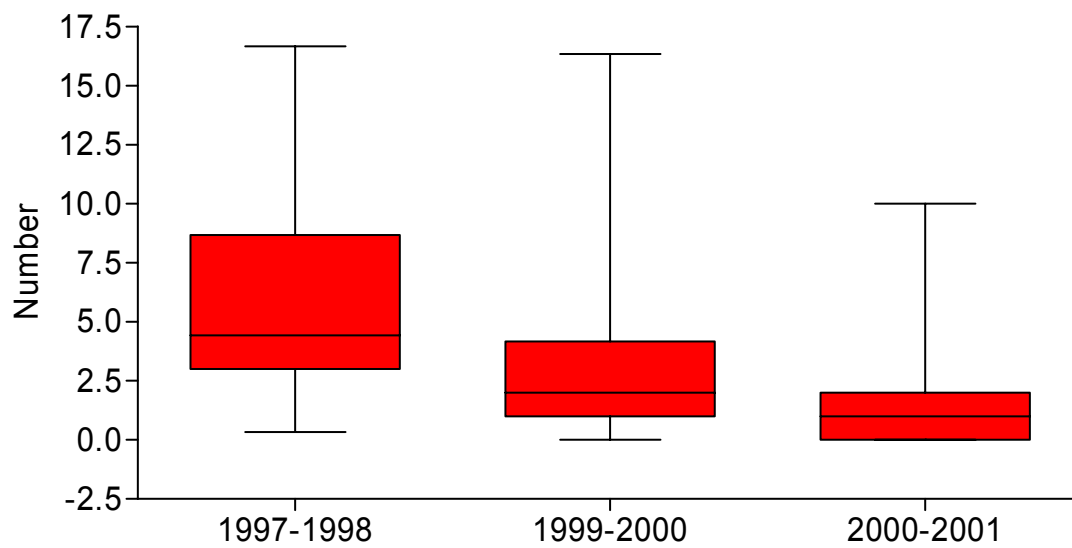


Figure 6.17: Number of pups killed at the Wolf Bay seal colony per day.

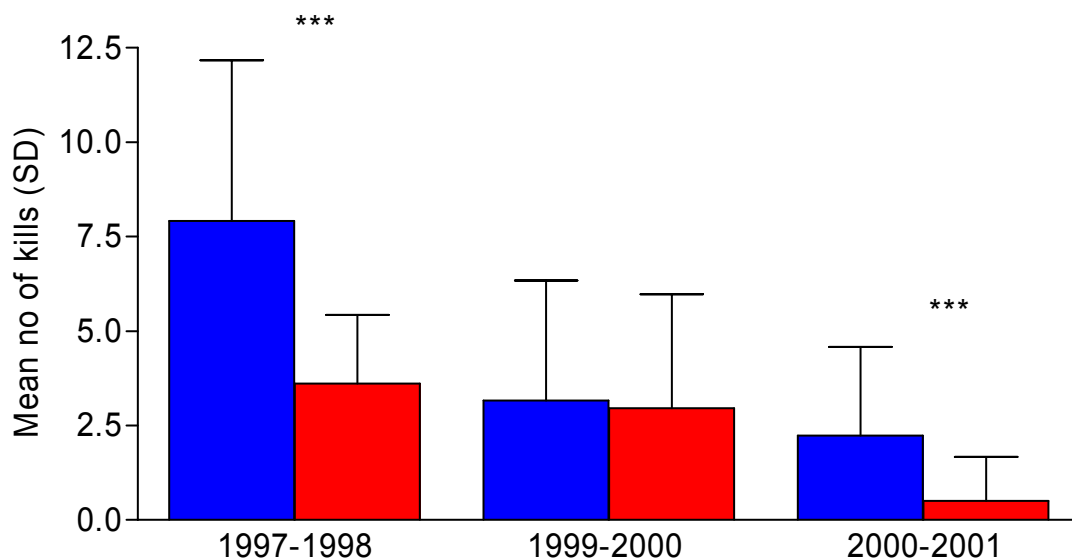


Figure 6.18: Mean number (\pm SD) of pups killed during different years and months (blue = December/January, red = February/March)

6.3.6 Mass Kill Events

Mass kill events occurred throughout the study period. The average number of killed pups per mass kill event was 3.31 ± 1.62 (SD) pups and did not differ between years (Kruskal Wallis Test $H = 0.27$, $p = 0.87$) (Figure 6.19). Significantly more pups were killed per mass kill in January than in December in 1999-2000 and 2000-2001 (Mann-Whitney U-Test: 1999-2000 $U = 32$, $p = 0.012$; 2000-2001 $U = 21.5$, $p = 0.011$), but there was no difference in 1997-1998 (t-test $t = 1.02$, $p = 0.33$) (Figure 6.20). Guarding by adult females (Chapter 4) did not influence the number of pups killed per mass kill event (Mann-Whitney U-Test $U = 506$, $p = 0.61$) (Figure 6.21).

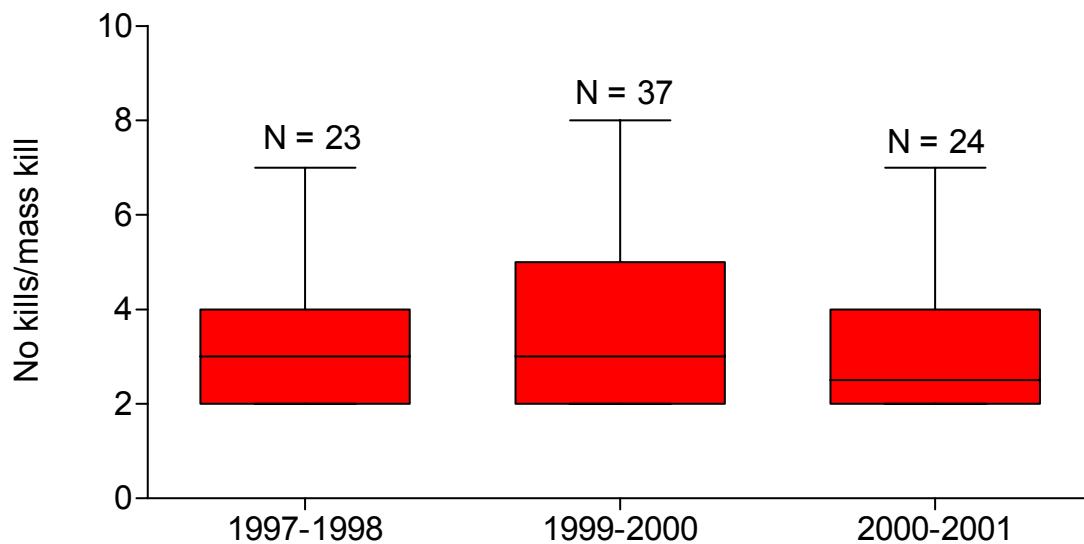


Figure 6.19: Number of killed seal pups per mass kill event at the Wolf Bay seal colony in different years.

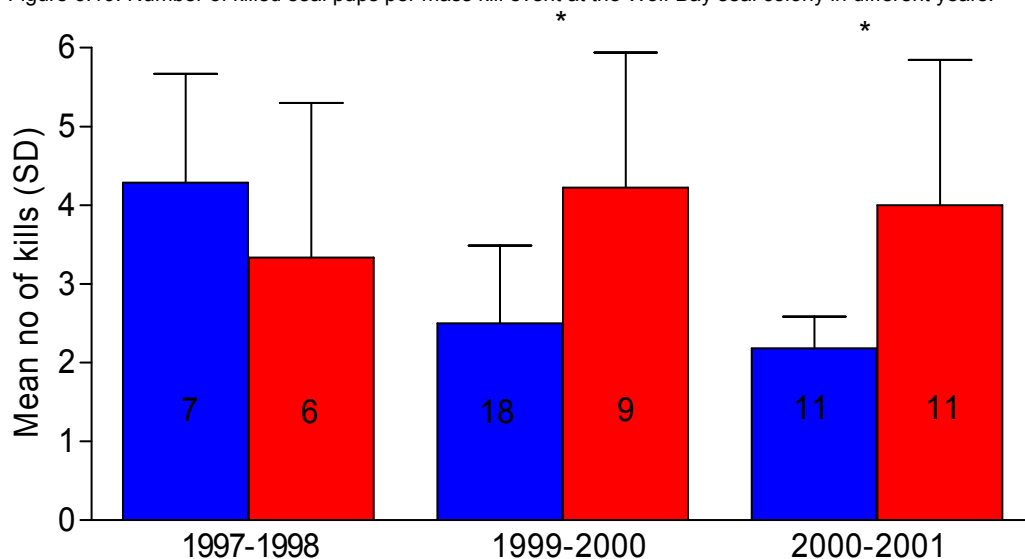


Figure 6.20: Number of killed seal pups per mass kill event at the Wolf Bay seal colony in different months for different years (blue = December, red = January, N = numbers in bars)

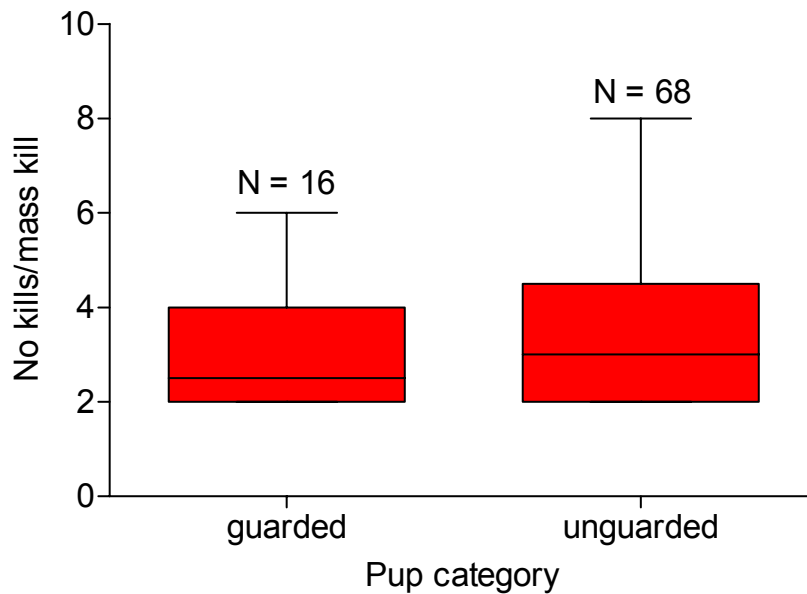


Figure 6.21: Number of seal pups killed per mass kill event during the period when they were mainly guarded or increasingly unguarded by their mothers.

6.4 Discussion

6.4.1 Brown Hyena Foraging Behaviour

a) Search for Prey

Brown hyenas cover vast distances in order to find food (Mills 1978, Owens & Owens 1978), travelling an average distance between large meals of 9.2 km in the southern Kalahari (Mills 1984). They are mostly nocturnal, but under cool environmental conditions can also be active until midday and from late afternoon (Mills 1978, Owens & Owens 1978). However, Kalahari brown hyenas were only active during daylight 6.2% of the time. Brown hyenas along the coastal Sperrgebiet spent on average 6.3% (0.3% to 23.8%) of the day during daylight hours at the seal colony. Therefore, they showed higher activity during the day than it is described for Kalahari hyenas, assuming, that brown hyenas remained active after leaving the seal colony (e.g. feeding, finding a resting site). The difference in climatic conditions between the Kalahari and the coastal Namib Desert may be the cause for the differences in activity. However coastal brown hyenas show different activity patterns during different seasons. They visited the seal colony throughout the day in autumn, before the peak of the pupping season, but with the progressing summer and increasing air temperatures they arrived earlier, spent less time at the seal colony and hence left the colony earlier.



However, not only environmental factors play a role in brown hyena activity and attendance patterns (see below).

Brown hyenas are solitary foragers (Mills 1978). Prey availability and acquisition influence this foraging strategy and the use of predominately small prey items leads to this behaviour (Kruuk 1975). Nevertheless, brown hyenas can congregate for communal scavenging at large carcasses (Owens & Owens 1978). Communal feeding was not observed in this study, but a maximum of two brown hyenas had overlapping foraging times on five occasions. Intraspecific interactions were only observed between two pairs of brown hyenas. Each hyena reacted to the other brown hyena once it was detected, and they either stared intensely at each other from a distance of 5 to 10 metres or they displayed certain body positions indicating a tendency to flee, appease or attack as described by Mills (1990). Direct body contact never occurred and it is unknown whether the animals belonged to the same social unit. After the encounter, both hyenas continued foraging at the seal colony, not directly avoiding each other (compare with Owens & Owens 1978), but usually walking away in opposite directions.

While searching for prey, brown hyenas walked relatively quickly alongside the seal colony or in between the seals. A similar fast walk is described by Mills (1978) and Owens & Owens (1978), who calculated a speed of three to six kilometres per hour. While walking the head is held slightly down, and the hyenas stop frequently, head held upright, to sniff the air or to stare into the distance. The wind plays an important role for olfactory detection of prey, but they are also very capable of visually detecting prey (Mills 1978, Owens & Owens 1978). Brown hyenas foraging at seal colonies stopped frequently and either looked around or stared at a specific group or individual seal, possibly using both visual and olfactory senses, as sniffing was observed on many occasions.

Brown hyenas encountered many non-violent mortalities while foraging at the seal colony (Chapter 4) and therefore were expected to use this easy and abundant food source instead of engaging in hunting (Estes 1967). However, other large predators do not occur in the study area, and brown hyenas can fill the vacated niche and become active hunters (Estes 1967). Such behaviour is seen with foxes (*Vulpes vulpes*) and wildcats (*Felis silvestris*) in Europe and America, where they become successful predators in the absence of wolves



(*Canis lupus*) (Estes 1967). This development is reflected in the general foraging behaviour of brown hyenas at the seal colony. Brown hyenas spent the major proportion of time searching for prey (for a temporal change in time budget, see below), interrupted by phases of standing, while looking around and staring at seals, which ultimately led to approach of the seals and subsequent hunting. Although brown hyenas scavenged as often as fed on kills, the foraging sequence shows a clear preference for hunting-related behaviours, and approaches to seals with the apparent intent to kill outweighed the scavenging side of the sequence.

Scavenging is the “consumption by an animal of a carcass, which neither it, nor others of its species, killed” (Kruuk 1972a). In this study, however, the cause of pup mortality often could not be determined. Therefore scavenging occurred on carcasses that were not killed by the focus animal during the observation and could hence include non-violent mortalities, jackal kills (see Chapter 8), or hyena predations from another individual or the same individual, killed during a previous visit to the seal colony. Furthermore, the definition of hunt by Mills (1990) specifically developed for Kalahari brown hyenas of “any interaction between a brown hyena and potential prey, where the brown hyena moved towards the prey at increased speed, provided that there was no carrion in the vicinity” could also not entirely be accepted for this study. Chasing seal pups was not necessary for capture, with only a few exceptions, and carrion was usually in the vicinity. Therefore the definition was modified as a determined movement towards the prey with no carrion in the immediate vicinity, for example next to the live pup.

Since hunting plays a major role in the foraging strategy at seal colonies, questions concerning the killing instinct and trigger for hunting should be addressed. The killing instinct of brown hyenas seems strong, but consumption depends on the palatability of the prey or the hyena’s hunger state (Goss 1986, Skinner et al. 1995). Hunting is usually triggered by stimuli that come from potential prey species (Estes 1967; see below).

b) Brown Hyena Hunting Technique

Hyenas are most closely related to cats and viverrids and generally show a felid lifestyle concerning mating and parental care but a canid lifestyle regarding

hunting and killing behaviour (Schaller 1972). The combination of instinct and learned behaviours plays an important role in the development of hunting and killing techniques (Eibl-Eibesfeldt 1956, Eaton 1970, Endler 1991). The grasping of prey with the mouth precedes the grasping of prey with the forepaws as done by many felids. A precisely aimed killing bite is a more recent method and learned by trial and error (Eibl-Eibesfeldt 1956), whereas undifferentiated biting, tossing and throwing is primitive (Eisenberg & Leyhausen 1972). An aimed bite to the head or neck region is typical for cats, which kill their prey by breaking the braincase or separating the vertebrae (Leyhausen 1965 cited in Kleiman & Eisenberg 1973). Such a killing bite is used by many carnivores, including marsupials, insectivores and primates, but often depends on the defence abilities of the prey (Eisenberg & Leyhausen 1972, Ben-David et al. 1991). A subsequent shaking of the prey, known as the death shake, is often stimulated by the activity of the prey and is therefore a response to still-living prey (Eibl-Eibesfeldt 1956, Eisenberg & Leyhausen 1972, Ben-David et al. 1991).

Brown hyenas usually hunt alone, although they live in permanent clans (Skinner 1976, Owens & Owens 1978, Owens & Owens 1996). Teaching hunting techniques and gaining experience through “hunting games” by the cubs has not been observed (Owens & Owens 1979). Most hunting is directed towards small mammals (Skinner 1976, Mills 1978), and some brown hyenas show specialization of hunting techniques towards certain prey species, such as southern Kalahari brown hyenas hunting springbok lambs (*Antidorcas marsupialis*) (Mills 1978) and korhaans (*Eupodotis* spp) (Mills 1978, Mills 1990) or brown hyenas killing livestock (Skinner 1976). They are also known to chase their prey for up to 1.1 km (Mills 1978). The killing bite is often directed to the head and neck region (Skinner 1976, Mills 1978, Skinner et al. 1995), therefore using the feline strategy of killing rather than the canine one. Death shakes have been observed in the central Kalahari (Owens & Owens 1978) but not in the southern Kalahari (Mills 1978).

Brown hyenas along the costal Sperrgebiet are known to kill seal pups, hence choosing small prey, comparable to prey choice in Kalahari hyenas, with an aimed bite into the skull (Skinner et al. 1995, Wiesel 1998). All killing bites in this study were directed at the skull, whereas the majority of dead pups were



grabbed at the back, which might indicate that the specific killing bite is innate, although the degree of experience of the observed hyenas was unknown. Nevertheless, even though seal pups are small and seem easy prey, they have sharp teeth at birth and are extremely flexible in their movements and therefore can, although never observed, possibly injure the hyena if the killing bite is directed at other parts of the body. Killing bites are usually directed towards the most vulnerable part of the prey's body, which in the case of seal pups is the skull, as it is fragile and has open sutures (Rand 1956) and therefore ensures the quick death of the pup. Injuries can thus be avoided and the specialization of the killing bite could be a combination of innate and learned behaviour.

Death shakes occasionally occurred, but not exclusively as a response to still-living pups, and they were sometimes feeding related.

c) Brown Hyena Hunting Behaviour and Handling of Prey at Seal Colonies

Foraging at seal colonies was very successful. Brown hyenas obtained food in 90% of the visits. In the majority of the observations, the brown hyena encountered a dead pup first and only immediately killed a seal pup in 25% of the sequences. Nevertheless, once the hyena had killed a seal pup it did not return to a dead pup that it had not killed, and usually continued killing or returned to one of its previous kills before leaving the colony with or a without pup. The relative value of certain prey items will be discussed in Chapter 8, but in the Kalahari, although the contribution of killed animals to the brown hyena's diet is small, hunting is important and provides the hyena with the odd highly nutritional meal (Mills 1978).

Once the brown hyena had located a live pup with the intent to kill, it approached either in an upright position, walking slowly towards the seal while staring in its direction, or in a crouched position, holding its head low. The latter posture was used less frequently, but capture success did not differ between the uses of different postures. Standing before the approach of seals mainly led to the use of the crouched position, whereas the upright position of the walking behaviour was not changed during the upright approach. Stalking predators often lower their heads to reduce body size while approaching prey. This method usually decreases the flight distance of the prey (Schaller 1972). The crouched

body posture used by brown hyenas could serve this purpose, but eliciting a certain posture seems to be dependent on the preceding behaviour. However the majority of seals did not show any anti-predator behaviour (Chapter 4), making the use of the crouched posture seem unnecessary.

The behaviour of seal pups or adult seals might influence the method of approach. A stalking approach to pups surrounded by adults, with their mother or alert pups, might be more successful and requires further investigation. Chasing of seals did not take place, and the apparent lack of anti-predator behaviour of the seals (Chapter 4) suggests that brown hyenas could usually walk and approach the seals without triggering a response, irrespective of the body posture.

As an exception to the above described hunting method, two individual brown hyenas showed unusual hunting behaviour during incidental observations at seal colonies, as illustrated below:

1. August 2001: A brown hyena walked alongside the seal colony at Van Reenen Bay, followed by a jackal. The hyena approached a group of seals that had started to run towards the sea, possibly due to its presence (Chapter 4). As soon as most of the seals were in the sea, both the hyena and jackal walked to the area where the seals had been and lay down. After 15 minutes the hyena moved away and lay down away from the seals. 20 minutes later, it moved towards the seals and tried to kill a seal pup, but was unsuccessful. The seals again ran towards the sea. The hyena lay down again and stared at a female with pup, which had stayed behind, and tried to capture the pup, again unsuccessfully. The hyena lay down again and waited for the seals to return from the sea. Five minutes later the hyena got up and the seals once again ran into the sea. The hyena lay down again and the same thing happened twice more. After 20 minutes many seals were back on land and the hyena moved on its belly towards the closest seal, suddenly standing up, defecating and moving away from the seals. Thus, the brown hyena used an ambush approach as opposed to the previously described stalking approach (Curio 1976).

The hyena was limping on one of its hind legs, and this injury could have contributed to its unusual behaviour. However during the behavioural focus



animal observations at Van Reenen Bay, HbS was observed lying down in groups of seals. Whether HbS was the same animal observed in August is unclear.

2. September 2002: A brown hyena walked quickly after a group of seals at the Baker's Bay seal colony until they were at the water's edge and then attacked one of the last pups reaching the water. The hyena tried to grab the skull, but the pup defended itself. The hyena tried to kill the pup several times, following it deeper and deeper into the water until the pup was able to swim away. Five minutes later, the hyena walked quickly into another group of seals, ran after the fleeing animals and grabbed one of the running pups at the head. The hyena fed on the pup for 1 ½ hours before walking away from the colony, leaving the remains of the pup behind.

Both observations took place eight to nine months after the end of the seal pupping season. Brown hyenas might adapt their hunting behaviour to changes in pup availability and in relation to the pups' increased size, mobility and ability to defend themselves. This possible influence is discussed later (Chapter 7), but it is assumed that the observations mentioned above were individual hunting techniques, as other brown hyena observed during the same period showed the typical hunting behaviour described in this study. Nevertheless, this subject requires further investigation during times outside the seal pupping season.

Feeding at the seal colony took place in 85% of the hyena sightings and could occur at any time during the sequence (compare with Kruuk 1972b), although the first encountered and handled prey was fed on 70% of the time. The feeding rate of brown hyenas is described as more leisurely than that of spotted hyenas, and they often spend hours at a carcass (Owens & Owens 1978). While feeding on seals, brown hyenas often stopped for short periods, looked around, and competed with jackals. The same behaviour is described for brown hyenas in other environments (Skinner 1976, Owens & Owens 1978).

Brown hyenas also carried prey items away from the seal colony, either to protected feeding sites close by, returning later to the colony, or further inland. These items were not necessarily fed on before being removed from the colony. Items that were carried away from the colony were grabbed at the back or, on one occasion, the neck and back flippers were held together. They were regularly



dropped to release the grip before carrying them further. Whether the number of grip changes increased in the progressing pupping season with the weight of the prey item is unknown but this is definitely a possibility.

Kalahari hyenas store food to avoid detection by other scavengers or to provide cubs with additional food (Mills 1978, Owens & Owens 1978). The occurrence of caches in relation to the foraging behaviour at seal colonies will be further discussed in Chapter 8, also in relation to interspecific competition.

d) Brown Hyena Hunting Efficiency

A successful predation sequence starts with the encounter of the prey, which depends on prey density (Endler 1991). Following the detection and identification of the prey item, the prey will be approached and captured. The success of the latter two behaviours depends on the relative size of the predator to the prey, the mobility of both species, the prey density and the predator's experience (Schoener 1969, Lingle & Pellis 2002). The sequence ends with the consumption of the prey (Endler 1991). The predator should reach the last stage of the sequence as quickly as possible to avoid interruption through anti-predator strategies of the prey. Therefore hunting success usually reflects the efficiency of anti-predator behaviours (Schaller 1972).

Brown hyenas encountered significantly more pups per unit of time in January, after the peak pupping season, than in November. Likewise, the interval between kills was shorter in January than in November. The high density of pups after the peak pupping season seems to have influenced this pattern. Encounter rates of wolves with elk (*Cervus elaphus*) increased with elk group size and had positive effects on the attack success (Hebblewhite & Pletscher 2002). The change in density-dependent prey encounters also had a positive influence on the brown hyena's hunting efficiency and capture rate. Hunting efficiency increased from 14% in November to 47% in January, and significantly more pups were killed per unit of time in January. These high efficiency rates naturally differ from known hunting success rates of brown hyenas in other environments, where prey species have well-developed anti-predator strategies and do not occur in dense accumulations. Hunting success in those environments lies at between 5.7% and 13.7% (Mills 1978, Owens & Owens 1978, Mills 1984). Pienaar (1969) describes



the brown hyena as a more aggressive hunter than the spotted hyena, but Skinner (1976) states that is an error.

In other cross-ecosystem predator-prey systems, similar hunting success rates are found. Wolves preying on spawning salmon (*Oncorhynchus* spp) in high abundance had a hunting efficiency of 39.4% (Darimont et al. 2003), similar to our estimate of 47% in January. In polar bears (*Ursus maritimus*), 10% to 24% of all predation attempts on ringed seal (*Phoca hispida*) are successful, which represent a total of 8% to 44% of the annual pup production (Hammill & Smith 1991). Polar bear hunting success depends on anti-predator strategies regarding the breeding habitat of the seals and is one third less when seals are in protected lairs. However predation attempts increased with lair density and with the progressing pupping season.

In this study, the occurrence of creeping and hunting did not differ between the period before and after the peak pupping season, but the number of creeping events per unit of time was positively correlated to the number of hunting events. Thus increased effort resulted in increased success independent of prey density, which is also seen in brown bears (*Ursus arctos*) foraging on salmon (Gende & Quinn 2004). An increased tendency to attack due to greater hunting success can also increase with the vulnerability of prey, as capture success depends on the mobility of the predator versus the mobility of the prey (Sih & Christensen 2001) or with the prospect of a successful attack (Curio 1976). However, considering the lack of anti-predator behaviour of seals and despite the fact that the few reactions of seals mainly occurred late in the predation sequence (approach stage) it is surprising that many predation sequences are interrupted at that specific stage. The error could lie in the definition of an approach as a determined movement towards the prey, as the intent to kill remains unknown. Furthermore, as evolved scavengers brown hyenas could have a natural “shyness” towards live prey, especially since adult seals are larger in body size. Lastly the dense aggregation structure of the colony could have a confusion effect on brown hyenas so that they experience difficulties in concentrating on one specific individual (Krakauer 1995, Schradin 2000). Movement of prey can increase the confusion effect (Krakauer 1995). Strategic counter methods such as disrupting the group of prey animals to expose individuals were not observed during the



study, but the fleeing of seals towards the sea or increased alertness by moving elicited an approaching behaviour in hyenas in 52% and 40% of cases respectively (Chapter 4).

e) *Time Budget*

Prey encounter rates, hunting efficiency and capture rate are important factors in determining the optimal effort that should be spent for foraging behaviours expressed as time. However, the mechanism behind the decision to forage is hunger. Hunger is one of the internal factors that cause a predator to search for prey and to hunt and ultimately determines the amount of the captured prey item that is eaten (Curio 1976). The rate of prey capture is often one of the parameters through which the degree of hunger can be determined. Hunger also often increases the range of food items accepted, and selectivity increases with satiation (Chapter 7).

Prey has to be located efficiently in order to ensure economic feeding. Many predators choose familiar food, search for specific prey (Kruuk 1972a) or search in specific areas using the method of “area-concentrated search” (Curio 1976), when one prey type is associated with one area.

Brown hyenas spent significantly less time foraging at seal colonies in January, after the peak pupping season, when seal pup density was highest. Other species, such as European polecats (*Mustela putorius*), also decrease foraging time when they encounter aggregated and easy resources (Lodé 1999). Although the proportion of time brown hyenas spent feeding increased in January, the absolute time spent feeding did not differ between November and January. However, the time spent feeding on each prey item decreased (compare with Cook & Cockrell 1978), so that a larger number of different prey items was consumed (Chapter 8). Although the energy value gained from each prey item is unknown, two scenarios seem possible: (1) The brown hyena minimizes the time spent on each prey item by being more selective later in the season in order to obtain a specific energy or (2) the hyena maximizes its energy by using a constant feeding time per foraging period by selectively feeding on parts of the prey with high energy content.



How much time brown hyenas have to spend on activities other than foraging (e.g. territorial maintenance) to maximize their reproductive success is unknown, but the decrease in total foraging time at the colony could indicate that other activities are important. However the decrease in total time spent at the seal colony could also be due to an increase in air temperature in summer. Brown hyenas arrived significantly earlier at the seal colony and left the colony before midday in January, possibly to avoid high air temperatures, compared with November.

The number of hyena sightings per hour did not change over time, and hyenas therefore neither became more nocturnal nor visited the seal colony less frequently. Nevertheless, behavioural observations were only carried out during the day, and night-time foraging might show a different pattern.

Several parameters are important to determine optimal diet strategies (Schoener 1969, Schoener 1971). The search time depends on the speed of the predator and prey and the search area of the predator. Cape fur seals are relatively stationary, as they are found only at the seal colony, and brown hyenas travel directly to those colonies to find food, so that the time before arrival at the seal colony can be excluded from the search time. Furthermore the search area is confined to the colony area and brown hyenas possibly use an “area-concentrated search” pattern, as they learned to find a reliable food source to return to. Therefore the total time spent at the seal colony, and the walking part of this study’s sequences in particular, represent the brown hyena’s search time. The number of food items encountered per unit of time should increase with prey density and decrease the search time, but lower hunger might also influence the time spent searching. Brown hyenas spent a significantly smaller proportion of time walking in January than in November, therefore reducing the time to obtain energy, whilst the encounter rate per unit of time increased.

The pursuit time, expressed here as prey encounter interval and interval between kills, also decreased in January and therefore depends on prey density. Hence search energy expenditures were less in January, but pursuit energy possibly stayed constant and might have led to specialization (Chapter 7).

The handling and eating costs per item depend on the relative size of the feeder to the prey and are discussed in Chapter 8. Nevertheless it should be



mentioned here that feeding and handling times per prey item were lower in January, possibly in relation to the satiation of the brown hyena or to partial preferences in prey consumption. The capture rate and hunting efficiency were higher in January, possibly related to an increase in prey encounter times due to higher density of seal pups. Small prey are more susceptible to predators at higher densities (Khan & Galeb 2003), and this pattern is reflected in the results of this study.

The caloric value of different prey items (Chapters 7 and 8) is also of importance for the determination of an optimal diet strategy.

Lastly, the relative abundance of food items also affects the optimal foraging strategy. Cape fur seals are relatively abundant within the brown hyena's home range during the entire year compared to other potential prey species of similar size, and the total abundance of seal pups is higher in January than in November. Ideally a patch should be left when the rate of energy intake becomes equal to that of the entire habitat (see Charnov 1976 cited in Hills & Adler 2002) and therefore it is difficult to assess the brown hyena's perception of the optimal time to leave the seal colony "patch" in this case, as the rate of energy intake at seal colonies may always be higher than in the rest of its home range. However when regarding a single prey item as a patch, other conclusions can be drawn (Chapter 8).

Other factors may lead to daytime foraging by brown hyenas. The absence of human disturbance and the cool weather conditions along the coast enable brown hyenas to increase daytime activity in general. However, some seal colonies, such as the Baker's Bay seal colony and the Atlas Bay seal colony, lie in overlapping areas of the home ranges of brown hyenas from different clans (Chapter 5 and unpublished data). Temporal territoriality could explain daytime activity in those areas. Domestic cats (*Felis catus*), for example, use common trails through their territory but avoid each other in time (Curio 1976). Population size estimates and telemetry data analysis suggest this explanation for brown hyenas foraging at seal colonies (unpublished data), but more evidence is needed. Lastly predators often synchronize their activity with the main activity of their prey or are influenced by prey availability and vulnerability during different times of the day (Curio 1976). The spatial structure of the seal colony and the



attendance of different seal classes, as well as the behaviour of seals, changes in the course of the day and with the progressing season (Chapter 4).

Brown hyenas could choose to forage during the day to avoid adult seals at the colony. Female seals, for instance, defend their pups, and the fewer females are present at the colony the more seal pups are unguarded and therefore easy prey, in addition to the ones that wait for their mother's return from the foraging trip. In general, most adults are on land at night in contrast to daytime attendance, which shows large fluctuations. In summer the minimum number of adult female seals occurs from late morning to early afternoon, whereas in winter the minimum number of female seals is recorded in the early evening (David & Rand 1986) and the general flow to the sea is more variable. This seasonal difference is partly reflected in the brown hyenas' attendance pattern at the Van Reenen Bay seal colony. In autumn hyenas are active throughout the day, possibly influenced by cooler temperatures. Nevertheless the number of adult seals during the day before the peak pupping season in December varies, but certainly is less than at night. After the peak of the pupping season brown hyenas still forage during the day, despite higher air temperatures, but shift their activity into the morning hours, possibly choosing a time when adult seals move to sea for thermoregulation. If air temperature were the only influence on brown hyenas' activity pattern, they might become entirely nocturnal in summer.

6.4.2 Predation Rate at Seal Colonies

Brown hyenas scavenge and kill seal pups throughout the pupping season (Goss 1986, Skinner et al. 1995, Wiesel 1998). Dead seal pups are abundant during and shortly after the peak of the pupping season, and brown hyenas therefore do not necessarily follow the path of least effort by exclusively using those mortalities as food, not considering the value of different prey items (see Chapter 7). As active predators, they might therefore have an influence on the stability (persistence of the two species) of the predator-prey system (Slobotkin 1974). Several hypothesis exist concerning the effect of predation on prey, amongst others (1) the predation limiting hypothesis, where predation is the primary factor that limits prey density, (2) the predation-regulating hypothesis, where predation regulates



prey density around a low-density equilibrium, or (3) the predator pit hypothesis, where the prey population may escape past low-density threshold where they are regulated by predation and become regulated by food availability (Feldersnatch 2003). The establishment of most mainland Cape fur seal breeding colonies followed the initial aggregation of young seals with only a few mature females giving birth (Shaughnessy 1987). Initial growth of the colony was limited, and the failure to grow was attributed to brown hyena and jackal predation (Shaughnessy 1987). Once a certain threshold was passed, however, the spread of seals to the mainland could not be prevented by predation (Rand 1956), so that the latter of the three predation hypotheses seems to be the most appropriate one to describe the brown hyena-Cape fur seal predator-prey system, especially since the system may currently be donor-controlled (Chapter 5).

Brown hyenas kill seal pups that are subject to high non-violent mortality during the first month of their life (Chapter 4, De Villiers & Roux 1992). Pup mortality estimates were between 18% and 61% in this study, and no data are available about the survival of Cape fur seals to maturity. However even though brown hyenas prey on young animals with a low reproductive value, whether by choice or only due to the fact that pups are relatively small, show insignificant defence and occur at high density (Khan & Ghaleb 2003), they can contribute to the instability of the system by being a major source of mortality.

The predation rate at the Wolf Bay seal colony was 9.4%, 9.6% and 5.1% during different pupping seasons, as opposed to 22%, 61% and 18% non-violent mortality rates during the same times. Therefore predation appears to have a smaller impact on seal pups than non-violent mortality. Nevertheless prey choice within the pup age class can further influence the impact of predation-caused mortality (Chapter 7).

Furthermore, non-violent mortality is highest during the first month of the pup's life (De Villiers & Roux 1992) and decreases to almost zero at the end of January, unless environmental anomalies cause a disproportional high mortality, such as during the 1999-2000 pupping season, in which non-violent seal pup mortality did not decrease towards the end of the pupping season and was significantly higher than during the other years. Hyena predation, on the contrary, happened throughout the entire study period and also later (pers. observ.),



although significantly fewer pups were killed from February onwards during “regular” years (1997-1997 and 2000-2001) that show a regular non-violent mortality pattern.

Predation at the Wolf Bay seal colony was independent of the availability of non-violent mortalities. The predation rates in “regular” years were higher in December and January, when most non-violent mortalities were available, than in February and March, when non-violent mortality was almost zero. Furthermore during the 1999-2000 study period, when many seal pups regularly died of starvation, brown hyenas did not show any differences in the predation rate over time, despite the availability of non-violent mortalities.

The increased mobility of seal pups may also influence the predation rate. Most seal pups are relatively immobile in December and January (Chapter 4) and therefore easier to catch than later in the season, when they become more mobile and spend time in the water. During the 1999-2000 study period the general condition of pups was poor, which possibly limited their mobility, since the only way for a starving pup to conserve energy during the absence of the mother is to minimize movement. Hence brown hyenas could kill pups easily compared to the same period during “regular” years.

An increase in satiation might also contribute to the decline in predation rate, but seems unlikely as the absolute feeding times did not change between November and January (see above), and could remain similar during the course of the year. In addition the predation rate remained constant in 1999-2000, hence more pups were killed later in the season.

The absolute number of pups killed at the Wolf Bay seal colony differed between seasons and was positively density dependent. Pup production in the sample areas declined from 8 950 in 1997-1998 to 5 450 in 1999-2000 to 2 900 in 2000-2001. Over the same time, the total number of pups killed declined from 841 to 523 and 148 killed pups, respectively. The low number of predations in 2000-2001 is a conservative estimate, as the low pup production in that year may have affected the sample design from February onwards and brown hyenas possibly foraged extensively in other areas, not included in this study. The possibility that fewer brown hyenas foraged at the seal colony also cannot be excluded as a cause for a decline in the number of predations, but the abundance estimates



presented in Chapter 5 indicate that abundance remained relatively stable between 1997 and 2001.

6.4.3 Mass Kill Events

The occurrence of mass kill events and especially surplus kills raises questions about the motivation behind these kills, and about the failure of anti-predator behaviour of the prey species (Kruuk 1972b). Surplus food includes a kill that is greater than the predator's appetite or the continuation of hunting when the predator is no longer hungry (Macdonald 1976). Possible advantages of obtaining such surplus food are to return to the carcass when the predator is hungry again, to provide offspring or other members of the social unit with food, or to gain hunting experience (Kruuk 1972b). A generalist predator that feeds on a variety of prey items can gain advantage from surplus kills when the costs of making a kill are low. Specialists, however, have a constant cost involved in killing, as their hunting success depends on the abundance of prey, and the predictability of the resource plays a major role in the decision to hunt surplus food. Although increased abundance of food lowers the cost of searching for specialist predators, the costs of killing stay the same (Oksanen 1983). Therefore the only optimal surplus kill strategy is to utilize an unpredictable or indefensible resource. Evolutionary stable counter strategies of the prey to avoid surplus predation can be the synchronization of birth, especially when a particular age class is affected or when previously isolated prey is detected by a predator (Short et al. 2002). Furthermore inaccessible habitat selection, gregariousness, and specific anti-predator behaviour can minimize surplus predation (Kruuk 1964).

Mass kill events occur in a variety of circumstances. They can be single events taking place during unusual weather situations, when the prey species shows a lack of anti-predator behaviour (Kruuk 1972a). DelGiudice (1998) describes such a situation with wolves hunting white-tailed deer (*Odocoileus virginianus*) during a severe winter, where the poor condition of the deer led to surplus kills. Similarly, wolves killed excess reindeer (*Rangifer tarandus*) on a cloudy and rainy night (Björvall & Nilsson 1976), spotted hyenas killed an excess amount of Thomson's gazelles (*Gazella thomsonii*) on a dark, stormy night (Kruuk

1972a), foxes killed gulls (*Larus argentatus*) on a stormy, new moon night (Goethe 1956).

Secondly surplus killing can occur when prey animals are found in unusual habitats or predators gained access to otherwise inaccessible habitat, such as in the case of an arctic fox (*Alopex lagopus*) that destroyed an entire common eider (*Somateria mollissima*) colony by swimming to an island (Quinlan & Lehnhausen 1982) or foxes that killed black-headed gulls (*Larus ridibundus*) breeding in an unusual habitat (Kruuk 1972b). Thirdly prey animals confined to enclosures are susceptible to surplus predation, and leopards (*Panthera pardus*) and caracals (*Felis caracal*) are known to kill domestic stock in enclosures in surplus (Stuart 1986), although they can become accustomed to the superabundance of food and ultimately stop killing food in surplus. The occurrence of surplus killing can also be a regular event, but temporally restricted by storing food for times of food shortage. Surplus killing is a regular strategy in weasels (*Mustela nivalis*) during the cold season, and the same behaviour cannot be stimulated in the warm season despite superabundance of food (Jedrzejewska & Jedrzejewski 1989). Lastly some surplus kill occurrences are difficult to explain, such as least weasels (*Mustela nivalis nivalis*) and other small mustelids (*Mustela* spp) killing more than their energy need (Oksanen 1983, Sundell et al. 2003) without returning to the prey or storing the food.

In co-evolved predator-prey systems, surplus killing is usually found when prey abundance is high and when the needs of energetic maintenance and reproduction are easily met, so that leisure time can be spent on fat-accumulating behaviours, such as eating and resting (Oksanen 1983). Predators then usually seem to be unable to resist the temptation of killing easy prey, although it is uncommon when anti-predator behaviour is well developed (MacDonald 1976). The only regular occurrence of surplus kills is when prey animals are found in an unusual habitat (Kruuk 1972b), so that predators return to this area where they have previously encountered easy prey (Kruuk 1964), or when prey species are exposed to exotic or novel predators, such as in Australia, where predator-prey systems are imperfectly formed and surplus killing becomes an every day event and can be sustained over a long period of time without satiation of the behaviour (Short et al. 2002).



Since brown hyenas are not described as efficient hunters, references to multiple killing for this species are not common. Only Skinner (1976) describes the multiple killing of sheep (*Ovis* sp) in an enclosure. However mass kills of seal pups occurred throughout the study period. The average number of pups killed per mass kill event was 3.31 pups, but it is a conservative estimate. Observations at the Van Reenen Bay seal colony showed that mass kills are not spatially limited as per the definition in this study and that the remains of single kills found at the Wolf Bay colony could have been parts of mass kill events. Furthermore the number of carried-away pups is unknown at the Wolf Bay seal colony, and therefore recordings of single killing events could have been part of a mass kill event as well.

The number of kills per mass kill did not differ between years, but a density dependent pattern concerning the number of killed pups was observed. In 1997-1998 mass kill events contained the same number of pups in December, during the peak of the pupping season, and in January, after the peak of the pupping season. Seal pup production was good during that year (36 500 pups born) and seals were abundant at the entire seal colony. In contrast, in 1999-2000 and 2000-2001 pup production was lower (30 825 and 21 139 pups born respectively) and the density of seals was lower than in 1997-1998. Naturally the largest number of pups was present at the seal colony in January, after all the pups had been born, which is reflected in the number of pups killed per mass kill event for this time. The number of pups killed per mass kill event was significantly higher in January, when the largest number of seal pups was present, than in December, when pup numbers were still increasing.

The knowledge of stimuli that elicit a response, in this case the attack of prey, is of major importance (Manning & Stamp Dawkins 1992). Movement often is a strong stimulus (Curio 1976), but predators with easy access to prey are often also stimulated by visual and olfactory cues (Kossak 1989). The key stimulus to start feeding is usually the preceding catching and killing of prey where predation continues until certain key stimuli disappear (Kossak 1989). The system fails in situations when searching and hunting, which usually prevents catching and killing in satiated predators and therefore prevents the waste of energy, are of minor importance during the foraging sequence (Kruuk 1972b). In



this case the readiness to kill is not determined by hunger alone and often is attributable to overabundance of easy prey (Kruuk 1972b, Curio 1976).

Feeding occurred at any time of the foraging sequence (see above) and surplus killing was hence independent of the hunger state and without any relationship between eating and killing (Kruuk 1964). The excessive prey density and availability of vulnerable prey leads to an overstimulation and can hence trigger surplus killing (Kruuk 1972b), consistent with the findings of this study.

Cape fur seals are without doubt superabundant and might trigger the occurrence of mass kill events. The vulnerability of seal pups differs over time and could be influenced by the protective behaviour of the mother during the peak of the pupping season. However, the number of kills per mass kill event did not increase with an increase in unguarded pups. Thus the overall superabundance of food is the main trigger for brown hyenas engaging in surplus killing.

Brown hyena hunting behaviour during mass kill events (see above) was typical in comparison with descriptions of other authors. Foxes walked through a black-headed gull colony, grabbed gulls, killed them, and after shaking them, dropped them and carried on walking (Kruuk 1972b). Furthermore they were seen to walk from one gull chick to another, killing it and leaving it on the spot. Carcasses were often found widely spread out along the foxes' track, which seems to indicate that the fox was not necessarily distracted and hence killing was not triggered by other prey (Kruuk 1964) and their movement. Weasels show a similar behaviour of hunting immediately after killing and therefore kept hunting and feeding separated (Erlinge 1974).

6.5 Summary

Brown hyenas scavenge and kill seal pups at mainland Cape fur seal colonies. Killing of seals had a stronger representation in the foraging matrix and might therefore be the preferred method of obtaining food at the seal colonies. Brown hyenas killed seal pups with a single, precisely aimed bite into the skull, sometimes stalking their prey, but usually approaching the seals in an upright position. Kills and scavenged pups were almost always obtained at the colony, which supports the idea of seals being a predictable food source. Prey was regularly carried away from the colony to protected feeding sites or further inland.

The prey encounter rate and interval between kills depended on seal density, and increased density resulted in an increase of the capture rate and hunting efficiency from 14% in November to 47% in January. The time brown hyenas spent at the seal colony decreased with increasing seal density, but their activity also shifted due to climatic changes. Nevertheless, they were regularly active during the day, which indicates that the attendance pattern of adult seals might play a role in the choice of foraging time.

Brown hyenas killed seal pups throughout the study period. The predation rate was lower than the non-violent mortality rate, hence not a major cause of mortality, and was independent of the availability of non-violent mortalities, but the absolute number of kills was positively density dependent.

Mass kill events were recorded throughout the study period and are therefore not unusual occurrences. The overabundance of easy and vulnerable prey may lead to an overstimulus situation that triggers killing independent of the consumption of the prey or the hunger state.



Chapter 7

The Influence of Size, Sex and Age of Seal Pups on Brown Hyena Feeding Preferences

7.1 Introduction

Predators encounter a variety of prey species that vary in their abundance, vulnerability to predation, and ease of capture. These factors are further influenced by the distribution of age and sex classes and by the condition of the individual animal. Prey choice usually also follows the path of least effort, and the predator needs to keep a positive energy balance through either using carcasses if available or reducing the energy spent on hunting (Estes 1967).

This aim is often reached through hunting the doomed surplus, such as unfit adults in a poor condition that are less likely to escape (Hodges 2001, Sih & Christensen 2001). However, the degree to which such sub-standard prey in poor condition are captured and hence contribute to the predator's diet is influenced by the general difficulty of catching individuals of that species regardless of their condition (Temple 1987). Increased prey choice is therefore likely to be found for prey species that are difficult to catch. Nevertheless, besides weak or old prey animals, juveniles are usually extremely susceptible to predation (Schaller 1972) and predators such as spotted hyenas (*Crocuta crocuta*) and wolves (*Canis lupus*) often show preference of prey choice by hunting weak, old and young prey (Estes 1967, Husseman et al. 2003).

Some predators, however, specialise in killing offspring. The polar bear's (*Ursus maritimus*) ringed seal (*Phoca hispida*) diet for example comprises up to 100% pups, and areas with adult male seal presence are often actively avoided (Stirling & Archibald 1977, Hammill & Smith 1991). The naivety, lack of vigilance and relative small size of seal pups increases their predation risk and possibly leads to differential predation (Hodges 2001) regarding age classes.

Optimal diet theories suggest that the values of different food types can be judged by the gain of energy per unit handling time and can therefore be ranked. Higher-ranking food is consumed independent of its relative availability, and lower ranking items are added in rank order (Pyke et al. 1977, Krebs & Kacelnik 1993). Nevertheless, the choice of consumption of prey also depends on the type of

predator. Generalists, for example, feed on any prey they can capture, and the encounter frequency with prey items becomes the main factor in prey choice (Rosenheim & Corbett 2003).

The ease in which prey are found, captured and eaten varies and influences the optimal diet of the predator (Estabrook & Dunham 1976, Husseman et al. 2003). The combination of prey types that are eaten when encountered should maximise the intake of food value per unit of time, and parameters such as the absolute abundance of food, the relative value of the prey to the predator, and the relative abundance of all prey types influence the consumption of prey (Estabrook & Dunham 1976) and may lead to diet preferences (Sih & Christensen 2001). Diet preferences occur when a predator consumes some prey more frequently than expected based on relative abundance, and can be a result of either active predator choice, where a high degree of satiation leads to a switch to preferred food items and hence increased selection, or passive predator choice, where prey capture often depends on reflexes and satiation does not influence selection (Emlen 1966, Sih & Christensen 2001, Sukhanov & Omelko 2002).

The prey value is defined as the measurable net energy or caloric value of food (Schoener 1971, Krebs & Kacelnik 1993). This value is difficult to measure directly, as the costs that are involved in foraging behaviours such as searching, capture, and handling are difficult to assess. Nevertheless a relative value can be attributed to different prey species or individuals. Prey with lower escape probability, for example, should have a higher prey value than difficult to catch prey (Sih & Christensen 2001), and equal capture probabilities for individuals should decrease the overall value of prey in poor condition.

Coastal brown hyenas (*Parahyaena brunnea*) have access to a localised food source of relatively easy to catch prey. Furthermore carcasses of seal pups (*Arctocephalus pusillus pusillus*), which mostly died of starvation, are abundant during the seal pupping season (Chapters 4 and 6). Nevertheless seal pups, irrespective of being dead or alive, differ in their condition, which results in a different relative value of individual prey items and might lead to active prey choice and feeding preferences in brown hyenas. Additionally the growth pattern of male and female pups differs (Chapter 4), and hence the sex and age of the



pup might have a further influence on prey choice by brown hyenas. Brown hyenas both scavenge and kill seal pups, partly in surplus (Chapter 6). The objective of this chapter, therefore, is to investigate their prey choice regarding the capture of seal pups and the consumption of killed pups. The value of dead versus live pups, and pups differing in body mass, sex, and age was assessed, and it was investigated:

- (1) which factors influence the scavenging of seal carcasses,
- (2) whether brown hyena predation has an additive impact on seal pup mortality,
- (3) whether the sex and age of the pup influences the brown hyena's prey choice and
- (4) whether there are preferences in consumption of different prey categories.

It was predicted that carrion has a lower relative value than a killed pup and that, as a consequence,

- (1) brown hyenas would prefer live prey over scavenging starved pups, which are smaller and of lower value,
- (2) scavenging would decrease after the peak pupping season, when more live prey are available,
- (3) hyenas would preferentially kill larger and heavier pups, and
- (4) hyenas would preferentially kill pups that have recently nursed in order to get at the consumed milk.

7.2 Material and Methods

7.2.1 Study Area and Study Period

Brown hyenas foraging were observed from an observation hut at the Van Reenen Bay seal colony between November 2001 and January 2002 (Chapter 6). Mortality surveys of seal pups were conducted at the Wolf Bay seal colony during the seal pupping seasons in 1997-1998, 1999-2000 and 2000-2001 (Chapter 4).

7.2.2 Number of Scavenged Pups and Kills

During the continuous observations at the Van Reenen Bay seal colony (Chapter 6), the number of pups scavenged and killed by the focus animals and other

brown hyenas that were present at the seal colony was recorded. Scavenged pups were those that either died of non-violent mortality or were killed by jackals or a brown hyena other than the focus animal. To be considered scavenging, the focus animal had to be in direct contact with a pup by initially holding, licking or feeding on it. Sniffing at a carcass was not included in this prey category.

In the sample areas at the Wolf Bay seal colony, all fresh dead pups were marked with numbered metal or plastic tags at their front flipper during the study periods in 1997-1998, 1999-2000 and 2000-2001. It was recorded whether the pup died of non-violent mortality or brown hyena predation and to what degree it had been consumed. The study distinguished between pups that were not consumed (surplus), partly eaten (excessive) or completely consumed, where no meat or blubber was left for further consumption. The marked pups were checked on the next consecutive visit to the sample area and the tags were only removed once the pups were rotten. It was recorded whether the pup was untouched, further consumed (noting the eaten parts and the scavenging species if possible), whether it was moved or not present any longer, which indicated that it had been carried away by either a brown hyena or possibly a black-backed jackal. In contrast to brown hyenas, which are capable of carrying a dead seal pup, black-backed jackals usually have to drag the pup, as its weight exceeds a third of their own body weight. These drag marks can be seen and by following them, the pup could usually be discovered.

The number of pups that were further consumed by brown hyenas and the number of carcasses that disappeared were used to determine the number of pups scavenged by brown hyenas at the seal colony. Furthermore the periods during and after the seal pupping season were compared.

7.2.3 Mass of Seal Pups

The mass of all dead seal pups (relative value) was recorded (Chapter 4) and brown hyena predations were distinguished between surplus kills and excessive kills (Chapter 6). To estimate the total mass of excessive killed pups, which had been partially consumed, non-violent mortality pups were removed from the colony and taken to the laboratory at the Namibian Ministry of Fisheries and Marine Resources in Lüderitz, where total mass, standard length, girth, and

blubber thickness were measured. Furthermore the upper part of the body (“mass of skull”) was cut off just in front of the shoulder blades and the mass without skull, mass of the skull and length without skull, measured in a straight line from the last tail vertebrae to the cut off point between the shoulder blades, was determined. The skull was skinned and the brain was removed and weighed.

Excessive kill remains found at the seal colony were measured similarly: the remaining parts of the upper body were cut off in front of the shoulder blades and the mass without skull, length without skull, girth and blubber thickness were recorded.

Two different calculations were used to extrapolate the total mass of excessive kills: (1) the relative mass of the skull, compared to total mass, over time and (2) a correlation analysis using total mass and mass without skull. Both correction factors were compared for significant differences in their linear regression lines using the field measurements of excessive kills. Similar methods for analysing prey remains have been used in feeding ecology studies of brown bears (*Ursus arctos*) and sockeye salmon (*Oncorhynchus nerka*) (Quinn & Kinnison 1999).

For each pupping season the linear regression curves of the mass of live pups, pups that died of non-violent mortality, and brown hyena predations were compared, also distinguishing between male and female pups. Live pups were measured five to six times during each study period to determine their growth rates at the colony (Chapter 4).

7.2.4 Sex Ratio and Age of Pups

The overall sex ratios of live pups that were captured and weighed during and after the pupping season was calculated and compared with the overall sex ratio of brown hyena predations during the same periods. The sex of completely consumed pups and cached excessive kills could not be determined, which might influence these results.

The age of seal pups could only be determined up to three days (Chapter 4). The data set of the Ministry of Fisheries and Marine Resources for the Atlas Bay seal colony was analysed to determine the exact day during the pupping season when the majority of pups turned older than three days. The following

equation (compare with Chapter 4) was used to calculate the number of three-day old pups T on Julian day n

$$T_n = \sum_{i=n-3}^n B_i$$

with B being the number of pups born on Julian day i . The number of three-day old pups TD on Julian day n , assuming a closed population, was

$$TD_n = TD_{n-1} + B_{n-3}$$

To determine whether brown hyenas selected prey based on age, the proportion of hyena predations that were younger and older than three days were calculated for two time periods; the time before and the time after older pups (> 3 days) became more common than young (< 3 days) pups. Only predations occurring until 7 January were included, as no pups were born later past this date.

Additionally the growth rate of newborn pups up to an age of five days was determined to establish the mass-related value of older pups. Seal pups at the Atlas Bay seal colony were tagged at birth during the 2000-2001 pupping season by the Ministry of Fisheries and Marine Resources. The tagged pups were weighed regularly to obtain individual growth data.

To investigate whether the age-related guarding of the pups influenced brown hyena prey choice during the seal pupping season, the numbers of daily hyena predations before and after 10 December, the date of the switch from predominately guarded to unguarded pups (Chapter 4), were compared for differences.

7.2.5 Prey Choice Regarding the Consumption of Killed Pups

Consumption of killed pups was examined using data from the 1999-2000 and 2000-2001 study periods, as no data about excessive kill caches were collected during 1997-1998. Differences in the daily number of surplus kills, excessive kills and excessive kill caches (Chapter 6) between the time before, during, and after the seal pupping season (November, December, \geq January) and during each of these periods were examined to establish the regularity of the occurrence of these events. The mass of all surplus kills was compared with the extrapolated mass of all excessive kills to investigate consumption-related prey choice

regarding the mass of seal pups. Mass kill events including both surplus and excessive kills were analysed separately.

The possible influence of stomach content (milk) in consumption choice was investigated by holding dead pups upside down while strongly massaging the stomach to extract the milk. Milk content was often already visible in excessive kills as it was extracted while the hyena was feeding. The proportion of pups with and without milk for surplus and excessive kills was compared.

7.3 Results

7.3.1 Prey Choice Regarding Scavenged Pups and Kills

a) Van Reenen Bay Seal Colony

The daily number of observed kills and scavenged pups at the Van Reenen Bay seal colony did not differ (Mann-Whitney U-Test $U = 698$, $p = 0.19$) (Figure 7.1).

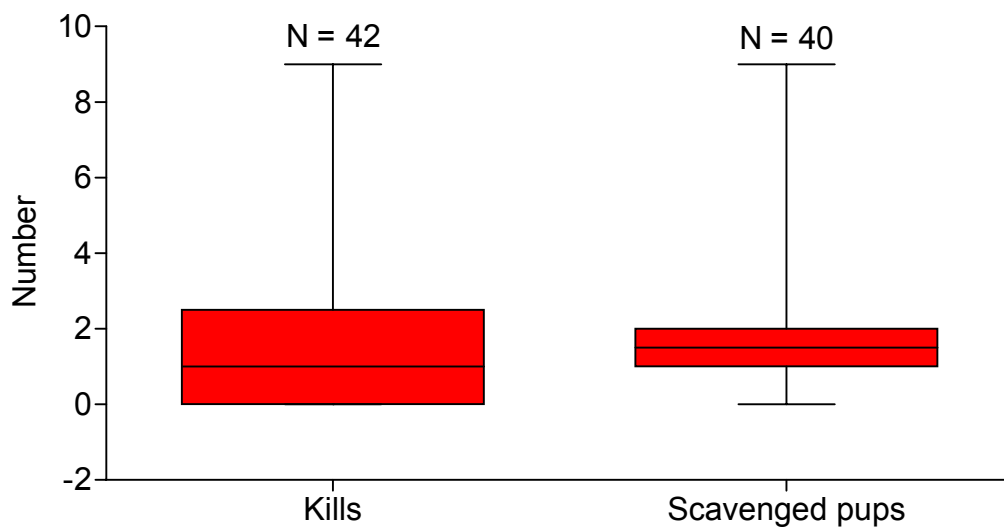


Figure 7.1: Daily number of killed and scavenged pups at the Van Reenen Bay seal colony (N = number of days).

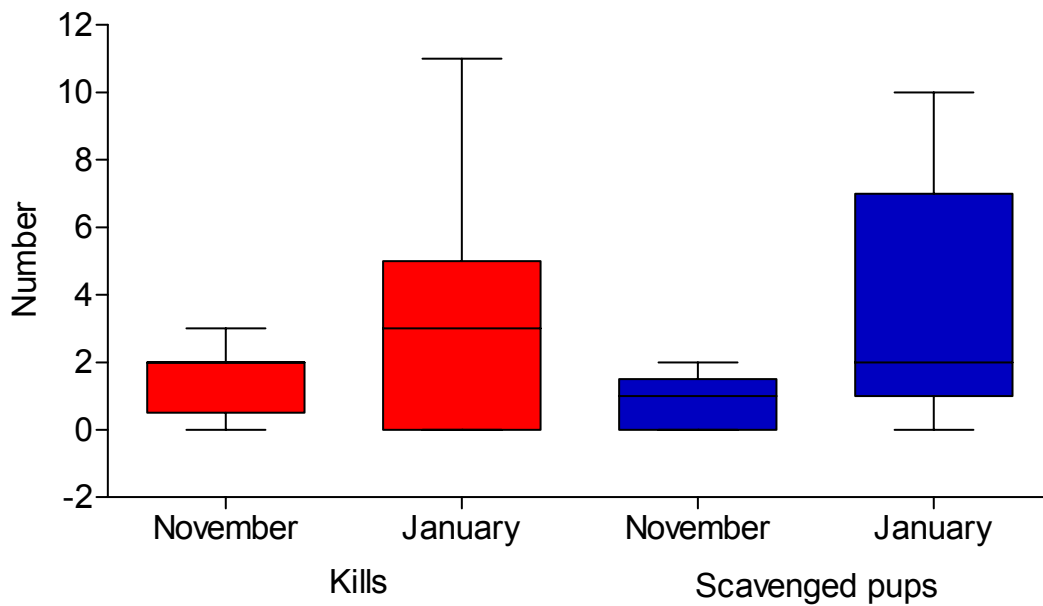


Figure 7.2: Daily number of kills and scavenged pups at the Van Reenen Bay seal colony in November (N = 9 days) and January (N = 11 days).

The daily number of kills at the Van Reenen Bay seal colony in November and January, before and after the peak of the pupping season, respectively, did not differ (t-test $t = 1.56$, $p = 0.14$) (Figure 7.2). The daily number of scavenged pups was higher in January than in November (t-test $t = 2.55$, $p = 0.020$) (Figure 7.2).

b) Wolf Bay Seal Colony

Although more pups were killed than scavenged at the Wolf Bay seal colony, the daily number of scavenged and killed pups did not differ significantly for either study period (Mann-Whitney U-Test, 1999-2000: $U = 5775$, $p = 0.093$ and 2000-2001: $U = 5692$, $p = 0.066$) (Figure 7.3). However, the results suggest a trend towards more kills. Differences in sampling frequency between days and periods (Chapter 6) precluded testing for differences in the daily number of kills and scavenged pups between November and January.

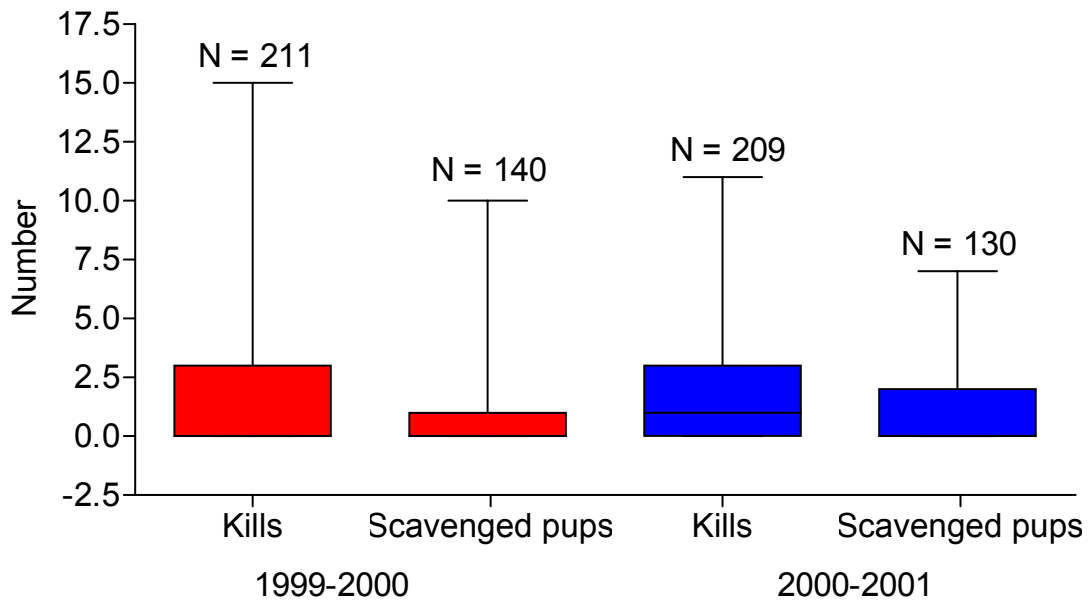


Figure 7.3: Daily number of killed and scavenged pups at the Wolf Bay seal colony during the study period in 1999-2000 and 2000-2001 (N = total number of pups).

7.3.2 Prey Choice Regarding the Condition of Pups

The percentage of skull mass (SKM) to total body mass changed over time (t in Julian days) (Figure 7.4):

$$\text{SKM} = -0.0483 t + 22.212 \quad r^2 = 0.0936$$

Therefore the extrapolated excessive kill mass (EKM) was:

$$\text{EKM} = x + (x * (-0.0483 t + 22.212) \%)$$

with the parameter x being the mass without skull.

The relationship of total body mass (TBM = EKM) to mass without skull (q) was described by the following equation:

$$\text{TBM} = 1.1467 q + 533.9 \quad r^2 = 0.9934$$

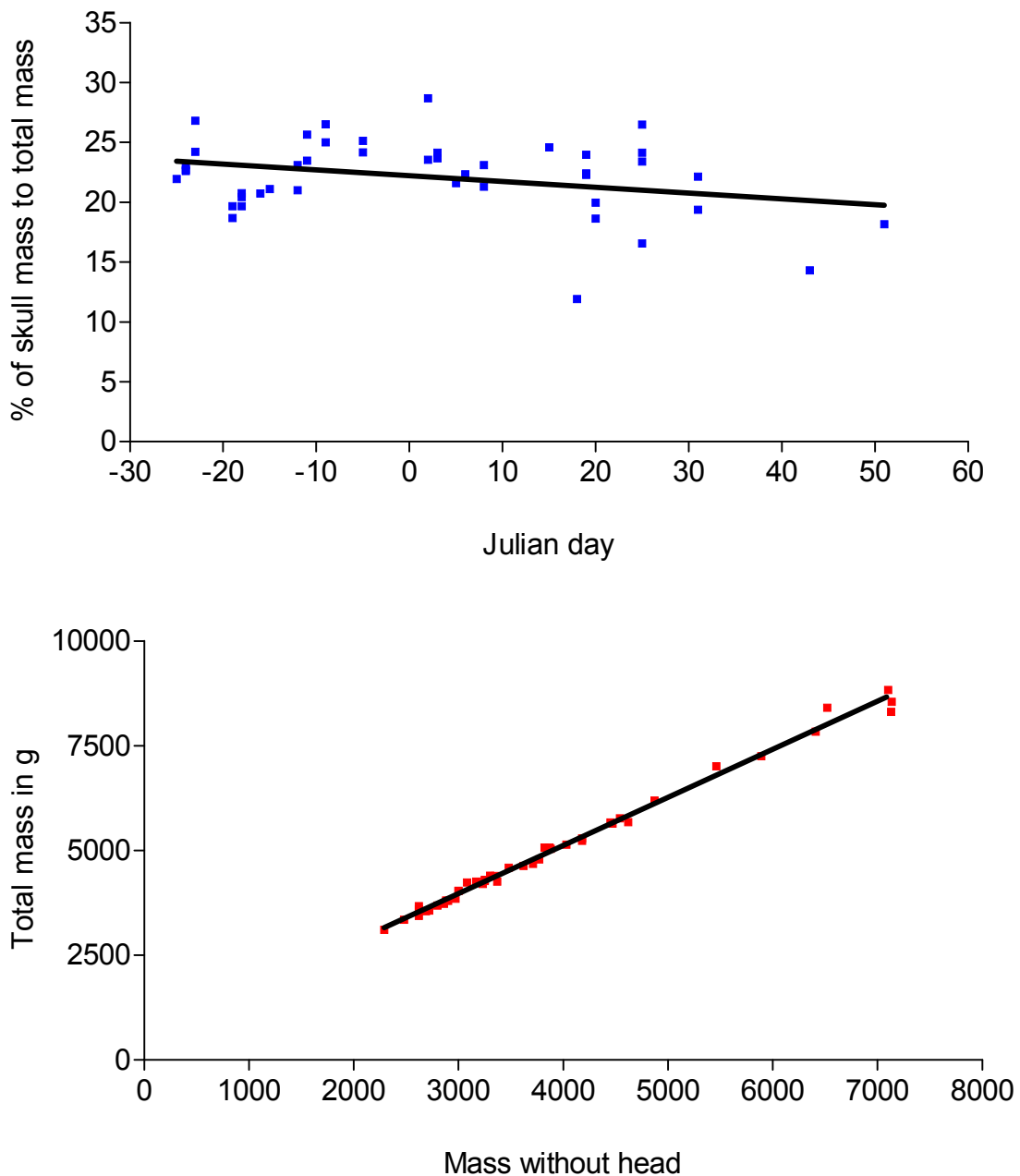


Figure 7.4: Correction factors to obtain the extrapolated excessive kill mass.

The comparison of the linear regression lines of both correction factors using field measurements of excessive kills showed no significant difference between the slopes, elevations and intercepts (slopes $F_{1,234} = 0.19$, $p = 0.66$; elevations $F_{1,235} = 0.59$, $p = 0.44$) (Figure 7.5).

For the subsequent analyses the correction factor calculated from the total body mass and mass without skull was used, as it resulted in a better r^2 value.

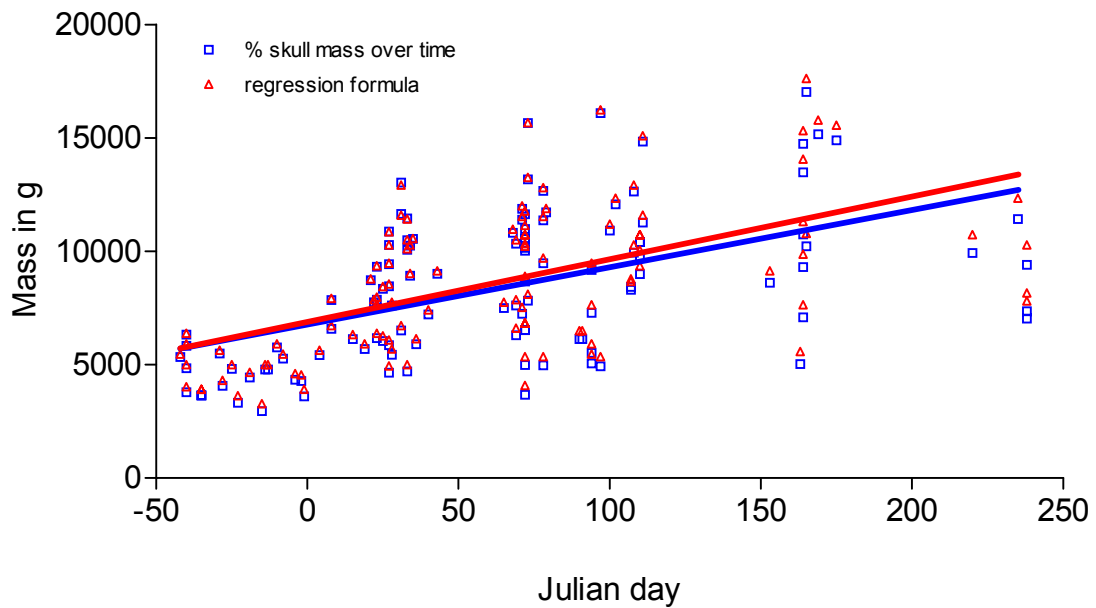


Figure 7.5: Linear regression curves of the correction factors percentage of skull mass and measurements of total body mass and mass without head.

Table 7.1: Results of the comparison of the linear regression curves of the change of mass of predation pups with growth curves of live pups and the change of mass of non-violent mortalities (nvm) during the three study periods. When slopes differed significantly, elevations/intercepts did not have to be tested for differences.

Study period	Category	Sex	Slope			Elevation/Intercept		
			df _n , df _d	F	p value	df _n , df _d	F	p value
1997-1998	Live	both	1,87	0.229	0.6337	1,88	1.912	0.1696
		male	1,45	0.234	0.6306	1,46	2.301	0.1361
		female	1,38	0.169	0.6831	1,39	0.544	0.4651
	NVM	both	1,359	20.692	< 0.0001			
		male	1,205	20.239	< 0.0001			
		female	1,150	1.886	0.1717	1,151	12.075	0.0007
1999-2000	Live	both	1,117	0.063	0.8018	1,118	1.714	0.193
		male	1,55	0.034	0.8551	1,56	1.246	0.269
		female	1,56	0.135	0.7148	1,57	0.583	0.4485
	NVM	both	1,783	25.027	< 0.0001			
		male	1,409	4.285	0.0391			
		female	1,367	16.978	< 0.0001			
2000-2001	Live	both	1,105	0.081	0.7771	1,106	2.292	0.133
		male	1,66	0.016	0.8989	1,67	2.487	0.1195
		female	1,35	0.139	0.7115	1,36	0.852	0.3622
	NVM	both	1,462	88.659	< 0.0001			
		male	1,257	54.092	< 0.0001			
		female	1,201	52.679	< 0.0001			

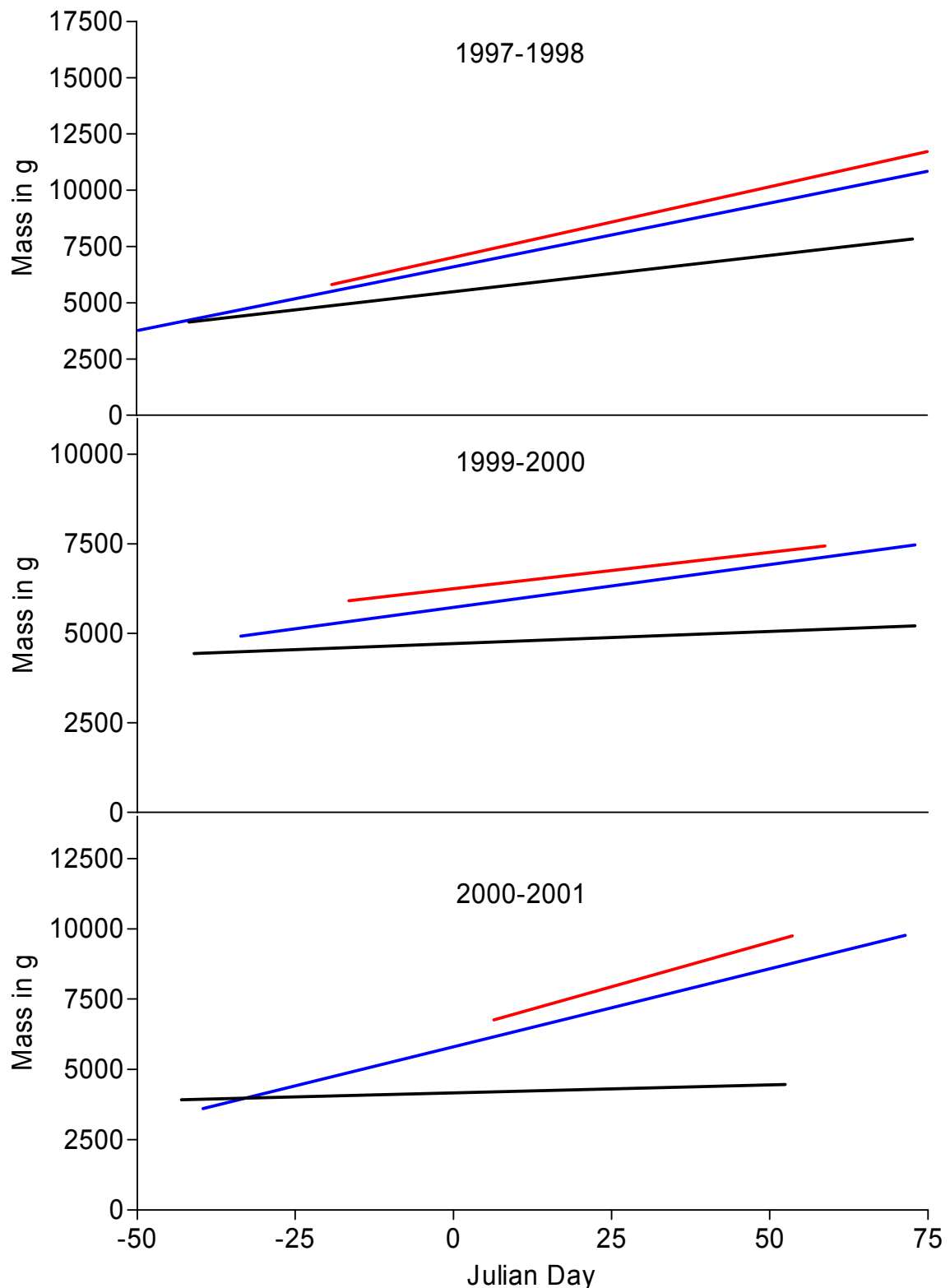


Figure 7.6: Linear regression curves of changes in the mass of live (red line), brown hyena predation (blue line) and non-violent mortality pups (black line) during the study period from November until March (Julian day 75) of the following year.

The growth curve (linear regression curves) of live pups and change of mass of brown hyena predations did not differ during any study period for either



sex or both sexes combined (Figure 7.6 and Table 7.1). However, the slopes of the curves of the change of mass of brown hyena predations were higher than those of the change in mass of non-violent mortality pups during all three study periods. The only exceptions were the female curves in 1997-1998, where the slopes were identical but the elevations differed.

7.3.3 Prey Choice Regarding Sex of the Pups

The overall sex ratio of male to female live pups was 68:32 in 1997-1998, 54:46 in 1999-2000 and 53:47 in 2000-2001. During the 1999-2000 pupping season significantly more female pups were killed than were proportionally present at the seal colony and after the 2000-2001 pupping season brown hyenas killed more male pups than were proportionally present at the seal colony (Table 7.2). This difference was highly significant. Other than that no significant differences could be detected.

Table 7.2: Results of Fisher Exact Test comparing the sex ratio of live pups with brown hyena predations during and after the pupping season. Ns = not significant, *female pups killed disproportionately ($p < 0.05$), ***male pups killed disproportionately ($p < 0.001$).

Year	During	After
1997-1998	ns	ns
1999-2000	females*	ns
2000-2001	ns	males***

7.3.4 Prey Choice Regarding the Age of the Pups

After 3 December each year, the number of pups older than 3 days exceeded the number of pups < 3 days. On average the number of young pups was double the number of older pups between the beginning of the pupping season (mid-November) until 3 December, and a ratio of 2:1 was hence conservatively assumed to be the expected value. Brown hyenas killed a larger number of older pups than proportionally present at the seal colony during this time (Fisher Exact Test $p < 0.0001$; Figure 7.8) and naturally killed more older pups after the switch took place.

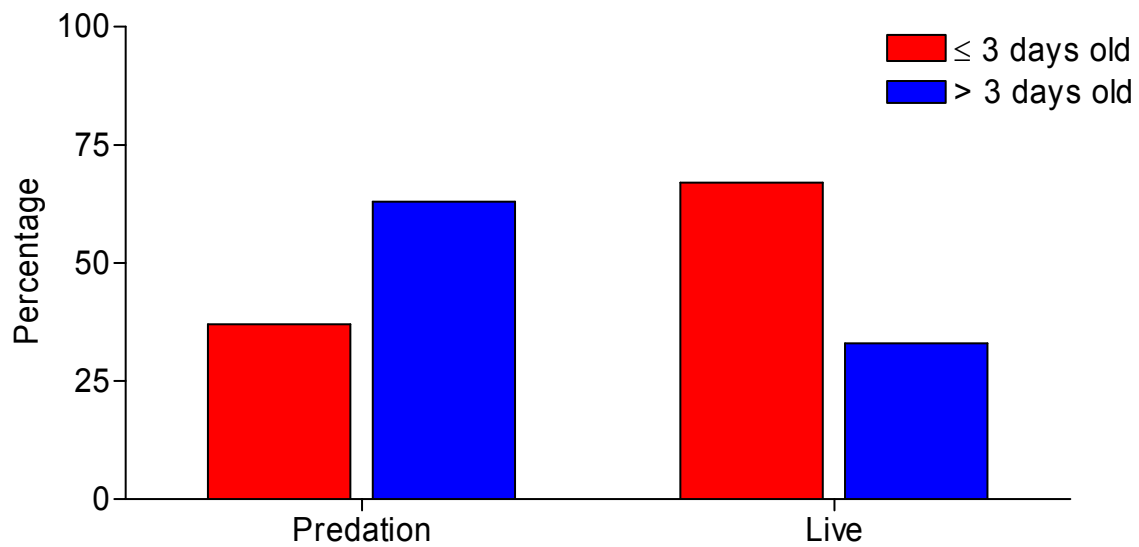


Figure 7.7 Percentage of hyena predations and live pups of different age categories at the Wolf Bay seal colony until 3 December.

The mass of 23 newborn pups at the Atlas Bay seal colony was determined at birth and a second mass measurement was taken up to five days later. The average gain in mass for one day old pups was -75 g (N = 2), for two day old pups 100 g (N = 3), for three day old pups 150 g (N = 3), for four day old pups 440 g (N = 10) and for five day old pups 940 g (N = 5).

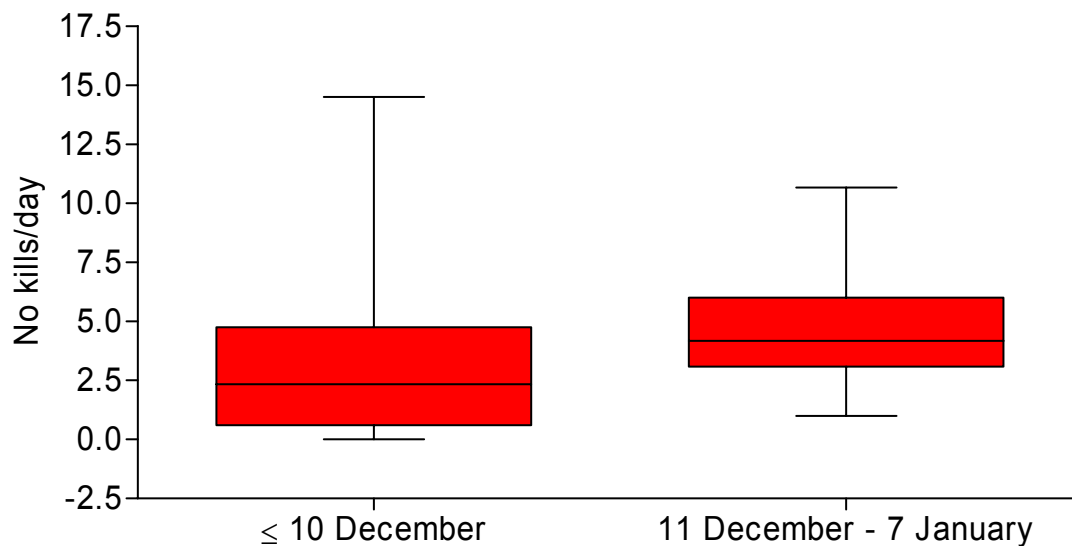


Figure 7.8: Number of hyena predations per day during the pupping seasons in 1999-2000 and 2000-2001 before the switch from the majority of pups being guarded to the majority of pups being unguarded



Brown hyenas killed significantly more pups per day when the majority of the pups were not guarded by their mothers any longer (Mann-Whitney U-Test $U = 218.5$, $p = 0.012$), in other words when they were older than six days (Figure 7.8).

7.3.5 Prey Choice Regarding the Consumption of Killed Pups

Surplus and excessive kills occurred throughout the two study periods in 1999-2000 and 2000-2001. Significantly more pups were killed in surplus in December and January than in November (2 years pooled, Kruskal Wallis Test $H = 13.0$, $p = 0.002$; Dunn's Multiple Comparison Test: Nov vs Dec $p < 0.01$ and Nov vs Jan $p < 0.01$) (Figure 7.9). Fewer excessive kill remains were found in November than in December and January (Kruskal Wallis Test $H = 16.2$, $p = 0.0003$; Dunn's Multiple Comparison Test: Nov vs Dec $p < 0.05$ and Nov vs Jan $p < 0.001$), but the combined data set for excessive kill remains and excessive kill cache remains did not differ between the periods (Kruskal Wallis Test $H = 2.85$, $p = 0.24$). The daily number of surplus kills was significantly higher than the daily number of combined excessive kills and caches in December (Mann-Whitney U-Test, $U = 1240$, $p < 0.0001$) and January (Mann-Whitney U-Test, $U = 2655$, $p = 0.0002$).

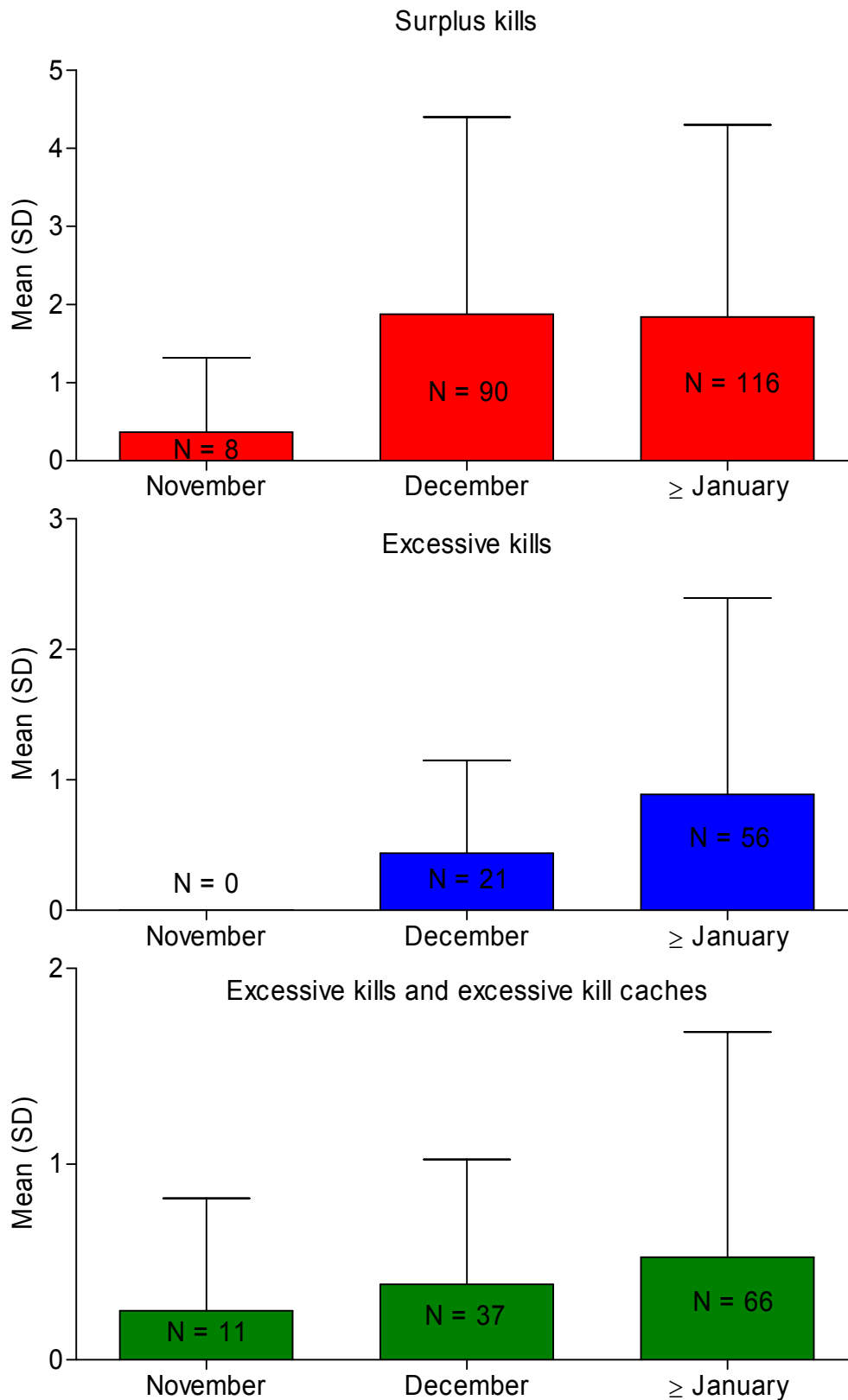


Figure 7.9: Mean daily number of surplus kills, excessive kills, and excessive kills and caches in November, December and from January onwards (N = total number of kills)

To investigate whether brown hyenas show prey choice regarding the consumption of pups, the mass of surplus kill predations was compared to the

mass of excessive kill predations. The slope of the surplus predations change of mass curve was significantly flatter than that for excessive predations ($F_{1,271} = 6.30$, $p = 0.013$) (Figure 7.10), and excessive kills were significantly heavier (Mann-Whitney U-Test $U = 4541$, $p < 0.0001$) (Figure 7.11), suggesting brown hyenas preferentially consumed larger seal pups.

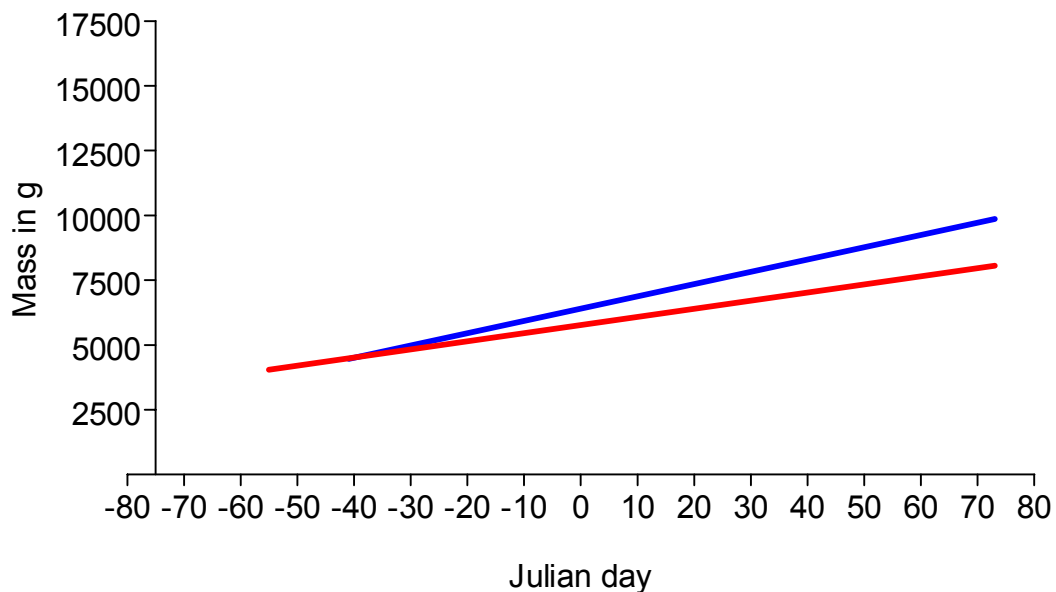


Figure 7.10: Linear regression curves of surplus predations (red line) and excessive predations (blue line).

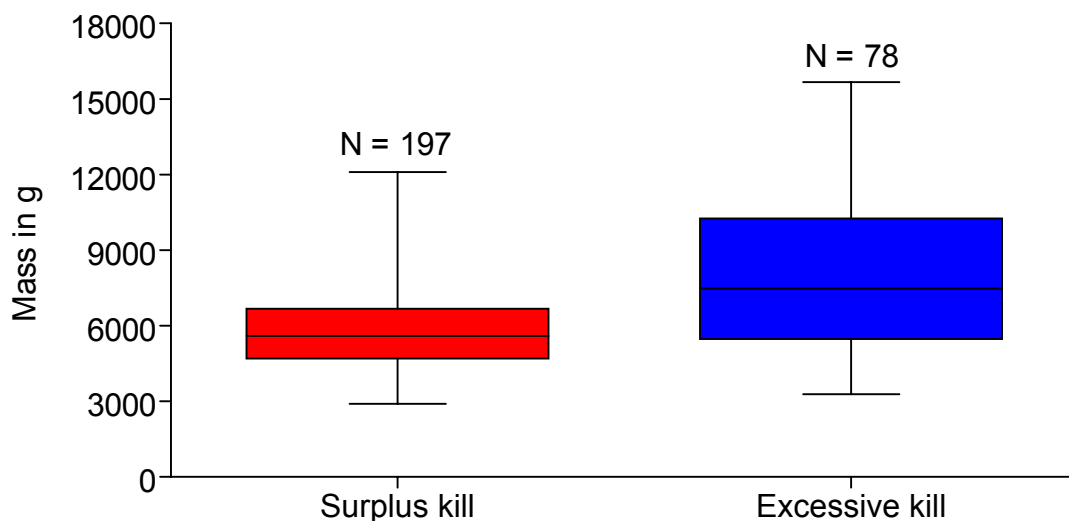


Figure 7.11: Median mass of surplus and excessive kills (N = total number of kills)

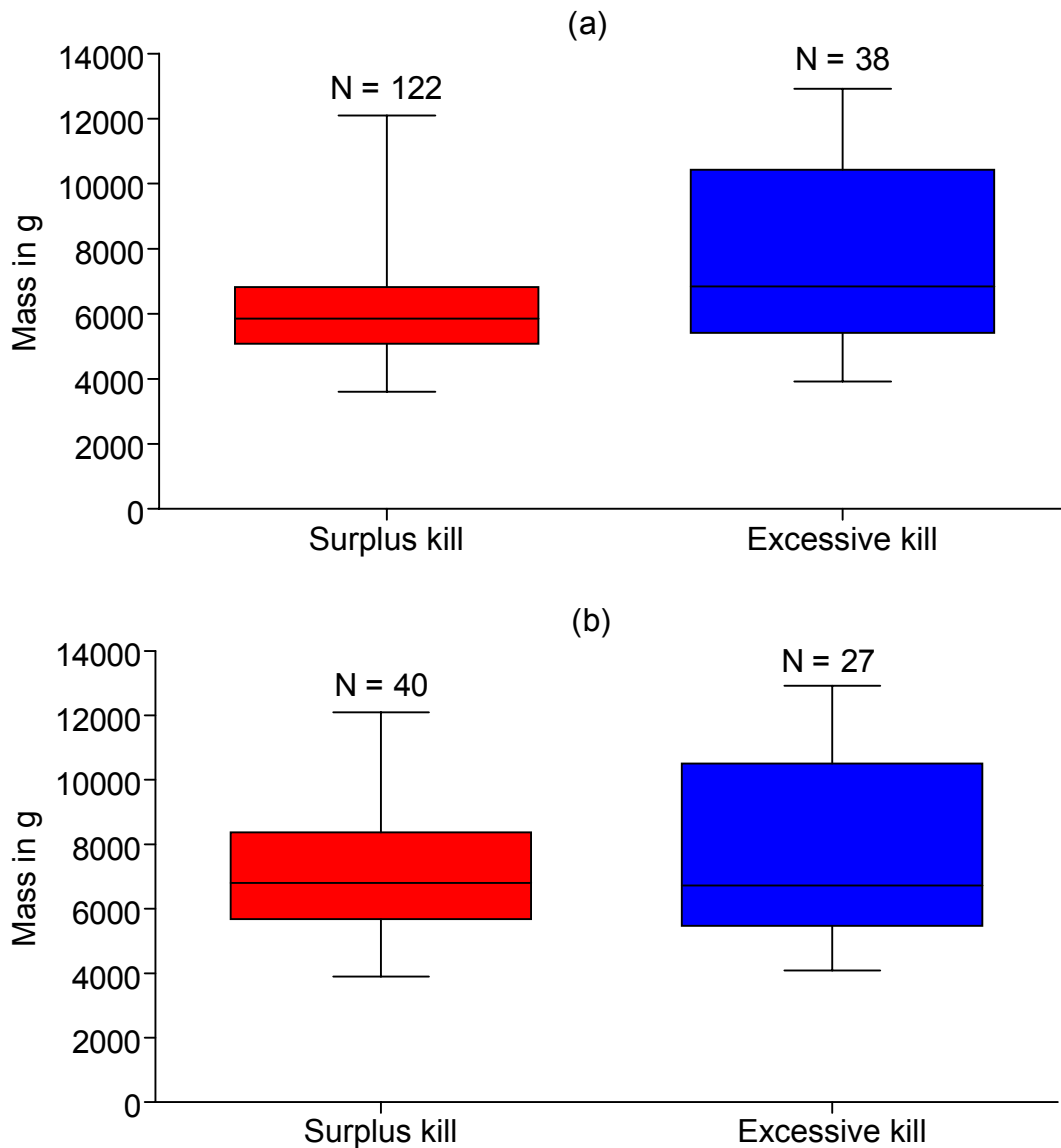


Figure 7.12: Median mass and 90% percentiles of surplus and excessive kills occurring in (a) all mass kill events (N = 84), and (b) mass kill events (N = 14) including the occurrence of both, surplus and excessive kills (N = total number of kills).

During mass kill events, the mass of surplus predations was also significantly lower than the mass of excessive predations (Mann-Whitney U-Test $U = 1519$, $p = 0.001$) (Figure 7.12a). However, in mass kill events where both surplus and excessive kills occurred at the same time, the masses of the two prey categories did not differ (Mann-Whitney U-Test $U = 506$, $p = 0.67$) (Figure 7.12b).

The stomach content of seal pups did not influence brown hyena prey choice, as the proportion of surplus kills and excessive kills with milk or without in the stomach did not differ (Chi² Test $\chi^2 = 0.037$, $df = 1$, $p = 0.85$).



7.4 Discussion

One of the general principles underlying optimal diet theories is that selectivity increases with increasing prey density and satiation (Emlen 1966, Sukhanov & Omelko 2002, Yearsley 2003). Predators generally maximise the food value to handling time ratio and minimise the search time, and the behaviour of the prey species may play an important role in successful prey choice (Kruuk & Turner 1967, Pyke et al. 1977, Krebs & Kacelnik 1993). A good indicator to describe prey choice is the investigation of the body condition of predations (compare with Sinclair & Arcese 1995). Body condition is often attributed to mass (compare with Temple 1987) and this study used a similar system to evaluate the value of certain prey items for brown hyenas. Mass is the overriding factor to determine the relative value of seal pups to brown hyenas, but sex and age classes differ in their mass (Chapter 4), so that male pups and older pups are automatically classed as being in a better condition than female pups and young pups, provided that they are not starving. This study assumes that brown hyenas cannot distinguish between male and female pups and if they show prey choice they can only visually determine the condition, sex and age of the pups by judging their mass or possibly mass to length ratio. As a consequence, if brown hyenas show prey choice regarding prey of higher relative value, they would choose kills over scavenged pups, and large pups, hence males and older pups or females and young pups of larger than average size, over small pups.

7.4.1 Capture of Seal Pups

a) To Kill or to Scavenge?

Freshly killed prey has a higher nutritional value to brown hyenas than the consumption of carcasses partly due to the higher moisture content and lack of decomposition, and brown hyenas are only likely to consume carrion, when they are hungry. However, energy expenditures for killing may be higher, but under some circumstances it can be advantageous to spend energy on hunting even when carcasses are abundant. Such situations arise when a predator is confronted with a high number of vulnerable prey. The time and energy that is then spent on searching, capturing and killing becomes negligible and can also lead to surplus predation (Chapter 6). Many successful predators, such as bears

(*Ursus americanus*, *U. arctos*) feeding on seal pups (*Erignathus barbatus*) or salmon (*Oncorhynchus* spp) also scavenge despite the availability of easy live prey (Smith 1980, Reimchen 2000, Ruggerone et al. 2000). Brown hyenas encounter live prey permanently while foraging at mainland Cape fur seal colonies (Chapter 6). Carcasses of seal pups are also encountered on a regular basis, but their availability changes over time. Most dead pups are available during the seal pupping season and up to four weeks later, as seal pup mortality is highest during that time (De Villiers & Roux 1992). Nevertheless live pups outnumbered carcasses throughout the season, and since the encounter rate for carcasses was lower than that of live pups, live prey is likely to be preferentially consumed.

However, energy spent on capturing and killing live pups has to be weighed against the energy spent on higher search costs for carcasses (compare with Cook & Cockrell 1978). Therefore the difference in energy spent to obtain food from a carcass or a kill is probably minimal and without considering the value of pups expressed in mass, brown hyenas would use carcasses and kills opportunistically. Data from this study support this suggestion. Although the daily number of scavenged pups and kills did not differ between November and January, the number of kills remained the same, whereas the number of scavenged pups increased in January, which coincides with the high availability of non-violent mortalities and hence increased encounter rate during that time (Chapter 4).

The major cause of death for seal pups is starvation (Chapter 4). A dead pup has therefore used its last reserves for survival and its caloric value is most definitely lower than that of still living pups regardless of their condition. In addition Cape fur seal pups that die of non-violent mortality were found to be on average lighter at birth than pups that survived until an age of two months (Kirkman et al. 2002a). Brown hyenas would therefore only choose to consume such low ranking carcasses when they are hungry (Curio 1976).

Although seal pups are killed throughout the year, the costs involved in capture and killing increase until the start of the next pupping season (when the next generation of vulnerable and easy prey are born), due to the decrease in pup density, increased size of the pups and defence ability of the pups. Brown hyenas



might therefore be more hungry at the beginning of the pupping season in November than later in the season and would use a decreasing number of carcasses, provided that the costs for using carcasses and kills are the same. This pattern cannot be seen in the results of this study. Furthermore if kills yield more energy per unit of handling time, brown hyenas would ignore low-ranking prey (Sih & Christensen 2001) according to the all-or-nothing prediction (Krebs & Kacelnik 1993), which also does not seem to be the case.

Additional behavioural observations of brown hyenas foraging at seal colonies outside the pupping season would reveal stronger support for the results of this study. The investigation of the encounter frequencies of carcasses and live prey during a foraging bout may show whether brown hyenas are true generalists, where the encounter frequency is the overriding factor in prey choice (Rosenheim & Corbett 2003) or whether there is a preference that depends on encounter and attack probability, capture success, probability of consumption and hunger state (Curio 1976, Sih & Christensen 2001).

However the availability of carcasses is less predictable than the availability of live prey and to practice killing regularly can be of advantage for times when no non-violent mortalities are around and also the killing in surplus might ensure a meal for the following day, although the latter suggestion is less plausible, as brown hyenas should have gained the knowledge about the year-round availability of seals as easy prey.

b) Condition of Seal Pups

Cape fur seal pups are easy prey with poorly developed anti-predator strategies towards terrestrial predators, and the size or condition of the pups should not significantly influence their escape probabilities (compare with Hodges 2001). In this study, brown hyenas killed seal pups of different conditions in proportion to their occurrence. The change of mass of predation pups was not different from the growth curve of live pups, which included pups in poor, moderate and excellent condition, and the elevations of the growth curves of live pups and the change of mass of hyena predations were equal. However, the change of mass curve for those pups that died of non-violent mortality was significantly lower and less steep than that of live and predation pups. The only exception was the



change of mass curve for female pups during the 1997-1998 study period where the change of mass was the same than for female live and predation pups, but the elevation was significantly lower.

If brown hyenas chose larger and heavier pups, the curve of the change of mass of predations would be higher and steeper than that of the representative live sample. However the results of this study suggest that brown hyenas are generalists that catch whatever is present at the seal colony while they are foraging, comparable to foraging strategies described for coyotes (*Canis latrans*) (Hernández et al. 2002). Similarly wolves killing semi-domestic reindeer (*Rangifer tarandus*) do not select their prey based on physical condition (Björvall & Nilsson 1976). Nevertheless these reindeer do not show regular anti-predator behaviour, similar to the lack of such behaviour in seal pups, and the lack of prey selection appears comparable to the occurrences of surplus kills and mass kill events as discussed in Chapter 6, where predators can easily kill animals in an excellent condition (Kruuk 1972a).

Under more natural conditions, wolves and also spotted hyenas are known to kill prey in a poor condition (DelGiudice 1998, Schaller 1972). However, brown bears that are exposed to a high abundance of salmon select larger salmon (Quinn & Kinnison 1999, Ruggerone et al. 2000), although the greater vulnerability of large salmon due to their greater length, differences in arrival pattern of size and sex classes, and differences in salmon behaviour could influence the choice for larger animals (Quinn & Kinnison 1999). This study clearly indicates that brown hyenas do not choose weak seal pups, but kill in proportion to the occurrence of seal pups of different conditions within the population and therefore also have an additional impact on seal pup mortality.

c) Prey Choice Regarding the Sex of the Pup

Although brown hyenas appear to capture or scavenge seal pups in proportion to their availability based on mass, since female pups are less heavy than male pups, the choice of heavy females in a good condition could yield similar results. It is difficult to obtain a reliable sex ratio estimate for seal pups throughout the season (Chapter 4). The most reliable sex ratio estimate seems to be the ratio at birth, whether there is a sex-related difference in non-violent mortality is unclear,



and the sex ratio of seal pups might therefore change considerably over time. Furthermore the sample size to calculate statistically analysable sex ratios has to be large, and capture of a sufficient number of seal pups is often not possible. In addition behavioural differences between sexes lead to biases in the sample (Kirkman et al. 2002b). Nevertheless, there was no difference in the sex ratios of hyena predations and live pups in the 1997-1998 study period. During the pupping season (December) in 1999-2000, significantly more female pups were killed than proportionally present at the seal colony. The sample of live pups showed a sex ratio in favour of males of 58%, but the sex ratio at birth was determined to be in favour of females (53%). This difference highlights the difficulty in obtaining reliable sex ratio estimates for seal pups and hence the difficulty of comparing the sex ratios of hyena predations with that of live pups. The same is true for the 2000-2001 study period, where significantly more male pups were killed by brown hyenas than were proportionally present at the seal colony after the seal pupping season (January). Although the sex ratio at birth was 54% males, the cross sample in January showed 55% females. The overall sex ratio calculated from all cross samples during all three study periods was male-biased and again highlights the difficulty in obtaining reliable estimates. Therefore no indication of sex-related prey choice can be given and more intensive studies are necessary to analyse such data sets. Nevertheless considering the results of the previous sections it seems rather unlikely that brown hyenas choose between sexes and again more probably kill what is proportionally present at the seal colony.

The visual differentiation of sexes through distinguishing features and choice of larger prey, as seen with bears preferentially killing large male salmon or females (Reimchen 2000, Gende et al. 2001) is unlikely to happen in Cape fur seal pups, as the sexual dimorphism at that age is small.

d) Prey Choice Regarding the Age of the Pup

Cape fur seal pups experience a loss in weight during the first 24 hours after being born (Roux pers. comm.), which is reflected in the results of this study. Newborn pups lost an average of 75 g during their first day of life, although the sample size was low. However, pups older than three days showed an average



increase in mass of close to half a kilogram and gained nearly one kilogram by day five. This gain in mass, although small, might be visually detected by predators and could lead to the choice of older pups. Brown hyenas showed a significant preference of older pups before 3 December, when most pups were younger than three days. Nevertheless this apparent prey choice could also be attributed to the behaviour of the female seal guarding her newborn pup, as older pups were unguarded and hence easier prey. Therefore brown hyenas rather indiscriminately killed pups regarding their age classes, similar to foxes killing chicks at a gull colony (Kruuk 1964)

e) Summary

Brown hyenas capture prey in proportion to their occurrence at the seal colony. An increase in the availability of carcasses leads to an increased use of this prey type. The mass of killed pups corresponded with the representative mass of live pups and further supports the fact that brown hyenas catch whatever is available. Prey choice regarding the sex of seal pups could not be determined, as the determination of the sex ratio from cross samples was unreliable. Older seal pups are preferred at the beginning of the pupping season, possibly not due to their larger size but rather indicating that the guarding of the pup by the mother influences brown hyena prey choice.

7.4.2 Consumption of Kills

Prey choice can ultimately happen after the prey has been killed. Brown bears, for example, kill many salmon, but only consume the larger animals (Gende et al. 2001). In brown hyenas the killing instinct seems to be strong (Goss 1986) and the readiness to kill does not seem to be determined by the hunger state alone (Curio 1976). Brown hyenas might use the opportunity to kill easy prey (Kruuk 1972b, MacDonald 1976) regardless of its condition, but might show prey choice in their consumption. Coyotes for example consume higher-ranking prey independent of its availability (Hernández et al. 2002). The large body size of the prey might be the stimulus leading to consumption and reflects the possibility that predators prefer a large to a light meal (Curio 1976, Ruggerone et al. 2000). In case of easy and overabundant prey such situations can lead to the



abandonment of low-ranking prey that has been killed (MacDonald 1976, Krebs & Kacelnik 1993).

Brown hyenas killed surplus prey that was not consumed at all throughout the study periods. Furthermore many pups were only partially consumed (excessive kill) or carried away (caches) from the seal colony. The number of surplus kills was significantly higher than the number of excessive kills and caches in December and January, hence during and after the peak of the pupping season. Chapter 6 already showed a possible positive influence of seal pup density on the number of pups killed per mass kill event. However, the occurrence of excessive kills and caches combined did not differ over time. Therefore surplus predation and consumption happened simultaneously throughout the study, and the stimulus to hunt surplus prey was most likely not hunger related.

The choice to consume certain pups and leave others could either be random or be related to attributes of the killed pups. Only the brain of excessive kills was consumed, but its implications will be discussed in detail in Chapter 8. The mass of all these partially consumed pups showed significantly more growth and was significantly higher than the mass of surplus predations. Brown hyenas therefore chose to consume heavier pups. The same pattern was detected for surplus and excessive kills occurring only during mass kill events, although the difference in mass was not significant for mass kill events where both surplus and excessive kills were recorded at the same time. The sample size was low with only 14 mass kill events that could be analysed and the difficulties in determining kills belonging to the same mass kill event (Chapter 6) could have influenced these results.

Although excessive kill predations were heavier than surplus kills, brown hyenas might choose prey not only based on size, but might also look for other attributes of the pups. The total body length of excessive kills could not be determined, and the pups could have been heavier not because they were larger, but because their stomachs contained milk. Brown hyenas were frequently observed holding the kill down in the belly region with one of their front paws and licking milk that was pressed out of the stomach, similar to black bears extruding chum salmon (*Oncorhynchus keta*) eggs by applying pressure on the abdominal



cavity (Reimchen 2000). Pups that have just been nursing might be detected by brown hyenas using olfactory cues, not just visual cues. Bears often preferentially consume the eggs of pre-spawn female salmon and are observed sniffing the anal region of their kills. They also seem to mistake small males for females and abandon them after sniffing the anal region (Gende et al. 2001). However, there was no significant difference in milk content of seal pups killed in surplus or those partially consumed, and brown hyenas therefore consumed larger pups regardless of their stomach contents. Significantly more pups were killed in surplus in December than partially consumed or carried away from the colony, and brown hyenas therefore consume prey of higher relative value independent of their availability. Thus, they are not entirely generalists as previously suggested, but show optimal foraging strategies regarding the consumption of prey.

7.5 Summary

In summary, brown hyenas are opportunistic regarding the capture of prey and scavenge or kill whatever is proportionally available at the seal colony. They do not choose the doomed surplus and have an additional impact on seal pup mortality. Surplus killing occurred throughout the season, and killing prey does not seem to be only hunger related; other stimuli might act. However, brown hyenas show prey choice regarding the consumption of seal pups and prefer heavier, more valuable prey.



Chapter 8

Consumption of Seal Pups and Factors Influencing the Feeding Time and Energy Budget of Brown Hyenas

8.1 Introduction

The consumption of prey forms the conclusion of a successful predation sequence (Endler 1991). As soon as the carnivore is satiated, a feedback mechanism prevents further eating, and consequently the hunt for further prey is inhibited (Kruuk 1972b). Nevertheless predators can gain from hunting surplus prey and subsequent caching of the prey when the costs of making a kill or finding carcasses are low (Oksanen et al. 1985, Short et al. 2002), for example when they are exposed to a high abundance of easy prey. This strategy is usually selected for in the smallest members of the predator guild (Oksanen 1983). The alternative to refrain from surplus killing is to secure resources through territorial defence so that future access becomes more predictable (Oksanen 1983, Oksanen et al. 1985). This strategy is predominately used by specialist predators, but depends on the defensibility of the resource. Therefore if a prey resource is unpredictable or indefensible, predators can increase the amount of prey captured to such a degree that the value of consuming the next prey item captured becomes zero (Oksanen et al. 1985), resulting in surplus kills. The stimuli eliciting surplus killing within easily accessible and abundant prey resource are mostly visual or olfactory cues, as well as the movement of the prey (Kossak 1989). The predator will continue to kill until the key stimuli disappear, often until all prey individuals are killed. As consuming these prey is not causally linked to killing, it can occur anywhere in the killing series (Kruuk 1972b).

Many carnivores only partially consume their prey items. Again if little effort is required to capture prey, partial consumption is possible (Gende et al. 2001). Hence when food becomes abundant, predators will show greater selectivity not only regarding prey choice but also regarding the degree of consumption of single prey items (Emlen 1966), especially if more than two bites are required to completely consume the prey, so that the prey value of the item changes over time (Cook & Cockrell 1978, Sih 1980). In these cases a prey item can be viewed as a patch where the valuable portion is fed on first, and consequently the net



intake rate on that prey item decreases so that it is abandoned before it is completely consumed. The strategy of the predator in this case includes the choice to continue feeding or to search for another prey item (Sih 1980).

Additionally nutrient constraints can lead to partial preferences in consumption of prey items (Pulliam 1975), so that maximising caloric intake becomes a secondary goal. Bears (*Ursus* spp), for example, target specific nutrients in salmon (*Oncorhynchus* spp) heads that can only be obtained from the diet and that are essential for their nervous system function (Gende et al. 2001).

Finally interspecific competition can also influence the consumption of prey, as energy and time has to be spent to reduce losses to competitors. Strategies to reduce losses are the reduction of feeding time through fast feeding or hunting of small prey, the defence of the kill, inconspicuousness, and caching or storing of prey (Lamprecht 1978). Brown hyenas (*Parahyaena brunnea*) benefit from food storing in the Kalahari as they reduce the chance to attract other dominant scavengers to the kill site and as the chance of stored food being recovered by competitors is lessened (Mills 1978), and hence they are able to secure a successive meal. The general motivation underlying caching behaviour is different from feeding, and caching, therefore, occurs independently of the hunger state and the number of prey items killed (Curio 1976) and can vary greatly. Often “leisure” time is spent as caching when the abundance of prey is high and energetic needs can easily be met (Oksanen 1983).

Brown hyenas kill surplus food, partially consume some of their prey and carry food away from the seal (*Arctocephalus pusillus pusillus*) colony, hence possibly store food (Chapters 6 and 7). Their only competitors along the southern coastal Namib Desert are black-backed jackals (*Canis mesomelas*), which are known to be considerable competitors to brown hyenas in other habitats (Owens & Owens 1978). The objective of this chapter is to examine the use of killed and scavenged seal pups by brown hyenas considering the value of prey items, the change in seal pup abundance, and the competition with black-backed jackals. It was investigated:

- (1) whether there is a difference in the consumption of killed and scavenged pups,
- (2) whether consumption depends on pup abundance,



- (3) whether feeding and handling times are influenced by seal pup abundance,
- (4) whether the occurrence of caches depends on hunting or scavenging success, and
- (5) whether there is prey choice regarding caches.

Furthermore the value of partially consumed parts of the seal body is discussed with regard to the energy requirements of brown hyenas (Chapter 5).

8.2 Material and Methods

8.2.1 Study Area and Study Period

Data were collected at the Van Reenen Bay seal colony between November 2001 and January 2002, observing brown hyenas foraging at the colony from an observation hut (Chapter 6). Seal pup mortality surveys were conducted at the Wolf Bay seal colony between November and March in 1997-1998, 1999-2000 and 2000-2001 (Chapter 4).

8.2.2 Consumption of Kills and Scavenged Pups

Dead pups found in the samples areas at the Wolf Bay seal colony were recorded (Chapters 4 and 6). It was determined whether there was a difference in the daily occurrences of surplus kills, excessive kills, cached excessive kills and completely consumed pups in general and between the period during the peak pupping season (November and December) and after the peak pupping season (\geq January). The same analysis was done separately for pups that were killed during mass kill events.

All fresh dead pups were marked with numbered metal or plastic tags at their front flipper and changes of their state were recorded on the next consecutive visits to the sample areas (Chapter 7). It was recorded whether the pup was untouched, further consumed, noting the eaten parts, whether it was moved or not present any more, which indicated that it had been carried away by either a brown hyena or possibly a black-backed jackal (Chapter 7).

The number of pups that were further consumed by brown hyenas and the number of carcasses that disappeared ("not found") were used to determine the



number of pups scavenged by brown hyenas at the seal colony. Furthermore the periods during and after the seal pupping season were compared.

The change in the state of marked dead pups was compared to investigate whether brown hyenas showed a preference for any of the three scavenged prey categories: hyena kill (surplus and excessive kills) and non-violent mortality.

8.2.3 Feeding and Handling Time

Feeding and handling times were recorded at the Van Reenen Bay seal colony (Chapter 6). Only feeding times longer than 30 seconds were included in the analysis, as the observation of actual feeding was not always clear during shorter periods. Handling time was defined as the time from the first contact with the prey item until it was either dropped and the brown hyena walked away or until the brown hyena left the colony area carrying the prey (Figure 6.1; yellow line). Handling time encompassed the following behaviours (see Chapter 6): the events of (1) hunting - kill, (2) hunting - contact attempt, (3) death shake and (4) dropping of the prey, and the states of (1) holding and (2) carrying of the prey. Feeding time was excluded from the handling time measurement.

For each focus animal observation, the total feeding and handling times were calculated and compared for differences between the times before and after the peak pupping season. Furthermore feeding times were compared between the two prey categories, kills (including return kills) and scavenged pups (including return carrion) (Chapter 6), as it was assumed that brown hyenas recognised their previous kills. Nevertheless return kills and return carrion were regarded as new prey items when they were approached again.

8.2.4 Competition with Black-Backed Jackals

a) Daily Attendance Pattern of Jackals and Predation Rate

The seal colony at Van Reenen Bay was observed daily from 07:00 until 19:00 or 20:00. Black-backed jackal numbers were recorded each hour. The counts only included black-backed jackals that were present in the beach area (Figure 6.1; yellow line), where the seals hauled out. Binoculars (Kamakura 8 x 32) and telescope (Kamakura 20 - 45x) were used to search the area for jackal presence. Furthermore the number of black-backed jackal kills per day was noted to



determine the predation rate using life tables (Caughley 1977, Chapter 4) for the time between 20 November 2001 and 31 January 2002.

b) Interspecific Competition

It was investigated whether interspecific competition with black-backed jackals influenced the brown hyenas' feeding time. Feeding times on prey items where competition occurred were compared with those without competition. Furthermore the proportion of time spent competing with black-backed jackals was compared for differences between the time before and after the peak pupping season. Competition behaviours were chasing jackals, attacking jackals and protecting the prey (Table 6.1).

8.2.5 Removal or Caching of Seal Pups

During all focus animal observations at the Van Reenen Bay seal colony, it was recorded whether the brown hyena carried a seal pup away from the colony, which was then regarded as a cache. Caches did not include incidences when brown hyenas carried seal pups to protected feeding sites in the visible area or when the same hyena returned later on the same day to the seal colony (intermediate caches). The study distinguished between caches of scavenged and killed pups and determined the percentage of focus animal observations in which a cache occurred.

At the Wolf Bay seal colony, only cached excessive kill remains indicated the occurrence of caches, but the number of additionally cached scavenged pups could be determined by examining of the change in the state of marked dead seal pups to obtain a better estimate of the number of cached pups. It was assumed that marked dead pups that were not present any more had been carried away by either a brown hyena or possibly a black-backed jackal. In contrast to brown hyenas, which are capable of carrying a dead seal pup, black-backed jackals usually have to drag the pup, as its weight exceeds a third of their own body weight. These drag marks can be seen and by following them, the pup could usually be discovered. Hence, all marked pups that could not be found were regarded as brown hyena caches.



8.2.6 Prey Choice Regarding Caches

The proportions of cached killed and scavenged pups were compared to determine whether brown hyenas preferred to cache certain prey categories before and after the peak pupping season and overall at the Van Reenen Bay seal colony. Furthermore the mass of surplus kills, cached surplus kills, and excessive kills without skull (representing the assumed mass of cached excessive kills at the Wolf Bay seal colony) was used to indicate a choice for caches based on mass. The mass of non-violent mortality caches was also compared to the mass of non-violent mortalities that were not cached.

8.2.7 Caloric Value of Brain Tissue

The brain of dead seal pups was removed and weighed on an electronic scale at the laboratory of the Namibian Ministry of Fisheries and Marine Resources (Chapter 7). Brain mass was compared for differences between periods, and the caloric value of brain tissue was determined by using the caloric value estimate for fat tissue of ringed seals (*Phoca hispida*) as described in Stirling & McEwan (1975).

8.3 Results

8.3.1 Consumption of Prey

a) Consumption of Kills

Of the seal pups killed by brown hyenas, 50.5% were killed in surplus, 32% were excessive kills, 6.5% were cached excessive kills, and 11% were completely consumed. During mass kill events, 62% of the remains were surplus kills, 26% were excessive kills, 3% were cached excessive kills, and 9% were completely consumed. The percentages for each of the three study periods are shown in detail in Table 8.1.

Table 8.1: Percentages of prey use for three study periods distinguishing between all predations and predations occurring during mass kill events (number of mass kill events in brackets).

Sample size	All predations			Mass kill events		
	172	321	262	80 (27) 1997- 1998	166 (50) 1999- 2000	95 (29) 2000- 2001
Study period	1997-1998	1999-2000	2000-2001			
Surplus kill	56	57	39	62.5	67.5	57
Excessive kill	38	28	29	30	21	25
Cached excessive kill	2	3	13	2.5	3	4
Completely consumed	4	12	19	5	8.5	14



The proportion of the different prey categories in the 2000-2001 period differed significantly from the periods 1997-1998 and 1999-2000. During 2000-2001, more pups were partially consumed, cached and completely consumed than killed in surplus (1997-1998 vs 2000-2001: Chi² Test $\chi^2 = 23.9$, $df = 3$, $p < 0.0001$; 1999-2000 vs 2000-2001: Chi² Test $\chi^2 = 11.2$, $df = 3$, $p = 0.011$). Nevertheless, data were pooled for the following analysis, as the same pattern was present during all years: the majority of pups were killed in surplus, followed by excessive kills, completely consumed pups and cached excessive kills.

The daily numbers of surplus kills (SK), excessive kills (EK), cached excessive kills (CE) and completely consumed kills (CC) differed significantly. Brown hyenas killed significantly more pups in surplus than were partially consumed (EK), completely consumed (CC), or cached (CE) (Kruskal Wallis Test $H = 43.2$, $p < 0.0001$, Dunn's Multiple Comparison Test: SK vs EK $p < 0.001$, SK vs CE $p < 0.001$, SK vs CC $p < 0.001$) (Figure 8.1).

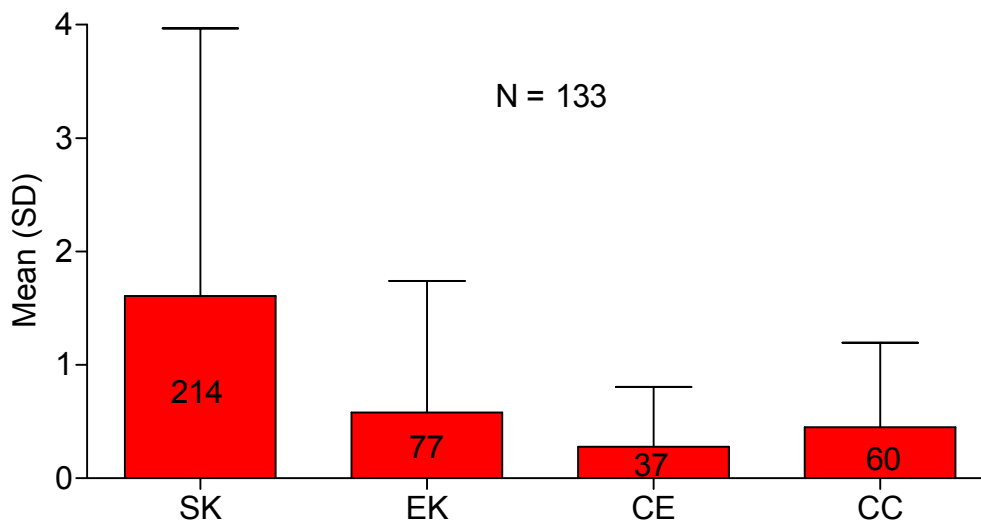


Figure 8.1: Daily number of surplus kills (SK), excessive kills (EK), cached excessive kills (CE) and completely consumed kills (CC) (N = number of data collection days, inserted numbers: total number of remains).

During the peak pupping season the daily numbers of surplus kills were greater than other kill remains (Kruskal Wallis Test $H = 21.4$, $p < 0.0001$; Dunn's Multiple Comparison Test: SK vs EK $p < 0.001$; SK vs CE $p < 0.01$; SK vs CC $p < 0.01$). After the peak of the pupping season there was no difference in the daily numbers between surplus and excessive kills, but the daily numbers of these two categories were significantly higher than the numbers of cached excessive kills (Kruskal Wallis Test $H = 32.7$, $p < 0.0001$; Dunn's Multiple Comparison Test: SK

vs CE $p < 0.001$ and EK vs CE $p < 0.01$) (Figure 8.2). Additionally more pups were killed in surplus than completely consumed (Dunn's Multiple Comparison Test $p < 0.05$).

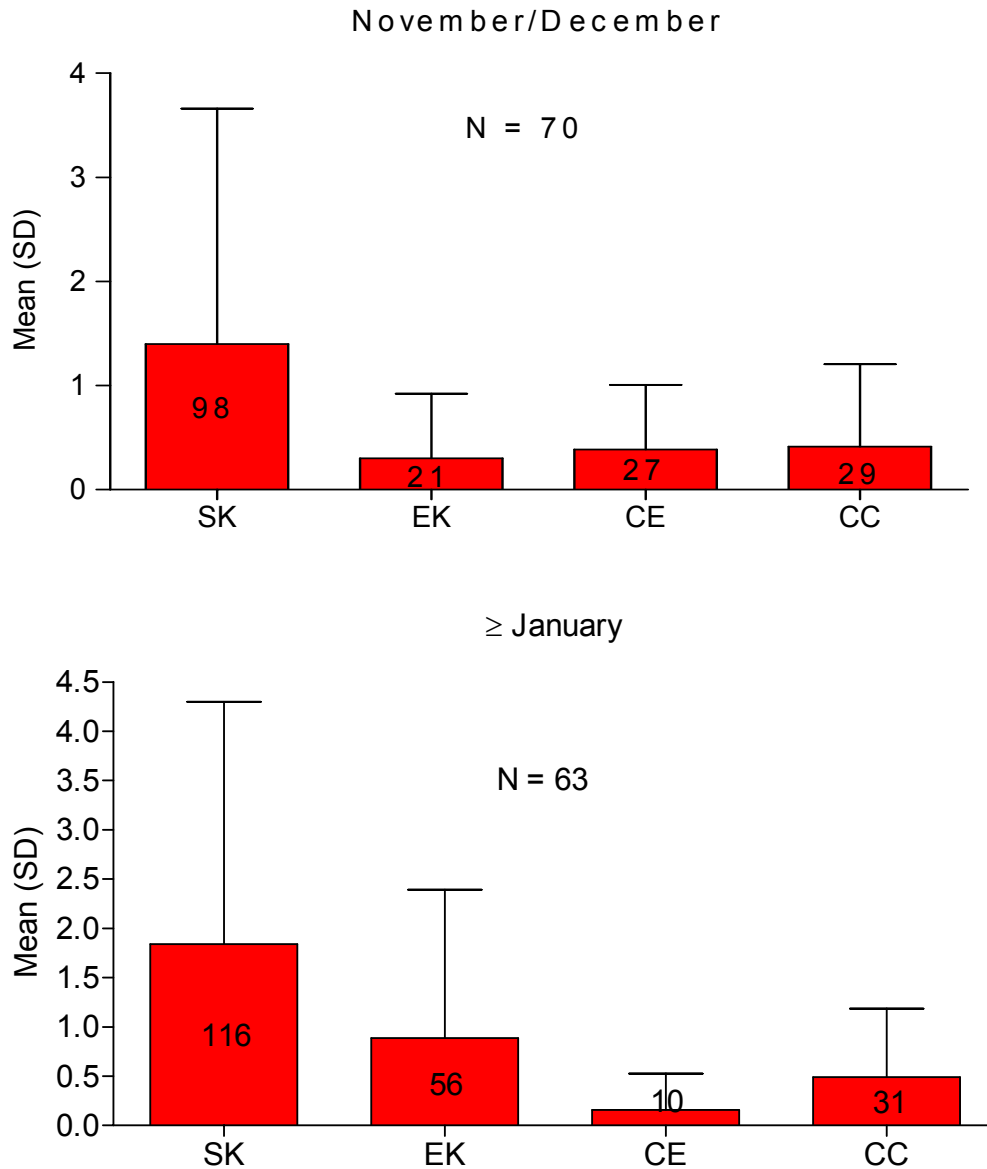


Figure 8.2: Daily number of surplus kills (SK), excessive kills (EK), cached excessive kills (CE) and completely consumed kills (CC) during different periods (N = number of data collection days, inserted numbers: total number of remains).

The daily number of surplus kills did not differ from those that were at least partially consumed (EK+EC+CC) either during or after the pupping season, or overall (Mann-Whitney U-test: pupping season $U = 2448$, $p = 0.10$; after pupping season $U = 1920$, $p = 0.34$; overall $U = 8686$, $p = 0.80$).

The daily numbers of surplus kills, cached excessive kills and completely consumed kills did not differ seasonally (Mann-Whitney U-Test: SK $U = 2007$, $p =$

0.37; CE U = 1837, p = 0.088; CC U = 1988, p = 0.32), but the daily number of excessive kills was significantly lower during the pupping season than after the pupping season (Mann-Whitney U-Test U = 1629, p = 0.009).

In mass kill events (Figure 8.3), brown hyenas also killed significantly more pups in surplus than were partly consumed (EK), completely consumed (CC) or cached (CE) (Kruskal Wallis Test H = 101.5, p < 0.0001, Dunn's Multiple Comparison Test p < 0.001). Additionally the daily number of excessive kills was higher than that of cached excessive kills (Dunn's Multiple Comparison Test: p < 0.05).

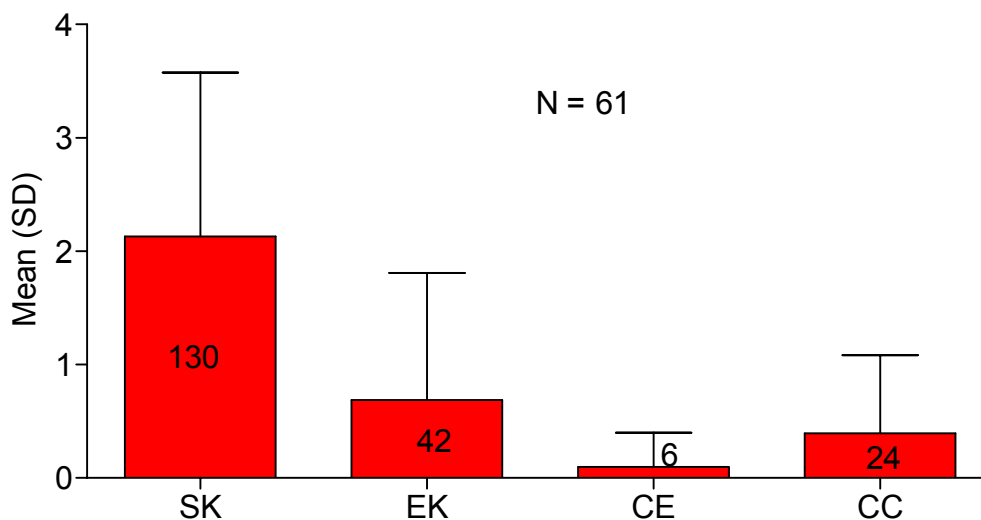


Figure 8.3: Number of surplus kills (SK), excessive kills (EK), cached excessive kills (CE) and completely consumed kills (CC) per mass kill event (N = number of mass kill events, inserted numbers: total number of remains).

The number of dead pups per kill category for each mass kill differed between periods as before, with the exception that the number of excessive kills before and during the peak pupping season (November/December) was not significantly higher than the number of cached excessive kills (November/December: Kruskal Wallis Test H = 49.6, p < 0.0001; Dunn's Multiple Comparison Test: EK vs CE p > 0.05; SK vs EK/CE/CC p < 0.001; January: H = 57.6, p < 0.0001; EK vs CE p < 0.01; SK vs EK/CE/CC p < 0.0001) (Figure 8.4).

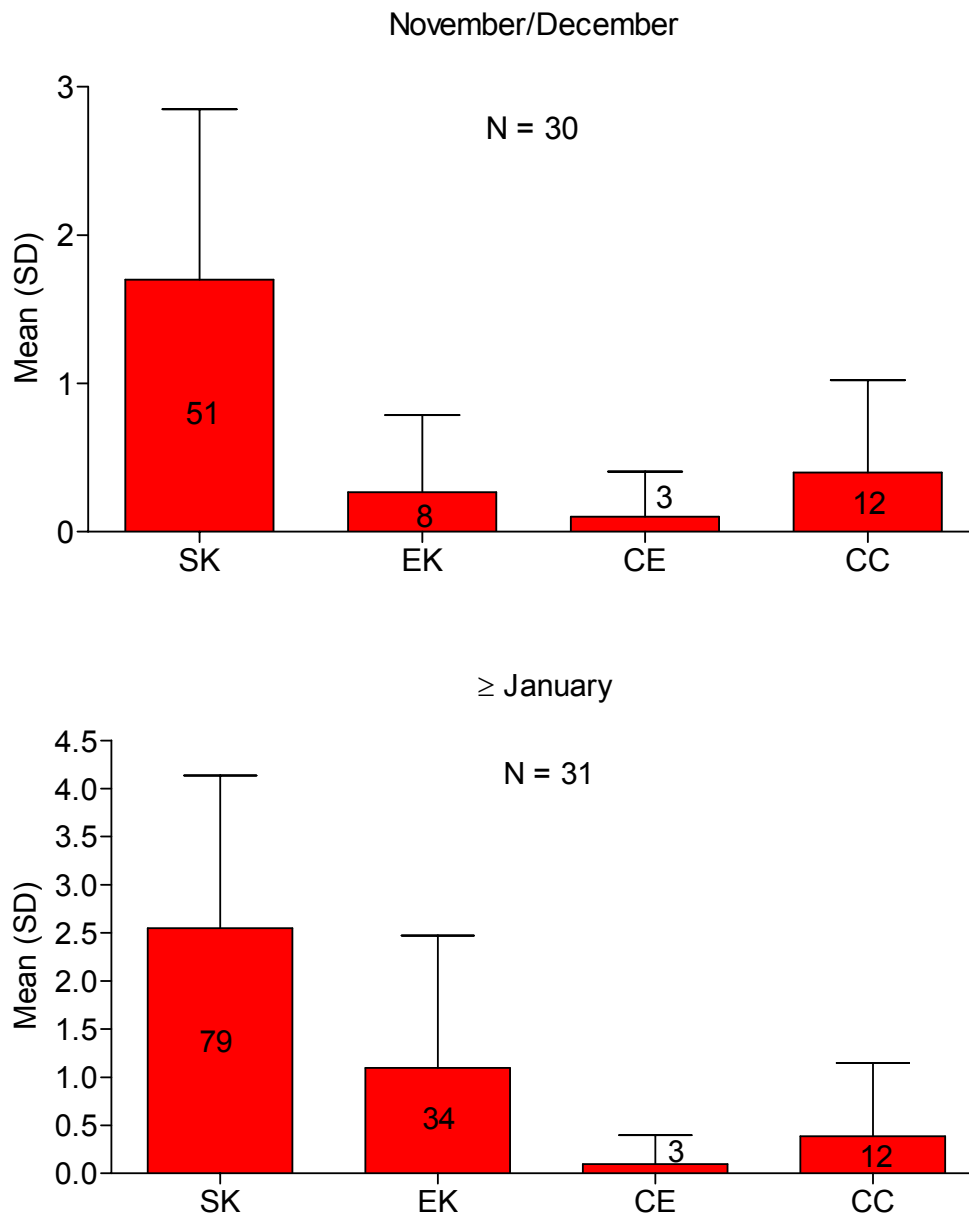


Figure 8.4: Number of surplus kills (SK), excessive kills (EK), cached excessive kills (CE) and completely consumed kills (CC) per mass kill event during different periods (N = number of mass kill events, inserted numbers: total number of remains).

During mass kill events, brown hyenas killed significantly more seal pups in surplus than non-surplus (all other categories combined) during and after the pupping season, and overall (Table 8.2).

Table 8.2: p values of the comparison of surplus kills and non-surplus kills during mass kill events in general (entire study period), during the pupping season (Nov/Dec) and after the pupping season (≥Jan)

Mann-Whitney U-Test	General	November/December	≥January
U	1124.0	233.0	313.5
p	0.0002	0.0013	0.0187

After the peak pupping season, the daily number of surplus and excessive kills per mass kill event increased (Mann-Whitney U-Test: SK $U = 322.5$, $p = 0.040$, EK $U = 304$, $p = 0.019$), whereas the daily number of cached excessive kills and completely consumed kills remained the same (Mann-Whitney U-Test: CE $U = 463.5$, $p = 0.99$, CC $U = 738$, $p = 0.69$).

b) Consumption of Scavenged Pups

Pups killed by brown hyenas (SK and EK) were more likely to be scavenged than non-violent mortalities (1999-2000: Chi² Test $\chi^2 = 10.8$, $df = 1$, $p = 0.001$; 2000-2001: Chi² Test $\chi^2 = 75.2$, $df = 1$, $p < 0.0001$) (Figures 8.5 and 8.6). The brain of carcasses was only consumed in four cases, twice on non-violent mortalities in 1999-2000 (0.03% of carcasses) and once on surplus kills during both seasons (1.2% of the carcasses in 1999-2000 and 1.8% in 2000-2001).

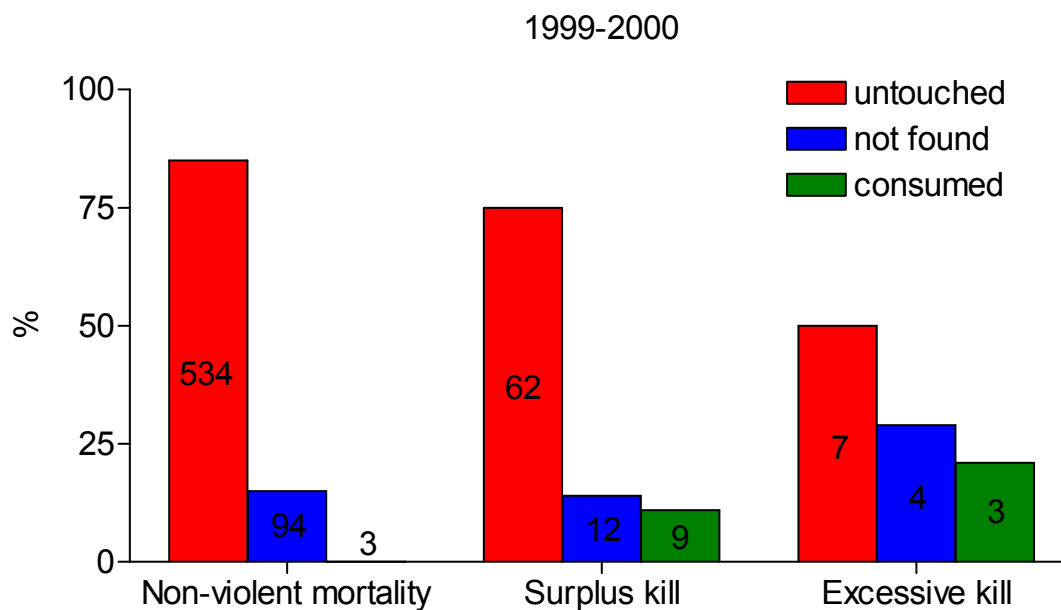


Figure 8.5: Number and proportions of not scavenged (not touched) and scavenged (not found, consumed) marked, dead seal pups at the Wolf Bay seal colony during the 1999-2000 study period.

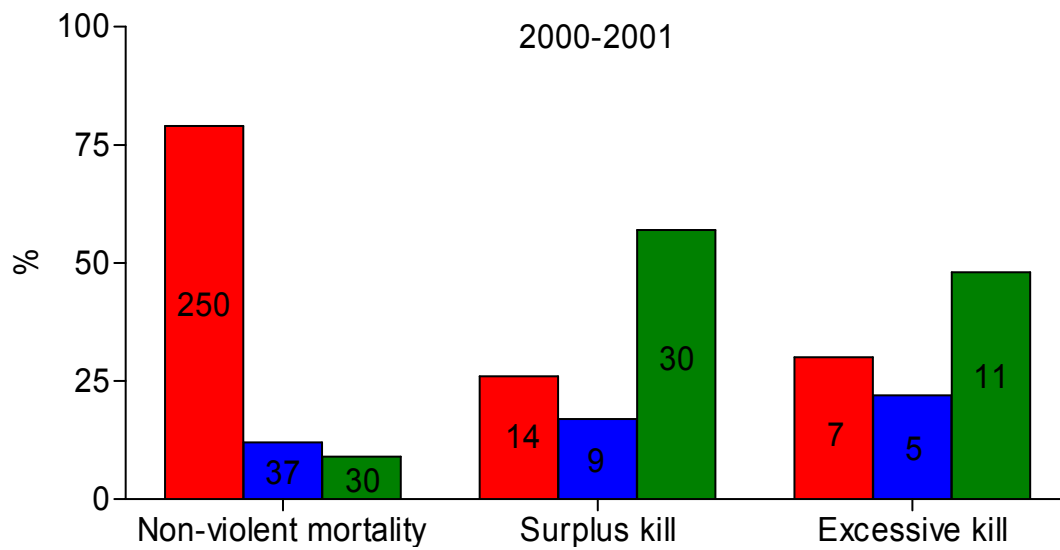


Figure 8.6: Number and proportions of not scavenged (not touched) and scavenged (not found, consumed) marked, dead seal pups at the Wolf Bay seal colony during the 2000-2001 study period.

8.3.2 Feeding and Handling Time

The proportion of time spent feeding and handling per focus animal observation was significantly lower in November than in January (t-test: feeding time $t = 1.37$, $df = 26$, $p = 0.004$; arcsine square root transformed handling time $t = 2.56$, $df = 26$, $p = 0.017$) (Figures 8.7 and 8.8).

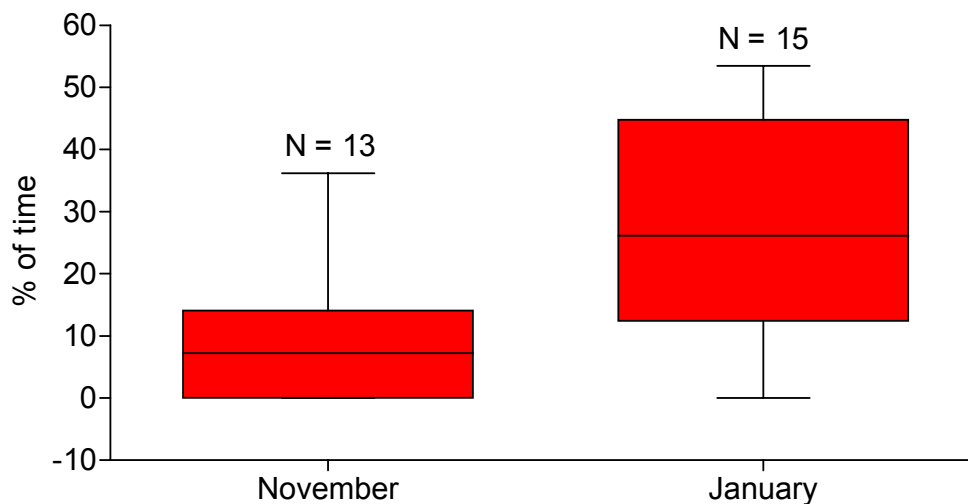


Figure 8.7: Percentage of time spent feeding per focus animal observation in November and January (N = number of focus animal observations).

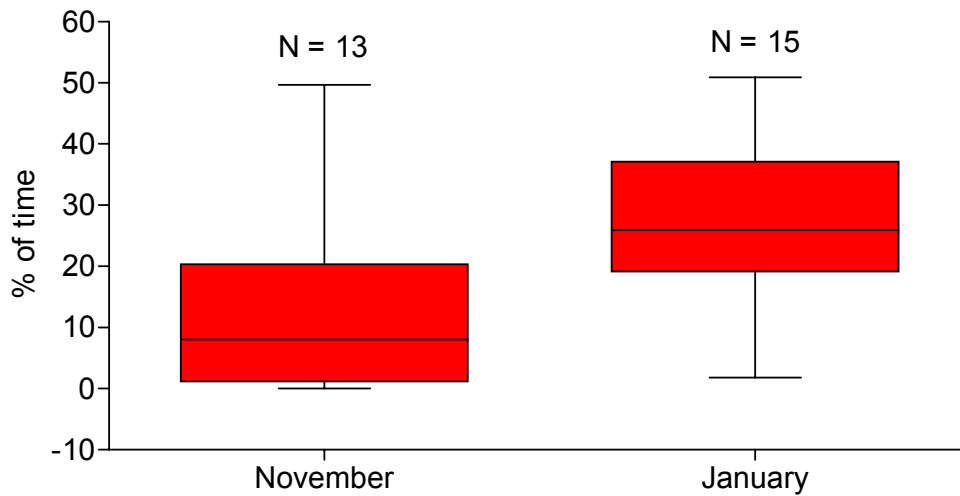


Figure 8.8: Percentage of time spent handling per focus animal observation in November and January (N = number of focus animal observations).

The amount of time spent feeding on scavenged and killed pups did not differ (Mann-Whitney U-Test $U = 1225$, $p = 0.82$) (Figure 8.9), but feeding times on scavenged and killed prey items were significantly shorter in January than in November (Mann-Whitney U-Test $U = 278$, $p = 0.013$) (Figure 8.10), as were the handling times (Mann-Whitney U-Test $U = 261.5$, $p = 0.002$).

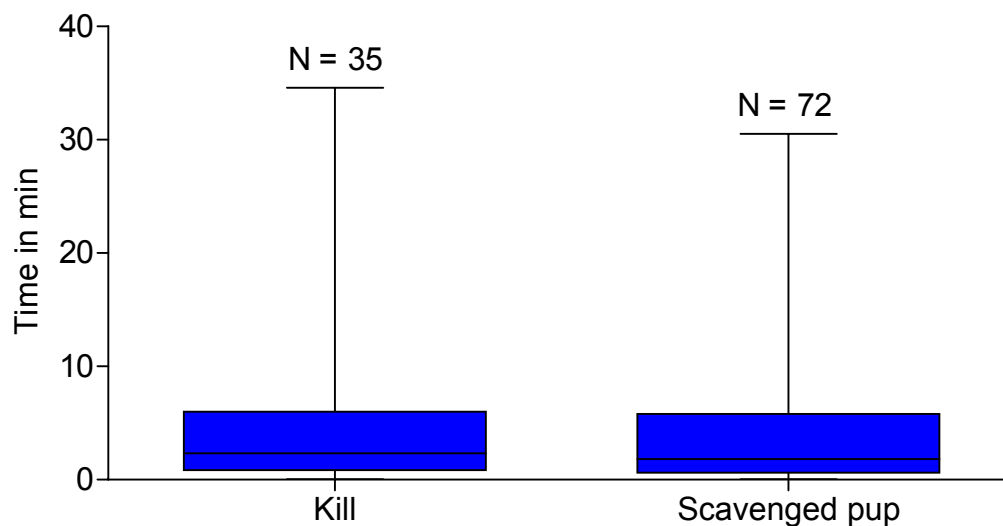


Figure 8.9: Feeding times on kills and scavenged pups at the Van Reenen Bay seal colony between November 2001 and January 2002 (N = number of prey items).

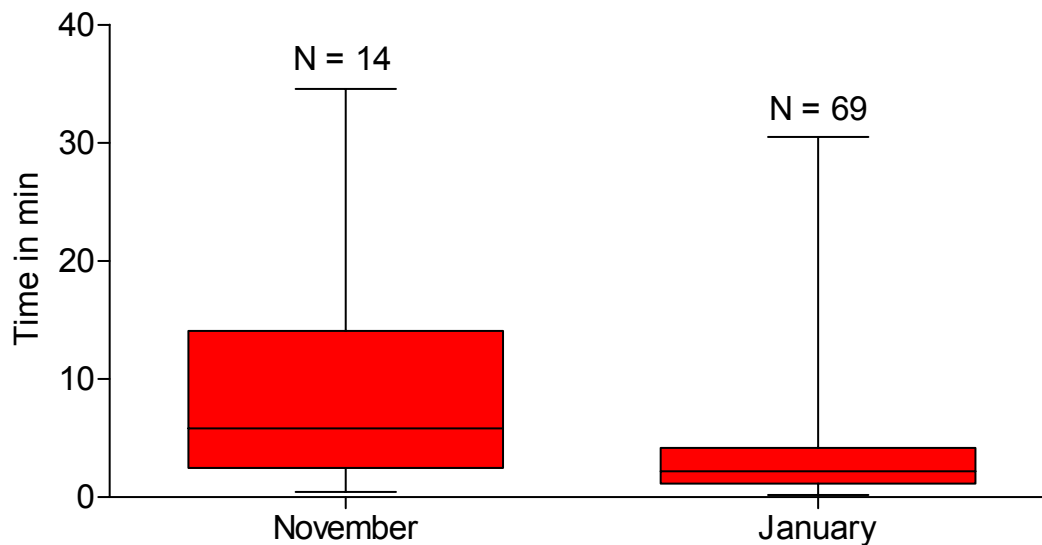


Figure 8.10: Feeding times on kills and scavenged pups in November and January (N = number of prey items).

8.3.3 Competition with Black-Backed Jackals

a) Attendance of Black-Backed Jackals at the Van Reenen Bay Seal Colony

The average number of black-backed jackals at the seal colony changed during the course of the day (Figure 8.11). More jackals were present at the colony in the morning and evening than in the afternoon (Kruskal Wallis Test $H = 89.4$, $p < 0.0001$, Dunn's Multiple Comparison Test $p < 0.05$ for 7:00 h to 9:00 h vs 13:00 h to 17:00 h; 10:00 h vs 15:00 h to 17:00 h; 19:00 h vs 17:00 h).

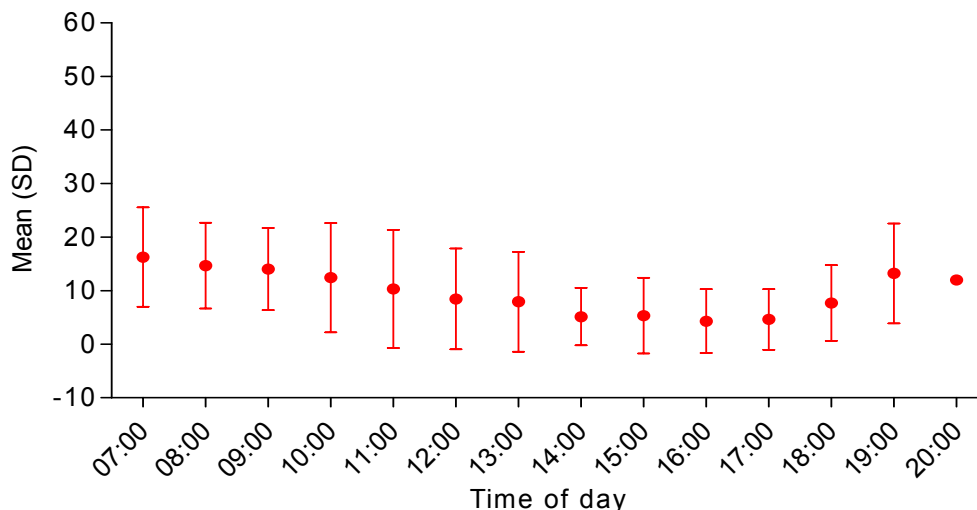


Figure 8.11: Mean (\pm SD) number of black-backed jackals during hourly counts at the Van Reenen Bay seal colony.

The mean number of jackals present at the colony per day also differed significantly between the three observation periods (Kruskal Wallis Test $H = 24.6$,

$p < 0.0001$; Dunn's Multiple Comparison Test Nov vs Dec $p < 0.001$; Nov & Dec vs Jan $p < 0.05$), with low jackal numbers in December (Figure 8.12). There were always more jackals present at the seal colony per hour than brown hyenas (Mann-Whitney U-Test $U = 1.0$, $p < 0.0001$), and the ratio between brown hyena and jackal presence per hour did not change significantly over time (Kruskal Wallis Test $H = 0.30$, $p = 0.86$).

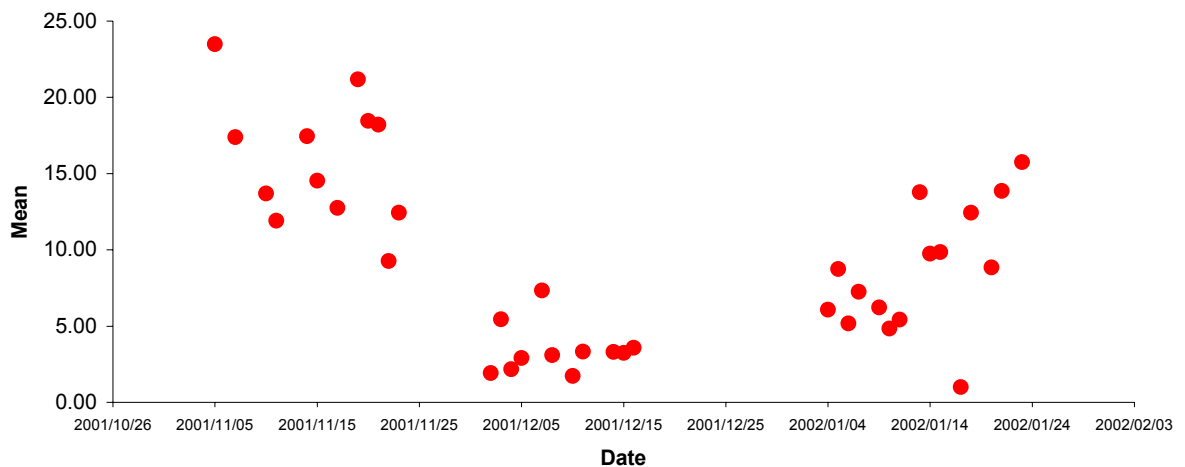


Figure 8.12: Mean number of jackals present at the seal colony during the observation period.

b) Seal Pup Predation

The number of jackal kills per hour did not differ during and after the peak pupping season (t-test $t = 1.67$, $df = 24$, $p = 0.11$) (Figure 8.13). The predation rate (% of pups killed) was 12.4% until the end of January, and the number of jackal kills per day was not correlated with the number of jackals at the colony (Pearson Product Moment, $r = 0.12$, $p = 0.52$).

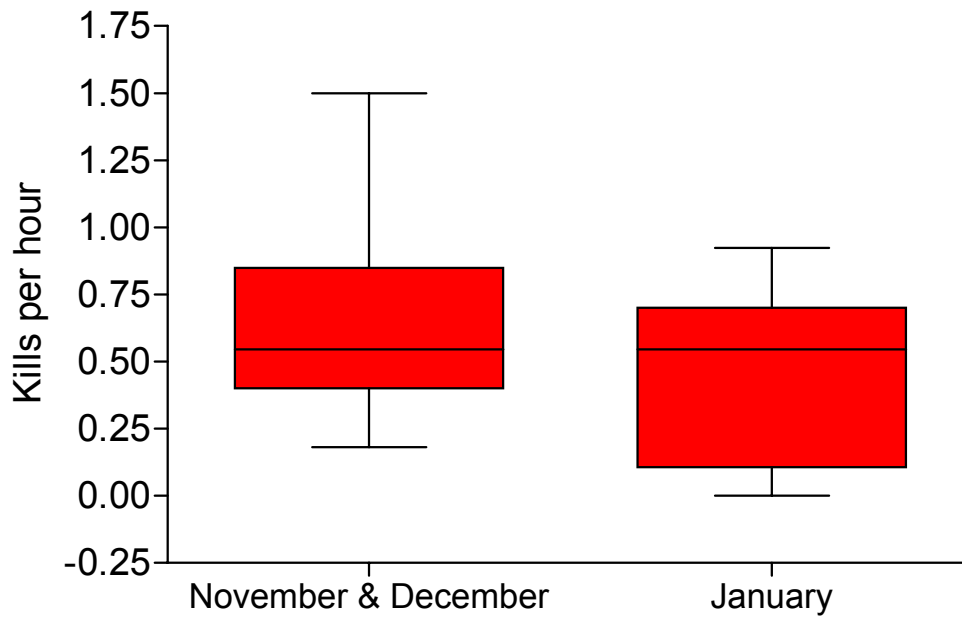


Figure 8.13: Number of jackal kills per hour at the Van Reenen Bay seal colony during (November & December) and after the peak of the seal pupping season (January).

c) Interspecific Competition

Brown hyenas spent significantly more time competing with jackals before the pupping season than afterwards (Mann-Whitney U-Test $U = 72$, $p = 0.023$) (Figure 8.14).

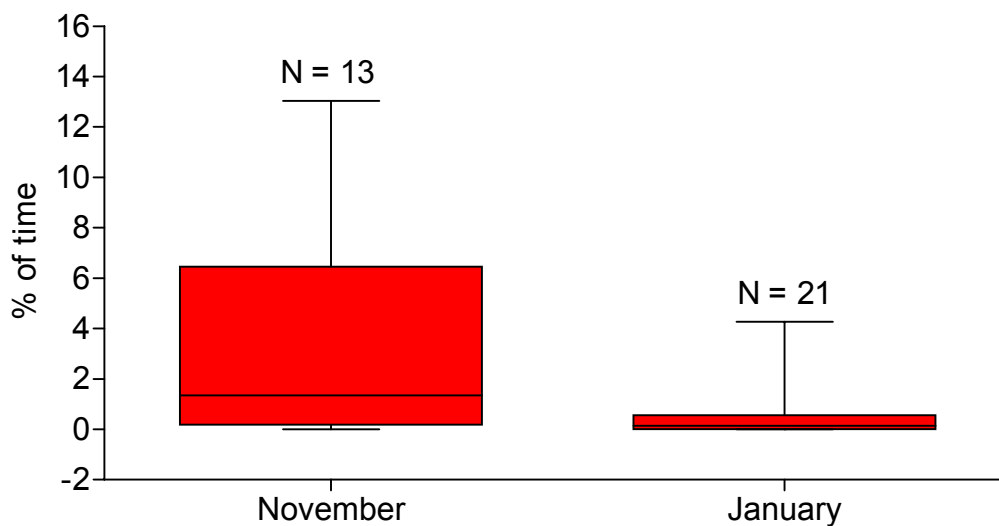
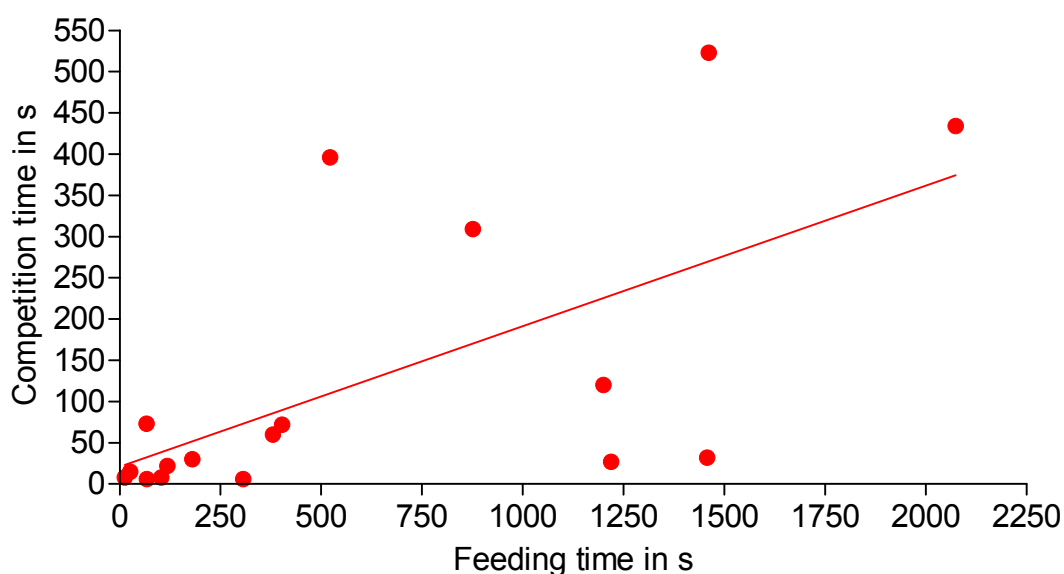


Figure 8.14: Percentage of time spent on interspecific competition per focus animal observation before and after the peak pupping season.



Feeding times were significantly longer when brown hyenas competed for the prey item with black-backed jackals (Mann-Whitney U-Test $U = 305$, $p = 0.013$; number of observations: 69 without competition and 15 with competition), and feeding time was correlated with competition time per prey item (Spearman Rank Correlation, $r = 0.69$, $p = 0.002$) (Figure 8.15).

Of the 79 seal pups observed scavenged by brown hyenas, 21.5% had been killed by jackals. Brown hyenas fought over their own kills with jackals twice but never lost their kills to jackals.



Cached excessive kill remains made up 8% of all predations found at the Wolf Bay seal colony for the 1999-2000 and 2000-2001 study periods. Another 17% of all marked predations (SK and EK) whose change in state was noted as “not found” may also have been cached by brown hyenas.

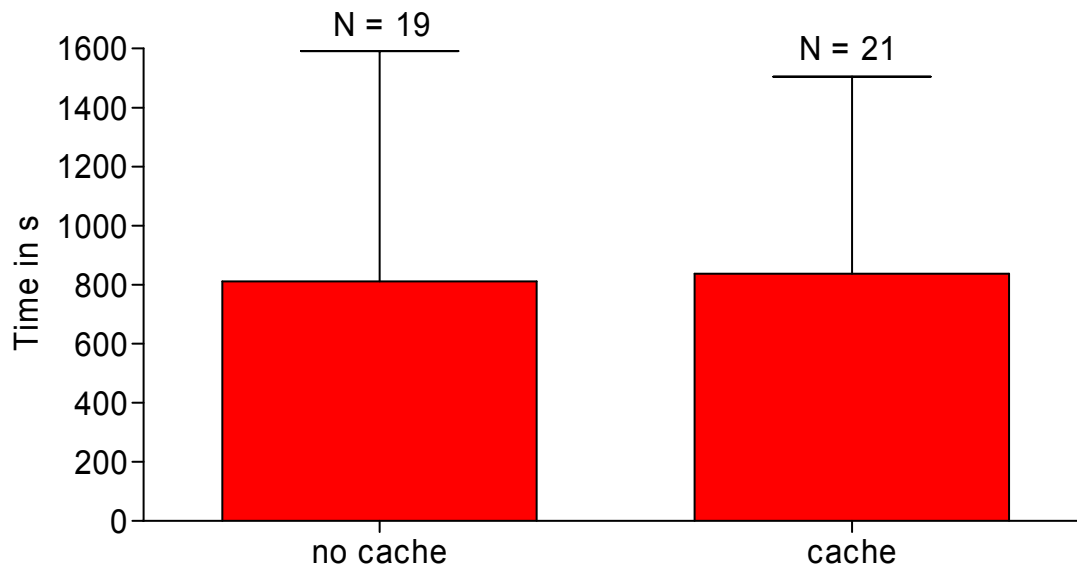


Figure 8.16: Mean (SD) total feeding time during the focus animal observations with and without the occurrence of caching behaviour (N = number of focus animal observations).

8.3.5 Prey Choice Regarding Caches

a) Kill versus Scavenged Pup

Brown hyenas did not show a preference for either of the two cache categories, cached kill and cached scavenged pup (Mann-Whitney U-Test $U = 735$, $p = 0.18$). The daily number of cached scavenged or killed pups also did not differ before and after the peak pupping season (Mann-Whitney U-Test: scavenge $U = 87.5$, $p = 0.47$; kill $U = 79$, $p = 0.27$).

b) Surplus Kills versus Excessive Kills

The use of surplus kill and excessive kill carcasses as caches at the Wolf Bay seal colony did not differ (Chi² Test $\chi^2 = 1.60$, $df = 1$, $p = 0.21$), but including cached excessive kills into the analysis suggested that a larger proportion of excessive kills was cached (Chi² Test $\chi^2 = 48.2$, $df = 1$, $p < 0.0001$). However, the

number of immediately cached surplus kills remains unknown and the latter result might therefore be an overestimate.

c) Mass of Cached Predations

The masses of surplus kills and excessive kills without skull did not differ (Mann-Whitney U-Test $U = 7172$, $p = 0.39$) (Figure 8.17). Although the mass of cached excessive kill remains (skull bones) that were found at the seal colony could not be determined, it was assumed that the mass was similar to the mass of excessive kills, which were measured at the seal colony. Consequently the masses of cached surplus kills and excessive kills without skull were compared. The comparison of the linear regression curves of these two categories did not differ (slopes $F_{1,94} = 2.11$, $p = 0.15$; elevations $F_{1,95} = 2.56$, $p = 0.11$) (Figure 8.18).

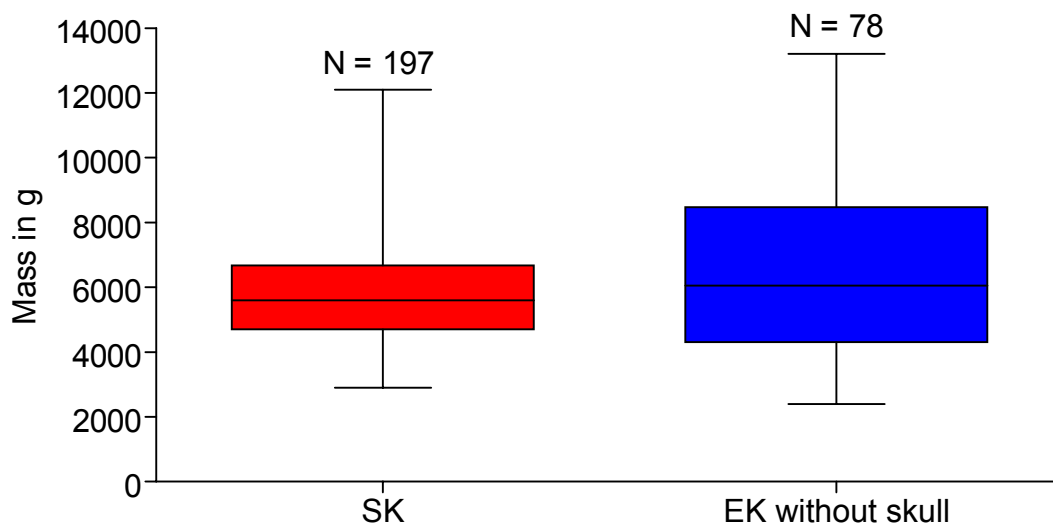


Figure 8.17: Comparison of the mass of surplus kills and excessive kills without skull found at the Wolf Bay seal colony during all three study periods (N = number of kills).

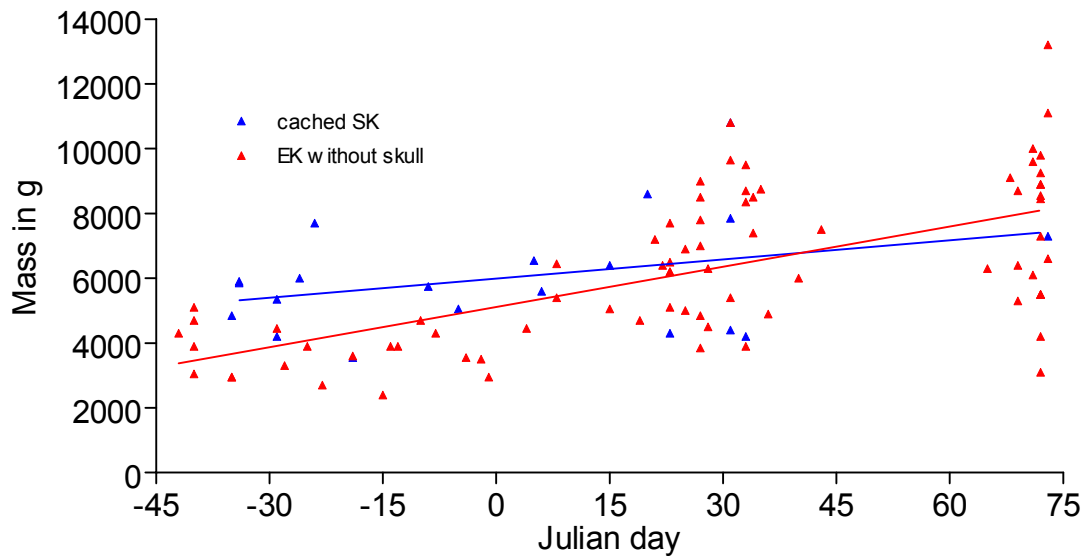


Figure 8.18: Linear regression curves of the mass of cached surplus kills and excessive kills without skull.

Furthermore the linear regression curves of cached surplus kills also did not differ (slopes $F_{1,159} = 0.40$, $p = 0.53$; elevations $F_{1,160} = 0.51$, $p = 0.47$) (Figure 8.19), and therefore brown hyenas did not chose to cache larger surplus kills than proportionally present at the seal colony.

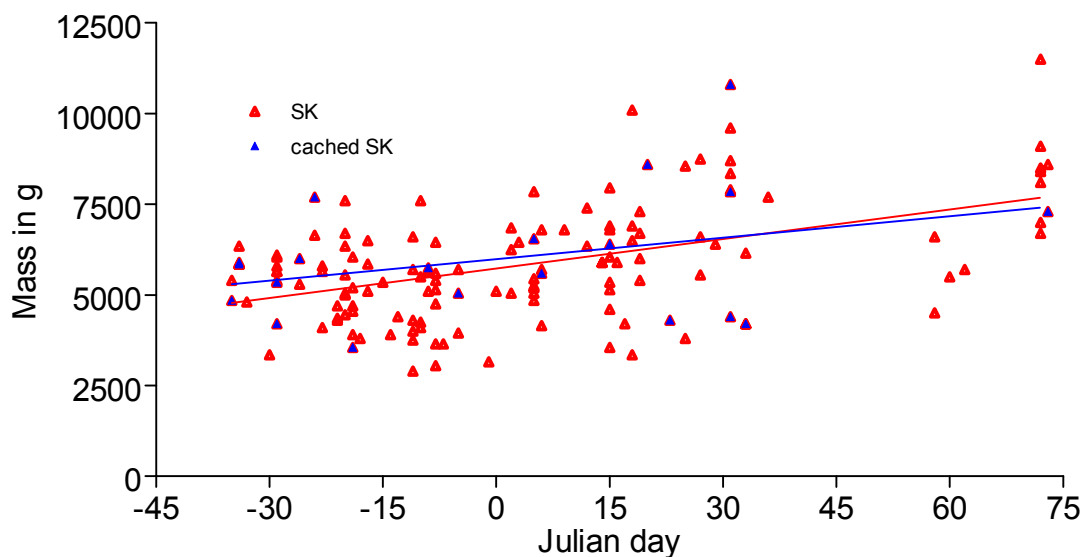


Figure 8.19: The mass of cached surplus kills and all surplus kills found at the Wolf Bay seal colony over time.

d) Mass of Cached Non-Violent Mortalities

The comparison of the mass of cached non-violent mortalities (“not found”) and uncached non-violent mortalities showed no significant differences (Mann-Whitney U-Test $U = 20800$, $p = 0.40$) (Figure 8.20).

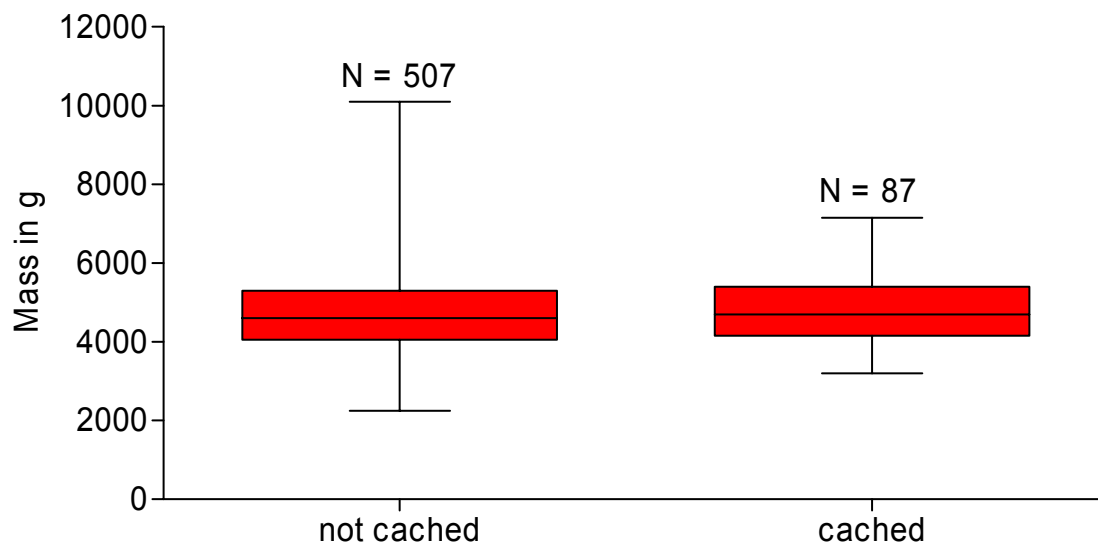


Figure 8.20: Median mass of cached and not cached non-violent mortalities.

8.3.6 Value of Brain Tissue

The mass of the brain of dead seal pups measured during the study period was 158 ± 32.4 g (SD), ranging from 118.8 g to 261.0 g, and did not differ between December and January (t-test $t = 0.58$, $df = 35$, $p = 0.57$) (Figure 8.21). Brain mass represented on average $3.4\% \pm 0.6\%$ (SD) of the total body mass of the pup, and the mass of the pup and the brain were correlated (Pearson Product Moment $r = 0.69$, $p < 0.0001$).

The caloric value of ringed seal fat is 8.7 kcal/g of fat (Stirling & McEwan 1975). Therefore the average caloric value of Cape fur seal pup brains during the study period was estimated to be 1374.6 kcal.

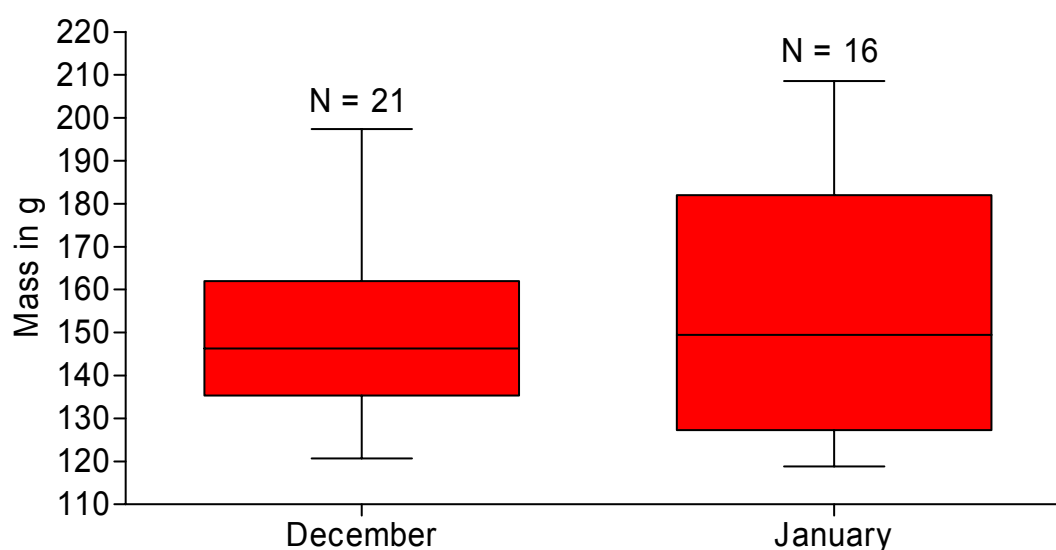


Figure 8.21: Median mass of the brain of seal pups in December and January.

8.4 Discussion

8.4.1 Consumption of Prey

a) Consumption of Kills

Many predators that are faced with a superabundance of easy prey capture prey in excess of their daily maximum intake ability. They either refrain from doing anything with the surplus food or show preferences for certain body parts of the prey (Schaller 1972, Oksanen et al. 1985). Brown hyenas at the Wolf Bay seal colony killed between 39% and 57% of their prey in surplus. The only other record of brown hyenas engaging in surplus killing is described by Skinner (1976), where 10 sheep (*Ovis* sp) were killed in a kraal and only three heads were consumed. This situation represents a typical surplus kill event for prey that does not show the regular anti-predator behaviour, either due to unusual weather situations or due to confinement. Bad weather situations, for example, lead to surplus killing by wolves (*Canis lupus*). Wolves that usually consume all of the white-tailed deer (*Odocoileus virginianus*) they kill either consumed nothing or only up to 33% of deer killed during a multiple killing event (DelGiudice 1998) and Miller et al. (1985) described a surplus of 72% for wolves killing caribou calves (*Rangifer tarandus groenlandicus*).

Nevertheless there are plenty of incidents of surplus killing that occur regularly in natural predator-prey systems, usually when the combination of high prey abundance and easy catch ability are met. Foxes (*Vulpes vulpes*), for



example, only consume 12% of their black-headed gull (*Larus ridibundus*) kills and 17% of their sandwich tern (*Sterna sandvicensis*) kills (Kruuk 1964, Kruuk 1972b). These birds were breeding on sub-optimal habitat, but there are also examples of seasonal predator-prey systems in which surplus killings occur throughout the specific season. During the salmon run for instance brown (*Ursus arctos*) and black bears (*Ursus americanus*) capture a large amount of surplus prey (Frame 1974, Gende & Quinn 2004). Polar bears (*Ursus maritimus*) are also known to kill ringed and bearded seal (*Erignathus barbatus*) pups without consuming them (Stirling & McEwan 1975, Stirling & Archibald 1977, Smith 1980).

Often a higher proportion of prey is consumed, when the abundance of the prey species is low (Stirling & Archibald 1977, Gende et al. 2001), as occurred in this study. Brown hyenas consumed proportionally more prey during the 2000-2001 study period, when seal pup abundance was lower than during the other two years. Nevertheless in general more pups were killed in surplus than in the other consumed prey categories, but in total the proportion of surplus kills and non-surplus kills was equal. After the pupping season, however, the proportion of excessive kills within the non-surplus kill category increased, which might indicate a higher degree of selectivity for brain tissue when seal pup abundance and density is great (compare with Emlen 1966). This selectivity can also be seen in brown and black bear consumption of salmon (*Onchorhynchus* spp), where less biomass per captured fish is eaten when availability is high and energy-rich body parts are preferred (Gende et al. 2001). But in general, the proportion of partially-consumed pups was higher than that of completely consumed or cached pups. Partial consumption was without exception directed at the brain of the seal pup.

The closest sympatric relative of the brown hyena, the spotted hyena (*Crocuta crocuta*), generally consumes almost 100% of a carcass (Schaller 1972), but brown hyenas are described as more leisurely feeders (Owens & Owens 1978). However, apart from spending a considerable amount of time separating pieces of a carcass for storage, they occasionally show a preference for fat and brain tissue (Skinner 1976, Owens & Owens 1978). Feeding on seal pups has only seldom been described and reports are inconclusive. Goss (1986) observed brown hyenas crushing the skull and eating the head, followed by

peeling back of the skin and pulling the skin upwards to eat the rest of the body entirely, whereas Skinner et al. (1995) state that fresh carcasses were never completely consumed and that brown hyenas usually consumed the brain and intestines. These observations do not conform to the results of this study. Goss' (1986) observations of peeling back the skin, leaving the skin and core of skeleton behind, was observed to be the mode of feeding for black-backed jackals rather than that of brown hyenas, and similar behaviour has been observed in arctic foxes (*Alopex lagopus*) (Smith 1980). Brown hyenas that completely consumed pups usually only left pieces of the skin behind, but the skeleton was entirely consumed. Partial consumption of fresh kills only included the consumption of brain and not of intestines, and an otherwise intact pup with only the head missing was found as remains.

Partial consumption and preference for specific tissues is a widespread phenomenon and usually occurs when prey can initially not entirely be consumed (Cook & Cockrell 1978, Sih 1980) and when the energetic costs of capture are low (Oksanen et al. 1985) and prey availability is high (Gende et al. 2001). Brown hyenas show a strong preference for brain tissue when partially consuming seal pups. Predators frequently start eating their prey at the point where the killing bite was placed (Eisenberg & Leyhausen 1972), which could explain the initial consumption of the brain, but does not explain the premature abandonment of the kill. If prey availability allows a high degree of selectivity, brown hyenas could afford to exclusively use the energy-rich parts of the seal body, not considering potential nutrient constraints through unbalanced feeding and metabolic constraints at this point (see further below). Hence brown hyenas behave similarly to other species, such as polar bears that predominately feed on the blubber of ringed seals unless they are starved (Stirling & McEwan 1975), wolves that consume mainly the head of salmon (Darimont et al. 2003), and brown and black bears that consume eggs in female and the brain in male salmon (Reimchen 2000, Gende et al. 2001). In the latter examples the attributes of the fish play a major role and the size, sex and spawning status is important for the choice of consumption (Gende et al. 2001). However, brown hyenas seemed to kill seal pups in proportion to their occurrence at the seal colony and hence did not show preference towards the condition or sex of the pup (Chapter 7).



Nevertheless they partially consumed larger pups and the implications regarding the value of consuming larger pups will be discussed further below.

The consumption of pups during mass kill events showed a similar pattern to the analysis of all killing events together. The majority of pups were killed in surplus, followed by partially consumed pups, completely consumed pups and cached excessive kills. Nevertheless there were significantly more pups killed in surplus than in non-surplus, which indicates that stimuli, such as the abundance of pups at the kill site or the movement of prey, might elicit multiple killing and result in a larger amount of surplus food. More direct observations with regard to prey density and behaviour are necessary to further analyse this difference.

Brown hyenas again act as generalist predators (Chapter 7) through killing prey in surplus given the right circumstances of abundant and easy prey. The seal colonies are most probably indefensible resources where home ranges of brown hyenas of different clans overlap (Chapter 5). Nevertheless seal colonies are also a relatively predictable resource, particularly during the pupping season, when pups are superabundant and brown hyenas are able to kill surplus prey with little effort in order to ultimately choose valuable prey for consumption, as is also seen with bears feeding on salmon (Gende et al. 2001).

b) Consumption of Scavenged Pups

Brown hyenas showed a clear preference for hyena predations when scavenging carcasses. Between 38% and 72% of hyena predation carcasses were scavenged by brown hyenas, in contrast to 15% to 21% of non-violent mortalities. The brain of carcasses was seldom consumed (0.03% of non-violent mortalities and 1.2% to 1.8% of surplus kills) and brown hyenas preferred to consume other parts of the body. Adult wolves that exclusively consume the head of fresh salmon also consume other parts than the head of scavenged salmon carcasses (Darimont et al. 2003). As with the brown hyenas investigated in this study, black bears show a preference for brain with abandoned bear-kills as opposed to other salmon carcasses and generally consume more abandoned kills than other carcasses (Frame 1974).



8.4.2 Feeding and Handling Time

From the optimal diet point of view, differences in feeding and handling time should be observed between periods of low and high prey abundance. High prey density results in lower search costs and the predator will hence consume less of each item as a direct response to a shortened inter-catch interval (Cook & Cockrell 1978, Sih 1980). However, handling time is difficult to estimate for flexible predators that feed selectively, decrease prey consumption with increasing prey density, and kill without consuming (Oksanen et al. 1985), and feeding time might be a better indicator to determine optimisation.

Prey encounter intervals were shorter in January, after the peak of the seal pupping season, than in November, before the peak of the pupping season (Chapter 6). Brown hyenas therefore should decrease feeding and handling times per prey item in January. This pattern was seen in this study. Although the overall feeding and handling times per foraging bout were longer in January than in November, the feeding and handling times per prey item were shorter after the peak of the pupping season, when seal pup density was highest. The increase in total feeding time per foraging bout could result from a larger number of pups that were fed on, and the results from Chapter 6 regarding the use of scavenged pups support this suggestion. Whether also a greater number of kills were consumed after the peak pupping season could not be determined, as the data set was too small and as no relation between the number of killed pups and the number of consumed pups could be detected (compare with Kruuk 1964).

Feeding and handling times of killed and scavenged pups were similar. Goss (1986), however, describes long feeding times on kills and not previously-scavenged carcasses and shorter feeding times on previously-scavenged and old carcasses. The degree of decomposition of the carcasses that were consumed by brown hyenas during the course of this study could not be determined, but it is expected that the majority of them were fresh. The Van Reenen Bay seal colony, where these observations were carried out, is situated on a sandy beach and the tides and prevailing high swells wash many carcasses out to sea on a daily basis. Brown hyenas and black-backed jackals therefore have limited access to older carcasses.



8.4.3 Competition with Black-Backed Jackals

Competition can considerably influence the predator's feeding behaviour when many predators of the same or different species inhabit an area (Lamprecht 1978). Black-backed jackals, for instance, are regarded as considerable competitors of brown hyenas in the Kalahari (Owens & Owens 1978) as their diets greatly overlap (Mills 1990). The relationship between black-backed jackals and brown hyenas has been described as mutually of advantage and disadvantage: both species lose and gain food from each other, as black-backed jackals follow foraging brown hyenas and brown hyenas are alert to black-backed jackal activities in order to find food (Owens & Owens 1978, Mills 1990). Nevertheless, the advantages generally lie on the side of the jackals.

To investigate the impact of black-backed jackal presence on coastal brown hyenas, two factors had to be determined: (1) the encounter probability and relative density of both species and (2) the dependence of black-backed jackals on the use of brown hyena predations.

Along the Namib Desert coast, black-backed jackals are the second-most abundant mammal (Skinner & van Aarde 1991), most probably due to the existence of mainland Cape fur seal colonies, where they occur in large aggregations (Skinner & van Aarde 1981, Oosthuizen et al. 1997). Such overabundance of food also has implications for the growth of populations of other similar-sized carnivores, such as arctic foxes feeding on geese (*Chen rossii*, *C. caerulescens*) (Bantle & Alisauskas 1998, compare with Chapter 5).

Black-backed jackals were almost always present at the Van Reenen Bay seal colony during the study period. Hourly counts revealed an average of 9.5 jackals at the colony during daylight hours, ranging from 0 to 38 animals. Black-backed jackals outnumbered brown hyenas and were always more numerous at the seal colony, and thus the encounter rate between both species was relatively high.

Oosthuizen et al. (1997) recorded a maximum number of 70 jackals at the Van Reenen Bay seal colony, but it is unclear whether their counts additionally included jackals in the vicinity of the seal colony. Nevertheless, both studies found a high abundance of jackals at that seal colony. Jackal numbers were lowest between 13:00 and 17:00, which also corresponds to the findings of



Oosthuizen et al. (1997). Interestingly, a significant drop in jackal numbers was observed during the peak of the pupping season in December compared to numbers before and after the peak, both during this and Oosthuizen et al.'s (1997) study. The overabundance of seal carcasses and particularly seal placentas during the peak pupping season might explain this pattern. Female seals that had recently given birth could easily be approached by jackals, and they often stole the placenta while the female seal was occupied with her pup or even pulled on the not yet released placenta (compare with Oosthuizen et al. 1997). Obtaining food, therefore, required little time and effort, and jackals could afford to spend the majority of time resting in the nearby hummock dunes or engaging in other activities. From January onwards, hardly any pups are born and jackals have to spend more time foraging.

Although the easiest time to find food in the form of placentas was December, black-backed jackals killed new-born seal pups throughout the study period. Oosthuizen et al. (1997) described black-backed jackals as scavengers in December and active predators of seal pups for the remainder of the year. This study did not find a difference in the number of predations between December and January, and the cumulative predation rate was 12.4%. Oosthuizen et al. (1997) suggest that black-backed jackals are the cause of an annual pup mortality of 35.7%, but this rate seems to be an overestimate. Arctic foxes, for instance, can be significant predators of ringed seals, with a predation rate of 26.1% (Smith 1976). Nevertheless they exclusively killed recently born pups, which are small enough to be killed (Smith 1976, Andriashek et al. 1985). Other authors describe black-backed jackals as scavengers of drowned seal pups (Skinner & van Aarde 1981, Stuart & Shaughnessy 1984), indicating that killing has not been observed. Otherwise, hunting success of single black-backed jackals is described as low; effective killing requires more than two jackals (Lamprecht 1978), and the formation of packs increases the hunting success considerably (Estes 1967, Kleinman & Eisenberg 1973, MacDonald 1983). Such cooperation between jackals was also observed at the Van Reenen Bay seal colony.

Single jackals usually tried to kill the seal pup by grabbing the throat and suffocating it, using the same killing technique as coyotes (*Canis latrans*) killing



harp seal (*Pagophilus groenlandicus*) pups (Way & Horton 2004). Groups of two or more jackals, however, grabbed the seal pup at different parts of the body, often the flippers, and pulled in different directions, while one jackal usually continued suffocating the pup.

By March the seal pups' weight exceeds that of a black-backed jackal and they are increasingly mobile. Furthermore the tough skin and thick, protective layer of fur increases the difficulty for jackals even in groups to kill seal pups. Continuous significant predation throughout the year therefore seems improbable. Incidental observations show that jackals, even during the peak of the pupping season, have difficulty opening up pups and often only succeed around the umbilical cord, anal region, or base of the front flippers, where the skin is softer and thin. Other than that, many jackals feed on hyena predations, particularly excessive kill remains, gaining access to the meat through the top where the head is missing, peeling back the skin until the carcass is turned inside out, exposing the core of the skeleton. Other scavengers such as gulls (*Larus canus*, *L. philadelphia*), for example, prefer salmon that was partially eaten by bears, as it provided easy access to the preferred parts of a carcass (Frame 1974).

Therefore brown hyenas might be an important food provider for black-backed jackals, which should result in interspecific competition for hyena predations. Brown hyenas spent considerably more time competing with black-backed jackals in November, before the start of the pupping season, than afterwards, despite similar jackal numbers at the colony. Therefore competition was related to seal pup abundance, and high abundance after the peak of the pupping season resulted in a decrease in intraspecific competition.

In general brown hyenas were more successful than jackals in protecting their prey. Brown hyenas deprived jackals of their kills on several occasions, but never lost one to jackals while feeding on their own kill.

Brown hyenas spend more time competing with jackals during long feeding bouts. These longer feeding bouts might give jackals a better opportunity to steal pieces of meat, as possibly a larger amount of the carcass or kill is consumed and hence opened up, so that easy access for competitors is provided. Other than that, spending more time with a carcass attracts more competitors over time



(Lamprecht 1978) and gives more jackals the opportunity to detect the feeding site.

8.4.4 Removal or Caching of Prey

Carrying food away from the capture site can have several advantages. Inter- and intraspecific competition while feeding can be reduced (Lamprecht 1978, Reimchen 2000), excess food can be stored for later use (Oksanen 1983) and food can be carried to the den to provision offspring (Kruuk 1964, Mills 1990).

Avoidance of interspecific competition by storing parts of carcasses in holes as described for brown hyenas by Skinner (1976) did not seem to influence the brown hyenas' decision to carry prey away from the seal colony during this study. Brown hyenas carried pups away from the colony independently of the time they had spent competing with black-backed jackals. Furthermore the feeding time per foraging time was unrelated to the occurrence of caches. This result might indicate that brown hyenas carry food away from the colony to store it for later use or that they carry it to the den to provide cubs with additional food. Kruuk (1964) described a constant rate of caches for foxes that prey on gulls and states that the tendency to kill is independent on the tendency to carry food back to the den and hence the number of cached prey items is unrelated to the number of killed prey. This observation is consistent with the findings of this study. Brown hyenas carried prey away from the colony independent of the number of pups killed. Nevertheless, the use of a larger number of scavenged pups during a foraging bout led more frequently to caches than the use of a lower number.

The percentage of time coastal brown hyenas carried pups away from the colony was similar to the findings of other studies. Coastal brown hyenas cached seal pups during 76% of all observations, and Kalahari brown hyenas have been observed to cache food 70% of the time (Owens & Owens 1978) or to carry food to the den 66% of the time (Mills 1990). Goss (1986) states that lactating females carry 71% of all encountered prey items back to the den and that other clan members cache 60% of their remaining food.

Whether coastal brown hyenas return to their caches is unknown, but this study clearly suggested that there was a strong tendency to carry food away from the capture site. The number of non-violent mortalities and kills that were carried



away before the daily data collection commenced could not be determined, but the existence of excessive kill cache remains (8% of all remains) and the disappearance of marked dead pups (17% of marked predations) indicated that caching happened on a regular basis.

8.4.5 Prey Choice Regarding Caches

The decision to engage in caching behaviour has to involve the assessment of associated costs. Energetic costs will be relatively high when providing offspring with food, but the long-term genetic benefits of carrying food to the den most definitely outweigh the costs. Storing food for later use might result in a positive energy balance, if the same individual that cached the food is able to recover it. Nevertheless, anecdotal observations of the fate of brown hyena caches along the Namib Desert coast indicated that most of these caches were not used at all or were lost to black-backed jackals.

Carrying food to protected feeding sites, to store it, or to provide cubs at the den entails significant energetic costs for brown hyenas. The mean distance prey is carried in the Kalahari is 6.4 km, but distances up to 15 km are not uncommon (Mills 1990). Coastal brown hyenas carry food over similar distances, as one brown hyena was followed for 6 km carrying a seal pup before disappearing out of sight, and seal prey remains have been found even farther inland (pers. observ.). If high costs are involved in carrying food, brown hyenas might show different prey choice regarding caches than regarding the consumption of pups by caching less heavy prey to conserve energy while walking, hence choosing non-violent mortalities for instance (compare with Chapter 7). However, brown hyenas at the Van Reenen Bay seal colony did not show a preference for either of the two prey categories. They carried as many kills as scavenged pups away from the seal colony, and this pattern remained constant during the study period.

Surplus predations were heavier than non-violent mortalities and were hence more valuable, using mass as an indicator for value, but weighed less than excessive kills. However, the brain of excessive kills had been consumed, and the remaining mass of an excessive kill without head was not different from that of a surplus kill. Nevertheless the value of an excessive kill carcass might be



higher than that of a surplus kill for two reasons: (1) the brain tissue of carcasses was seldom consumed (see above) and therefore does not add to the caloric value of the cache and (2) the body of an excessive kill, being larger, contains more food than that of a surplus kill. Both factors would be likely to lead to a choice for excessive kills as caches due to their higher value compared to surplus kills of the same mass. However, brown hyenas surprisingly did not show prey choice regarding the caching of surplus and excessive kills, and heavier surplus kills were not preferred, nor were heavier non-violent mortalities. Therefore brown hyenas seem to follow the same strategy as when hunting, and cache pups in proportion to their availability within one prey category.

8.4.6 Value of Brain Tissue

Based on the above, brown hyenas appear to behave optimally regarding their choice of seal pups for consumption. As discussed previously, partial consumption can be optimal given the right circumstances. Furthermore predator species show preferences for similar tissues that are high in lipid content (Stirling & McEwan 1975, Smith 1980, Stirling & Lunn 1997, Gende et al. 2001, Gende & Quinn 2004).

For some predator species it is advantageous to maximise the energy value of a kill (Stirling & Øritsland 1995), especially looking at the accumulated energetic advantage over the course of a specific season, for example during the salmon run (Gende et al. 2001). The digestibility of fat is generally greater than that of protein (Best 1984 cited in Stirling & Øritsland 1995), and in polar regions bears require a high-energy diet to meet the metabolic requirements for thermoregulation and the search for food (Stirling & McEwan 1975). Therefore polar bears prefer to consume the blubber of seals and selectively prey on yearlings and adults, as their fat is greater than in newborn seals (Smith 1980, Stirling & McEwan 1995, Stirling & Lunn 1997). The digestion of protein also requires additional water and the consumption of fat tissue might serve to save water and keep a positive water balance (Stirling & Øritsland 1995).

Along the Namib Desert coast fresh water is present, but can potentially become limiting for some species. Furthermore the available food for brown hyenas may have a higher salt content, as it is of marine origin (Skinner & van



Aarde 1981). It is still unknown how brown hyenas keep a positive water balance, especially as they are able to survive for extended periods of time without fresh water (Owens & Owens 1978). Nevertheless, the combination of the difficulty in obtaining fresh water along the coast and the consumption of food with a possibly higher salt content might lead to the selection for brain tissue in the consumption of fresh seal kills. Furthermore although coastal brown hyenas in the study areas have access to seal colonies, they move great distances and their metabolic requirements associated with the energy cost of walking are high (Chapter 5). Mills (1990) calculated that Kalahari brown hyenas require 2.8 ± 0.78 kg of food per day. If their food entirely comprised of meat, they would gain a caloric yield of approximately 4200 kcal (compare with Schaller 1972), about one third more than the field metabolic rate calculated for the brown hyenas in this study (Chapter 5). Nevertheless, as scavengers their diet is more diverse and does not entirely consist of meat. In contrast coastal brown hyenas can meet their metabolic needs relatively easily by consuming the lipid rich parts of seal kills, namely the brain and blubber. The blubber layer of seal pups increases throughout the year and their corpulence is high in September and October, but drops steadily afterwards (Shaughnessy 1982). Therefore blubber as a lipid-rich food source is less predictable than brain tissue, as the energy status of brain tissue does not change over time and is a function of size rather than condition (Gende et al. 2001), which corresponds to the results of this study. The consumption of two brains per day could therefore be sufficient to meet the metabolic needs of coastal brown hyenas as calculated in Chapter 5. Nevertheless, it has to be noted that it is not assumed that brown hyenas exclusively consume brain, as other nutritional constraints are expected.

Lastly the additional consumption of seal milk could further increase energy intake and help regulate water balance. Fur seal milk is generally very concentrated and high in fat content (Bonner 1981). Cape fur seal milk contains 19% fat and 10% proteins (Rand 1956), and brown hyenas have been observed licking exposed milk from seal kills (Chapter 7).



8.5 Summary

Brown hyenas only partially consume a large proportion of their prey items, showing a distinct preference for brain tissue. Selectivity increases with seal pup abundance, expressed through a larger number of partially consumed pups and a decrease in feeding and handling time per prey item. Competition with black-backed jackals is greatest during the time of relative food shortage, but does not seem to influence the brown hyena's feeding-related time budget nor the occurrence of caching behaviour. Caching behaviour seems to be strongly developed and is independent of the number of pups killed. Prey choice regarding caches did not seem to exist, and pups were taken as caches in proportion to their occurrence. The choice for brain tissue consumption of killed pups could lead to a quick caloric intake to satisfy the brown hyena's metabolic requirements, but might also be related to keeping a positive water balance.



Chapter 9

Conclusions

The predatory and foraging behaviour of brown hyenas (*Parahyaena brunnea*) was observed at mainland Cape fur seal (*Arctocephalus pusillus pusillus*) breeding colonies in the southern Namib Desert. The objectives of this study were to

- (1) assess the availability, condition and accessibility of seals for brown hyenas,
- (2) evaluate the importance of the coast for brown hyena abundance, movement and energy budget,
- (3) determine factors influencing the foraging related time budget of brown hyenas,
- (4) assess feeding preferences, and
- (5) examine the consumption of prey.

Behavioural observations were conducted at the Van Reenen Bay seal colony and seal pup mortality data was recorded at the Wolf Bay seal colony. GPS collars were fitted on coastal brown hyenas to determine their movement.

Live seal pups were available for brown hyenas all year round, but their increasing size, mobility and activity, as well as the attendance pattern of adult females may influence the brown hyena's foraging behaviour. Many dead pups were available to scavenge during the pupping season and represented an easy and safe way to obtain food.

In general, predators and prey are mutually influenced by each others behaviours. In Chapter 4 the anti-predator strategies of Cape fur seals towards brown hyenas were reviewed and assessed with regard to their influence on the hyena's foraging strategies. Although Cape fur seals showed a near complete lack of anti-predator behaviour, the predator-prey system is possibly donor-controlled (Chapter 5) and the usual compensatory effect on prey populations that face novel or exotic predators is not expected (see Sinclair et al. 1998). The numerical response of predators to increased prey numbers as predicted by Holling (1959, 1965) could not be seen in this study (Chapter 5), and seasonality in the availability of seal pups, therefore, may limit brown hyena population

growth, and may contribute to the maintenance of large home ranges despite localised food sources. However, coastal brown hyenas' daily movements were less than that of inland ones, they have a lower field metabolic rate, and hence may consume less food.

Brown hyenas preferred to kill seal pups despite the availability of carrion (Chapter 6). The predation rate was unrelated to carrion availability, but the absolute number of kills was positively correlated to seal pup density. Increasing seal pup density led to an increase in brown hyena capture rate and hunting efficiency. Furthermore the overabundance of easy and vulnerable prey led to surplus kills.

However, brown hyenas foraged opportunistically by scavenging, killing and caching seal pups in proportion to their occurrence at the colony (Chapter 7 and 8), and hence, caused an additional impact on seal pup mortality by not only choosing the doomed surplus. The killing of seal pups seemed to be unrelated to hunger, and surplus killing occurred throughout the study period. Brown hyenas preferred to consume larger and heavier prey, but a large proportion of the brown hyena's prey was only partially consumed (Chapter 8). Selectivity increased with seal pup density, and feeding and handling times per prey item were reduced.

Brown hyenas showed a preference for brain tissue, and the consumption of brain tissue may quickly satisfy the brown hyena's metabolic requirements, or may be important to keep a positive water balance.

Although black-backed jackals (*Canis mesomelas*) outnumber brown hyenas and are their main competitors at seal colonies, they did not influence the brown hyena's foraging strategy.

Brown hyenas, therefore, behave opportunistically regarding their feeding preferences and optimally regarding the consumption of seals. Seal pup density influences the brown hyena's predatory and foraging behaviour, and seasonality in seal availability may limit brown hyena abundance and influence their movement patterns.

Future observations of foraging brown hyenas outside the pupping season and at night could yield additional interesting information about adaptations in predatory and foraging behaviour to changes in seal behaviour, abundance and attendance.



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Appendix



Figure 1: Brown hyena carrying killed seal pup away from the seal colony.



Figure 2: Dead seal pups washed up at Wolf bay beach during the seal pupping season.



Figure 3: Dead seal pups floating in the sea at Wolf Bay beach during the seal pupping season.



Figure 4: Seal pups that died of heat stress during the seal pupping season.



Figure 5: Seal kill completely consumed by brown hyena.



Figure 6: Surplus kill (note plastic tag on left front flipper).



Figure 7: Haemorrhaging through bite marks under the skin of a surplus kill (note the crushed skull).



Figure 8: Excessive kill.



Figure 9: Cached excessive kill (skull bone remains) and clearly visible blood trail of freshly killed pup.



Figure 10: Seal pup consumed by black-backed jackal.

Appendix

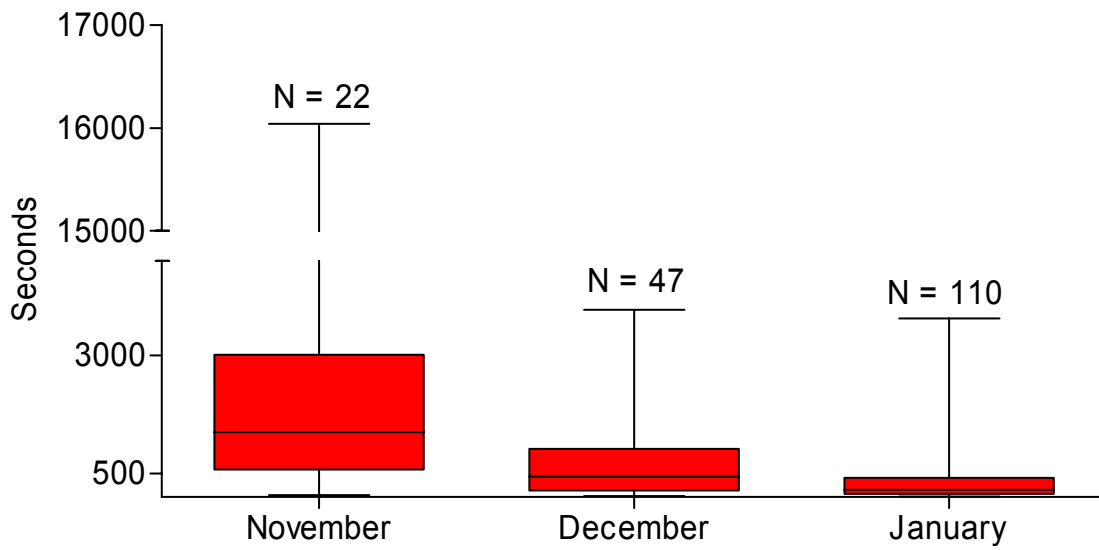


Figure 11: Interval between prey encounters (in seconds) before, during and after the peak pupping season.

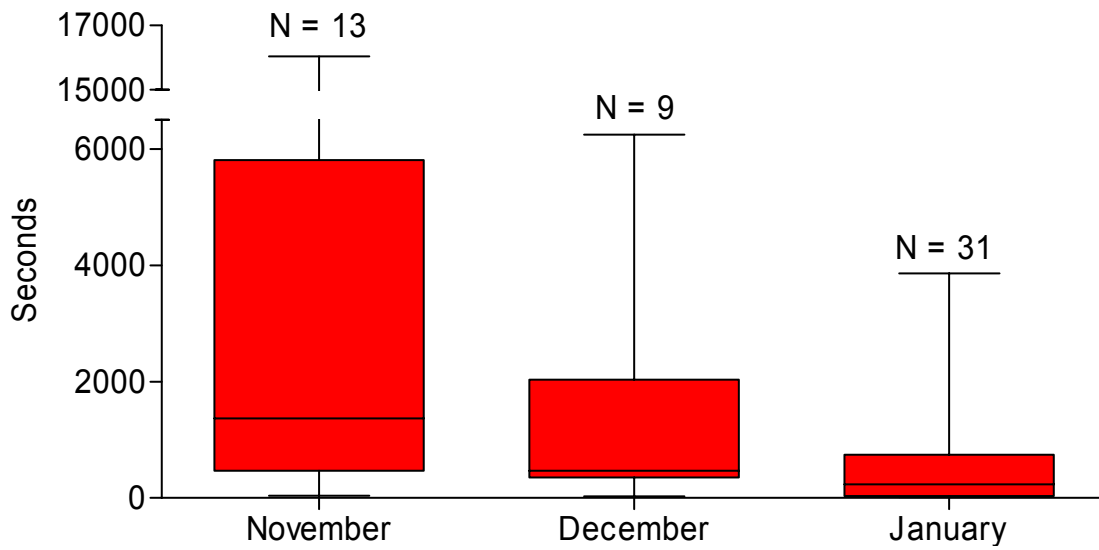


Figure 12: Interval between kills before, during and after the peak pupping season.

Appendix

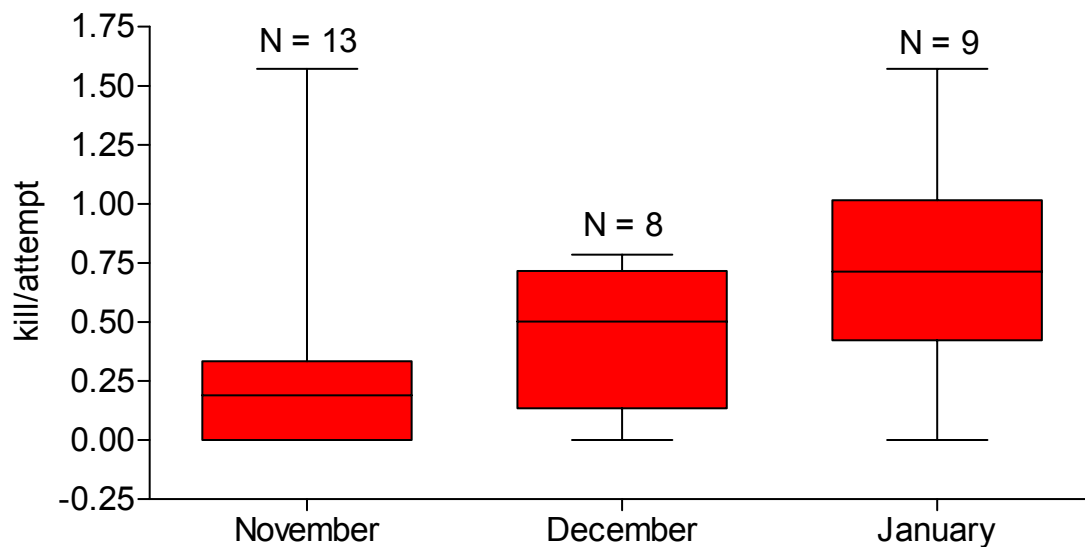


Figure 13: Hunting efficiency of brown hyenas before, during and after the peak of the pupping season.

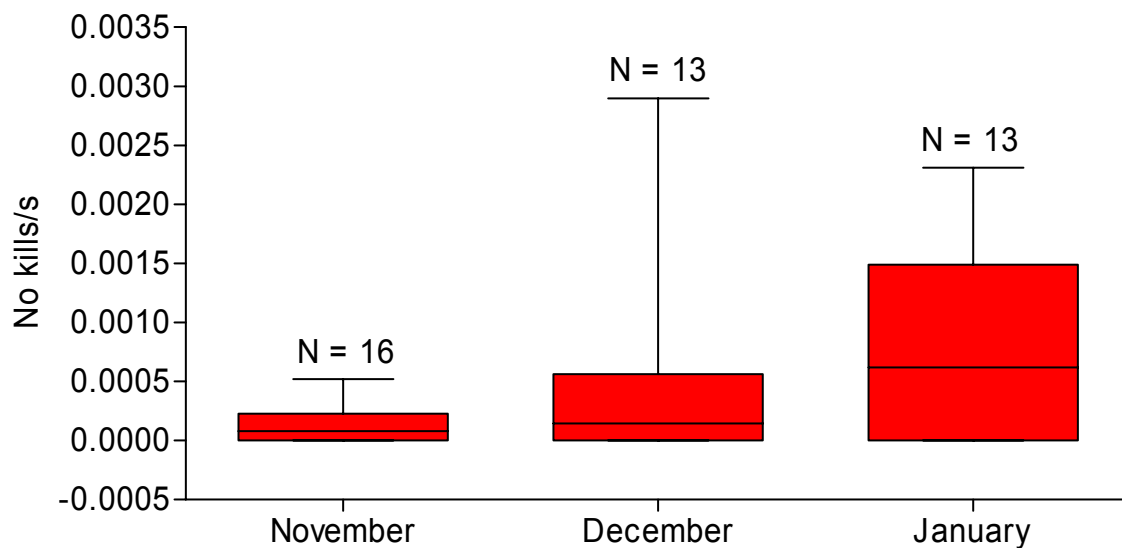


Figure 14: Capture rate before, during and after the peak pupping season.

Appendix

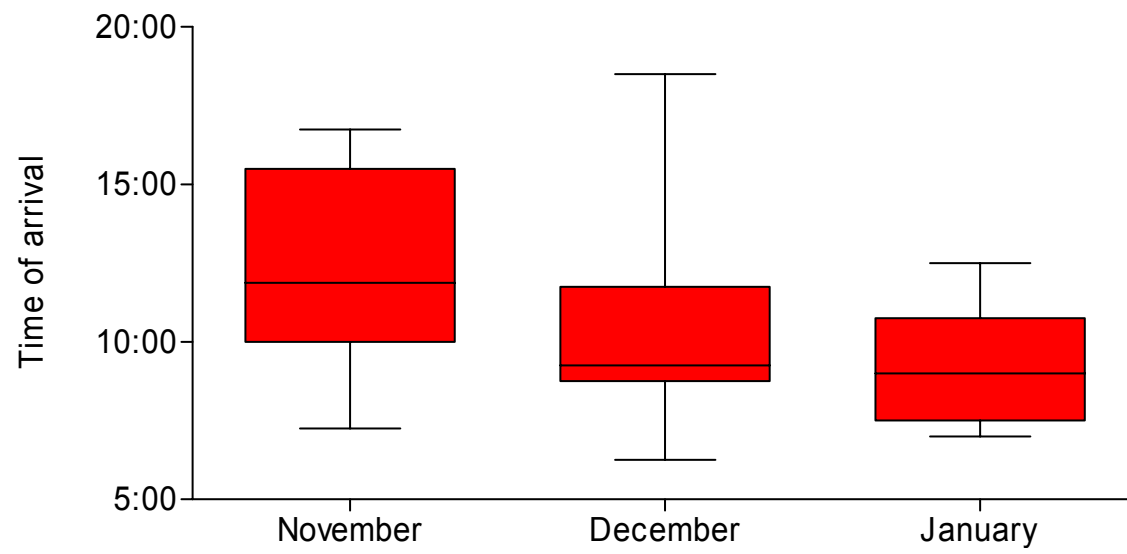


Figure 15: Time of arrival of brown hyenas at the Van Reenen Bay seal colony before, during and after the peak of the pupping season.

Eidstattliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig angefertigt habe. Wörtliche und inhaltliche übernommene Stellen aus anderen Quellen sind als solche kenntlich gemacht und die Inanspruchnahme fremder Hilfe ist namentlich aufgeführt.

A handwritten signature in black ink, reading "Ingrid Wiesel". The script is cursive and fluid, with the first letters of each word being capitalized and prominent.

Ingrid Wiesel