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Reproductive Behaviour, Endocrinology and Captive Breeding of the Malayan Sun bear (Ursus malayanus)

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Heather Hesterman

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Abstract

A better understanding of Sun bear (Ursus malayanus) reproductive biology is essential to implement more effective management of zoo populations. The objective of this study was to document and describe reproductive behaviour, monitor ovarian and testicular cycles, and review approaches to captive breeding. Because Sun bears exhibit no fixed breeding period in captivity, identifying a set of behaviours associated with oestrus, pregnancy and impending parturition are important. During 1997 three male:female pairs at two zoos were studied for periods of up to <10 months. Bears spent the majority of time in solitary behaviours, but oestrus was marked by and an increased rate of affiliative encounters, with females actively soliciting the male, and exhibiting characteristic behaviours including rolling, backward walking and inguinal presentation. Oestrus lasted ~2 weeks, the end being marked by rapid loss of sexual interest, and mutual avoidance. During mid-late gestation females became increasingly intolerant of the male, and altercations were common. Several weeks before term females acted reclusive, and extensive nesting occurred when suitable material was available. Parturition occurred ~3 months after mating, with pseudopregnancy lasting an equivalent period to 'true gestation', and being accompanied by similar behaviour changes and overt physical signs (e.g. mammary Separation of the female, provision of a high level of isolation and maintenance of privacy was necessary for successful rearing to occur.

Faecal sex steroids were analysed in samples collected from 13 (9 male:4 female) Sun bears housed in zoological parks in North America and New Zealand, over periods of <27 months. Male samples were assayed for testosterone and female samples for oestradiol 17 β and progestagens. Testosterone levels were often elevated during mating periods, with peaks frequently accompanying breeding behaviour and copulation. There was no significant effect of season (p>0.05) on testosterone concentrations, which fluctuated throughout the year, with most animals showing sustained increases in androgen excretion at 4-6 month intervals. The mean length of the follicular and luteal phase was 11.2 \pm 1.3 days and 93.3 \pm 3.0 days, respectively. Increased faecal oestradiol concentrations were associated with the onset of oestrus behaviours and breeding activity; an analysis of endocrine-behaviour data suggests that these behaviours may serve as useful indicators of physiological oestrus. The pattern of oestradiol and progesterone metabolite excretion during pregnancy and pseudopregnancy was similar, indicating that sex steroid monitoring may be of limited use for unequivocal pregnancy diagnosis in ursids.

Analysis of studbook data and breeding records from Sun bears in North American and New Zealand zoos revealed that reproduction in these populations is strongly seasonal with the majority (>75%) of births occurring during summer and autumn. A bimodal pattern of reproduction was observed, resulting from sharp peaks in the birth rate during July and October. Findings suggest a correlation between breeding activity and monsoon patterns in this species' native habitat. The factors limiting reproductive success in captive Sun bear populations are not understood. Difficulties confirming pregnancy, coupled with the failure of some zoos to separate potentially pregnant females or implement remote surveillance, reduces reliable statistics for birth or neonate mortality and prevents an investigation of the causes of cub fatality. A review of breeding records from various zoos indicates that standardising approaches to husbandry might also improve Sun bear reproduction in captivity.

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Chapter 1

General Introduction and Literature Review

1.1 GENERAL INTRODUCTION

1.1.1 Systematics

The Family Ursidae contains eight species of bears in three subfamilies: Ailuropodinae (the Giant panda), Tremarctinae (the Spectacled bear), and Ursinae (the remaining members) (Stirling 1993). Numerous molecular genetic methods have been used to resolve systematic relationships between bears, pandas, and racoons (O'Brien 1993), as a result of which the Red panda (Ailurus fulgrens) is now classified as a racoon. The Giant panda (Ailuropoda melanoleuca), and the Spectacled bear (Tremarctos ornatus) are allocated separate subfamilies due to chromosomal and morphological differences between these bears and all other members of the Ursidae. Of the six remaining species, the Brown bear (Ursus arctos), the American black bear (Ursus americanus), the Asiatic black bear (Ursus thibetanus), and the Polar bear (Ursus maritimus) are most closely related. The Sloth bear and Sun bear were previously classified as Melursus and Helarctos respectively because they possess some unique characteristics (Wozencraft & Hoffmann 1993), but Wozencraft & Hoffmann (1993) place both these species in the genus Ursus and that classification is followed here.

Geographic isolation has led to genetic differences at the subspecific level between island and mainland populations of the Malayan Sun bear. Two sub-species are recognised - a nominate race *U. malayanus malayanus* from mainland SE Asia and Sumatra, and *U. malayanus euryspilus* on the island of Borneo (Fain 1996).

1.1.2 Status and Distribution of the Malayan Sun bear

Sun bears are tropical mammals inhabiting the rainforests of South East Asia. They have been reported living at all elevations, from swampy lowland forests (Santiapillai & Santiapillai 1996) to 2800m above sea level (Blouch 1984 cited in Santiapillai & Santiapillai 1996). Formerly the species ranged from Malaysia and Indonesia in the east, up through Cambodia, Thailand, Laos, and Vietnam; north to Southern China. Despite a relatively wide distribution, it is thought that Sun bear populations may have been in low numbers, or widely dispersed, for several decades (Kuhme 1990; Kurt 1990).

In China the last live Sun bear was caught in 1972, and there have been no recorded sightings since the early 1980s (Ma 1983). The species is reputably rare in this area

(Fan & Song 1997), with the Chinese Ministry of Forestry (MOF) estimating that approximately 400 Sun bears remain in the wild (Mills et al 1997). Their present distribution is reported to include Northern Burma (Servheen 1993), but it is unknown whether any remain in Bangladesh (Ma 1983; Mills & Servheen 1991). The bears are no longer found in India (Ma 1983) and evidence suggests that populations in this region may have been depleted early in the 1900s. Hunting returns from one province revealed that *U.malayanus* represented only 1% of nearly 4000 bears killed between 1910-1917 (Higgins 1932 cited in Kuhme 1990).

Sun bears and Asiatic Black bears (*U. thibetanus*) are sympatric in Laos, Thailand, Burma, Cambodia, and Vietnam where their range overlaps as much as 50% (Hovey & Bunnell 1993). It is unknown, however, whether habitat exclusion or predation by the larger Asiatic Black bear, affects habitat use or distribution of the Sun bear (Garshelis & Smith 1996). The Malayan bear is the only bear species to inhabit Sumatra and Borneo.

Populations that exist on the Malaysian mainland and its island states are believed to be in decline (Mills & Servheen 1991), as are those in Indonesia (Santiapillai & Santiapillai 1996). There are no estimates of the distribution or number of Sun bears remaining in the wild, but their range has clearly contracted over the last 50 years (Servheen 1993) and they are described as one of the rarest mammals in Northern Sumatra (Kurt 1990).

1.1.3 Sun Bear Biology

The Malayan Sun bear is the only ursid that has not been studied in the wild (Garshelis & Smith 1996; Servheen 1997). Consequently, very little is known about them and field study of this species is considered to be the most important research need in bear biology today (Servheen 1997). Most information on Sun bear behaviour and habits in the wild has been inferred from morphology and reported sightings, including anecdotes from forest rangers, local villagers, and game hunters (Servheen 1996; Santiapillai & Santiapillai 1996). Where appropriate, information on the natural history of other bear species has been included in this section for comparison.

1.1.3.1 Physical Characteristics

The Sun bear is the smallest member of the ursid family. Adult body length is $\sim 1.2 - 1.5$ m, with a weight range between 27-65kg, and males are approximately 20% larger

than females (Stirling 1993). In the wild, an individual greater than 50kg is considered large (Domico 1988), but in captivity their weight may exceed 100kg (Kitchener 1998)¹. Their pelage is short (<1cm) and sleek, and predominantly black, fading to a light colour around the muzzle; most individuals have a unique crescent-shaped yellow or orange chest patch. It is thought that their loose-fitting skin may assist in defence by allowing them to turn easily when attacked by a large predator (Kitchener 1992). The Sun bear has short bandy legs, naked soles, and long, strongly curved claws, making it exceptionally well adapted to climbing.

1.1.3.2 Habits

Wild Sun bears are reported to be nocturnal (Domico 1988), and to descend from the trees to forage at night. During the day they are said to sunbathe and sleep in trees at elevations of up to 7 metres, and to build nest-like platforms from broken vegetation (Domico 1988). Apparently, Sun bear tree nests resemble those made by Orang-utan so closely that even local people cannot distinguish between them (D. Middleton pers comm. 1997). Similar nest-like structures are built by other forest-dwelling bear species. For instance, Asiatic Black bears and Spectacled bears bend thin limbs toward the trunk to create such platforms, but these are mainly constructed for feeding from outer branches (Reid 1993; Weinhardt 1993). Spectacled bears may also use these structures for sleeping, as some have been found to contain layers of foliage, and appear to have been used for lengthy periods (Weinhardt 1993). The extent to which Sun bears build arboreal 'nests', or the purpose they would serve, is unknown.

Although most species of bear use dens, particularly for overwintering, there is no report that *U. malayanus* does so. Living in the tropics means not having to cope with extreme climatic changes, so it is unlikely that Sun bears would undergo a seasonal period of torpor characteristic of bears living in temperate regions.

1.1.3.3 Diet

With the exception of the Polar bear (*U. maritimus*) which is almost exclusively carnivorous, and the herbivorous Giant panda (*A. melanoleuca*), all other bears are omnivores (Stirling 1993). Sun bears are extremely rapid foragers, which may reflect

¹ Weights provided for nine individuals included in this study ranged from 72 kg for females (mean 82 kg) to 108 kg for males (mean 95 kg).

an ecological adaptation to the ephemeral nature of food resources in a humid, tropical environment jungle (Laurie & Seidensticker 1977; Domico 1988). Their natural diet is predominantly fruit (Kunkun 1985, Lekagul & McNeely 1977 cited in Joshi et al 1997) but also includes shoots, palm tree hearts, invertebrates, lizards, birds, and small mammals (Domico 1988; Stirling 1993). The Sun bear is sometimes referred to as the 'honey bear' because of their fondness for feeding from wild beehives. They can easily access the honeycombs using their sharp, sickle-like claws and incredibly long tongue, thought to be an adaptation to this type of feeding (Servheen 1993).

In addition to the loss of plant and animal species associated with original forest cover, herbicide use associated with plantation maintenance reduces the availability of natural foods (Servheen 1996). As the bears move out of disturbed areas they are brought into increasing contact with people living near the forest's edge. Predictably, the opportunistic nature of bears results in them frequently raiding plantations and adjacent settlements. Sun bears are considered dangerous pests by local villagers, and are often shot for damaging crops such as bananas, coconuts, and oil palms (Santiapillai & Santiapillai 1996).

The natural diet of Sun bears is predominantly frugivorous (Kunkun 1985 cited in Joshi et al 1997; Lekagul & McNeely 1977 cited in Joshi et al 1997), and includes many different fruit types (Servheen 1993). Fruiting trees in tropical forests often flower synchronously, so cycles of abundance vary throughout the forest (Servheen 1993). Movement of some tropical mammals has been linked to fruiting cycles, which led Servheen (1993) to suggest that Sun bears may also vary their areas of use. Most ursids are known to move in response to the availability and distribution of food sources (T. ornatus: Weinhardt 1993; U. arctos, U.americanus, U., U.maritimus: reviewed in Joshi et al 1995). Studies of Sloth bears (U. ursinus) in Nepal revealed a shifting seasonal home range that is related to their diet; the location of this primarily myrmecophagous (insectivorous) bear is determined by their ability to excavate termites (Joshi et al 1995), rather than in response to areas of ripening fruit (Laurie & Seidensticker 1977). The more opportunistic nature of Sun bears, and availability of alternative foods in areas of human settlement, may permit Sun bears to be less nomadic in habit than other species (Garshelis & Smith 1996). However, in managing wild populations it is important to discern causal factors underlying area use so that reserves can be developed accordingly (Joshi et al 1995; Garshelis & Smith 1996; Servheen 1996).

1.1.3.4 Social System

Mammalian social organisation evolves under the influence of resource availability, competition for resources, and predation risk (Herrero 1978; Macdonald 1983). The patchy distribution and variable quantity and quality of food favoured by most ursid species means little would be gained by forming groups to defend this resource. Bear do not commonly hunt large prey so there are few advantages to sharing kills (Herrero 1978; Stirling & Derocher 1993), and mature individuals are generally well equipped for defence. Also, as opportunistic omnivores, association is not necessary to exploit food resources; ultimately a bear's 'optimum' feeding strategy is solitary foraging and hunting (Herrero 1978; Stirling & Derocher 1993). However, individuals congregate at sites that offer seasonal abundance of high quality foods, such as streams during salmon-spawning, and garbage dumps. Although hierarchies are developed at this time the bears do not form stable social organisations (Stonorov & Stokes 1972; Bledsoe 1975; Herrero 1978).

Sun bears have been reported travelling in pairs (Fetherston 1940 cited in Kuhme 1990; Domico 1988), and Kurt et al (1990) alleges that this species lives in clans of up to four members. Nothing, however, is confirmed, and despite such anecdotal evidence it is more likely that Sun bears are predominantly solitary in the wild, as all other ursids are known to be. Sightings of two or more individuals together may be associations between males and a female in oestrus, a mother and her offspring, or the temporary affiliation of immature siblings. Field studies of other bear species indicate that prolonged associations are formed only between mothers and cubs and frequently persist for several years (Bunnell & Tait 1981). Siblings have been known to remain together soon after separation from their mother (Craighead et al 1969; Bledsoe 1975; Laurie & Seidensticker 1977), which may reduce attacks on the immature bears (Garshelis 1993) or predation by large males (Stonrov & Stokes 1972). Reports that pairs of adult Sun bears have been seen accompanied by cubs (Domico 1988) could involve females which have entered a post-weaning oestrus and attracted a male. Female bears have been known to tolerate cubs during and after oestrus periods (Jonkel

& Cowan 1971), and males will periodically associate with a female and cubs, to assess her sexual status (Barber & Lindzey 1983; Ramsay & Stirling 1986).

1.1.4 Threats to Wild Populations

Until basic information is obtained on the number of Sun bears remaining in the wild, and their biology and behaviour, the future for this species remains uncertain. Habitat destruction through deforestation, coupled with poaching for the Asian commercial bear trade in medicine, food, and exotic pets (Mills 1992) are operating synergistically to accelerate the decline of the Sun bear.

1.1.4.1 Habitat Destruction

Since 1900, forest cover has contracted considerably, and resources diminished within the Sun bears' range (Santiapillai & Santiapillai 1996). The accelerating rate of human population growth has resulted in mass conversion by logging companies or settlers of large tracts of primary rainforest to secondary growth. Development of forest areas for agricultural use and plantation crops such as cocoa, rubber, and oil, as well as the exportation of timber, result in habitat fragmentation and exclusion of the Sun bear from its prior range. Malaysia and Indonesia export more tropical hardwoods than any other country world-wide and due to this demand it is estimated that lowland forests now cover a mere 10% of Sumatra (Santiapillai & Santiapillai 1996). In 1986 the IUCN reported 49% wildlife habitat loss in Indonesia and Malaysia. Habitat loss runs as high as 80% in Vietnam (Servheen 1993), where deforestation is occurring at an estimated 3110 km² per year (Collins et al 1991 cited in Mills & Servheen 1991). Habitat disturbance has reduced the availability of food, and presumably other resources, to animals like the Sun bear.

1.1.4.2 The Bear Trade

All bear species face serious threat from an escalating international trade in bears and their parts. With the exception of the American black bear (*U. americanus*), and the Polar bear (*U. maritimus*), the other six species of bears, are currently listed by the IUCN as threatened or endangered (Mills & Servheen 1991). As bear populations world-wide decline in number, the market value of bears and their parts increases. Asia forms the hub of the bear trade, and Sun bears are frequently sold as pets, or their parts used for food and medicine.

1.1.4.2.1 Bears as Pets

Keeping cubs as pets is popular in Taiwan, Thailand, Laos and Malaysia (Mills & Servheen 1991) and Buddhists in Thailand often take in, and care for, bears, to earn religious merit in the afterlife (Mills 1992). Young animals are removed from the wild by forest villagers or employees of timber companies, and may sell for as little as US\$10 to greater than US\$5000 (Mills & Servheen 1991). Once a cub matures and becomes difficult to handle, owners try to give them away to monasteries or already overcrowded government facilities, but often these unwanted animals enter the market for food and medicine (Mills 1992).

1.1.4.2.2 Bears as Food

Sun bears are eaten opportunistically by indigenous tribes in Malaysia and aboriginals of Kalimantan and Burma (Mills & Servheen 1991). In Asian cultures strongly influenced by Chinese, bear parts represent an economic indicator (Mills 1992); and have been found on Chinese menus since the beginning of the Ming Dynasty in 1368 (Mills 1993). Restaurants in China, Hong Kong, Japan, Singapore, South Korea, Thailand, and Vietnam serve bear (Mills & Servheen 1991), at prices reaching as high as \$700 for bear-paw entree (Mills 1993). Bear meat is prized both as a status symbol and for certain holistic properties it is believed to convey.

South Korean and Taiwan Chinese are known to book tours to Thailand to partake in bear banquets, where the animals are killed to order (Mills 1993). While alive, the caged bear may be set on hot coals to braise the feet, or lowered into a tub of hot water (Mills 1991). The animals' loud, desperate cries have sometimes alerted locals; and led informed forestry officials to the sites of these illegal feasts (Mills 1991). Bears from Thailand are also exported overseas for consumption - in 1988 30 live bears were discovered after being smuggled into South Korea to fortify the Korean Athletic Team (Mills & Servheen 1991).

1.1.4.2.3 Bears as Parts

The extent of the trade in bear parts is just becoming realised with recent evidence that it now represents a global underground network that includes the United States, Canada, Russia and South America (Knights 1996). The demand for bear gallbladders is the major driving force behind the international trade in bears. It is undoubtedly the most coveted part of the bear and ranks alongside rhino horn as one of the most potent ingredients in Asian pharmacopoeia (Mills & Servheen 1991). The market for bear

gallbladders alone, present a threat to Asian bear populations that is proportional in magnitude to the continued destruction of their habitat (Mills & Servheen 1991; Mills 1993). A recent survey has indicted that the demand for bear gall bladders and bile is still strong (Mills et al 1997), and an increasing body of evidence suggests that the Asian demand for bile is having negative impacts on wild populations of non-Asian species including the American black bear (*U. americanus*), the Brown bear (*U. arctos*), the Polar bear (*U. maritimus*) and the Spectacled bear (*T. ornatus*) (Mills 1995 cited in Mills et al 1997).

Pharmaceutical use of bear parts and their bile dates as far back as the 7th Century, and these products are revered in traditional Chinese medicine for an ability to combat a myriad of illnesses (Mills 1992). When dried the gallbladder is said to resemble a fig, and weighs between 50 to 150 grams (Mills & Servheen 1991). A recent survey of 11 Asian countries determined that per gram, prices for gallbladders run as high as \$US210 - in league with the cost of some forms of heroin, and 12 times the price of gold (Mills & Servheen 1991).

Bile salts produced by the gallbladder contain high levels of ursodeoxycholic acid (UDCA) which has clinically proven medical properties (Mills 1992). Levels of UDCA in this organ are significantly higher in bears than other mammals (Mills 1992). Bile salts or the entire gallbladder is dried down for retail; and resulting products are prescribed for a range of disorders from liver cirrhosis and heart disease to relatively minor complaints including localised infections. They are also reputably effective at treating diseases of the liver and gallbladder (Mills & Servheen 1991; Mills 1992).

Since 1955 Japanese scientists have been able to synthesise UDCA from cow bile, and this product is even readily employed in Western medicine as a remedy to dissolve gallstones, circumventing the need for surgery (Mills 1992). Unfortunately, even flooding the market with this cheaper, synthetic form of bile does little to slow the trade in bears, as Chinese medicinal tenets decree that bile from wild bears has superior curative properties (Mills 1992).

Although extraction of bile from live, caged bears has been practised successfully in North Korea for approximately 20 years the methodology behind this practice remains somewhat shrouded (Bai 1986 cited in Mills & Servheen 1991). Basically, the process

requires surgical placement of a fistula into the gallbladder, and an attachment serves as an external tap for draining bile (Mills & Servheen 1991). To prevent the animal from removing the appendage a steel plate may be harnessed over the site, and restrictive cages confine any movement that could dislodge the fixture.

The welfare of farmed bears is poor - captive conditions are uncomfortably small, there is a high level of disease, and post-surgical infections are common (Mills & Servheen 1991). Draining of bile also seems to cause considerable distress to the animals. Investigators who viewed this process first-hand described a bear in a frantic state, scraping and clawing wildly at the cage during the 5 minute 'milking' procedure in which approximately 2 mL of bile is drawn (Mills & Servheen 1991). Each bear may yield up to 20 mL per month over a 3-4yr period (Mills & Servheen 1991), so there can be considerable profit involved in farming bears. Chinese governments recognise the high consumer demand for bear gall products and encourage development of bear farms (Ball 1996a). Efforts by the International Fund for Animal Welfare (IFAW) have increased public awareness of this practice. Following negotiations with IFAW, in 1994 the Chinese government ceased issuing licences to new bear farms and began to close unlicensed establishments (Robinson 1997). By 1996, however, more than 10 000 bears were kept in captivity for this purpose, and it was the goal of the Chinese government to increase this number to 40 000 by the year 2000 (Robinson 1997).

Approximately 90% of farmed bears originated in the wild, and were captured before the China Wildlife Protection Law was established in 1989, but it is argued that the capture rate (<10 000 animals p.a. from 1984 - 1989) to supply bear farms is unlikely to have caused any significant impacts on wild populations (Fan & Song 1997). Despite legislation one report suggests that in China wild populations continue to be exploited to offset the high mortality and low reproductive rate in captivity (Mills et al 1997). Following negotiations between IFAW and Chinese authorities, efforts are being made to improve conditions on existing bear farms and reduce the farmed bear population by 33%, toward the aim of phasing out the practice through development of a herbal alternative to bear bile (Robinson 1997).

While extraordinarily little is known of the ecology or behaviour of Asian ursids, scientists from countries involved in bear farming, have devoted considerable research effort toward perfecting bile extraction techniques, and to improve the captive breeding

record in these institutions (Mills & Servheen 1991). Somewhat ironically, even bile from farmed bears cannot curb the trade in bear galls. This rests once again, on the strength of ancient pharmacopoeia dictate - that full potency is attained only from bears in the wild.

1.1.4.2.4 Wildlife Trade Laws

National and international laws attempt to control the trade in SE Asian wildlife. The Sun bear, listed in the highest conservation priority by the World Conservation Union (IUCN), is classified as Endangered and has been rated on Appendix 1 of CITES (Convention on International Trade in Endangered Species) since 1975 (Servheen 1996). These are the highest classifications designated to endangered species.

The extent to which Sun bears are protected varies because not all countries are party to CITES, and others fail to implement the ban. In some cases national trafficking laws have been legislated to protect wildlife, but lucrative market prices result in illicit hunting. Corrupt officials are even known to participate in operations or turn a 'blind eye', and enforcement of punishment is rare (Mills & Servheen 1991). A recent case led to conviction of the former director of the Forest Resources Conservation Project in Laos, for his involvement laundering wildlife across the Mekong river - a notoriously 'porous' border between Laos and Thailand (Mills & Servheen 1991). As political barriers dissolve between adjacent countries, patrolling and law enforcement to reduce wildlife trafficking is likely to become even more difficult.

Hunting bears is illegal in Indonesia, Laos, peninsular Malaysia, and within reserve areas of Sarawak (Mills & Servheen 1991). The practice is also restricted to forest reserves in Burma, and licenses must be sought to hunt bears in Thailand and Sabah. Local tribes in some areas are permitted subsistence use of these animals (Mills & Servheen 1991).

Sun bears are sometimes illegally killed by villagers and forestry workers who considered them a pest, but primarily they are killed to meet the demand from wildlife brokers who often finance entire poaching operations (Mills & Servheen 1991). Keeping Sun bears as pets is also illegal in some Asian countries, but loopholes in the law make prosecution difficult. For instance, in Thailand all individuals are permitted to keep two of most wild animal species. If found in possession of numerous bears, a wildlife trader only has to claim that surplus animals belong to his spouse, siblings, or

children to evade the present law (Mills & Servheen 1991). Investigators of the Asian bear trade have identified two key areas that will assist conservation efforts - strengthening of CITES and domestic laws within Asian countries, and providing education that promotes the intrinsic and ecological importance of bears to these various cultures (Mills & Servheen 1991).

1.1.5 Captive Sun bear Populations

1.1.5.1 Summary of North American and European Populations

Although Sun bears have been present in zoological parks around the world since the 1930's (Kolter 1995), there is growing concern for the current status of captive populations in both North American and European zoos. A recent international survey by the Captive Breeding Specialist Group (CBSG) recorded 269 individuals, dispersed widely among the world's zoos (Ball 1994). Generally, the breeding of Sun bears in captivity has been inconsistent and poor, and this situation has changed little in recent years.

Within North American zoos of nine recorded births between 1992 and 1998 only five cubs survived; in general, the captive population has been declining since the 1970s (Ball 1993), and as at December 31 1993 numbered as few as 60 individuals (Frederick 1998). An estimated 50% of these Sun bears are 20 years or older, so considered beyond breeding age (Ball 1994). There is also a strong population skew, with almost twice as many females as males represented in North American zoos (Frederick 1998).

As at 8 August 1999, the population of Sun bears within European zoos similarly numbered approximately 60 individuals (Kolter 1998d). There have been ten births since 1994 (including a set of twins), and eight young have survived. A population summary of captive Sun bears in Europe revealed that since 1961 births have contributed to population growth during only 9 of 35 years (Kolter 1995). As the number of deaths per year often outnumber the birth rate, imported animals have contributed more to population growth in European zoos than reproductive success (Kolter 1995).

Unlike the NA captive population, the majority of Sun bears in Europe are considered within breeding ages (Kolter 1995; Kolter 1998d). However, a similarly skewed sex ratio is also apparent in these zoos; females outnumber males by 2:1, and

mortality/fertility calculations predict a negative growth rate for the male Sun bear population (Kolter 1995). Kolter (1995) suggests two reasons for the strong population skew: 1) low representation of males may reflect preferential importation of females due to a tendency of European zoos to maintain Sun bears in harems; or 2) males may have a higher death rate among unsexed neonates.

1.1.5.2 Captive Breeding Protocol

The Taxon Advisory Group (TAG), also known as the Bear Advisory Group (BAG), was developed under the auspices of the American Zoological Parks and Aquariums (AZA), and makes recommendations for captive bears in North America. In the past the BAG has encouraged breeding of Sun bears to compensate for the continual decline in zoo stocks (AZA BAG Report 1994). Now that the origin of many captive NA bears is in question, the 1996 Species Survival Plan (SSP) recommended only animals of known lineage be bred in 1996/7 to reduce potentially deleterious inbreeding (Ball 1996b). The European Studbook Co-ordinator has also advised a breeding moratorium for Sun bears of unknown origin (Kolter 1995). The long-term management goal for captive bears is that members represent a self-sustaining breeding population that retains 90% of the heterozygosity in current wild populations for 100 years (1994 AZA BAG Report).

1.1.5.3 Conservation Initiatives

A regional studbook for the Sun bear was developed in North America in 1992 (Ball 1996a), and the first European studbook was published in 1994 (Kolter 1995). These publications contain annual population summaries, information on animals in participating institutions, present demographic analyses and current work, and outline proposals and protocols for future research. In 1996 the Sun and Sloth bear Management Group developed a Species Survival Plan (SSP). The SSP outlines a five-year action plan for conservation activities that include *in situ* and *ex situ* projects.

1.1.5.3.1 In-Situ Projects

As fragmentation of the Sun bears' natural habitat continues at an alarming rate, monitoring free-ranging populations of this potentially fragile, environmentally-sensitive species will prove crucial to its continued existence in the wild. In response to strong concerns about the number of Sun bears that remain in the wild, a pilot field study was initiated in Thailand during 1994 and 1995. This collaboration between the

Royal Thai Forestry Department and US researchers was developed as an in-situ conservation project set out in the Sun and Sloth Bear Species Survival Plan (SSP) for 1997-2001. The primary objective of the study was to generate information on the natural history of the Sun bear by determining factors such as habitat use, seasonal range shifts, and quantifying home range sizes to assist with future conservation efforts in the wild (Garshelis & Smith 1996).

Sun bear sightings and sign were poor in several wildlife parks and sanctuaries surveyed in western and eastern Thailand, evidently due to heavy poaching activity in these areas (Garshelis & Smith 1996). For this reason an alternative study site was established in the Maenam Phachi region on the border of Burma, adjacent to Thailand's' largest National Park. Due to the remote nature of the area it is less accessible to poachers, so a higher number of bears was anticipated. Although extensive bear sign was noted during a preliminary study (Garshelis & Smith 1996), trapping in the area did not prove very successful (D. Garshelis pers comm. 1997).

A second field study to monitor Sun bear populations on the island of Borneo has been proposed (Servheen 1996). The main aim of this project would be to assess the impacts of perpetual logging on the bears, to determine whether they can survive in areas of forest that have been converted to secondary growth. In 1997 a preliminary field study began in Borneo, which incorporates research areas from both aforementioned projects and also involves attempted reintroduction of several human-habituated Sun bears (G. Frederiksson pers comm. 1999).

1.1.5.3.2 Ex-Situ Projects

1.1.5.3.2.1 Forensic Genotyping

A difficulty facing law enforcement agencies is the inability to distinguish between a gallbladder from a bear, and one from an unprotected animal (Mills & Servheen 1991). US scientists are perfecting two contemporary forensic techniques as analytical support: mitochondrial DNA (mtDNA) testing (Fain et al 1994), and profiling of bile acids (Espinoza et al 1994). These methods respectively identify the type of animal the gallbladder came from, and which species it belongs to. A US transplant expert is developing an alternative method, culturing bear liver cells for the production of genuine bile (Marks 1996). It is hoped that the latter method will reduce pressure on wild bear populations by providing consumers with a more credible form of bear bile.

1.1.5.3.2.2 Genotyping Captive Populations

In 1993 collaboration between Woodland Park Zoo, Seattle, and the United States Forensic and Wildlife Services (USFWS) forensics was established to determine genetic variation among NA populations of Asian bear species (Fain & Ball 1996). This recommendation was initiated out of genetic concern, due to the uncertain origins of the majority of the NA captive population. The founding stock of many of these Sun bears were unspecified as wild-caught or captive-born animals, and often their origin remained undocumented. Nuclear and mitochondrial DNA (mtDNA) analyses are being conducted to determine genetic relationships among captive Sun bears in NA zoos which will assist in making breeding decisions for future captive management (Fain & Ball 1996). A similar genetic study of European captive populations began in 1994 (Kolter 1995).

In 1994 the BAG recommended importation of up to 20 known-origin Sun bears from SE Asia to act as founders (Ball 1994). An import permit was approved in 1996, and ten animals (one male:nine females) on loan from Sabah, Malaysia were distributed as pairs among NA zoological institutions (Frederick 1998). The bears are adult (ranging in age from ~5-15 years), and were considered non-releasable because they had been kept as pets since infancy.

1.1.5.3.2.3 Reproductive Biology

The application of non-invasive hormonal monitoring techniques has been proposed for describing reproductive cycles in three Asian bear species - the Sun bear (*U. malayanus*), Sloth bear (*U. ursinus*), and Asiatic Black bear (*U. thibetanus*) (Monfort & Johnston 1993). The Spectacled Bear (*T. ornatus*) from South America has also been included in this approach which aims to define the reproductive biology of previously unstudied members of the ursid family.

Reproductive parameters including gestation length and seasonality are unclear for all Asian bear species except the Giant panda (Monfort & Johnston 1993); further knowledge is essential to enhance future captive breeding attempts of other ursids. Measuring reproductive steroids in urine and faeces are non-invasive methods that eliminate stress associated with conventional blood sampling, and permit frequent and long-term sampling regimes to be conducted. Captive breeding programs have shown that contemporary non-invasive methods are particularly useful for co-ordination of

assisted reproductive techniques in the Giant panda (Hodges et al 1984; Kubokawa et al 1992). A further potential use of these techniques is for confirming pregnancy in bears, because traditional methods such as blood sampling and ultrasound analysis require physical and chemical restraint which can compromise the female and jeopardise foetal survival (Ball et al 1996).

1.2 LITERATURE REVIEW:

REPRODUCTIVE BIOLOGY AND BEHAVIOUR OF THE URSIDAE

1.2.1 Reproductive Parameters

Bears are notoriously difficult to study in the wild. They are widely distributed, present in low densities within remote locations and, despite a somewhat shy nature, they can be extremely formidable subjects (Herrero 1978, Derocher & Stirling 1993). For these reasons zoo records comprise the majority of available literature on reproductive biology of the Ursidae. Collectively, studies of free-ranging and captive animals have revealed that the reproductive rates of bears are among the lowest of all terrestrial mammals (Bunnell & Tait 1981). Knowledge of reproductive parameters such as the average age at first parturition, average litter size, and average duration between litters, is required to calculate the reproductive rate for a population (Herrero 1978). Determining the reproductive rate of populations is crucial to an understanding of reproductive strategies in ursids, and necessary for effective management of these animals (Herrero 1978; Bunnell & Tait 1981). There is no scientific knowledge concerning the reproductive biology of free-ranging Sun bears (Garshelis & Smith 1996; Servheen 1996).

1.2.1.1 Reproductive Maturity

Natality rates including age at first reproduction are linked to environmental factors, and strongly influenced by the nutritional status of the female (Rogers 1976; Bunnell & Tait 1981). In captivity, female Sun bears may reach reproductive maturity as early as 3.5 years, but do not usually conceive before they are 6 years old (Dathe 1970; Schaller 1994; Kolter 1995). These findings are consistent with data from studies of other species (*U.ursinus*: Jacobi 1975; *U.americanus*, *U.arctos*: Herrero 1978; *U. maritimus*: Ramsay & Stirling 1986; *U.thibetanus*: Reid 1993; *A.melanoleuca*: Hodges et al 1984; *T.ornatus*: Weinhardt 1993).

There is less information on the age that males become sexually mature but published reports suggest a similar range. Male Sun bears in European zoos usually breed after the age of 5 or 6 years (Kolter 1995); and male Brown and Polar bears become sexually mature after 4 years (Palmer et al 1988) and 5 years (Erickson et al 1968) respectively. Male American black bears usually mature at approximately the same age as other bears

(Palmer et al 1988), but may become reproductively active earlier in regions where there are increased opportunities to breed (Garshelis & Hellgren 1994).

Bears are long-lived animals; their average lifespan is over 25 years in the wild or captivity (Bunnell & Tait 1981, Prator et al 1988; Kurt 1990; Seidensticker 1993b). The age of reproductive senescence is uncertain, but indications are that females remain capable of breeding for most of their life (Bunnell & Tait 1981). In captivity, American black bears and Brown bears have produced young after 25 years (Nowack 1991), and similar observations have been reported for Sun bears (Kolter 1995). Some individual variation can be presumed - for example, there is a report of a 37-year-old Polar bear giving birth (Latinen cited in Nowack 1991). Male bears over 25 years are considered post-reproductive (Palmer et al 1988), and in captivity some Sun bears have continued to breed until approximately this age (Kolter 1995).

1.2.1.2 Seasonality

Most bears are seasonal breeders, mating takes place during spring and summer, and cubs are born during winter (Stirling 1993). Some Asian species are exceptions. Asiatic black bears (*U. thibetanus*) also give birth in winter, but may breed during autumn (Kitchener 1992), and there is no evidence of a fixed breeding season in captivity for the Sri Lankan sub-species of Sloth bear (*U. ursinus inornatus*) (Domico 1988) or the Sun bear (Dathe 1970; Kolter 1995; Schwarzenberger et al 1997). If cubs are removed prior to the subsequent mating period (Baker 1912; Erickson et al 1964), or if the female loses young prematurely (Herrero 1980; Ramsay & Stirling 1986) seasonally breeding bears will produce young annually. Usually, however, parturition occurs in alternate years or after a three year breeding interval (Herrero 1980; Schaller et al 1985; Stirling 1993).

The reported length of behavioural oestrus in ursids is from 5-7 days (Monfort & Johnston 1993), but some individual variation is apparent, as cycles lasting up to 27 days in length have been recorded (Craighead et al 1969). Reports of behavioural oestrus in Sun bears indicate a range from 1 (Dathe 1963) to 7 days in length (Domico 1988; Schaller 1994). Female bears typically have a monoestrus cycle, but evidence of a second period of heat in the breeding season shows that polyoestrus cycling can occur in some species (*U. arctos:* Dittrich & Kronberger 1962; Craighead et al 1969, Tsubota

et al 1985 cited in Tsubota & Kanagawa 1986; Tsubota & Kanagawa 1986; *T. ornatus*: Bloxam 1976; *U. americanus*: Barber & Lindzey 1983, Rowlands & Weir 1984).

1.2.1.3 Gestation Length

Many carnivores have prolonged gestation due to an arrest in development of the ovum following fertilisation, referred to as 'embryonic diapause' or, more commonly, 'delayed implantation' (Mead 1989). During this delay the early stage embryo remains free within the uterus for a variable period of time depending on the species (Mead 1989). In Brown bears, implantation and resumed growth of the foetus may not occur for nearly six months (Tsubota et al 1987). Delayed implantation is believed to occur in most species including the American black bear (Wimsatt 1963; Erickson et al 1964), Asiatic black bear (Dittrich & Kronberger 1963), Brown bear (Dittrich & Kronberger 1963; Tsubota et al 1991; Tsubota et al 1994; Göritz et al 1997), Polar bear (Derocher et al 1992) and Giant panda (Hodges et al 1984). In most species of bear pregnancy lasts between 6 to 9 months (Kurt et al 1990; Stirling 1993), but the Giant panda has an abbreviated period of delay, and gives birth after only 95-108 days (Monfort et al 1989). Most reports indicate the length of pregnancy in Sun bears at approximately 95 days (Dathe 1961; Pagel & Kuhme 1992; Schwarzenberger et al 1997), although gestation lengths of between 174-240 days have been recorded (McCusker 1974).

1.2.2 Reproductive Strategies

The mating system of free-ranging bears is influenced by environmental variables such as population density and distribution of individuals (Herrero 1978). The distribution of females rather than the distribution of food resources is thought to influence organisation and dispersion of solitary male bears (Macdonald 1983). The average home ranges of mature black and Brown bear males are approximately four times larger than females, and overlap numerous female 'territories' (Bunnell & Tait 1981). The areas of use by male Giant pandas also include ranges of several females but are only slightly larger in comparison (Schaller et al 1985; Pan & Lu 1993). Polar bears do not have stable home ranges due to the unpredictable nature of arctic sea ice and associated food availability (Ramsay & Stirling 1986). Members of this species travel widely and change distribution frequently, but space themselves according to food resources, congregating at ice floe edges to feed (Ramsay & Stirling 1986).

In all species of bear studied less than a third of the adult female population is available for mating during the breeding season (Bunnell & Tait 1981; Schaller et al 1985; Ramsay & Stirling 1986). This is due to the late age at which bears become sexually mature, and a long interbirth interval (Herrero 1978; Bunnell & Tait 1981). The lengthy period between each females' availability to breed is an outcome of the several years of maternal care that they invest in rearing young (Herrero 1978; Bunnell & Tait 1981). Males roam widely during the breeding season to locate females in oestrus, and compete with rivals to obtain 'rights' to this important resource (Bunnell & Tait 1981; Stirling & Derocher 1993).

Adult male bears are at least 1.5 times larger than adult females of the same species (Herrero 1978; Stirling 1993); this level of sexual dimorphism implies that they have a polygynous mating system (Stirling & Derocher 1993). Ursids with strong arboreal habits show reduced dimorphism, but Stirling & Derocher (1993) suggest this represents a selective limitation on body size that would prevent compromising locomotive or feeding activity within trees. The similarity in gender size of both Sun bears and Sloth bears has been interpreted as a possible propensity towards more social habits in these species (Macdonald 1983).

Studies of wild bears indicate that males select mates (Herrero 1978), and high levels of intrasexual competition lead to intense conflicts between males during the breeding season (Herrero & Hamer 1977). At this time males become extremely aggressive, and use overt threat displays, vocalisation and fighting to establish a dominance hierarchy (Herrero & Hamer 1977; Herrero 1978; Barber & Lindzey 1983; Ramsay & Stirling 1986; Schaller et al 1985; Garshelis & Hellgren 1994). The age and social status of males appears to decree their access to oestrus females (Garshelis & Hellgren 1994). Studies support this theory, recording that the highest-ranking, most mature males participate in the majority of breeding each year (Craighead et al 1969; Barber & Lindzey 1983; Schaller et al 1985).

In populations where females are widely dispersed, male reproductive fitness is maximised by copulating with as many females as possible, and remaining with a single mate during the breeding season confers little advantage (Herrero 1978; Bunnell & Tait 1981). This situation is likely to represent the most common breeding scenario for bears - a male and female meet, copulate, and part (Bunnell & Tait 1981). The

reproductive strategy of grizzly bears appears to be influenced by density-dependence, resulting in a plasticity in reproductive behaviour (Herrero & Hamer 1977). In areas where bears congregate near a concentrated food source, a high level of promiscuity in both sexes has been reported (*U. arctos:* Sparrowe 1968; Erickson et al 1968; Craighead et al 1969; *U. americanus*: Jonkel & Cowan 1971; *U. maritimus*: Ramsay & Stirling 1986). Female grizzlies have been observed copulating with up to four different males in a single day (Hornocker 1962 cited in Barber & Lindzey 1983; Craighead et al 1969), illustrating the extent of promiscuity in some free-ranging populations. In areas with higher densities of individuals even the most aggressive males have difficulty isolating and defending females (Hornocker 1962 cited in Herrero 1978), and inter-male aggression is less apparent (Sparrowe 1968; Craighead et al 1969; Garshelis & Hellgren 1994). Associations between males and females are relatively brief in these situations, and may last from as little as several minutes to hours in length (Mundy & Flook 1963; Sparrowe 1968; Craighead et al 1969; Ramsay & Stirling 1986; Barber & Lindzey 1983).

During the breeding season pairs may also form longer associations, and remain together from over a week to a month in length (*U.arctos*): Mundy 1963 cited in Hensel et al 1969; Dean 1976 cited in Harting 1987a, Herrero & Hamer 1977, Brady & Hamer 1992; *U. americanus*: Barber & Lindzey 1983; *U. maritimus*: Ramsay & Stirling 1986; *T.ornatus*: Orejuela 1988). During the mating season courting pairs of Brown bears, Polar bears, and American black bears may travel together and remain in close contact (Jonkel & Cowan 1971; Herrero & Hamer 1977; Barber & Lindzey 1983; Ramsay & Stirling 1986; Brady & Hamer 1992).

There is an increasing body of evidence that in some areas male Brown bears isolate a female from other adult males during her breeding period (Sparrowe 1968; Herrero & Hamer 1977; Harting 1987a; Hamer & Herrero 1990; Brady & Hamer 1992), and similar behaviour has been reported in Polar bears (Ramsay & Stirling 1986). Males reportedly 'sequester' the female by confining her to a remote area such as mountain summit or range (Hamer & Herrero 1990; Brady & Hamer 1992). Although the males use repetitive herding and displacement to prevent their mates leaving the females also make numerous 'mock' attempts at escape (Herrero & Hamer 1977; Hamer & Herrero

1990; Brady & Hamer 1992), behaviour which Hamer & Herrero (1990) suggest may serve as a test of male vigour.

Another potential reproductive function of pair bonding and mate-guarding in bears is to ensure procreation (Bunnell & Tait 1981; Hamer & Herrero 1990). Some carnivores, like canids, ovulate spontaneously (Milligan 1982; Rowlands & Weir 1984) but copulation or a similar stimulus is necessary to induce ovulation in other species. Induced, or 'reflex' ovulation has recently been confirmed in American black bears (Boone et al 1998), and is suspected to occur in other ursids (Ewer 1973 cited in Schaller et al 1985) with the possible exception of the Giant panda (Schaller et al 1985; Kleiman 1983). As the interval from coitus to ovulation can take several days (Milligan 1982), male bears could gain advantage by sequestering a female during her breeding period to avoid sperm competition, and ensure paternity of a litter (Bunnell & Tait 1981; Ramsay & Stirling 1986).

1.2.3 Communication

With the exception of females and their young, bears are solitary for most of the year. During the breeding season, individuals use olfactory, auditory, and visual signals to communicate. These take the form of chemosensory signals, vocalisation, and behavioural displays. In solitary canivores olfactory and auditory cues are important signals for establishing long-distance contact; and behavioural displays are primarily used to convey intent during closer encounters (Kleiman 1983). Communication during the reproductive season permits sexes to initiate, maintain, and synchronise breeding.

1.2.3.1 *Marking*

The function of marking activities by ursids remains somewhat controversial (Herrero 1972; Pelton 1993). In the wild and in captivity, bears rub their back, shoulders and sides against objects, and also bite, claw and peel bark from trees (Tschanz et al 1970; Schaller et al 1985; Harting 1987b; Seidensticker 1993a). Some researchers consider this type of marking communicates a visual signal and/or deposits scent in the environment (Tschanz et al 1970; Colmenares & Rivero 1983; Schaller et al 1985; Pelton 1993), while others contend that these behaviours are self-maintenance activities (Herrero 1972; Craighead 1972; Geist 1972; Harting 1987b). Marking behaviour is also considered an important component of agonistic rituals (Etkin 1963 cited in Jonkel & Cowan 1971; Colmenares & Rivero 1983), and may assist in the establishment of

dominance hierarchies (Pelton 1993). It is possible that bears marking activities serve a territorial purpose (Pelton 1993), but some scientists refute this theory (Herrero 1972; Craighead 1972; Stonrov 1972), due to the limited evidence for home range defence in these animals.

Although the main purpose of environment marking in bears remains unresolved, these activities are performed with increasing tendency prior to and during the reproductive season (Tschanz et al 1970; Laurie & Seidensticker 1977; Kleiman 1983; Schaller et al 1985; Pelton 1993), which may facilitate breeding synchrony between males and females (Pelton 1993). Nondomestic canids and large felids also exhibit these behaviours at the onset of the breeding season in association with reproductive activity (canids: Kleiman 1968; felids: Kleiman 1974).

Giant pandas have unique anal glands that are reduced or absent in other ursids (Kleiman 1983; Ewer 1985). Both sexes adopt a variety of postures to distribute a thick, sticky secretion from these glands on horizontal or vertical surfaces (Morris & Morris 1966 cited in Schaller et al 1985; Kleiman et al 1979; Schaller et al 1985), and during peak oestrus the female may mark the male (Frese 1985). During threat displays American black bears (Jordan 1974) and Brown bears (Colmenares & Rivero 1983) dribble urine on their belly or legs, and mark the ground or bushes in their proximity, but urine is more often prominently used for scent-marking by Giant pandas and closely related procyonids (Schaller et al 1985). Male and female members of these species scent-mark with increasing frequency during the breeding season (Kleiman 1983; Schaller et al 1985).

1.2.3.2 Olfaction

Scents and pheromones are important for conveying information about the sexual status of animals, and their use is widespread among carnivores, rodents, ungulates, and primates (Beach 1976; Nelson 1995). Courtship behaviour in mammals is strongly underpinned by olfactory cues and associative behaviour patterns including anogenital investigation, marking and urine investigation (Dewsbury 1979). Males of numerous species use olfaction to detect chemosensory cues from females in oestrus (Beach 1976; Nelson 1995) and such signals are thought to play a role in ursid communication (Jordan 1974; Colmenares & Rivero 1983; Kleiman 1983; Stirling & Derocher 1993; Swaisgood et al 1999). During the reproductive season males frequently check odour

trails to track oestrus females (Schaller et al 1985; Orejuela 1989; Kurt et al 1990), and Polar bears are said to walk tens of kilometres in a straight line to a receptive female (Stirling & Derocher 1993) indicating the potency of olfactory cues.

Bears also investigate the reproductive status of females by following, and sniffing and/or licking the females' hindquarters, anogenital region, and urine (Meyer-Holzapfel 1957 cited in Ewer 1985; Craighead et al 1969; Tschanz et al 1970; Herrero & Hamer 1977; Kleiman et al 1979; Hamer & Herrero 1990). Olfactory and gustatory inspection of the anogenital region is common to many male mammals, and may be accompanied by a grimace or distinctive curl of the upper lip known as the 'flehmen' response (Beach 1976; Nelson 1995). Flehmen is thought to assist in transmitting female sex hormones to an olfactory receptor area in the roof of the mouth known as the vomeronasal organ (Wysocki 1979 cited in Nelson 1995). This response is characteristic in numerous ungulate species, and present in carnivores including domestic dogs and cats (Beaver 1994), and non-domestic Felids (Verberne 1970). Flehmen has been reported in a Sun bear during a mating attempt (Dathe 1963 cited in Ewer 1985) but other accounts are not evident, which may indicate this behaviour is less common, or more difficult to detect in ursids.

1.2.3.3 Vocalisation

In general, information on the vocal communication of bears is poor, and detailed research has primarily focused on the Giant panda (Peters 1985; Schaller et al 1985). Giant pandas have an extensive vocal repertoire of up to 11 different complex and graded calls and sounds, much wider than the vocalisation reported for other species of bear (Peters 1985). During the breeding season male and female Giant pandas are especially vocal, and use a variety of calls to advertise their location and reproductive status, and facilitate association between breeding individuals (Peters 1985; Schaller et al 1985).

In contrast to canids, vocalisation in most bears is usually associated with serious agonistic behaviour (Henry & Herrero 1974; Kleiman 1968; Latour 1981; Colmenares & Rivero 1983; Peters 1985; Forthman 1995). During oestrus the female Giant panda emits a series of high-pitched bleats and chirps to attract and communicate with males; this type of vocalisation is also used by females of the closely related Red panda (Ailuridae) and racoons (Procyonidae) (Kleiman 1983; Peters 1985; Schaller et al

1985). Other species of bear studied do not appear to have an equivalent sound to signal appeasement or affiliative intent (Peters 1985; Schaller et al 1985). Although Kleiman (1983) noted that conspicuous vocal communication has not been reported accompanying breeding activity of other ursids, several accounts indicate affiliative vocal interchange may occur in some species. Like the Giant panda, female Spectacled bears may vocalise with increased frequency during oestrus (Rosenthal 1989b; Weinhardt 1989), and Asiatic black bears are said to make 'clucking' noises while courting (Law et al 1992). Male American black bears (Henry & Herrero 1974) and Spectacled bear (Orejuela 1989) have been said to use low pitched vocalisation when approaching an oestrus female, which may assist to communicate their affiliative intent.

1.2.4 Behaviour of the Male

The period of spermatogenesis in most ursids is seasonal, and precedes and exceeds beyond the females breeding period (U. americanus: Erickson et al 1964, Palmer et al 1988, Garshelis & Hellgren 1994; U. arctos: Erickson et al 1968; Tsubota et al 1997; A. melanoleuca: Platz et al 1983; Masui et al 1985; U.maritimus: Palmer et al 1988; U. thibetanus: Komatsu et al 1995). In seasonally breeding animals levels of the male hormone testosterone rise during the reproductive season, promoting spermatogenic activity and facilitating aggressive behaviour (Lincoln 1981; Nelson 1995). In a number of mammalian species adult males undergo a seasonal rut characterised by high levels of intrasexual aggression and display during the breeding period (Sadleir 1969; Nelson 1995). A seasonal rise in testosterone levels has been observed in male American black bear (McMillin et al 1976; Palmer et al 1988), Polar bear (Palmer et al 1988), Giant panda (Bonney et al 1982; Kubokawa et al 1992), and Brown bear (Tsubota & Kanagawa 1989). Testosterone peaks prior to the onset of breeding in ursids (*U.arctos*: Tsubota & Kanagawa 1989; *U. americanus*: Garshelis & Hellgren 1994), which may assist in establishing social hierarchies early in the season (Garshelis & Hellgren 1994). Boars use antagonistic displays and fighting to establish a social dominance hierarchy that will gain them breeding opportunities with females (Herrero 1978; Ramsay & Stirling 1986; Barber & Lindzey 1983; Schaller et al 1985; Garshelis & Hellgren 1994), and studies of the American black bear have found a supporting correlation between increased testosterone and a heightened incidence of aggressive behaviour between males (Garshelis & Hellgren 1994).

Bears have a linear dominance hierarchy; the largest males are dominant over other boars, followed by females with cubs, single sows, and lastly, juvenile members of the population (Stonrov & Stokes 1972; Herrero 1980). Sexual competition between bears is thought to have resulted in evolutionary selection of large, aggressive males (Herrero 1978; Stirling & Derocher 1993), and during the breeding season, dominance displays are common (Herrero & Hamer 1977; Barber & Lindzey 1983; Ramsay & Stirling 1986; Schaller et al 1985). In free-ranging populations little inter-sexual or intra-sexual conflict or fighting involving females has been observed, apart from in defence of cubs (Ramsay & Stirling 1986; Wielgus 1986 cited in Harting 1987a).

During antagonistic display ursids primarily use head and body postures to communicate their social status and intimidate others (Stonrov & Stokes 1972; Jordan 1974; Egbert 1978 cited in Harting 1987a; Peters 1985). The establishment of a dominance hierarchy between males does appear to reduce the incidence of physical fighting (Hornocker 1962 cited in Bunnell & Tait 1981; Lindzey 1983). Agonistic behaviour by bears includes lunges and paw-swatting, charging attacks, and ritualised threat (Jonkel & Cowan 1971; Stonorov & Stokes 1972; Bledsoe 1975; Herrero 1980; Schaller et al 1985; Harting 1987a), and is frequently accompanied by growling, barking or roaring vocalisation (Jonkel & Cowan 1971; Peters 1985; Harting 1987a).

The canine teeth are bared during threat display, and used as weapons when fighting (Bledsoe 1975; Herrero 1980; Stirling & Derocher 1993; Valkenburgh 1993), sometimes becoming badly broken as rivals clash with open jaws (Ramsay & Stirling 1986; Stirling 1993). Although the majority of agonistic interactions between bears end without physical contact (Jonkel & Cowan 1971; Stonrov & Stokes 1972; Bledsoe 1975; Barber & Lindzey 1983; Herrero 1980; Forthman 1995), inter-male battles can result in severe injury or death (Stonorov 1972; Bunnell & Tait 1981; Ramsay & Stirling 1986). The highest incidents of intraspecific wounding are reported during the breeding season as a result of intensive inter-male competition for oestrus females (Pearson 1975 cited in Bunnell & Tait 1981; Schaller et al 1985; Ramsay & Stirling 1986; Wielgus 1986 cited in Harting 1987a; Garshelis & Hellgren 1994).

As testosterone levels decline toward the end of the mating season, the frequency of inter-male conflict wanes (*U. maritimus:* Latour 1981; *U. americanus:* Garshelis & Hellgren 1994), leading to speculation that in bears aggression may indeed be facilitated

by seasonal elevation in testosterone (Palmer et al 1988; Garshelis & Hellgren 1994). In Polar bears agonism between males takes on an inhibited, somewhat ritualised form (Lono 1980 cited in Ramsay & Stirling 1986). Polar bears are a very aggressive species (Geist 1972; Latour 1981; Ramsay & Stirling 1986), and have an enhanced level of sexual dimorphism, with males reaching up to twice the size of females (Kingsley 1979 cited in Ramsay & Stirling 1986). It has been postulated that in this species, reduced aggression during the non-reproductive season may permit males to assess rivals strength and skill when resources are not at stake, and chances of serious injury are low (Latour 1981).

1.2.5 Behaviour of the Female

In free-ranging populations, bears in oestrus are identified by the presence of attracted males, and their behaviour toward potential mates (Craighead et al 1969; Schaller et al 1985; Harting 1987a). Within zoos, Giant pandas have been the subject of much research due to the high profile and conservation status of this species. As a result, the reproductive biology and behaviour of the Giant panda has been documented in great detail and so forms the basis of most available literature in this section (Kleiman et al 1979; Kleiman 1983; Bonney et al 1982; Hodges et al 1984; Murata et al 1986; Chadhuri et al 1988; Monfort et al 1989; Kubokawa 1992).

The period of sexual activity in females of mammalian species is regulated by the ovarian hormones, oestrogen and progesterone (Beach 1976; Concannon et al 1979; Wildt et al 1981; Beach et al 1982; reviews in Dewsbury 1979 and Nelson 1995). In most mammalian species an increase in oestrogen levels is responsible for the behavioural 'heat' elicited by females (Beach 1976). Female mammals use a succession of behavioural cues as oestrus ensues - initially to attract males, and later to communicate their readiness to mate (Beach 1976). Beach (1976) coined the term 'proceptive' to describe the sexually solicitous behaviour used by females in early oestrus, to associate with, and gain the attention of males. Some researchers refer to this stage of sexual activity that precedes acceptance of intromission as 'pro-oestrus' or the proceptive phase, and use the term oestrus to describe the phase of the ovarian cycle when the female permits breeding.

During the proceptive stage of oestrus bears adopt submissive posturing in the presence of adult males, initiate contact with them, invite play, and present their anogenital area for inspection (Herrero & Hamer 1977, Bonney et al 1982, Kleiman 1983, Murata et al 1986; Harting 1987a). Female bears may also mount and thrust their pelvis against the male (Henry & Herrero 1974; Bloxam 1976; Kleiman 1983; Kuhme 1990); female mounting is a response widespread in numerous species, and thought to elicit reciprocal mounting from the male (Beach 1976). Giant pandas are reputed to be restless during heat – characteristic behaviours include rubbing, rolling, and writhing for prolonged periods, and frequent vocalisation to males (Kleiman et al 1979; Schaller et al 1985; Murata et al 1986). Predictable indicators of oestrus in non-domestic canids (Kleiman 1968) and large felids (Sadlier 1966; Kleiman et al 1979) also includes presentation to males, mounting behaviour, rubbing, rolling, and frequent vocalisation.

Behaviour-endocrine correlates of oestrus have been reported for a variety of non-domestic felids (Schmidt et al 1979; Schmidt et al 1983; Seal et al 1987; Schmidt et al 1988; Wielebnowski & Brown 1988; Graham et al 1995), wolves (Seal et al 1979), African wild dogs (Monfort et al 1997) and Giant pandas (Bonney et al 1982; Murata et al 1986). Proceptive behaviour in these species is often associated with increased excretion of oestrogens, but receptivity and mating may not take place until levels of this hormone decline.

1.2.6 Courtship and Copulation

Bears have been described as having little or no courtship behaviour (Kurt et al 1990), and on some occasions no prelude is evident immediately prior to copulation (Mundy & Flook 1963; Sparrowe 1968; Ludlow 1974; Egbert 1978 cited in Harting 1987a). Numerous reports indicate, however, that pairs may form a temporary affiliative association for up to several weeks prior to copulating (Herrero & Hamer 1977; Barber & Lindzey 1983; Ramsay & Stirling 1986; Harting 1987a; Orejuela 1989; Brady & Hamer 1992). During this period, mated pairs engage in repeated bouts of olfactory investigation, and non-aggressive physical contact including play and wrestling (Hornocker 1962 cited in Harting 1987a; Craighead et al 1969; Herrero & Hamer 1977; Schaller et al 1985; Hamer & Herrero 1990; Kuhme 1990).

Postures and movements used during affiliative social interactions are morphologically and contextually similar in ursids, procyonids, and canids (Kleiman 1983). These include play invitations, chasing, pawing, inhibited biting, and rolling over (Henry & Herrero 1974; Burghardt 1975; Kleiman 1983). Mock-fighting seems to be a common

component of ursid courtship behaviour (A. melanoleuca: Kleiman 1983; U.ursinus: Kitchener 1992; U. malayanus: Kuhme 1990). For non-social species such as bears, this may be necessary to allow individuals to assess the reproductive status of a partner without serious conflict (Ewer 1985).

The female mammal also plays an important role in timing of breeding activity by signalling her readiness to mate (Doty 1974 cited in Kleiman et al 1979; Beach 1976), or 'receptivity' (Beach 1976). The onset of receptivity marks the transition from courtship to copulation (Beach 1976), and is thought to be mediated by a reduction in circulating oestrogen coupled with a progressive increase in progesterone levels (Concannon et al 1977; Chakraborty et al 1980; Beach et al 1982). When ready to breed, the Giant panda female solicits male attention by walking backward, lifting her tail to present the anogenital region, tossing and shaking her head, and calling (Kleiman et al 1979; Kleiman et al 1986). She co-operates with male attempts to copulate by standing when mounted, and may assume a stereotyped mating position to assist intromission (Beach 1976; Dewsbury 1979; Nelson 1995). Female bears may crouch or arch their back (*U. americanus:* Ludlow 1968; *A. melanoleuca:* Kleiman et al 1979; Roberts & Kessler 1979 cited in Schaller et al 1985), in a lordosis posture, similar to that observed in other mammals (felids: Kleiman et al 1979; canids: Dewsbury 1979; rodents: Nelson 1995).

Bears display the typical carnivore mating posture - the male mounts and clasps the standing female from behind (Kleiman 1983). He may remain draped over the female during copulation, or stands upright behind the female with forepaws in the centre of her back (Mundy & Flook 1963; Sparrowe 1968; Ludlow 1974). Giant pandas tend to copulate with the female half-seated and the male squatting behind (Kleiman et al 1979; Schaller et al 1985), which may be necessary as these bears cannot become fully bipedal (Kleiman et al 1979). Neckbites and holds are used by male felids when mating (Ewer 1985), and canids during sexual play (Henry & Herrero 1974). Similarly, male bears usually mouth and bite the females' nape, ears, face or back while mounted and during copulation (*U.arctos:* Mundy & Flook 1963, Herrero & Hamer 1977, Tsubota & Kanagawa 1986; *U. americanus*: Ludlow 1974; *U.maritimus:* Meyer-Holzapfel 1957 cited in Ewer, 1968; *A. melanoleuca*: Kleiman et al 1979; Schaller et al 1985).

The female bear can be quite mobile during intromission, and may walk about, pawing, and sniffing at the ground while the male remains draped over her back, or actively copulating. The general pattern observed during ursid copulation is mounting of the female, and periodic thrusting movements by the male, followed by quivering of the males hindlegs which is thought to indicate ejaculation (Meyer-Holzapfel 1957 cited in Ludlow 1968; Tsubota & Kanagawa 1986). If the male does not dismount immediately following ejaculation, the female terminates contact using aggressive vocalisation and behaviour, or lurching out from below the male and running away (Ludlow 1974; Bloxam 1976; Herrero & Hamer 1977; Kleiman et al 1979; Schaller et al 1985).

Recorded mount durations for bears vary from less than 5 minutes in American black bears, Brown bears, and the Giant panda (Mundy & Flook 1963; Ludlow 1974; Schaller et al 1985) to an hour or longer in the Spectacled bear (Bloxam 1978; Orejuela 1989). Mounting length in Brown bears averages 23 minutes (reviewed in Tsubota & Kanagawa 1986), and the reported range for American black bears is between 0.5-29 minutes (Schaller et al 1985). Frequent mounting and copulation occur over the female's receptive period which may last from several days to weeks in length (*U.arctos*: Meyer-Holzapfel 1957 cited in Ludlow 1974, Dittrich & Kronberger 1962, Hornocker 1962 cited in Barber & Lindzey 1983; Craighead et al 1969; Tsubota et al 1985 cited in Tsubota & Kanagawa 1986; Tsubota & Kanagawa 1986; *T.ornatus*: Bloxam 1976, Orejuela 1989; *U. americanus*: Ludlow 1974; *A. melanoleuca*: Kleiman 1983). The pattern of frequent mounting and copulation is characteristic of species with induced ovulation, lending further credence to the presence of this reproductive mechanism in ursids.

Even when male and female bears consort for a lengthy period during the breeding season, the relationship between the pair remains tenuous. Despite extensive bouts of play and intimate contact, throughout the courtship both animals periodically demonstrate aggressive behaviour toward their partner (Herrero & Hamer 1977; Harting 1987a). The temporary nature of the association between bears is typical of courtship and mating patterns in solitary, dangerous species (Ewer 1985). Copulation occurs when the female reaches peak oestrus, and pairing dissolves when the female is no longer receptive (*U. arctos:* Craighead et al 1969; Herrero & Hamer 1977; *U. americanus*: Rogers 1977 cited in Bunnell & Tait 1981; Barber & Lindzey 1983; *T.*

ornatus: Orejuela 1989). In some mammalian species ovulation is associated with an increase in progesterone, and it is suggested that rising levels within the female may cause reduced tolerance of the male (Beach 1976).

The amicable interaction between sexes that is observed over the reproductive season is rare at other times of year (Bledsoe 1975; Henry & Herrero 1974 cited in Ramsay & Stirling 1986; Kleiman et al 1979; Forthman 1995). Sex-specific differences in habitat use have been documented for American black bear, Brown bear (Bunnell & Tait 1981; Weilgus & Bunnel 1994), Polar bear (Derocher & Stirling 1990), and Sloth bear (Joshi et al 1995). These studies suggest that segregation is related to the avoidance of males by females and subadults, and their social exclusion by adult males. Male bears compete for food resources and are highly aggressive (Stirling 1993). As an exemplar of this, cannibalism is observed more often among ursids than any other mammal, and is conducted predominantly by males (Kurt et al 1990). The removal or killing of subadults by mature males is also thought to be an important strategy in regulation of population density among bears (Bunnell & Tait 1981).

Female bears with dependent young will not associate with adult males even during the breeding season (Bunnell & Tait 1981; Weilgus & Bunnell 1994). In some mammals, lactation inhibits oestrus, and males will kill the young to bring the female back into heat and gain a breeding opportunity (Blaffer Hrdy & Hausfater 1984). Studies suggest that male infanticide serves this purpose in ursids (Weilgus & Bunnell 1994), and it is known to occur in the Brown bear (Weilgus & Bunnell 1994), American black bear, and Polar bear (Geist 1972; Bunnell & Tait 1981).

Chapter 2

Solitary and Inter-Sexual Behaviours of the Malayan Sun Bear (*Ursus malayanus*)

2.1 INTRODUCTION

Sun bears (*Ursus malayanus*) are tropical mammals inhabiting the rainforests of South East Asia. Formerly the species ranged from Malaysia and Indonesia in the east, to as far north as Southern China. Rapid loss of habitat through deforestation and poaching for the illicit trade in bear parts is placing increasing pressure on this species in the wild. There are no estimates of the distribution or number of Sun bears that remain, but populations in Malaysia and Indonesia are believed to be in serious decline (Mills & Servheen 1991; Santiapillai & Santiapillai 1996).

There is little information about Sun bear biology, with no field studies having been conducted in the bear's natural habitat where it is becoming increasingly scarce. In general, knowledge has been inferred largely from published anecdotes, zoo breeding records and studbook data from captive populations. Although this species has been maintained in captivity since the 1930s, behavioural research is limited to several papers of general observations made at European zoos (Kuhme 1990; Schaller 1994; Steffen 1998).

The breeding of Sun bears in captivity has been inconsistent and poor, and currently only approximately 120 individuals remain in western zoos. The species has recently become a higher conservation priority in the zoo community, with the development of regional studbooks in North America and Europe in the 1990s (Ball 1993; Kolter 1995), and more recently, a five-year Species Survival Plan (Ball 1996a). This increased status appears justified in terms of our limited knowledge of the species, and steadily declining populations in captivity and the wild. The factors limiting reproductive success in captive Sun bear populations are not understood, but an improved understanding of this species' behaviour is fundamental to future conservation attempts.

Understanding a species' social requirements is paramount to providing more effective captive management strategies (Kleiman 1980). In the past problems breeding bears have been overcome by adapting conventional approaches to husbandry, based on a better understanding of ursid behaviour. Providing the female with an environment conductive to rearing young has been identified as the key factor contributing to improved captive breeding success in bears (Rosenthal 1989b; Partridge 1992; Linke 1998). Separation of pregnant females from conspecifics, providing access to a suitable

maternity area, and maintaining a high level of privacy are crucial, particularly during the periparturient period.

The objective of this study was to provided detailed information on solitary and intersexual behaviour of breeding pairs in zoos to assist in identification of reproductive activity in the Sun bear. Other ursids have a distinct breeding season so that even if copulation is not observed, dates of parturition can still be estimated and preparation for birth made ahead of time. With Sun bears however, because copulation and birth can occur at any time of year (Dathe 1970; McCusker 1974; Kolter 1995) it is important to identify a set of behaviours associated with oestrus and impending parturition to develop more effective strategies for management of captive breeding programs. Although having comparatively frequent mating periods to other species of bear, the less predictable occurrence of reproductive activity may have contributed to difficulties breeding them in captivity.

2.2 MATERIALS AND METHODS

2.2.1 Study Group One: Wellington Zoological Gardens (WZG)

2.2.1.1 Animals and Breeding History

One female (Studbook # 607) and one male (Studbook # 617) Sun bear were observed at Wellington Zoological Gardens (WZG), New Zealand (41°15' S). 'Chomel' the female, is one of twins born at Miami Metrozoo, Florida on 02 August 1988; 'Bakti' the male, is a singleton born at San Diego Zoological Gardens, California on 17 September 1989. The bears were imported as a potential breeding pair from San Diego Zoo in April 1992. At the start of this study the female was c. 9 years, and the male c. 7.5 years old.

The pair remained together permanently from their arrival until 1996. Breeding activity was first noticed in 1993, and periodically each year thereafter. On several occasions during 1994 and 1995 keepers observed the female exhibiting preparturient behaviours (nest-building, excessive grooming), and isolated her in a den, but there was no evidence of birth. In January 1996, the female again showed late-gestational activity and, as a precaution, was separated from the male in the evenings. On the morning of 20 January 1996, cub vocalisation from the audio monitor confirmed that a birth had taken place. No further vocalisation was heard, and when the female was released several days later, there was no evidence of young. Further prepartum behaviours were noted by keepers in April 1996, but again, without result.

2.2.1.2 Maintenance and Enclosures

The bears were maintained on a diet of various forms of protein (frozen fish, fresh poultry, eggs, dog biscuits (Hill's Science Diet, Canine Maintenance Formula; Hills Pet Nutrition, Kansas, USA) and a selection of fruit and vegetables. They were fed most of their diet at approximately 9am, and the remainder at unscheduled intervals during the day. Water was available to the animals *ad libitum* from the moat or waterfall within the main exhibit. The pair have remained in good health since their arrival at Wellington Zoo; weights recorded for the adults in 1997 were 107.5 kg for the male, and 85.0 kg for the female.

In general, the bears had unrestricted access to outdoors 24hrs/day. At times, temporary separation and alternative housing of the pair was necessary for husbandry purposes.

Observations have been classified into periods to reflect changes in grouping and location of individuals during this study (Table 2.1).

Table 2.1: Observation dates, composition of study groups and their location

Observation Period	Date (1997)	Study Animals (Studbook #)	Sex (M:F)	Location
I	01 Jan - 31 Jan	617 / 607	1.1	WZG, Main Enclosure
II	14 Feb - 15 Feb	606 / 608	1.1	ZSSD
III	17 Feb - 02 Mar	606 / 598	1.1	ZSSD
IV	06 Apr - 17 Aug	617 / 607	1.1	WZG, Main Enclosure
V	19 Aug - 31 Aug	607	0.1	WZG, South Den
VI	01 Sep - 23 Sep	617 / 607	1.1	WZG, Main Enclosure
VII	24 Sep - 27 Oct	607	0.1	WZG, Maternity Wing
VIII	28 Oct - 18 Nov	617 / 607	1.1	WZG, Main Enclosure
IX	19 Nov - 18 Dec	607	0.1	WZG, Maternity Wing

Main Enclosure

The bears occupy a large, concrete enclosure (34.8m x 10.7m) that faces east, separated from the public by a 1m wide wet moat and a viewing barrier (Figure 2.1). Water is supplied by a recycling system, fed by a waterfall that runs down through the terraced exhibit from the top of the enclosure. The rear portion of the exhibit is heavily vegetated, and the animals are prevented from entering this area by an electric wire. Accessible vegetation growing throughout the enclosure included a variety of grasses, small flowering plants, and several shrubs. The exhibit is furnished with a large tree stump, and a tall, dead gum set upright in concrete. Numerous logs, and several bark pits are distributed throughout the exhibit.

Concrete dens are located at either end of the enclosure; the south den (4.9m x 2.8m x 2.0m) consists of adjoining rooms with a wooden bunk (0.4m height) in each; the north den (4.4m x 2.4m x 2.1m) has adjoining rooms, the rear room contains a single bunk (0.5m high) (Figure 2.2). Individual holding areas are connected by a series of manually operated doors, and keeper entrances are located at both ends of the exhibit.

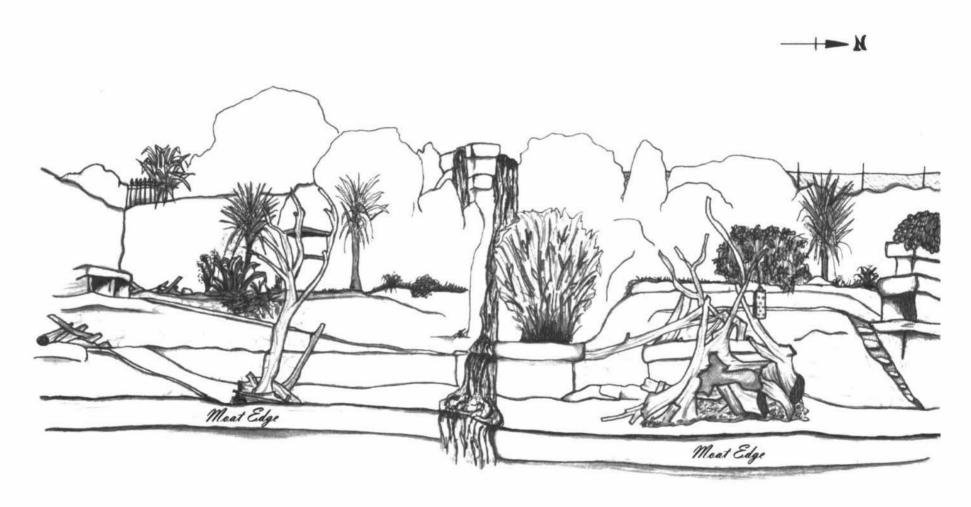


Figure 2.1: Sun bear exhibit at Wellington Zoological Gardens - the naturalistic enclosure contains a variety of features including live vegetation, dead trees to climb and a waterfall.

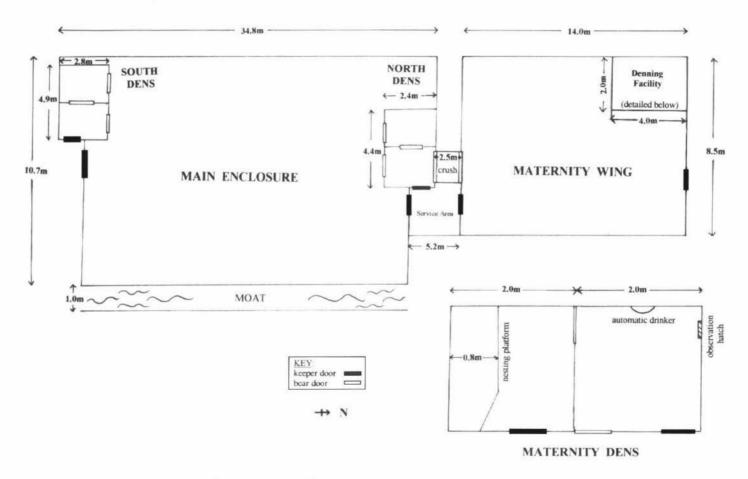


Figure 2.2: Plan drawing of Sun bear enclosures at Wellington Zoological Gardens. Public access is restricted to the main enclosure (exhibit), and the private maternity wing is located adjacent to the north dens. The maternity wing includes a denning facility located in the far northwest corner; see plan inset. Maternity dens contained video and audio equipment positioned in a false ceiling above the nesting platform. Note: diagram not drawn to scale, all measurements are approximate.

Maternity Wing

The maternity wing is adjacent to the north den, and connected by a raceway/crush that serves as a passage to move animals between these areas (Figure 2.1). The maternity enclosure was converted from a pre-existing bear exhibit now isolated from the main public thoroughfare. The enclosure is a deep concreted grotto (14m x 8.5m) with bark chips covering 2/3 of the ground surface. It is furnished with a large, dead tree set in concrete, woodpiles, and numerous logs. Keeper entrances are located at either end of the enclosure.

A complex containing a pair of adjoining dens (4m x 2m x 3.4m) is located at the northwest corner of the maternity wing; the room furthest from the north service entrance contains a nesting platform (1.77m x 0.77m). A single doorway for the bear, leads into the facility through the northmost den. The inner rooms are connected by a manually operated door, and service doors close each den from outside. Water was available *ad libitum* from a trough in the outside enclosure, or an automatic drinker indoors.

Audio and closed-circuit visual monitoring equipment was set up in a false ceiling above the nesting platform. Low level light was provided by a 50 watt redlight/infrared bulb. Footage was obtained by use of a black and white security camera fitted with a 22 mm superwide lens (Burle Security Systems, Ireland) and recorded on a time-lapse VCR (Hitachi). When the bear was indoors, behaviour was observed on a video monitor (Hitachi) in a surveillance room adjacent to the northernmost den.

2.2.1.3 Sampling Methods

Data were collected at Wellington Zoo from 02 January to 18 December 1997. There was a break in observations from February to April 1997, while supplementary research was conducted in the United States (see Table 2.1), and behaviour notes for this period were compiled from keeper records. During the study animal management records for the bears concerning events that occurred outside sampling periods also served as sources of qualitative information.

In general, the pair were observed for 2-6 days each week between 8.00am-5.00pm from a site in the public viewing area that permitted surveillance of the majority of the main enclosure. The occurrence and length of observations were at times constrained by management changes to husbandry routines, and severe weather. For instance, in

winter the bears often retreated into dens and remained there for most of the day. A subject was recorded as "out of sight" when view of the animal was obscured, or when it entered a den. If the male and female were simultaneously out of sight within the same den, this was also noted. During periods when the female was isolated (V, VII and IX see Table 2.1), remote video monitoring permitted recording of her behaviour for up to 24 hours per day.

Solitary and social behaviours were recorded by continuous focal sampling (Martin & Bateson 1993), using a stopwatch to time the onset of each behaviour. Additional information on these, and uncoded behaviours of interest were noted qualitatively. When the bears were paired, each subject was observed in 30 minute blocks; when they were separated only the female was observed. During interactions the role of a subject (*initiator* and *terminator*) was noted when it appeared obvious. The end of an encounter was defined as when a pair broke contact and/or did not react to each other for 10 seconds. When possible, morphological changes of the female's vulva² were graded and scored during the observation session.

Behaviour data are presented as the mean \pm SE. Mann-Whitney test was used to determine if there were any significant (p<0.05) differences in the frequency or duration of behaviours between oestrus and pregnancy.

²This parameter is a potential physical indicator of female reproductive status.

2.2.2 Study Group Two: San Diego Zoological Gardens (ZSSD)

2.2.2.1 Animals and Breeding History

One male (Studbook # 606) and two female Sun bears (Studbook # 608 and #598) were observed at San Diego Zoological Gardens (ZSSD), U.S.A. (32°48' N). This study site was chosen because Sun bears had successfully bred at this zoo in the past. The male is one of twins³ born at Miami Metrozoo, Florida on 02 August 1988; female #608 was also born at Miami, on 18 October 1988; and female #598 was born at Baltimore Zoo, Maryland on 07 October 1987. The animals from Miami Zoo were transferred to San Diego Zoo in April 1989, and female #598 arrived in May 1989. At the onset of this study the male, 'Ringo' was c. 8.5 years old; the two females 'Moon' (#608) and 'Muffin' (#598), were aged c. 7.5 and c. 8.5 years respectively.

Keepers first observed breeding activity between the male and female #598 in November 1990 when the male was 2.5 years old, and the female 3 years old. No further reproductive encounters were noted until December 1995 when the male was observed mounting female #608 - the pair were both c. 7 years of age. At the start of this study none of the subjects was a proven breeder.

2.2.2.2 Maintenance and Enclosures

The bears were maintained on individually tailored diets consisting of protein in the form of dog biscuits (Zu Preem Omnivore Diet, Premium Nutritional Products, Inc. Kansas, U.S.A), and a selection of vegetables and fruit. Most of the food was given to the animals when they entered the indoor enclosures in the afternoon. Water was available from automatic drinkers indoors, and *ad libitum* outdoors from another automatic drinker, the waterfalls or moat.

The outdoor exhibit is a spacious gunite enclosure (42.7m x 12.2m x 4.3m), situated in a hillside that faces east. The animals are separated from the public by a pair of wet moats and viewing barrier. Water runs from a waterfall at the far northeast corner, down through the exhibit to fill the stream, then is filtered and recycled. Sheltered cavelike areas containing heating pads (covered electric heating coils) are set into the ground at several sites. The enclosure is furnished with a mass of large eucalyptus limbs, logs, and several bark pits.

³ Coincidentally, his twin is 'Chomel' (#607), the female at Wellington Zoo.

Off-exhibit, the bears occupy a building that contains two bedrooms (3.3m² each), a sunroom (5.6m²), and a cubbing den (1.4 m²). Each bedroom is furnished with a wooden shelf (~1m high) bracketed to one wall to serve as a bunk, and a heating element set into the concrete floor. Holding areas are connected by a series of manually operated doors and chutes. A complete description of these facilities is given in Michel (1990).

Four bears (1Γ:3E) were moved in pairs between the indoor enclosures and an outdoor exhibit. The third female kept at San Diego Zoo was not included in the study; this animal was considered by management to be post-reproductive (>16 years), and therefore was no longer paired for breeding. Study subjects were exhibited outdoors between 9.00am and 4.30pm, when they were exchanged for the second pair. Data collection occurred in two periods (Table 2.1) determined by the composition of individuals. At the start of this study the male had been paired with female #608 for approximately 8 months.

2.2.2.3 Sampling Methods

Data were collected at San Diego Zoo between 14 February and 02 March 1997. Initially the pair studied were male #606 ('Ringo') and female #608 ('Moon'). On 16 February female #608 was removed for husbandry reasons, and from 17 February female #598 ('Muffin') was paired with the male for the remainder of the study. Supplementary notes of events that occurred outside sampling periods have been compiled from keeper records.

The bears were observed for up to 6 days each week between 8.30am - 4.30pm, from a site in the public viewing area providing surveillance of most of the main enclosure. The occurrence and length of observation sessions were chiefly determined by management changes to husbandry routines and procedures. Periods of observation were also affected by separation of the male and newly introduced female following serious aggression.

Solitary and social behaviours were recorded by continuous focal sampling (Martin & Bateson 1993), using a stopwatch to time the onset of each behaviour. Each animal was observed in 30 minute blocks, and additional information including uncoded behaviours of interest were noted qualitatively. During interactions the role of a subject as *initiator*

or *terminator* was noted. The end of an encounter was defined when a pair broke contact and/or did not react to each other for 10 seconds. When possible, morphological changes of the female's vulva were graded and scored during the observation session.

2.2.2.4 Supplementary Information

Additional information has been compiled from unpublished keeper reports provided on six pairs of Sun bears (six males:seven females) housed at six other North American zoos (Table 2.2).

Table 2.2: Source of supplementary specimen reports/keeper notes on Sun bear behaviour.

Site	Behaviour records Jan 1994 - Jan 1996		
Minnesota Zoo, MN (MZG) U.S.A.			
Miami Metrozoo, FL (MMZ) U.S.A	Nov 1989 - May 1997		
Oakland Zoo, CA (OZG) U.S.A	Jun 1996 - Jul 1997		
Metro Washington Park Zoo, OR (MWPZ) U.S.A	Apr 1995 - Feb 1997		
St Louis Zoo, MO (StLZ) U.S.A	Jul 1995 - May 1997		
Woodland Park Zoo, WA (WPZ) U.S.A	Feb 1996 - Sep 1996		

2.3 RESULTS

The Sun bears at San Diego Zoo (Study Group One) were observed for a total of 55 hours over 2 weeks; and those at Wellington Zoo (Study Group Two) were observed for a total of 1005 hours over 10 months. The results are firstly presented in the format of a descriptive ethogram and behaviour summary (Section 2.3.1), followed by an analysis of the collected data. Although the focus of this research is inter-sexual and reproductive behaviour of captive Sun bears, much of the study represents preliminary information on other aspects of the bears' behaviour, including solitary habits and non-reproductive interactions. Where appropriate, therefore, the results section includes a comparison of these aspects of Sun bear behaviour with the literature reported for other ursids.

2.3.1 Ethogram

2.3.1.1 Solitary Behaviour

2.3.1.1.1 Inaction

Sun bears tended to sit with hind legs held straight out in front rather than in the typical bent-knee posture of a dog. The forelimbs touched the ground, rested in the 'lap' or hung loosely at the animal's sides. The bears also sat in a 'cradle' position formed by holding the hind feet in the air at an angle of nearly 45 degrees, and balanced on their sacral area. Some animals rocked gently back and forth in this position. The animals occasionally rested in a semi-hanging position by hooking their claws into an overhead crevice to support the body.

When basking, bears oriented toward the Sun sitting fully upright with chest exposed, and head slightly raised with the eyes partially closed. Basking occurred throughout the year and has been reported for other captive Sun bears (Feng & Wang 1991). Free-ranging Sun bear are said to Sunbathe and sleep high in trees (Domico 1988). Captive bears preferred to rest several metres above the ground, either hanging over a large bough or sitting in the crotch of a tree (Figure 2.3b). Other favoured resting sites included tree platforms and elevated areas of the enclosure such as the roof of a den. They usually reclined on their front or side, but occasionally slept in a curled or supine position.

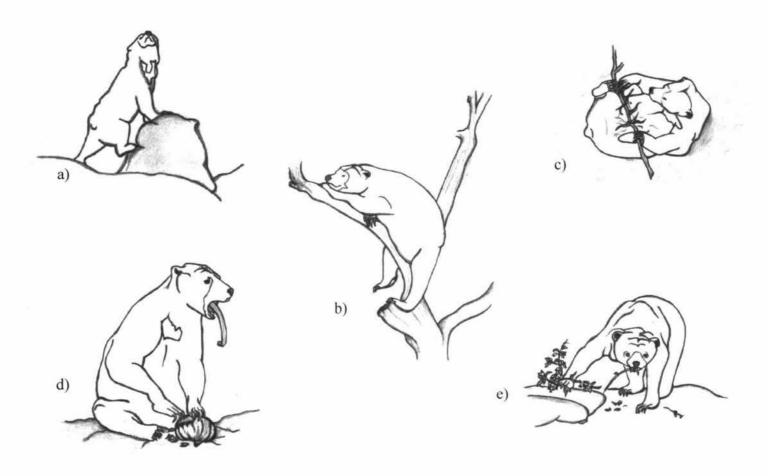


Figure 2.3: Solitary behaviours of the Sun bear. Foraging: a) olfactory scanning was commonly associated with food-finding, d) and e) while the strong dextrous claws were used to manipulate items during feeding. Note the long tongue in d) used to access food in deep holes and crevices. b) Rest sites were typically located several metres above the ground in a tree. c) Twirling sticks with all four feet was a common form of play.

2.3.1.1.2 Locomotion

All ursids are plantigrade, and although they usually remain quadrupedal, with the exception of the Giant panda (Kleiman 1983) bears can also walk fully upright. When walking on all fours the Sun bear has a characteristic swaggering gait that is attributed to slightly in-turned legs - a trait considered to be an adaptation to an arboreal habitat (Servheen 1993). During high-intensity encounters or when animals became alarmed they exhibited more rapid quadrupedal movement in a trot or run. Generally the bears only became bipedal during agonistic display, when traversing difficult substrate, exploring new domain or soliciting for food. During the day they readily climbed trees and other structures within the exhibit to search for food. Descent from any height was always rump first.

Although Sun bears at both zoos had access to deep moats and pools only one individual was observed swimming. However, all the bears stood, lay or waded in shallow water on a frequent basis, as has been observed at other zoos (Steffen 1998). Captive Sun bears are known to swim (Michel 1990; Feng & Wang 1991), but a contradictory report (Usher-Smith & Kolter 1998) suggests that swimming is not a common behaviour for this species.

Stereotypic locomotion occurred in all bears, including a fourth individual at San Diego Zoo that was not a study subject. In most animals this consisted of repetitive invariable pacing at particular sites within an enclosure. At Wellington Zoo the onset of pacing activity appeared to be represent a "food anticipation behaviour" (Jordan & Burghardt 1986) as it predictably occurred prior to regimented feeding times.

The development of chronic stereotypic activities in captive animals is a widely recognised problem, and common in zoo bears (Keulen-kromhout 1978; Carlstead et al 1991; Ames 1992). These apparently purposeless behaviour patterns are thought to develop in captivity due to the absence of appropriate environmental stimuli that would otherwise lead to useful outcomes in free-ranging animals (reviews in Carlstead et al 1991; Wechsler 1991). Pacing is a common stereotypy of captive bears; and can be effectively reduced or remedied by providing animals with a program of environmental enrichment (Law et al 1990; Carlstead et al 1991; Wechsler 1991; Ames 1992). Essentially, environmental enrichment involves altering feeding regimes, and

introducing novel and manipulatable objects to animals to increase the complexity of their captive setting.

Other behaviour problems seen in the study animals included stereotypical swimming, repetitive swaying and swinging of the head, tongue flicking, persistent autogrooming and prolonged inactivity. The male at Wellington Zoo was frequently observed eating his faeces (coprophagy). These behaviours are typical of the type of 'abnormal' patterns exhibited by animals in captivity; the general consensus is that their presence implies a state of compromised welfare in an individual (Keulen-kromhout 1978; Carlstead et al 1991; Ames 1992; Lyons et al 1997). General observations rather than methodological analysis of the effects of environmental enrichment on Sun bears were included in this study. Husbandry practice is closely related to behaviour displayed by the animals and will be considered further in Appendix A.

2.3.1.1.3 Feeding

The natural diet of Sun bears contains a wide variety of fruits, shoots and other vegetation, invertebrates, and some small vertebrates (Domico 1988; Stirling 1993a). In captivity this omnivorous species is fed mainly on fruit or vegetables supplemented with fresh meat (usually poultry or fish⁴), commercial dog biscuits and eggs as sources of protein. A mixture containing smaller food items such as seeds, nuts, dried fruit and grains was also available to the animals in this study. This dried mixture was often scattered or hidden throughout the enclosure to stimulate foraging behaviour and to prolong the availability of food.

More occasional treats included honey and/or honeycomb, coconuts, peanut butter, and ice blocks containing fruit or fish. Many species of bear other than the Giant panda also include a variety of vegetation such as grasses, berries, roots, seeds and nuts in their diet (Bacon & Burghardt 1976a; Laurie & Seidensticker 1977; Kurt 1990; Stirling 1993a; Kolter 1998c). Animals housed at Wellington Zoo had *ad libitum* access to fresh grass and small plants growing within their enclosure (species were not identified), and both zoos provided a range of edible vegetation including species of bamboo, pine, fig and ginger (Appendix A).

⁴ Although pork has previously been included in the zoo diet of Sun bears (Schaller 1994), current opinion is that this meat should not be fed due to risk of infection with Aujetzki disease (Kolter 1998c).

Bears seemed to rely strongly on olfactory cues when seeking food and investigating potential food items. The upper lip was extended when encountering stimuli, which may facilitate detection and discrimination of odours (Bacon & Burghardt 1976a). Smell is the major sense used by bears for locating hidden food, but vision has also been demonstrated to contribute an important role in foraging (Bacon & Burghardt 1976a,b; Valkenburgh 1993). The American black bear has highly developed colour vision; this feature is thought to be common to ursids (Stirling 1993a), and aids in recognition of small or scattered food items and identification of edible fruits (Bacon & Burghardt 1976a).

As Sun bears foraged they walked about the enclosure with their noses held slightly above the ground, raising their heads to sniff upward intermittently, and poking their snouts into crevices. This type of foraging activity by ursids is termed "olfactory scanning" (Bacon & Burghardt 1976b) and represented the major component of locomotive foraging behaviour (Figure 2.3a). The bears also used their front paws extensively to rake, dig, and sort through vegetation and debris for edible particles. The forepaws and claws were frequently used to turn pieces of wood and stones while foraging - this particular behaviour is considered a fixed action pattern associated with food finding in bears (Burghardt & Burghardt 1972; Bacon & Burghardt 1976a; Kurt et al 1990). The animals readily entered the moat, standing chest deep and using their forepaws to scoop up food items. When items floated out further they plowed the water vigorously to create a directional flow that brought the object within reach.

Sun bears use their long, curved claws very effectively during feeding; for peeling or scooping the flesh from fruit and vegetables, tearing open rotten wood and plucking items out of cracks (Figure 2.3d). The dextrous claws and tongue were used simultaneously to access honey and small food items from deeper holes and crevices. Seeking and acquiring food by bears was conducted at a relatively rapid pace. This may reflect an ecological adaptation to the ephemeral nature of food resources in a humid, tropical environment jungle (Laurie & Seidensticker 1977; Domico 1988). Occasionally the bears fed in a more leisurely manner, fully or partially reclining and using their forefeet and hindlimbs to hold and manipulate food items.

Most small food items were simply licked up, or collected in the teeth and cracked prior to ingestion. Larger and more complicated food items such as fruit and vegetables with rind or containing large seeds, were held in the forepaws and manipulated to remove inedible or 'preferred' portions. In season, branches of *Eugenia* berries were provided to the animals. Bears obtained the fruit by surrounding it with an open mouth, then closing the jaws slightly and withdrawing their head, using the teeth and lips to strain the berries from the stem (Figure 2.3e). Branches of vegetation that were difficult to reach were bent and secured in the forepaws.

Some individuals deliberately placed and ate food off the dorsal surface of their forelimbs. The head was lowered to eat from this makeshift 'feeding station' or the animal carefully raised the forelimb to their mouth. This unusual feeding behaviour has been described for the American black bear (Bacon & Burghardt 1976a), and possibly reduces ingestion of unpalatable debris associated with ground feeding. Sometimes food was transported to a raised surface such as a stump prior to ingestion. In some cases the animals would carry food several metres into a tree for immediate consumption. As bears housed alone also exhibited this behaviour, it is unlikely to represent a tactic used solely to sequester food.

Most species of bear consume insects and other invertebrates as part of their varied diet (Bacon & Burghardt 1976a; Orejuela 1989; Law et al 1992; Stirling 1993a; Kolter 1998c). The exceptionally long tongue of the Sun bear is thought to be an adaptation to this type of feeding (Servheen 1993) and study animals sought insects within trees and stumps on a regular basis, targeting portions of the wood by sniffing and tapping at it with their long claws. Bark was easily peeled back using claws and teeth, and holes were probed to obtain insects and larvae from deep within the timber.

The Sloth bear of India and Sri Lanka is an ursid specialised to cope with a myrmecophagous (termite-eating) diet. This species has evolved several features including protrusible lips, a hollowed palate, and is missing a pair of upper incisors to facilitate suction of termites from within mounds. Feeding Sloth bears are reported to make very loud and conspicuous sucking noises that can be heard nearly 200m away (Laurie & Seidensticker 1977; Nowack & Paradiso 1983). Although lacking similar morphological adaptations, the Asiatic black bear is said to vacuum-feed (Law et al

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⁵ Presumably, a hollow sound would indicate rot had begun and insects could be present.

1992); it is possible that Sun bears obtain insects in this manner as audible snorting and sucking sounds were frequently heard to accompany this type of feeding.

Some individuals demonstrated an alternative method of capturing insects. From a reclining position the bear used a forepaw to trap insects that landed on their body. These insects were then carefully transferred to the mouth or licked up. In seasons when insects were abundant, catching and eating them could occupy the bears for lengthy periods. At other times, insects that landed on them were shaken off or ignored.

On several occasions the male at Wellington Zoo killed and ate small birds that ventured into the enclosure. Rather than sneaking up to a bird, the bear sat very still and allowed it to come close and peck at food nearby. When the bird was within reach, he made a hasty swiping motion either knocking the prey from the air or crushing it against an adjacent surface. The "paw slap" is a behaviour more commonly used by felids to stun or crush small prey, but has been observed in American black bears (Bacon & Burghardt 1976a).

Both bears at Wellington zoo had conspicuous begging habits. The animals stood upright or walked bipedally, and bobbed or waved their heads from side to side when soliciting attention. Begging behaviour was mainly directed toward their keepers at feeding times, because most of the daily diet items were distributed by hand from the front of the enclosure. Although there are signs at the entrance to Wellington zoo asking visitors not to feed animals, on numerous occasions members of the public were observed feeding the bears with 'junk food' from a nearby kiosk (e.g. hot chips, pies, icecreams and candies). As a result, the bears often directed begging behaviour toward zoo visitors with food⁶. It is well-known that zoo bears readily acquire begging habits, particularly when fed by the public (Keulen-kromhout 1976; Carlstead et al 1991).

2.3.1.1.4 Excretion

Both sexes urinated or defecated in a squatting position, and although certain locations were used more frequently than others excretion was not confined to limited areas. Animals with unrestricted access to outdoors did urinate and defecate within their dens,

⁶ When the extent of public feeding was brought to the attention of managers at Wellington Zoo, a sign was erected in front of this enclosure asking visitors to refrain from feeding the bears. The incidence of public feeding and begging both declined as a result.

but avoided soiling the bed. A degree of locus specific defecation was evident as excreta was infrequently deposited on paths of travel within the exhibit, and animals habitually dropped it in front of the keeper entrances. The Wellington Zoo bears also regularly deposited faeces and urine into the moat by backing over the edge. If the animals were released prior to periodic replacement of water in the exhibit they predictably entered the empty moat to defecate. As the moat represents the buffer zone between the public and the bears, these actions could be interpreted as marking the boundaries of their captive territory.

2.3.1.1.5 Self-Maintenance

The Sun bears often rubbed themselves against trees and other structures within their enclosure. Rubbing the neck, shoulders, sides and back was vigorously performed from a seated position or while standing bipedal against the limb of a tree or vertical surface. This activity was not site-specific but particular areas within enclosures were favoured. At these preferred locations rubbing resulted in the build-up of a thick, dark and tacky paste that contained some hair. The accumulated secretion had little perceptible odour. Sometimes the animals held pieces of fruit, bark or grass sod in their forepaws and repeatedly rubbed the item over their head, face and nape.

As noted for other ursid species, grooming movements by Sun bears were neither frequent nor complex, and were not conducted in any predictable sequence (Burghardt & Burghardt 1972; Kleiman 1983). Grooming involved licking and nibbling of the pelage and body; and was largely independent of scratching - performed with the claws of the fore or hind feet. During oestrus and pregnancy females exhibited an increasing tendency to groom their forepaws, nipples and anogenital area. Preparturient females elicited a specific grooming action unseen at other times in these individuals, or by males and non-pregnant females. This was characterised by extensive licking of the forearms, and performing repeated strokes over the head, ear, and face in the typical face-washing pattern elicited by rodents and cats. To permit analysis of this type of activity, attention to particular anatomical areas were recorded in addition to frequency and duration of grooming bouts.

Most species of bear enjoy water (Burghardt & Burghardt 1972; Keulen-kromhout 1978; Stirling 1993a) which assists in cleaning the fur and cooling the body (Kleiman 1983). Sun bears often stood or wallowed in shallow water during hot weather and after

physical exertion. Periodically, some individuals stood or sat in drinking troughs. When wet, they shook themselves vigorously to shed excess water from the short fur.

2.3.1.1.6 Play

Bears sometimes played with inanimate objects, rolling about, pouncing on, or manipulating items such as an empty bucket, leafy branch or pieces of wood. During solitary play the mouth was held slightly open and head cocked to one side. Some animals targeted non-food items floating in the moat; splashing, swiping and repeatedly biting at them in an animated manner. Play objects were also batted about with the forepaws, or juggled and twirled on all four feet when the animal lay on its back (Figure 2.3c). Solitary play was infrequent and generally unpredictable in occurrence.

2.3.1.1.7 Reproduction

This category incorporates distinct activities that became highly apparent during oestrus, pregnancy and the periparturient period. With the exception of *rolling*, solitary behaviours associated with these reproductive states were performed exclusively by females. Interestingly, Sun bears exhibited some analogous behaviours to those that characterise Giant panda reproduction. Common activities indicative of oestrus included conspicuous restlessness, *masturbation*, *backward walking*, and the use of affiliative calls (Kleiman et al 1979; Kleiman 1983); behaviours evident during pregnancy and the periparturient period were *nest-building* and *cradling* of objects (Kleiman 1983).

Rolling

During rolling bears lay and writhed on the ground in a manner similar to dogs. Oestrus seemed to invoke a state of body surface irritability in females as rolling became especially evident at this time.

Masturbation

Females in heat scratched at and rubbed their vulva with the forepaws or using an object such as a piece of bark or grass sod. This activity was accompanied by intermittent sniffing of the claws or object that had been in contact with the genitalia.

Backward walking

While moving about an enclosure the bears sometimes walked backward several steps to change direction or avoid a conspecific. Walking in reverse appeared to be a ritualised and distinctive component of female behaviour during oestrus. A bout of

backward walking (after Kleiman et al 1979) could last as long as 1 minute and cover a distance of up to 10 metres. Conspicuous *nickering* sounds were often emitted during backward walking (see Section 2.3.1.2.3), and the head was raised and lowered slowly and rhythmically. Females walked backward either toward or away from a male, but this behaviour was not exclusively exhibited in proximity to a mate, or in the presence of other bears.

Inguinal presentation

Females solicited male attention by lying supine with the rear legs relaxed and presenting their anogenital region. "Inguinal presentation" has been observed during sexual play in American black bears (Henry & Herrero 1974).

Denning and Nesting

Bear dens are excavated from earth or snow, or the animals may utilise a naturally occurring tree hole or rock cave (Stirling 1993a). With the exception of the Giant panda, temperate species of bears construct dens for overwintering where they enter a state of lethargy similar to hibernation. A shortage of food makes this behaviour imperative to survival, and it is during this period that females gestate and give birth to extremely small cubs. Although the Polar bear does not experience winter food shortage, pregnant females still enter dens (Valkenburgh 1993). Sun bears and other ursids from warmer climates do not undergo seasonal torpor either, but pregnant females also utilise dens (Stirling 1993a). Presumably, this reclusive behaviour is essential for supporting and raising such altricial young (Stirling 1993a).

The construction of day beds or 'nests' is a behaviour trait common to most ursids (Stirling 1993a; Kolter et al 1998) including the Polar bear (Ames 1992). Male and female bears use a variety of vegetative materials to build nests that can measure up to 1.5m in diameter (Kolter et al 1998). Free-ranging Spectacled bears and Asiatic black bears create arboreal nests (Reid 1993; Weinhardt 1993; Kolter et al 1998), and Sun bears are also said to nest high in the canopy (Domico 1988; D. Middleton pers comm). Asiatic black bears and Spectacled bears in zoos do create 'tree nests' using branches, twigs and other materials found in their enclosure (Law et al 1992; Kolter et al 1998). Although study animals made frequent use of the skeletal trees in their exhibits for

climbing and resting, arboreal nest-building was never observed⁷. Sun bears in other zoos have been reported to nest build when appropriate materials are available (Steffen 1998); possibly live trees and a selection of leafy boughs, branches and twigs are necessary to promote this naturalistic activity.

At Wellington Zoo, nests were discovered on several occasions prior to and during the study. The bowl-shaped nests of straw were usually built overnight upon the sleeping platforms (~0.5m high) within their dens. The depth of a typical nest was less than 20cm, and the diameter rarely larger than 1m. Both sexes engaged in nest-building, because structures were present in individual dens when the male and female had been separated. Several reports confirm that this species nests in captivity (Dathe 1963, Dathe 1966, Kuhme 1990; Pagel & Kuhme 1992; Schaller 1994), but nest-building has not been described in any detail.

Little information is available on the nesting behaviour of pregnant free-ranging ursids, but conspicuous nest-building activity is often apparent in zoo bears nearing term (*U. malayanus:* Dathe 1963, Dathe 1966, Pagel & Kuhme 1992; *U. maritimus:* Hanning 1992; *U. ursinus:* Law et al 1992; *A. melanoleuca:* Kleiman 1985; *T. Ornatus:* Bloxam 1976, Rosenthal 1989a). Female bears preparing for birth have been described as broody and reclusive, spending increasing time indoors resting and preparing a nesting site up to a month prior to delivery (Bloxam 1976; Peel 1979; Kleiman 1985; McDonald 1989; Schaller 1994). Providing a late-gestational bear access to nesting material and a suitably secluded area has been considered imperative to their successful rearing of young in captivity (Keulen-kromhout 1978; Rosenthal 1989b).

On 02 May 1997 the Wellington Zoo female was observed carrying corn husks and medium sized branches in her mouth. She made five trips from various areas of the main enclosure to transport the items to an outdoor shelter adjacent to the closed south dens. Further observations of nest-building were not possible as this area of the exhibit is obscured from view. On the 06 May 1997, the remains of two cubs were discovered in the main enclosure; one of the young was found in the nest that the female had begun to build four days earlier.

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⁷ Personal communications with staff from various zoological institutions corroborate an apparent absence of arboreal nesting among captive Sun bears.

The loosely formed nest was arranged in a semicircle ~0.8m in diameter and constructed of wood, twigs, grasses and other unidentified vegetation. Several large branches had been gnawed and splintered, but numerous pieces up to 50cm long and 10cm in diameter were found within and outside the entrance to this outdoor den. Although the perimeter of the nest was well formed there was no bedding material on the damp and compacted earthen floor.

Bears usually bed their nests heavily using materials such as twigs, pine needles, grasses, ivy, mosses, lichen and leaves (Craighead & Craighead 1970; Burghardt 1975; Dee 1989; Reed 1989; Kuhme 1990; Law et al 1992 Stirling 1993a; Kolter et al 1998). Bedding material acts both to ventilate the nest, and reduce loss of body heat to the ground; this is particularly important for ursids, which give birth to extremely altricial young. The purpose, if any, of the large pieces of wood that were found within this female's nest is unclear.

In August 1997 the Wellington Zoo female again exhibited nesting behaviour, collecting coconut husks and large branches in her mouth and transporting the material to the same site. At this time the animal was given access to the interior of the den and video monitoring was set up to permit surveillance. The following description details typical nesting activities by this Sun bear:

When entering a den for the first time the female carefully investigated her new environment, walking about, sniffing and periodically standing upright to tap on the walls. After several minutes her attention became focused on a thorough olfactory investigation of the nesting material. In addition to straw, a range of naturalistic material was provided such as twigs, bamboo stems, leafy branches, palm husks and fronds. The female often gnawed extensively at wooden structures, and the splintered timber was incorporated into the nest along with the other materials.

Nest-making commenced with "shuffling" (Molloy 1989) among the vegetation, using scraping motions of the forepaws to rake the material into a large pile. To gather the nesting material closer, she leant forward and encircled it with the forelimbs, pulling it toward the body in a motion described as "hay-hugging" (Blurton 1991). When most of the vegetation was heaped in front of the bear, she began to separate the material. Separation was accomplished by teasing the straw apart with the long claws of her

forepaws, tossing it into the air and sifting the material through the claws. The bedding material was also draped over the head and muzzle and combed off with the claws, as has been observed for Asiatic black bears (Law et al 1990). The animal climbed down from the nesting platform numerous times to collect further straw and plant matter from the floor of the den. Nesting material was carried in the mouth, tucked under the forepaw, or pressed between both forepaws and transported while bipedal.

Binding of the material occurred as it was pressed between overlapping forelimbs and tangled with synchronous, outward rolling motions. This action was used to bend long strands of bamboo and other vegetation into more manageable shape. To shape the nest, the bear used her forepaws in an outward circular motion, tucking the outer edges under with the claws and periodically nosing the bedding into position. Both forepaws were used simultaneously during nesting to lift, drag and tuck the straw into position. From time to time lengthy investigations of the nest were performed - nosing at the perimeter and tucking under loose strands with the mouth or forepaws. Turning frequently during construction of the nest resulted in a 'doughnut' shaped around the seated animal. When seemingly satisfied with a completed nest the bear usually curled up and slept.

Invariably, as the animal changed position numerous times during sleep the nest became flattened and required some reconstruction. Often, it was completely dismantled and remade. To disassemble the nest, the female scraped and kicked the vegetation onto the floor, then climbed down and used the forepaws to rake any remaining material from the platform. Any bedding that became soiled by contact with the wet floor or a faecal pile was carefully separated from the dry clean straw that was collected and returned to the bed.

Cradling

The Wellington zoo female was sometimes observed 'mothering' inanimate objects. Often, these were food items such as a piece of fruit or a bone but 'cub-size' pieces of wood and bark were also favoured. The bear investigated a potential item at great length; sniffing and sometimes turning it over and over before collecting it in the forepaws or mouth, and rolling slowly onto one side. The item was cradled gently against her chest, and attentively sniffed, licked and transferred from mouth to paw. "Cradling" (after Kleiman 1985) is considered to represent a maternal care pattern as the

actions resemble the way a mother bear physically supports her young cub during grooming and nursing bouts (Peel et al 1979; Kleiman 1983; Villares et al 1985).

2.3.1.1.8 Miscellaneous

Behaviours included in this category occurred infrequently and/or were difficult to assign to a specific context. They included *carrying* objects in the mouth or forepaws when not associated with nesting or feeding, and *sentinel* behaviour when animals expectantly waited for keepers in advance of predictable feeding times.

2.3.1.2 Communication

Ursids communicate using visual, olfactory and auditory signals (Pruitt & Burghardt 1977; Stirling 1993a). There is still limited knowledge of the sensory systems of bears, but their hearing is thought to be fairly acute (Pruitt & Burghardt 1977; Domico 1988; Kitchener 1992), they can recognise visual signals up to a distance of 60m (Pruitt & Burghardt 1977), see in colour (Bacon & Burghardt 1976b), and are endowed with an impressive sense of smell (Stirling 1993a; Kitchener 1998).

Apart from the distinctive coloration of the Giant panda, coat patterning is fairly conservative among the Ursidae (Stirling & Derocher 1993). Asiatic black bears, Sloth bears and Sun bears have a unique light coloured u- or v-shaped patch on the chest. It has been suggested that the striking contrast of this 'chevron' may assist intraspecific communication, particularly in densely forested areas (Stirling & Derocher 1993). Despite the visual acuity of bears it is more likely that their long distance identification of conspecifics is facilitated by prior knowledge of an individuals' differences in gait and other behaviours (Kleiman 1983).

Gross body postures and movements are thought to play the primary role in conveying information and intent to other bears (Stonrov & Stokes 1972; Jordan 1976; Pruitt 1976; Kleiman 1983). Bears appear to have a reduced repertoire of social signals which has been attributed to their predominantly solitary nature, the short tail that precludes its use as a signal device, and their poorly developed facial musculature (Lorenz 1953 cited in Jonkel & Cowan 1971; Egbert & Stokes 1976; Krott 1961 and Ewer 1968 cited in Pruitt 1976; Kurt et al 1990).

Indeed, the use of highly specific visual signals by Brown bears (Egbert & Stokes 1976) and Giant pandas (Kleiman 1983) are assumed to constitute a relatively minor role in

intraspecific communication; however, American black bears communicate using a diverse repertoire of facial expressions that involves complex and graded positioning of their ears and jaw (Drahos 1951 cited in Jonkel & Cowan 1971; Burghardt & Burghardt 1972; Henry & Herrero 1974).

Olfactory signals are thought to be a prevalent method of communication between bears (Burghardt & Burghardt 1972; Jordan 1976; Colmenares & Rivero 1983; Kleiman 1983; Stirling & Derocher 1993). Although scent glands are reduced or absent in most ursids (Kleiman 1983; Ewer 1985; Kitchener 1992) they are well developed in Giant pandas. This species lays scent-marks using secretions produced by the enlarged anal glands and urine. American black bears and Brown bears also use urine for scent-marking (Jordan 1976; Colmenares & Rivero 1983). Some researchers have suggested that rubbing activity may help distribute olfactory signals within the environment (Tschanz et al 1970; Colmenares & Rivero 1983; Schaller et al 1985; Pelton 1993).

Many mammals make use of scents to convey information about their sexual status (Beach 1976; Nelson 1995), and these signals are strongly suspected to play a role in ursid communication (Jordan 1976; Colmenares & Rivero 1983; Kleiman 1983; Stirling & Derocher 1993). During the breeding season males follow odour trails of oestrus females (Schaller et al 1985; Orejuela 1989; Kurt et al 1990) in some cases for many kilometres (Stirling & Derocher 1993). Males show a strong interest in female urine and 'test' a female's sexual status by sniffing and licking the anogenital region (Meyer-Holzapfel 1957 cited in Ewer 1985; Craighead et al 1969; Tschanz et al 1970; Herrero & Hamer 1977; Kleiman et al 1979; Hamer & Herrero 1990).

Vocalisation is usually associated with agonistic interactions between bears (Burghardt & Burghardt 1972; Henry & Herrero 1974; Jordan 1976; Latour 1981). Giant pandas are however reputedly vocal during the breeding season and are known to emit a variety of affiliative sounds (Kleiman et al 1979; Kleiman 1983; Peters 1985; Schaller et al 1985). Male American black bears (Henry & Herrero 1974), Polar bears (Wemmer et al 1976) and Spectacled bears (Orejuela 1989) emit low pitched vocalisation when approaching an oestrus female, that may assist in communicating affiliative intent. The use of vocal signals varies between species, and is speculated to be more important for communication between forest-dwelling bears because of the restricted vision in forests (Herrero 1980; Stirling & Derocher 1993).

2.3.1.2.1 Environmental signals

In the wild and in captivity, bears are often observed biting, clawing and peeling bark from trees (Tschanz et al 1970; Schaller et al 1985; Harting 1987b; Ames 1992; Seidensticker 1993a). Some researchers consider this marking communicates a visual signal used by individuals to advertise their presence (Tschanz et al 1970; Colmenares & Rivero 1983; Schaller et al 1985; Pelton 1993), while others contend the behaviour plays a role in self-maintenance (Herrero 1972; Craighead 1972; Geist 1972; Harting 1987b). Marking may in fact, serve to maintain nails and teeth in a good condition, and also act as an enduring signal of presence or passage. It is of note that American black bears typically peel the trunks of fir trees to feed on the vascular tissue (Kimball et al 1998).

Gnawing and biting of wood appears to be a characteristic behaviour of captive Sun bears (Steffen 1998; Kolter 1998), and those at Wellington Zoo periodically peeled bark and scratched and gnawed the hardwood of dead trees in their enclosure. This activity could engage individuals for up to 15 minutes at a time but close inspection of the areas revealed no evidence of purposeful foraging *i.e.* there were no signs of fresh sap or insect use of the timber. On several occasions a claw sheath, and in one case a small incisor was found embedded in the wood. Evidence of this activity was also found in dens where the animals had chewed, sometimes intensively, at the wooden sleeping platforms and support beams.

2.3.1.2.2 Olfactory Communication

Apart from rubbing, Sun bears did not demonstrate any discernible scent-marking activity. All animals engaged in periodic olfactory investigation of conspecifics by sniffing near, or making nasal contact with the body of another individual. Sniffing was usually directed toward the head, nape and shoulder region but pairs also engaged in mutual naso-nasal contact. Both sexes displayed interest in each other's anogenital region but females did not engage in extensive inspection of males. Males sniffed and/or licked the vulva of permissive females and used their claws to hold the short tail aside for closer scrutiny. The periodic inspection of a partner's anogenital region became much more frequent when females were in oestrus. Sniffing and/or licking of female urine, and to a lesser extent their faeces, was common. Females showed minimal interest in male excreta at any time.

2.3.1.2.3 Auditory Communication

Vocalisation by Sun bears was predominantly associated with agonistic interactions. Both sexes produced a range of graded sounds similar in context to those reported for other ursids (*U.americanus*: Jonkel & Cowan 1971, Herrero 1980; Jordan & Burghardt 1986; *U.arctos*: Egbert 1978 in Harting 1987a; U.maritimus: Wemmer et al 1976; *U. ursinus*: Forthman 1995; *A. melanoleuca*: Kleiman 1985, Peters 1985). Acoustic quality within the exhibits was reduced by loud waterfalls and observer distance which prevented any systematic recording of vocalisation, but whining, moaning, growling, huffing, barking, and roaring were heard. The occurrence of particular vocalisations was used to qualify the intensity of agonistic encounters.

During oestrus and late gestation female Sun bears emitted a conspicuous and repetitive *nickering* call. In the call repertoire for this species, the signal is relatively high-pitched and was almost exclusively uttered in the presence of a male. It did not, however, necessarily accompany partner-directed activity, or induce any apparent response from the male. Nickering also appeared to function as a short-distance contact call and was predictably issued during reintroduction of a pair. In Giant pandas the sound occurring in similar contexts is termed "bleating", but it is emitted by both sexes and frequently precedes physical contact between a pair (Kleiman 1983).

With the exception of agonistic vocalisations, the only audible sounds heard from the two male Sun bears included in this study were "clacking" and deep "popping" noises during reintroduction to a mate. These calls were not heard from females and occurred less frequently or predictably compared to female nickering vocalisation.

2.3.1.2.4 Visual and Tactile Communication

Visual signals between bears at long to medium range depend on the use of gross body posturing; during close range interactions the majority of display and visible signals between bears involve their anterior region – primarily head and neck postures. Graded facial expressions were part of most interactive behaviours used by Sun bears, but the very small ears of this species may restrict their use in signalling.

Facial expressions primarily involved a variety of jaw positions and retraction of the highly mobile lips. During agonistic and aggressive interactions vocal threat preceded any physical action and occurred in conjunction with a range of visual signals.

Affiliative episodes were rarely preceded or accompanied by audible signals, with the exception of females soliciting attention during oestrus.

Solitary and interactive behaviours between male and female Sun bears consisted of complicated interplay between olfactory, auditory, visual and tactile signals, and are described fully below. To qualify encounters, interactions have firstly been grouped into contact and non-contact behaviours, and categorised further by functional context (affiliative and agonistic). Activities not exclusively associated with a specific category (e.g. wrestling) have been included in their most prevalent context. Behaviours are not listed in any particular order, such as by intensity or frequency.

2.3.1.3 Interactive behaviour: Non-Contact

2.3.1.3.1 Affiliative

Approach

One bear orients toward another and makes a steady approach. Approaching preceded most affiliative interactions, but was occasionally associated with agonistic intent.

Sniff

A bear makes nasal contact with a portion of another animal's body. Generally, olfactory investigation of another individual was confined to areas of the head, neck and shoulders or the anogenital region. When pairs were introduced or prior to affiliative encounters, animals predictably engaged in naso-nasal contact (*mutual sniffing*).

Submissive posturing

During affiliative or agonistic interactions individuals acted submissively by withdrawing slightly and rolling onto their back, usually with the head turned to one side and eyes averted. Females in heat often exhibited submissive posturing in response to an approach by, or the close presence of, a male.

Play

Play behaviours were defined as a series of actions exclusively affiliative in nature and involving minimal contact between a pair. A typical play session consisted of soliciting behaviour (play invite) that resulted in feigned fighting manoeuvres and rapid pursuit (play chase). Repeated visual contact and approach toward another animal often preceded their invitation to play. Within several feet of a partner, the initiator made a sudden lunge toward the other bear, often punctuated with a quick swat or nip and withdrew rapidly to observe the reaction of the other animal. Delivery of a playful nip

usually resulted in confrontation or play chase by the bear that was bitten. Sometimes bears tried to invoke play by running repeatedly to and from an unresponsive partner in an exaggerated manner. Lively play could include lengthy pursuit and clambering within trees. With the exception of interactions that were disrupted by outside influence (visitors, keepers, environmental disturbance), most encounters were terminated by one animal "facing away" (Stonrov & Stokes 1972) *i.e.* turning the head horizontally away from the other bear.

Head-jockey

The "head-jockey" (after Burghardt 1975) was a distinctive playful interaction between two bears seated close to and facing, each other. It involved ritualised mutual head bobbing, lunging and weaving, and periodic nosing of the face, ear and neck region. Aside from occasional play bites, the bears' mouths remained slightly open or closed. A heightened frequency of play-biting marked the transition of a head-jockey bout into the more intense "jaw wrestling" (see contact behaviour).

2.3.1.3.2 *Agonistic*

This category includes independently and mutually elicited behaviours that had the ability to provoke a response from a partner, and incorporated both antagonistic and apparent indifference.

Look

Direct look or lengthy stare at another bear in the absence of any other noticeable interaction. This behaviour became mutual when a pair engaged in eye contact (*mutual look*). Maintaining a fixed gaze on another individual while *approaching (look-approach)* usually conveyed an intention to interact.

Avoidance

Generally, bears practised mutual avoidance of conspecifics and actively maintained varying "individual distances" (Herrero 1980) of up to 20 metres. The level of spacing was primarily dependent on the current status of an individual and was restricted by the enclosure dimensions (e.g. den vs. public exhibit). Avoidance behaviour was commonly used to terminate interactions, and could be preceded by low moaning noises.

Sun bears avoided close contact with each other by "facing away" (Stonrov & Stokes 1972), threat display (see *head down threat* and *jaw gape*) and physical retreat.

Lowering and turning the head prevented eye contact, and served to circumvent an interaction when animals encountered each other during general activity (e.g. foraging). Individuals trying to prevent an interaction with an approaching conspecific also used avoidance behaviour.

Theft

Attempted procurement of items (usually food) nearly always resulted in altercation. The 'thief' approached and grasped the desired article in mouth or paw, and tried to wrest it from another. Possible outcomes were submission and abandonment of the item (permit theft), or mutual threat display. Sun bears foraged and fed separately, and usually became defensive if interrupted by conspecifics. Brief aggressive episodes between predominantly compatible animals often involved competition for food. The reaction of individuals appeared to vary with the type of food, for example favoured items (honeycomb or chicken carcasses) were defended much more vigorously against theft. Occasionally theft was permitted without any apparent defence.

Follow

Following was defined as instances when a bear followed within one body length of another. Although it may be possible to determine following between free-ranging subjects at distances of 5-10m (Herrero & Hamer 1977), restrictions of a captive environment increased the probability of chance that two animals could be moving in the same direction at any greater distance. Males often had an outstretched neck when following an oestrus female, and repeatedly smelt or tasted her anogenital region.

Herd

The male at Wellington Zoo "herded" (after Murie 1981 cited in Harting 1978a) the female by circling and repeatedly blocking and intercepting her direction of travel (Figure 2.4). Strong nudges at her sides and neck, and leaning or pushing with his entire body, head or paw were used to off-balance the female and re-orient her in a particular direction. The male would become increasingly insistent when the female remained non-compliant and intensify his herding effort by using open mouth threats (jaw gape) and biting the female's sides and heels.

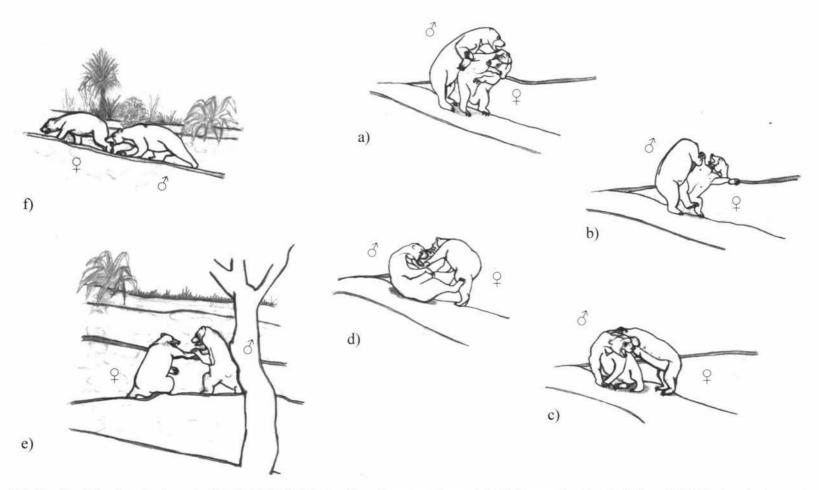


Figure 2.4: Herding behaviour by the male 'Bakti' (#617) Wellington Zoo. Sequence shows a) Bakti intercepting female ('Chomel' #607) after she leaves the secluded upper south area of the exhibit (see Figure 1). Bakti asserts his dominance by standing over the female and threatening her with jaw gaping, which b-d) results in a bout of wrestling before she eventually complies, e-f) running back up the exhibit with the male nipping at her heels.

Jaw gape

Sun bears communicated a range of intentions using graded opening of the jaws. The "jaw gape" is a component of social behaviour common to canids and ursids (Burghardt & Burghardt 1972). As this visual signal was not restricted to a particular context the presence of supplementary signals (*e.g.*, gross body posture and vocalisation) were used to determine the overall nature of the interaction.

Depending on the type and intensity of an interaction, the mouth was held open to varying degrees. When used in an affiliative or mildly agonistic context the angle between jaws was ~20 to 60 degrees, and teeth were not visible. Jaw gaping was often used to signal when approaching a partner in a potential conflict situation, and mutual gaping was common during low-intensity agonistic encounters.

During increasingly intense agonistic interactions the gape continued to widen in a graded manner, until the lips were fully retracted and teeth exposed. The use of jaw-gaping in this context ("jawing" Stonrov & Stokes 1972; "open mouth threat" Forthman 1995) was readily distinguished by accompanying whining or growling vocalisation. During high-intensity agonistic interactions bears sometimes snapped their jaws together loudly.

Threat

During low intensity threat the aggressor held its head low and muzzle perpendicular to the ground, but maintained eye contact. Lateral presentation and a characteristic stiff-legged walk also sometimes preceded a "head-down threat" (Egbert & Stokes 1976) (Figure 2.5). Overt threat display that implied serious intent of injury was predictably accompanied by vocalisations. Audible sounds progressed from a low whine expressing mild irritation, to a threatening growl; and during extreme agonism, from barking to continuous, very loud roaring.

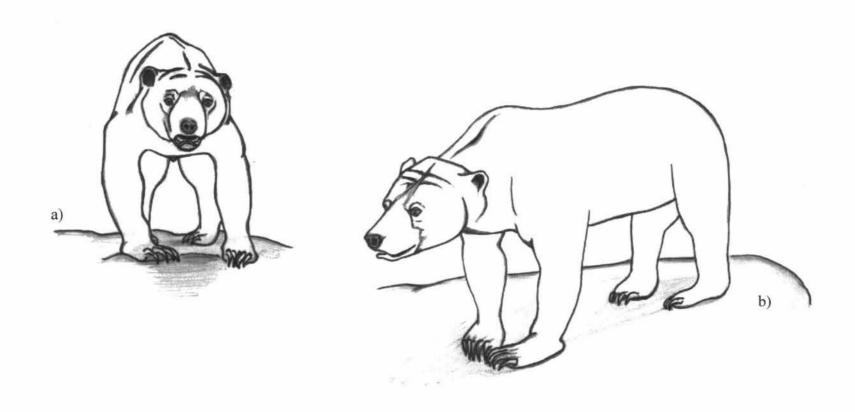


Figure 2.5: Threat posturing by the male Sun bear ('Bakti' #617), Wellington Zoo. Body is held stiffly with ears back and mouth slightly open during a) head-down threat, and b) lateral presentation.

Charge

Threat and warning signals (including calls and body posturing) preceded all physical attacks directed toward another bear. The challenger elicited an explosive bark at the onset of a direct charge, accelerating and roaring during a rapid run toward their opponent. Generally, the distance covered during charges was less than 10m but in highly aggressive situations a fleeing rival could be pursued much further. If a pursuing individual got close enough, it sometimes bit or swatted the rump of the animal in flight. Ambivalent charges involved repeatedly bounding at an opponent over a distance of several metres.

Termination of a charge was abrupt when the subject under attack pivoted to confront their aggressor. Both bears usually rose to a semi- or fully-bipedal stance and began an exchange of threat posturing, parrying and vocal display. Most charges were truncated, and ended without physical contact between animals (the "false charge" Herrero 1980), but in some cases, direct confrontation erupted into bouts of serious fighting.

Escape

To withdraw from agonistic bouts a subordinate animal rolled or slowly backed away with head held low or assumed a defensive posture (*i.e.* bipedal stance with teeth exposed). Once eye contact was broken the deferring bear stalked slowly away with its head down; sometimes both individuals simultaneously terminated an encounter in this manner. During high intensity agonism the escaping bear ran quickly from the other, and often turned several times to check that it was not being pursued. Retraction from more aggressive encounters was usually accompanied by agonistic vocalisation (moaning and whining) from the deferring individual.

2.3.1.4 Interactive behaviour: Contact

2.3.1.4.1 Affiliative

Bodily contact

Sun bear pairs sometimes spent prolonged periods in physical contact without apparent reaction from either animal. After approach and gaining attention of the partner (*mutual look at*), the initiator sat or lay closely enough to cause bodily contact. While in contact a pair rarely engaged in any other solitary or interactive behaviour. Bodily contact could involve adjacent positioning of bodies, or merely the forelimb of one individual resting over part of the other animal. Pairs sometimes rested or slept for considerable periods of time with one bear partially on top of the other.

Hug

At times Sun bears were observed in direct contact in an upright seated position, with the foremost animal positioned between the hind legs of their partner. The male usually sat behind, often with his forelimbs wrapped about the female's middle. This intimate positioning resulted after one animal intentionally backed into a seated partner; or was pulled down by that animal. The animal behind sniffed frequently at the female's head and neck region. On one occasion a hug preceded copulatory activity - the male gripped the female's scruff between his teeth, pulled her onto all fours and mounted without releasing his grip.

Allogroom

When a pair rested close to, or touching one another, one individual began bouts of sniffing toward the head, neck and shoulder regions of the partner. If these actions did not provoke a response from the recipient their attention intensified, leading to closer inspection, parting of the pelage and licking and nibbling the other animal. The Wellington female routinely approached her resting mate from behind, and leaned heavily on his back which appeared to reduce his struggling during her persistent grooming sessions. Mutual grooming was rarely observed.

Jaw-wrestle

This mutual behaviour resembled the *head jockey* (see Section 2.3.1.3.1), except the bears made repeated physical contact. Bouts of "jaw wrestling" (after Burghardt 1975) often followed *head jockey*, as a pair engaged in repetitive silent interlocking and twisting of the jaws. Periodical biting of the partner's muzzle and cheeks occurred.

Muzzle-suck

This unusual behaviour was only observed between the pair at Wellington Zoo, and was initiated exclusively by the male. After making naso-nasal contact, he licked the female's nose then gently seized her muzzle or upper jaw in his mouth and began to suck⁸ (Figure 2.1). One or both bears sometimes cradled the partner's head from behind, and both animals' usually kept their eyes closed during this intimate interaction. While *muzzle-sucking*, the bears either lay side by side facing each other, or one animal stood quadrupedal above the prostrate partner. The positioning of the pair sometimes

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⁸ The female did not appear to participate in sucking activity, which caused noticeable rhythmic hollowing of the male's cheeks.

changed without breaking contact. All undisturbed bouts were terminated by the female and met with resistance from the male.

To terminate muzzle-sucking the female pulled away from the male with her head or body and sometimes emitted a low whine. Reluctance by the male to release his mouth-hold led to struggling by the female. Often the male then tightened his grip behind her head, sometimes requiring her to use her own claws to pry free. Upon termination of muzzle-sucking the bears withdrew from each other, and engaged in exaggerated licking to remove the foam that had accumulated around their muzzles. Occasionally this behaviour occurred immediately after the animals had fed, but although loud sucking noises could be heard there was no evidence of regurgitation.

Vulva stimulation

"Vulva stimulation" (after Henry & Herrero 1974) usually involved a male approaching a female from behind to 'check' her genital region (see *sniff* Section 2.3.1.3.1). However, oestrus females readily 'presented' to males by lying on their back with the rear limbs relaxed (see *inguinal presentation* Section 2.3.1.1.7). The reclining female permitted her mate to approach and perform lengthy olfactory and gustatory inspection of her genitalia. Sometimes the male secured the supine female with a forepaw while sniffing, licking and occasionally biting at her pelvic and anogenital region. Females appeared tolerant of male attention, considering their extreme vulnerability while in this position. As evidence of their complete ease, females also lay with the forelimbs fully extended behind their head during this intimate interaction.

Mounting

Initiation of mounting often began with sniffing and light physical contact such as pawing or placing a paw on the mate. Mounting behaviour involved either the male or female bear climbing partway onto the partner, "standing over" (Henry & Herrero 1974 after Fox) them with extended forelimbs, and clasping. Mounting of the partner from behind or the side was primarily associated with reproductive interactions, but also occurred as a component of affiliative encounters (e.g. during play wrestling). Although both sexes engaged in periodic mounting behaviours, females were never seen to perform pelvic thrusting. As males sometimes reposition themselves after climbing onto a female there was no clear way to distinguish sexual from non-sexual bouts of mounting.

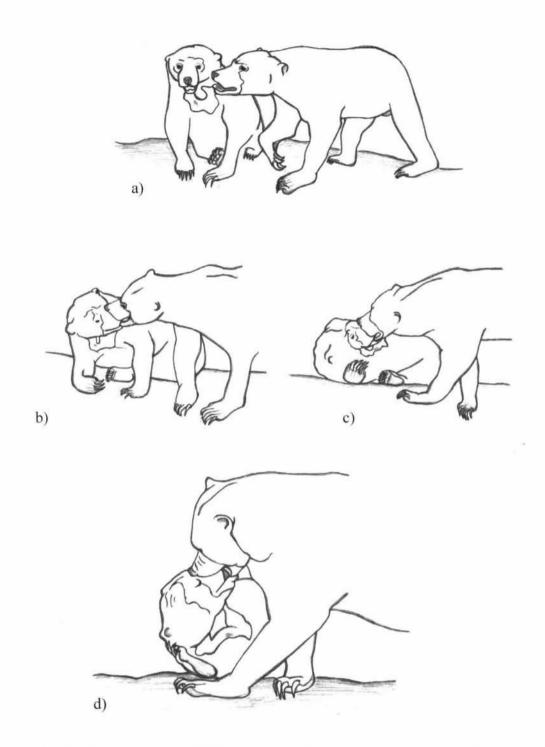


Figure 2.6: Muzzle-sucking between Wellington Zoo Sun bears. Sequence shows a) male ('Bakti' #617, on right) approaching the seated female ('Chomel' #607); b) following naso-nasal contact he seizes her upper jaw in his mouth and c-d) begins to suck, while the female lies back submissively.

Prolonged mounting behaviour between sexes often occurred between the San Diego pair prior to copulation. The male mounted the female from behind and positioned his body so he was *draped* over the female. His rear legs remained in contact with the ground and his forelegs hung loosely by her sides. If this behaviour was met with resistance and the female attempted to manoeuvre out from under the male, he clasped her tightly around her middle. While mounted the male mouthed or held the nape of the female in his teeth ("neck bite" Ludlow 1976 after Ewer 1973) or rested his head between her shoulders. Short bouts of non-intromissive thrusting could occur periodically. Leisurely locomotion of this pair during such coupling was not unusual (*walk drape*) when the female, seemingly unperturbed by her 'jockey', continued with solitary activities such as foraging. Dismounting by the male, or being thrown off by the female terminated a bout of mounting between a pair.

Copulation

Erections of the males' penis were sometimes noted following multiple mounts and thrusting without apparent intromission. Lengthy mounts (>5 minutes) associated with intromission and periodic bouts of thrusting culminated in visible tremors of the male's hindquarters. Observations of these consecutive activities during mounting were used to define copulation in the absence of confirmed intromission or presence of ejaculate.

Male Sun bears either copulated from a rear orientation, with extended forelegs pressing down on the females' back, or while in a semi-squatting position while clasping their mate around the abdomen (Figure 2.7). Sometimes, if the female backed up or was pulled downward by the male, a pair could continue to copulate from a seated position. The male often mouthed, bit or gripped the female's shoulders and nape while copulating. After separation the pair commonly distanced themselves by walking or running several metres from their partner. A pair rarely remained in contact following copulation.

During mating activities females sometimes appeared to become agitated, attempting to dislodge the male by twisting out from under him or suddenly lunging forward. This evasive action was often preceded and accompanied by intense agonistic vocalisation (growling, barking and roaring) by the female. These vigorous efforts dislodged the male, or he dismounted voluntary, and in either case there followed threat displays or aggression.

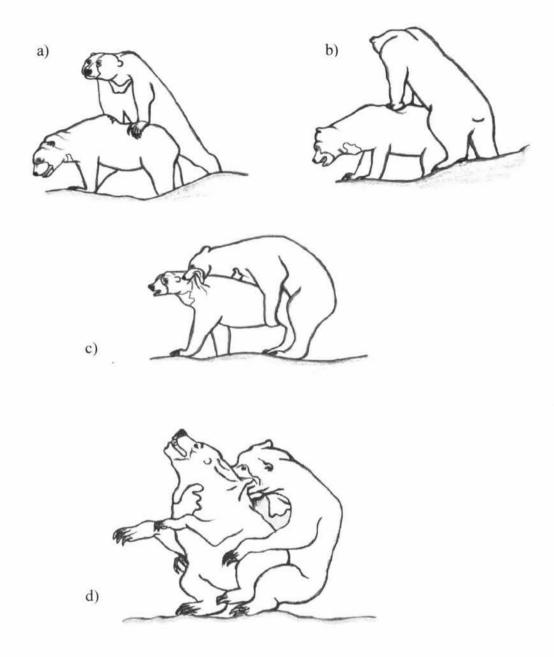


Figure 2.7: Copulation between the male ('Ringo' #606) and female ('Muffin' #598) at San Diego Zoo. a)

Male 'tests' female's willingness to mate by standing over her with his paws on her back, before
b) positioning and mounting from a rear orientation. Note lordosis position of female. The
copulatory posture shown in c) is typical of ursids, with the male keeping a firm grip the female's
nape; d) copulation was sometimes conducted in a semi-seated position.

2.3.1.4.2 *Agonistic*

Sustained contact between bears was more likely during affiliative interactions, whereas agonistic behaviour was primarily limited to display; having the potential to incur serious mutual injury. Even bouts of seemingly affiliative wrestling could rapidly deteriorate into hostile and less inhibited interchange of swiping and biting. This was particularly likely if a participant was repeatedly grappled after making several attempts to terminate an interaction.

To an extent, the relatively loose fit of the Sun bears' skin may reduce physical injury during fighting, but bleeding from abrasions, punctures and gashes was often evident after intensive bouts of wrestling. The most frequent site of wounding was the neck and shoulder region, and to a lesser extent the back and hindquarters. Although none of the injuries sustained between the study animals required medical treatment, inter- and intra-sexual attacks between captive Sun bears in other zoos have resulted in serious wounding, fractures and even a fatality (Schaller 1994; Kolter 1998b; Steffen 1998).

Biting

The bears' teeth were partially or fully exposed during threat behaviour, wrestling and intense agonism. During serious conflict one bear would sometimes grasp the neck of the other in its teeth and hold it for several seconds ("inhibited bite" Henry & Herrero 1974). The other animal remained static and averted their gaze when arrested in this manner. Restrained biting also occurred during mildly agonistic interchanges (e.g. when one animal was attempting to drive another either away from or toward an area) but these were not accompanied by any audible vocalisation. Despite the direct contact between animals during some encounters, serious biting was infrequent. High-level agonistic and aggressive bouts of wrestling were those most likely to intensify into an exchange of biting, and did occasionally cause wounding. To bite another, an animal typically lunged forward, stretched out its neck to strike at the head and shoulders of its opponent, then quickly withdrew.

Drag

Bears sometimes used a mouth-grip to *drag* each other in a particular direction. An animal grasped the loose skin of their partner's head or nape firmly between their teeth and pulled hard. By continually backing one individual could drag another several metres. *Dragging* was usually preceded by repeated *looking* and *approaching* a partner, and was frequently accompanied by *jaw gaping*. It was most likely to occur after

prolonged indifference of the partner. On several occasions animals dragged each other by the muzzle or jaw or seized them by a back leg. Low intensity whining and growling by the initiator sometimes accompanied dragging, particularly when the behaviour met with resistance.

Wrestling

This boisterous activity was a common form of physical contact between Sun bears, occurring during affiliative and agonistic interactions. It was not always possible to categorise play-fighting from more serious wrestling activity because the context of an interaction could change within a bout.

Wrestling bouts were often conducted in a bipedal stance, particularly during highintensity agonistic encounters. Initiation of a typical wrestling bout involved approach, and sniffing of the partner followed by non-contact agonistic display, jaw-gaping and exaggerated feints of swiping and biting. The partners' reaction determined the course of an interaction - nonchalance resulted in deference or persistence on behalf of the initiator; amicable defence met with a parried exchange of play fighting; and a hostile response led to reciprocal aggression, or defence and retreat by the initiator.

Characteristically, a wrestling pair engaged in bouts of mutual grappling; feinting and lunging, pushing and grabbing each other. Periodic swiping and biting occurred but was restrained. Even during playfighting the bears demonstrated their great strength, and were capable of physically lifting and throwing a rival to the ground. Termination of wrestling bouts was rarely mutual; and typically concluded when one animal struck a forceful blow or delivered a powerful bite to the other, then rolled away or withdrew abruptly.

2.3.1.5 Summary Ethogram of Solitary and Inter-Sexual Behaviours

Agonistic and affiliative sexual behaviours are listed in approximate order of increasing intensity or frequency (Table 2.3). Activities not exclusively associated with one specific category have been included in their most prevalent context.

Table 2.3: Summary ethogram of solitary and inter-sexual behaviour.

SOLITARY BEHAVIOUR

Inactive

Standing, Sitting, Basking and Resting or Sleeping

Active

Locomotion

Bipedal or quadrupedal walking, Pacing, Climbing, Wading, Running and Playing.

Feeding

Foraging and ingestion; also included soliciting for food.

Self-Maintenance

Licking and nibbling or scratching the pelage and body; and rubbing against trees/ structures in an enclosure.

Miscellaneous

Excretion of faeces and urine, carrying non-food items, and expectant waiting prior to predictable feeding times ("sentinel"); other behaviours of interest that occurred infrequently were recorded as qualitative notes.

Reproductive

With the exception of *rolling*, solitary behaviour associated with reproductive activity was performed exclusively by females.

Rolling

A bear lay and writhed on the ground.

Backward Walking

The animal reversed on all fours; sometimes the head was raised and lowered slowly and rhythmically, and *nickering* vocalisation accompanied the action (see Non-Contact Affiliative behaviour).

Inguinal Presentation

A female lay supine with the rear legs relaxed, presenting their anogenital region.

Masturbation

The bear scratched or rubbed its vulva with the forepaw or on objects.

Cradling

A forepaw was used to cradle inanimate objects (e.g. pieces of fruit or bark) against the upper body.

Nesting

Nesting material (vegetation such as branches, plant husks) was collected and transported in the mouth or paw. The nest was constructed by "shuffling", "hayhugging" and "binding".

INTERACTIVE BEHAVIOUR

Non-Contact

Affiliative

Approach

One bear oriented toward another, and approached it. See also *look*(below).

Submissive

The subject withdrew slightly and rolled onto its back; its head was usually turned to one side and eyes averted from the dominant individual.

Sniff

A bear made nasal contact with a part of another bear's body. When a pair engaged in naso-nasal contact the behaviour was termed *mutual sniff* (MUT SNF).

Play

Typical play sessions between a pair consisted of play invitation that resulted in a series of feigned fighting manoeuvres and rapid pursuit (play chase).

Head Jockey

A pair seated close to and facing each other engaged in ritualised mutual head bobbing, lunging and weaving. Periodic nosing of the partner's face, ear and neck region occurred. Aside from occasional play biting, the bears' mouths remained slightly open or closed.

Nicker

Only females elicited this call. The signal was repetitive in form and relatively highpitched in comparison to all other vocalisations (see Non-contact Agonistic behaviour).

Agonistic

Look

An individual directly looked or stared at another bear without any other noticeable interaction. Eye contact between animals was defined as a *mutual look* (MUT LK). When an individual maintained a fixed gaze during its approach the behaviour was termed *look-approach* (LK APR).

Avoid

Bears avoided each other by physically retreating or facing away from an approaching individual.

Theft

The attempt to procure an item (usually food) from another by grasping the desired article in mouth or paw. Submission and abandonment of the object by the 'owner' was termed *Permit Theft* (PM THFT).

Follow

Following was defined as instances when a bear followed within one body length of another.

Herd

A male circled and repeatedly blocked and intercepted a female's direction of travel. Physical nudges with the body, head and paws were used to off-balance and reorient the female in a particular direction.

Jaw Gape

During amicable behaviour or mild agonism the bears held their jaws open from \sim 20 to 60 degrees, and the teeth were not visible; intense agonism was signalled in a wider gape with the lips fully retracted and teeth exposed. Pairs engaged in *mutual jaw gaping* (MUT JGP).

Threat

A bear held its head low and muzzle perpendicular to the ground, or postured using lateral presentation or a characteristic stiff-legged walk. Serious intent was accompanied by graded audible vocalisation, progressing from a low whine or growl to barking or continuous roaring.

Charge

A challenging bear elicited an explosive bark at the onset of a direct charge, accelerating and roaring during a rapid run toward their opponent.

Escape

To withdraw from an agonistic bout the subordinate bear rolled or slowly backed away and assumed a defensive posture. During high intensity agonism the escaping bear ran quickly from the other.

Vocalisation

With the exception of *nickering* (see Non-contact Interaction), vocalising was predominantly associated with agonistic interactions. Both sexes produced a range of graded sounds including *whining*, *moaning*, *growling*, *huffing*, *barking*, and *roaring*. The occurrence of vocalisations was used to qualify the intensity of encounters.

Contact

Affiliative

Bodily Contact

Physical contact occurred between a pair without any apparent reaction from either animal.

Hug

Bears were in direct contact in an upright seated position, with the foremost animal positioned between the hind legs of their partner.

Allogroom

A bear licked and nibbled the pelage or body of another individual. *Mutual grooming* between animals was also observed.

Jaw Wrestle

Two bears engaged in repetitive silent interlocking and twisting of the jaws; periodic biting of the muzzle and cheeks occurred.

Muzzle suck

A bear sucked the upper jaw or entire muzzle of another bear.

Vulva Stimulation

A male made olfactory and/or gustatory inspection of a female's anogenital region.

Mount

Mounting included the male or female climbing partway onto their partner, "standing over" them, and in males, sometimes involved clasping. This behaviour was defined as 'Male on Top or Female on Top. See also drape (below).

Drape

A male mounted a female from behind and positioned his body so it was *draped* over the female. His rear legs remained in contact with the ground and forelegs hung loosely by her sides; his head rested on the female's shoulders or back. Locomotion of a pair during such coupling was termed *walk drape*.

Copulation

Correctly positioned mounting of the female by the male was associated with intromission and periodic bouts of thrusting that culminated in visible tremors of the male's hindquarters.

Agonistic

Drag

A bear used a mouth-grip to *drag* another in a particular direction. Usually the skin of the partner's head or nape was seized and pulled while backing up.

Wrestle

A pair engaged in bouts of mutual grappling - feinting, lunging, pushing and grabbing each other. Periodic *swiping* and *biting* also occurred. Wrestling was conducted in a quadrupedal or bipedal stance. High intensity encounters were characterised by less inhibited physical striking, and audible vocalisation.

2.3.2 Study Group One: San Diego Zoological Gardens (ZSSD)

2.3.2.1 Pair A: Studbook #608 and Studbook #606

The first pair studied comprised the female Moon (#608), and male Ringo (#606), the individuals on exhibition during daylight hours when the study began. After two days the bears were separated following the unexpected birth of a cub⁹. Because of the short sampling period, results for Pair A are considered only qualitatively.

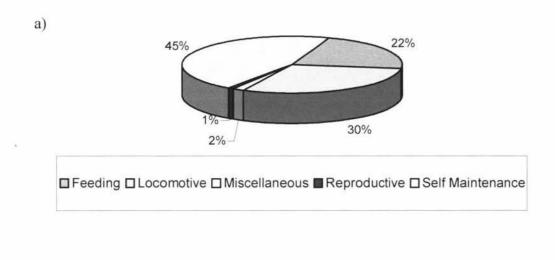
The bears spent most time in solitary behaviours, with interactions accounting for less than 10% of their daily activity. They were active for approximately 30 minutes each hour in mainly feeding and locomotion.

Typically, in the morning, they began foraging immediately after their release onto exhibit, seeking food that had been distributed by their keepers. This initial feeding was conducted more hurriedly than subsequent foraging activity, which was interspersed with periods primarily devoted to rest and other solitary activities. 'Purposeful' locomotion (i.e. moving between areas to forage and climb) represented a high proportion of the bears' active time budget, but both individuals also had a habit of stereotypic pacing. They either travelled back and forth repetitively past the single entrance to the exhibit (~8m), or tracked a large 'figure of eight' between the entrance and the passage to the northern end of the exhibit (~20m). Pacing was characterised by an increase in tempo, periodic head-swinging and an abrupt, regimented 'about-turn' at both ends of the route.

Although no baseline data were collected on these bears prior to the study, several aspects of the female's behaviour indicated a restless state. While the male rested high in the boughs, Moon paced back and forth past the exhibit entrance, and periodically returned to the sleeping male. Each time she climbed to within 1m distance of him, sat momentarily, then descended and walked back to the entrance. When the female did sit for longer periods she appeared unsettled, often turning, shuffling, and reacting to any sudden noise. Moon also spent a relatively high percentage (45.7%) of time in self maintenance activities on 14 February; and focused attentively on grooming her nipples and ventral area (Figure 2.8a).

⁹ Subsequently, the male was paired with a second female for the duration of the study (see Section 2.3.2.2)

On 15 February, the female's restlessness intensified, as her activity levels increased from 44.6% to 64.5% of her total solitary budget (Figure 2.8b). A high proportion of time spent "sentinel" - sitting and peering through the exhibit entrance, accounted for a large increase in miscellaneous activity. The proportion of self maintenance also reduced, but the frequency remained high (at ~5 bouts per hour), and Moon's grooming pattern altered in a distinctive way: she repetitively licked her forelegs and paws, then rubbed them over her head in a manner resembling face-washing in cats.



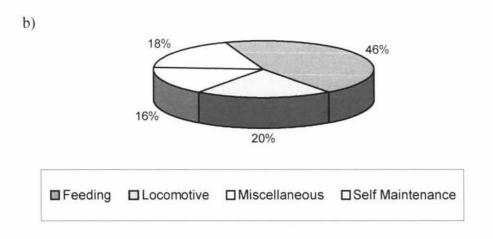


Figure 2.8: Solitary activity budgets for female 'Moon' (#608) showing relative proportion of each behaviour category a) 14 February 1997; b) 15 February 1997.

The rate of interactions increased sharply on 15 February (Figure 2.9a) with agonistic displays, and interactions almost exclusively initiated by the female. Moon kept a close watch on the male, and exhibited high levels of threat behaviour - using warning vocalisation and jaw gaping whenever he was nearby (Figure 2.9b). The male appeared largely unresponsive to these displays. Affiliative behaviours also increased in frequency and Moon appeared to seek the male's attention by approaching him and sitting in contact. Several times she briefly groomed his sides and back.

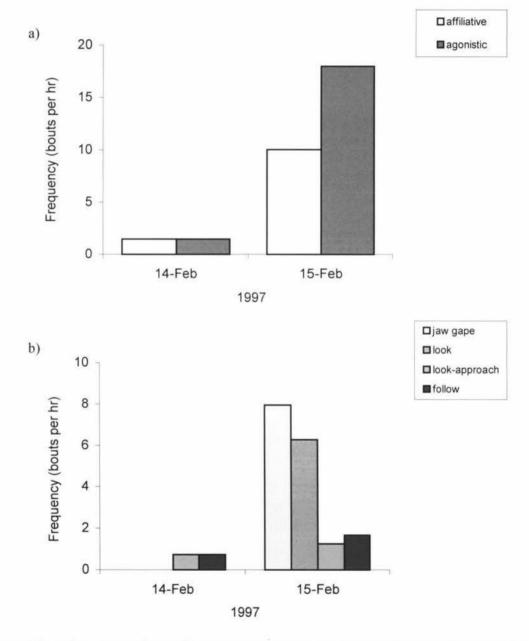


Figure 2.9: a) frequency and type of interactive behaviours; and b) types of agonistic behaviour directed toward the male by the female Moon (#608) in Pair A.

By the afternoon of 15 February Moon's behaviour had become increasingly agonistic (Figure 2.9b). On one occasion she approached the sleeping male and began to vocalise aggressively. Getting no response, she then bit his rump, seized some skin, and attempted to drag him out of the tree. Despite this act of extreme antagonism the male did not reciprocate, but attempted to evade subsequent encounters by avoiding eye contact and maintaining a greater distance from the female.

Early the following morning (16 February), it was discovered that overnight Moon had given birth within the indoor holding area. She was sitting hunched over a heating pad with the live cub between her hind legs. The male was moved to a separate room, and the cubbing den at the rear of the facility was prepared to provide more privacy for the mother and her cub. The birth was unexpected because, although the pair had been kept together for nearly eight months, reproductive activity had never been seen (Keeper log books).

After the birth the keepers were able, periodically, to observe the mother and neonate through a small hatch in the cubbing den. Moon was reportedly attentive to her young vocalising, cradling, and grooming it; however, suckling had still not been confirmed 48 hours after the birth. On 18 February the mother left the cub in the den and did not return, whereupon zoo staff decided to intervene, and the cub was removed for veterinary inspection. At 341.0 grams the female cub was within the normal weight range for newborn Sun bears (Appendix B), but its nose and paws were severely abraded and its stomach contained very little milk. The cub was, therefore, removed for hand-rearing in the Zoo's nursery because of its poor physical condition, and the mother's reduced interest in continuing to rear it herself (Plate 2.1).

Reports suggest that these type of abrasive injuries are likely to have been sustained during the cub's frantic rooting about for milk (Quick 1969; Hess 1971).



Plate 2.1 Sun bear cub 'Niah' (#657) born at San Diego Zoo, 16 February 1997. The female cub was removed for hand-rearing because the dam was unable to feed it. The cub's paws and nose became severely abraded during frantic rooting about for milk. Photo was taken 19 February when Niah was -96 hours old. (photo: J.Hawes)

2.3.2.2 Pair B: #598 and #606

2.3.2.2.1 Encounters

From 17 February 1997 Ringo was paired with a second female named Muffin. For several days indoor encounters between the bears were staged for approximately 30 minutes, prior to their release each morning onto exhibit. Initially the pair were introduced within the largest indoor holding den, to facilitate separation if that became necessary. The bears were permitted to interact each day, but were maintained in separate rooms overnight. Behavioural data collected during morning encounters has been included in the results.

2.3.2.2.2 Solitary and Interactive Behaviours

To preserve the chronological sequence of events during the study, results are presented here as an interplay between solitary behaviours and interactions. Firstly, a quantitative analysis of the major categories of solitary and interactive behaviours is given, followed by a more detailed (quantitative and qualitative) investigation of the development of independent behaviours and interactions between the pair.

The bears spent the majority of their time in solitary activities (female mean 81.1%; male mean 86.62%), with rest (inactivity) and foraging representing priority behaviours. The female was more active, and had a considerably lower mean rate of resting (16.9 \pm SE 2.8 mins per hour) than the male (28.5 \pm SE 5.9 mins per hr); but their average rate of feeding was similar, and occupied approximately 20 minutes each hour (female 20.5 \pm SE 4.9 mins; male 17.5 \pm SE 5.2 mins).

Feeding accounted for the greatest proportion of active solitary time in both bears (female 58.1%; male 72.1%) (Figure 2.10). The bears fed immediately when released each morning and in general other activities were not observed for at least 20 minutes after they entered the exhibit. For the female the distribution of other sub categories: *locomotion, reproduction, self maintenance* and *miscellaneous*; was surprisingly even (~10%). In comparison, the male spent more time in locomotive activity, but very little time in self maintenance or reproductive behaviours.

A gradual increase in activity was observed for both sexes over the two week period (Figure 2.11). For the male this was caused by more feeding and locomotion. Data for the female showed a similar trend in feeding, and changes in levels of reproductive and self maintenance behaviours. Reproductive behaviours will be considered in detail in Section 2.3.2.2.3.

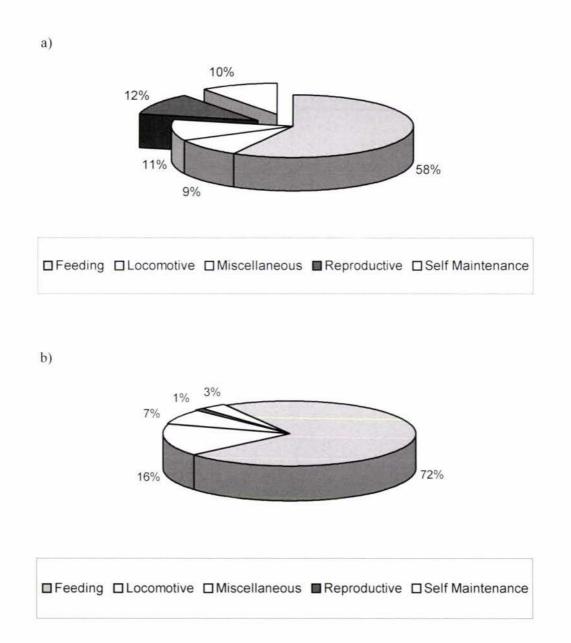


Figure 2.10: Time budget showing relative proportion of solitary behaviours over two weeks 17 February - 02 March 1997 for a) the female Muffin (#598) and b) the male Ringo (#606).

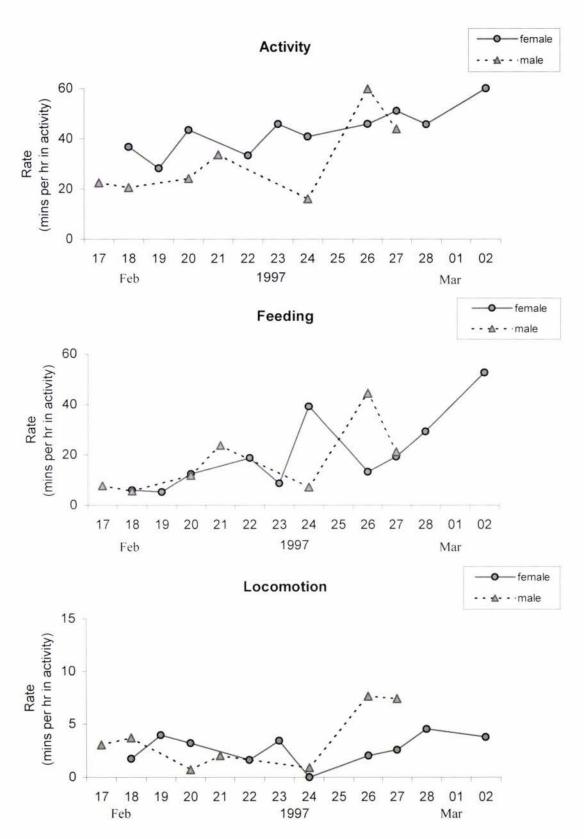
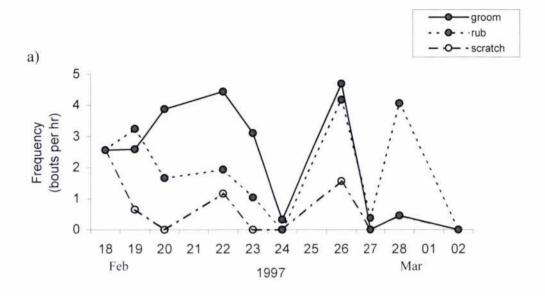


Figure 2.11: Daily activity levels 17 February - 02 March 1997 for the male and female (#606, 598), and rates of feeding and locomotion.

Self-maintenance behaviours included rubbing, scratching, and grooming. During the first two days of introduction both animals often rubbed themselves against the bars of the cage during encounters, and at particular sites in the outdoor enclosure. Rubbing usually lasted less than one minute (mean bout length $48.3 \pm SE$ 28.7 secs). After the second day of introduction, the male was rarely observed rubbing and this behaviour also declined for the female. Scratching was uncommon, but for the female followed a similar pattern to rubbing. Grooming was performed by both sexes in short bouts lasting less than 30 seconds (mean $29.7 \pm SE$ 5.0 secs), and was infrequent in the male.

Overall self-maintenance behaviours were much less apparent for the male, but trends were evident for the female (Figure 2.12a) for instance, common peaks of activity in the three maintenance behaviours. All self maintenance behaviours declined in frequency after 22 February, and rose again on 26 February. Grooming was the most prevalent behaviour, but bouts of rubbing became particularly conspicuous on 26 and 28 February. Self-maintenance activity declined to assumed baseline levels by the end of the study. The mean duration of grooming bouts increased steadily over the two week period (Figure 2.12b) with anogenital grooming noted from 22-24 February and 26 February.



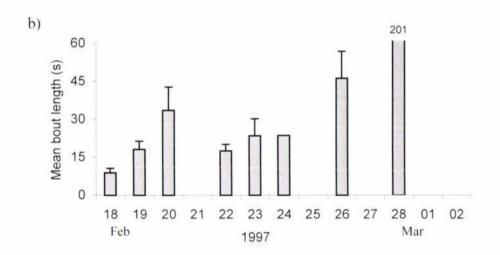


Figure 2.12: Pattern of self-maintenance activities for female 'Muffin' #598 18 February - 02 March 1997. a) The frequencies of behaviours; b) mean length of grooming bouts. Bars show 1 standard error.

On average, interactions accounted for less than 20% of the bears' time budget (female mean 18.9%; male mean 13.4%). During the first few days encounters initiated by the male provoked mainly agonistic responses from the female. Over two weeks, however, as the female underwent oestrus, their relationship graduated from habituation through to the expression of complex social and reproductive behaviours. The following paragraph describes the behaviour of Ringo and Muffin during their first introduction:

When the male was first let into the room containing the female he cautiously approached her and the pair began mutual sniffing and jaw gaping; they then circled each other emitting low growls. Ringo attempted to assert his dominance by rearing

over the female, biting her, and 'standing over' with his forepaws placed on her back. Muffin reacted by throwing him off, standing upright, snapping and swiping. She moved away rapidly, but was unable to retreat more than a few metres due to their confinement. The pair grappled while standing erect, and locked their jaws together, twisting and pushing. After several minutes they disengaged with loud growls and roars. Subsequent altercations arose when the male tried to approach or sniff the female. The level of interactions waned over approximately 10 minutes, and the animals distanced themselves at opposite ends of the den. For the remaining 20 minutes the female paced rapidly back and forth past the den exit, and kept the male at bay using threat postures and loud agonistic vocalisation. When released onto exhibit they actively avoided each other at first, and generally maintained a large individual distance (>5 m). Ringo continued to act assertively over several hours by periodically approaching and initiating contact with Muffin which led to his being rebuffed and high levels of agonism.

This was typical of the sequence of encounters over the first few days with the male pursuing the reluctant, and aggressive female. During the first few days, they usually actively avoided one another, but occasionally the male attempted to interact with the female. Sometimes Muffin kept Ringo at a distance with threatening behaviour, but he persisted. A close approach was typically followed by mutual sniffing (naso-nasal contact), intermittent growling, and an exchange of wide jaw gaping with canines fully exposed. Threat often escalated into vigorous bouts of bipedal wrestling (Figure 2.13). Although the bears emitted loud, high intensity vocalisation (barking and roaring) during encounters, the only injuries sustained were relatively minor scratches and punctures of the skin, indicating considerable physical restraint during fighting.

Despite the intensity of the altercations the male continued to try to dominate the female by standing over her, grasping her tightly with his front paws and gripping the loose skin of her neck in his teeth. He also dragged the female about by the skin, or a hind limb, and would force her to the ground by getting behind, twisting her nape, and using his full weight to hold her down. Although Muffin was the smaller animal, she was very heavy and able to resist Ringo to some extent. Several times she charged the male chasing him the full length of the enclosure, then grasping, biting, and pinning him to the ground.

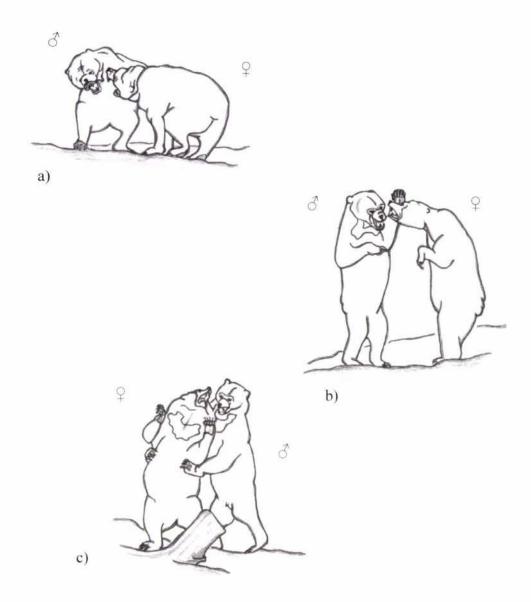


Figure 2.13: High-intensity aggression during introduction between the male ('Ringo' #606) and female ('Muffin' #598) at San Diego Zoo. Initial encounters led to intense confrontation, with both animals displaying high-level threat, rearing onto their hind legs and engaging in violent physical contact. The jaws were held wide to display the teeth, and encounters were accompanied by loud and constant roaring.

On the second day of introduction fighting between the bears intensified, causing obvious wounds. The male retreated from one encounter bleeding heavily from a gash several inches long on his shoulder. A few minutes later, when the female approached, he rolled submissively onto his back, and soon after the pair briefly groomed each other's wounds. Zoo staff separated the male so that his shoulder could be examined, but the injury was not judged to be serious, and he was released back with the female.

The level of interactions between the pair varied over the two week period, but a steady rise in affiliative behaviour and a complementary reduction in agonism was evident for the female (Figure 2.14). Trends for the male were less clear, but he showed more affiliative behaviour toward the female after several days. Altercations occurred every day but were relatively mild once the male established his dominance (Figure 2.15). Muffin became increasingly submissive toward the end of the first week.

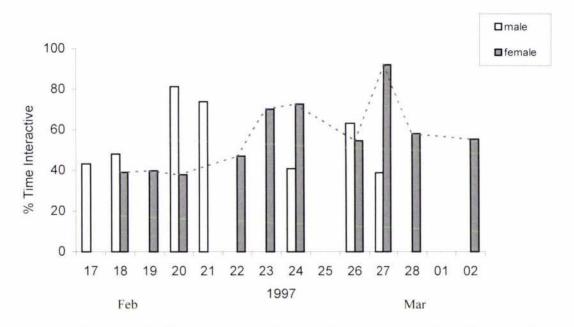


Figure 2.14: Proportion of affiliative interactions between the male Ringo (#606) and female Muffin (#598) 17 February - 02 March 1997.



Figure 2.15: Aggressive behaviour declined following repeated encounters between the male ('Ringo' #606) and female ('Muffin' #598) at San Diego Zoo. Confrontations were still intense but the bears primarily communicated threat through jaw gaping and body posturing, rather than engaging in physical contact. The sequence of events is the opposite to that observed during initial encounters (Figure 2.13).

As agonism declined and the female became increasingly tolerant, at times the male would approach and the two bears would sit in contact. Bodily contact occurred frequently but briefly during the day usually lasting less than 30 seconds (mean $26.9 \pm 8 \pm 3.3$ sec). Hugging was a more proximate form of contact (see ethogram for details) that emerged during the first week, and was also brief ($24.7 \pm 8 \pm 3.7$ sec). Bodily contact between the bears persisted throughout the study, but hugging was rarely observed after 23 February (Figure 2.16).

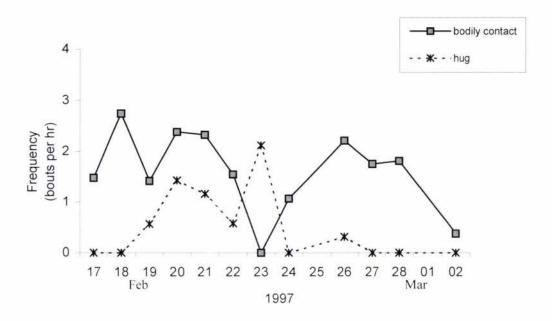


Figure 2.16: Rate and form of body contact between the male Ringo (#606) and female Muffin (#598) 17 February - 02 March 1997.

Interactive behaviours clearly changed in frequency over the two week period (Figure 2.17). For instance, jaw gaping, a primary component of threat and representative of high levels of agonism, was initially exhibited at a very high rate by both bears, and frequently used by the female to deter the male. Gaping reduced in intensity several days after introduction, however, to become a tiny component of the agonistic repertoire (Figure 2.17a).

Wrestling persisted over the two weeks (Figure 2.17b), but the form of this interaction altered from short bouts in the first week (mean 29.1 \pm SE 3.1 sec; max 90.5 sec); to longer ones during the second (mean 77.3 \pm SE 23.2 sec; max 357.0 sec). Moreover,

wrestling became less frequent or intense¹¹ in the second week and took on an apparent playful quality.

Mutual play was rare (data not shown), but another interaction that appeared to reflect the growing bond between the pair was head jockeying (Figure 2.17c). This display began on 20 February and occurred regularly each day. Generally, bouts of head-jockeying increased steadily over the period, but their frequency waned halfway through the second week.

¹¹ Vocalisation also no longer accompanied wrestling after the 20th February.

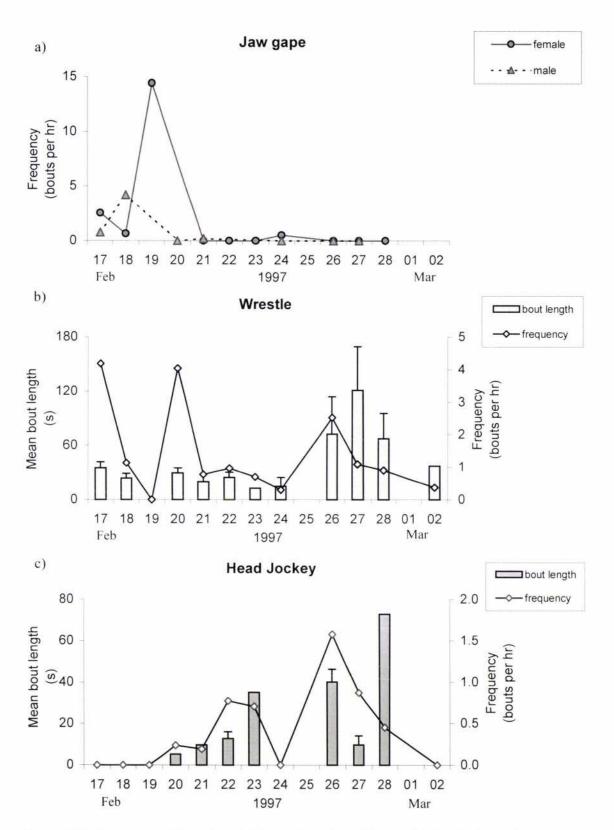


Figure 2.17: Frequency and duration of a) jaw gaping, b) wrestling, and c) head jockeying between Ringo (#606) and Muffin (#598) 17 February - 02 March 1997. b) and c) are mutual behaviours. Bars show 1 standard error.

2.3.2.2.3 Reproduction

The development of reproductive behaviours by the female was rapid, and distinctive activities were apparent within several days of introduction to the male. Backward walking (Figure 2.18) was first seen on 20 February, and was a very noticeable activity when performed about 8 times per hour. Bouts lasted for 20 seconds on average (18.5 ± 50.7 sec), and were sometimes accompanied by perceptible nickering from the female. After this date walking backward was still observed on a regular basis, but bouts were shorter and occurred less frequently.

Inguinal presentation by the female began on 19 February (Figure 2.18b), with an initially modest increase in frequency reaching a high peak on 23 February. This transient peak represented a five-fold increase over original levels, and at a rate of 20 bouts per hour was a prominent component of reproductive behaviour on that day. The female usually presented in response to affiliative contact from her mate, but after 23 February, even an approach by Ringo was sufficient to elicit inguinal presentation. Bouts of inguinal presentation were observed until 28 February, but less frequently, at only 1-2 bouts per hour.

Rolling occurred in a less obvious pattern than other reproductive behaviours (Figure 2.18c). It was less common than backward walking or inguinal presentation, but the frequency varied. Most bouts of rolling were vigorous and lasted approximately 40 seconds (mean $39.8 \pm SE 9.8$ sec), but sessions lasting up to several minutes were observed on 23 February. Rolling occurred on most days until 26 February, and then ceased abruptly. An overlay of the rate of the female's separate reproductive behaviours (Figure 2.19) demonstrates common increases in frequency on 23 and 26 February.

Another behaviour that accompanied the onset of oestrus in the female was solitary play. Typically, play consisted of the bear lying on her back, twirling or juggling branches or small objects with all four feet. As with episodes of mutual play, occurrences were uncommon, but a rise in the frequency of solitary play was recorded on the same day as her peak of reproductive activity (data not shown).

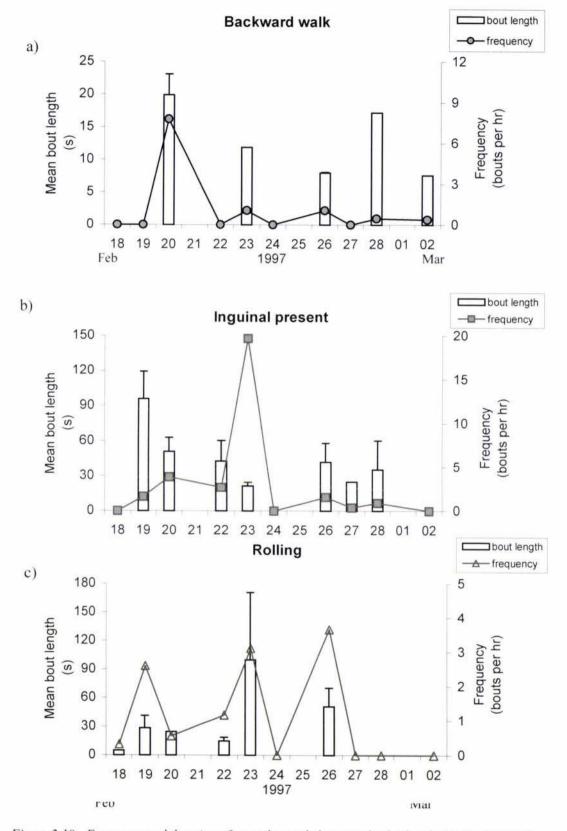


Figure 2.18: Frequency and duration of reproductive behaviours by the female Muffin.(#598) 17
February - 02 March 1997 a) backward walk, b) inguinal presentation, c) rolling. Bars represent 1 standard error.

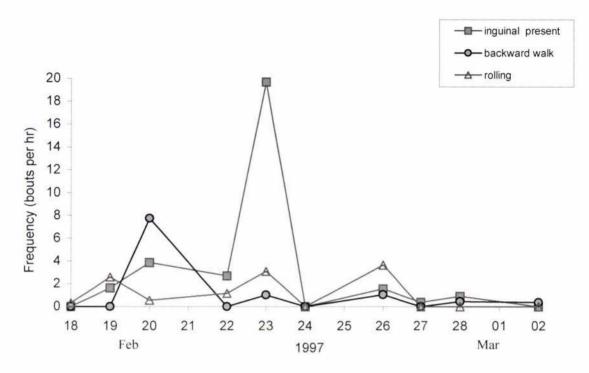


Figure 2.19: Overlay of the rate of reproductive behaviours (inguinal presentation, backward walking, and rolling) for the female Muffin (#598) 17 February - 02 March. Note common increases in frequency on 23 and 26 February.

The balance of interactions between the sexes changed as the female's reproductive cycle progressed. At first the male would approach the female, follow her, and initiate interactions, but during the second week, the female became increasingly assertive. In addition to soliciting his attention with the expression of reproductive behaviours Muffin began to regularly approach and follow her mate around the exhibit (Figure 2.20). On 22 February, Muffin began to actively pursue the male, and increased the frequency of this behaviour sharply on 23 February.

Olfactory communication is likely to have assisted the bears in gauging the sexual status of their partner. Bouts of sniffing occurring 1-3 times each hour were usually directed toward the head and shoulders of the other animal. The frequency of sniffing was higher for both bears at first, but mutual sniffing (naso-nasal contact) persisted throughout the study with little change (data not shown). Periodic investigation of the partner's anogenital region was performed by both sexes and, less occasionally, the male sniffed the female's urine and faeces (Figure 2.21a). The combined frequency of odour 'testing' was highest on 23 February, and the data suggest that the primary target of olfactory investigation was the anogenital region.

Occasionally, when the female lay supine she permitted the male to undertake a more thorough investigation of her genitalia (Figure 2.21b). Gustatory and tactile stimulation of the vulva lasted approximately 30 seconds on average (mean $36.5 \pm SE 13.3 \text{ sec}$), and was accompanied by periodic sniffing from the male. This behaviour appeared relatively early in the study (19 February), and was frequent during the first week. Vulva stimulation was not observed after 26 February (Figure 2.21b).

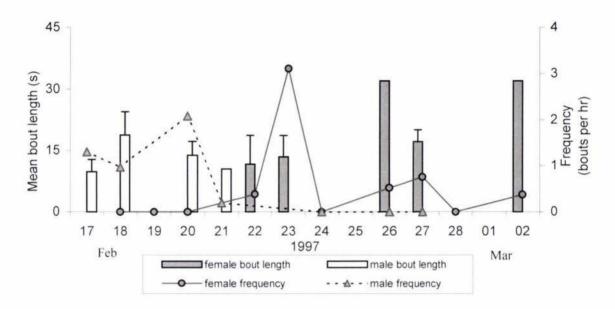


Figure 2.20: Rate and bout length of following for the female Muffin (#598) and male Ringo (#606) 17 February - 02 March 1997. A well-defined shift in interaction and rise in frequency for the female accompanied onset of oestrus around 21 February. Bars show 1 standard error.

0.50

0.00

02

Mar

01

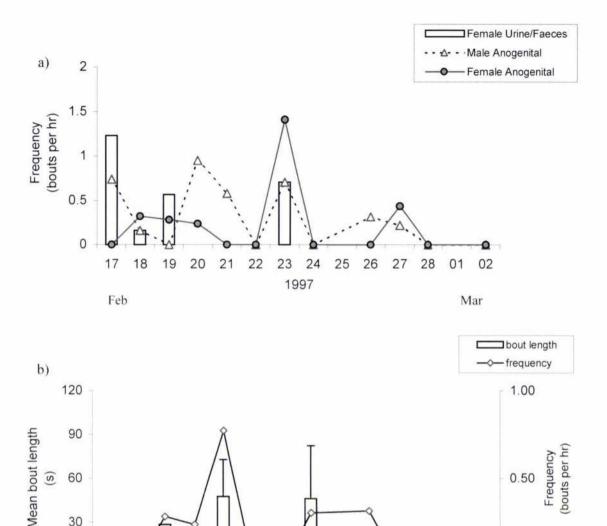


Figure 2.21: a)Frequency and focus of sniffing between the male Ringo (#606) and the female Muffin (#598) 17 February - 02 March 1997; b) frequency and duration of vulva stimulation. Bars show I standard error.

1997

24

25

26

27

28

60

30

0

17

Feb

18

19

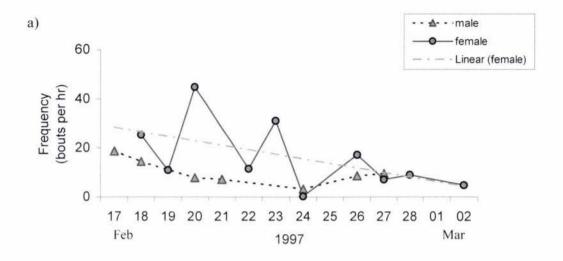
20

21

22

23

Interactions appeared to be largely controlled by the female, while the male assumed an essentially passive role. There was a steady decline in the female's rate of agonism after the first week, with a corresponding, but brief increase in affiliative behaviour (Figure 2.22). A similar, but slight trend in agonism and affiliation was observed for the male. A rise in the female's affiliative behaviour was obvious on 20 February, followed by a dramatic increase on 23 February. Few interactions occurred on 24 February, and two days later affiliative behaviours were rare. Interactions between the bears tailed off near the end of the second week.



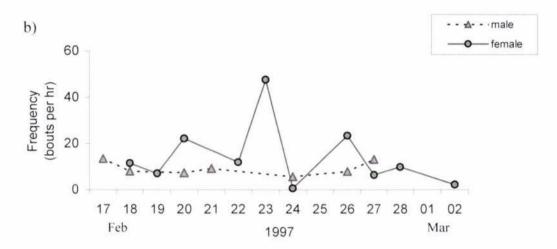


Figure 2.22: Daily rates of a) agonistic and b) affiliative behaviours between the male Ringo (#606) and the female Muffin (#598) 17 February - 02 March 1997. A linear trendline has been added to a) to depict regression of female agonism over the two week period.

Mounting was seen regularly from the time the bears were first introduced. The behaviour did not occur in exclusively sexual contexts, and initially appeared to be used primarily for asserting dominance. It also occurred during wrestling bouts. Often there was little prelude to a mount, but the outcome and sequence of such encounters were somewhat predictable. As described above (Section 2.3.2.2.2), initial attempts by the male to mount (or 'stand over') the female met with displays of extreme agonism. The rapid onset of oestrus led to increased compliance and acceptance of the male by the female. After several days she tolerated brief mounts with less resistance and terminated interactions using relatively mild forms of threat (jaw gaping and low growls).

The relative proportion of time the male and female spent "on top" varied over the two week period (Figure 2.23a). Initially, mounting behaviour was performed exclusively by the domineering male and, overall, he spent a much higher proportion (81.3%) of time on top. The temporary reversal in dominance on 19 February may have been a consequence of the serious attack by the female on the previous day (Section 2.3.2.2.2). In general, mounting was a less frequent behaviour for the female, but repetitive mounting of the male was obvious on 23 February (Figure 2.23b). The increase in proportion and time spent 'on top' by the female is a further indicator of her increasingly assertive role during the receptive period.

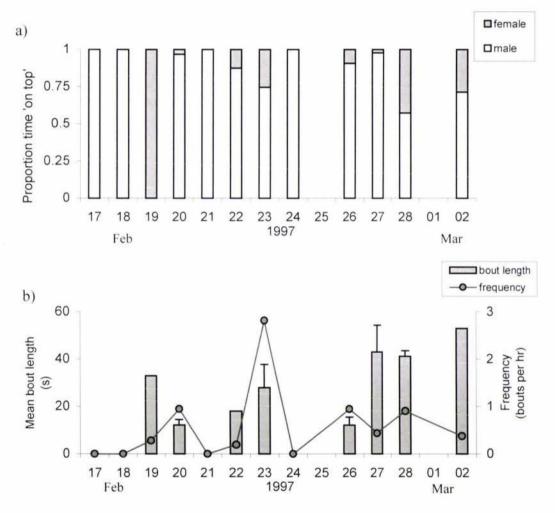


Figure 2.23: Copulatory behaviour of the male Ringo (#606) and female Muffin (#598) 17 February - 2March 1997. a) Relative proportion of time spent mounted by each sex b) frequency and duration of the female 'on top'. Bars show 1 standard error.

Mounting by the male was categorised as: *male on top, drape, walk drape* and *copulation* (see Ethogram; Section 2.3.1.1.7) to assist in analysing any change in the context of this behaviour when the female became receptive. Over 250 bouts of non-copulatory mounting were observed over the 14 day period, and most lasted less than 30 seconds (mean $24.9 \pm SE 3.7 sec$).

The female's readiness to mate at peak oestrus was clearly evident from her response to being mounted (Figure 2.24). At times during the first week, the male draped himself over the female as if testing her willingness to stand for mating. She began to encourage mounting toward the end of the first week by backing into the male; however, she acted uneasily when he did mount, often responding by moving forward or trying to dislodge him. On 23 February Muffin entered 'standing heat', and became receptive, from thereon willingly permitting all mounting attempts. Draping was not seen after this date.

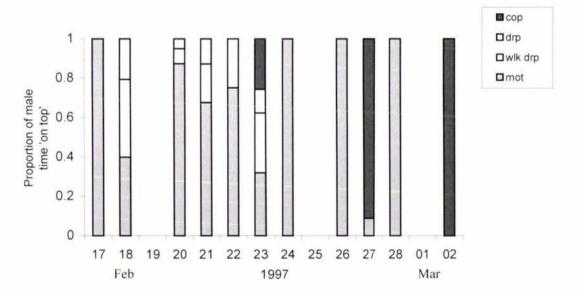


Figure 2.24: Mounting behaviour of the male Ringo (#606) 17 February - 02 March 1997. Cop = copulation;, drp = drape; wlk drp = walk drape; mot = male on top.. Note the disappearance of 'draping' after 23 February.

A comparison of mounting with and without copulation, revealed the highly intense and extensive nature of mating that took place on 27 February (Figure 2.25). Intermittent increases in the frequency of male mounting did not necessarily coincide with dates of copulation, and mounting began well in advance of the female's receptive period. The consistently elevated rate of mounting (Figure 2.25) reflects the persistence of mounting efforts from the male.

From the second day of introduction, pelvic thrusting by the male accompanied some mountings of the female, but intromission did not occur until she became fully receptive. Copulation was observed on three non-consecutive days (23 February, 27 February, 02 March), and lasted considerably longer than other forms of mounting, with an average duration of $6.3 \pm SE$ 2.4 min.

Copulation was repeated 3-5 times each day on 23 and 27 February, but only 1 episode was recorded on 02 March. On 27 February the pair copulated for extended periods, with each bout lasting between 5 and 22 minutes. The marked decline in frequency of male mounting toward the end of the second week (Figure 2.25), shows his waning sexual interest in the female. The female's oestrus cycle apparently ended on 02 March, since neither mounting nor copulation was observed after this date (Keeper log books). The whole breeding episode was successful, resulting in the birth of a live cub (#658) approximately 3 months later (see Postscript; Section 2.3.2.4).

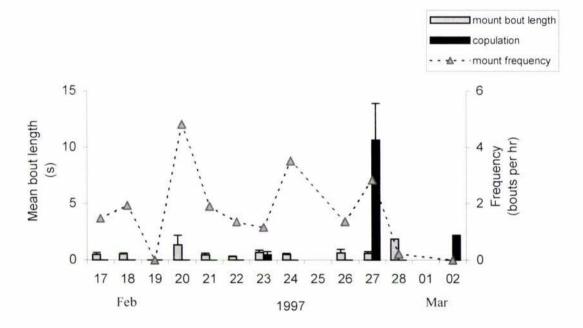


Figure 2.25: Frequency and bout length of non-intromissive mounting, and copulation by the male Ringo (#606) 17 February - 02 March 1997. Bars show 1 standard error.

2.3.2.2.4 Vulva Characteristics

Characteristics of the female's vulva were recorded each day to provide a physical indicator of oestrus. Size, colour and moisture were graded independently on a scale of 1-3, and a daily total was generated by adding scores from each feature (Table 3). When the female was first introduced to the male her genitals were small and pale in colour. Swelling of the labia and reddening of the vaginal mucosa became evident during the first week. During the receptive phase of oestrus the female's vulva was highly engorged, the labia slightly parted and the mucosa scarlet in colour. A clear to pale discharge was apparent from the first day, and the highest level of moisture was also observed at peak oestrus.

Table 2.4: Characteristics of the vulva prior to and during oestrus for Muffin (#598).

Date	Size	Characteristic Colour	Moisture	Total Score
17 Feb	1	1	2	4
18 Feb	2	2	2	6
19 Feb	2	2	2	6
20 Feb	2	2	3	7
22 Feb	3	2	3	8
*23 Feb	3	3	3	9 *
24 Feb	3	3	3	9
26 Feb	3	2	3	9
*27 Feb	3	3	3	9 *
28 Feb	3	3	3	9
*02 Mar	3	3	3	9 *

^{* =} copulation

2.3.2.3 Additional Observations

Ringo (#606)

The bears always foraged independently and normally food was jealously guarded, thus it was unusual to see the male deliberately carrying and presenting various items to his mate. The 'nuptial gifts' were typically food items *e.g.* a beef bone, pieces of fruit and leafy branches of *Eugenia* berries, but also included other vegetation such as a palm husk, fronds, and branches of spruce. This behaviour was seen on seven separate occasions, and occurred more often during the days immediately prior to peak oestrus. A final event was recorded on 27 February – the date of most intensive mating between the pair. It is unknown whether this behaviour represents an idiosyncrasy, or a genuine factor of courtship in Sun bears.

Muffin (#598)

Stereotypic pacing was evident in both sexes, but much more common in the female. This problem was well known to keepers and had been apparent since Muffin's was arrival at the zoo. After she was paired with the male, pacing did not become obvious until the final week of the study. Her speed during pacing was rapid, and bouts could last for up to 10 minutes. From 27 February pacing occurred regularly, from 2-3 bouts per hour.

One particular site favoured by the female for pacing was the ledge that divided the moats directly below the public viewing area. Access was difficult, and achieved by 'crabbing' bipedally about a vertical wall nearby. The narrow ledge was only approximately twice the body length of the bear, and consequently, only 3-4 steps could be taken in each direction. During the final days of the study Muffin's pacing became increasingly frantic - head-tossing and tongue-flicking as she reached either end of the route. The bear proved very difficult to distract from this disturbing activity, and rarely responded to the male's attempts at interaction.

A more unusual stereotypy exhibited by the female was termed "lick-spitting", as it incorporated components of self maintenance and ingestive behaviours. While sitting upright the forelegs were extended and inspected closely before she began to intensively lick the dorsal surface of the paws. Intermittent head-weaving and rapid tongue-flicking also occurred during the activity. It appeared as if something was being repeatedly licked off the paws, mouthed, and transferred back onto the paws from the tongue. At times, with the use of binoculars, tiny pieces of debris (wisps of straw, twigs, small

leaves) were identified on a forepaw, but the behaviour also persisted when no material was apparent. Bouts of lick-spitting could last for up to 10 minutes, and as with pacing, proved very difficult to disrupt. It is possible that this eccentric behaviour developed from self-maintenance, as the frequency of this activity followed the frequency of self maintenance activities (see Figure 2.12a; Section 2.3.2.2.2).

With the exception of pacing, the context of the behaviours described above was difficult to interpret so they were grouped within the Miscellaneous category for each individual.

2.3.2.4 Postscript

The pair were separated at the end of March 1997 and on 05 June, Muffin was relocated to the cubbing area. The den had been prepared in advance, but further alterations continued throughout the day. Section staff periodically checked on the bear which appeared to disturb her as she reacted by aggressively charging one keeper. Early on the morning of 06 June, the female gave birth to a single cub. Parturition was 103 days from the first mating between the pair, and 96 days had elapsed since the last observed copulation on 02 March. The mother and neonate were monitored at intervals during the day, and keepers reported that Muffin was attentive to her cub. In the afternoon, she was temporarily moved to another room in order to service the cubbing den.

By the following morning the cub had become relatively quiet, and once again, nursing had still not been confirmed. Veterinary staff darted the female with oxytocin (i/m) to assist with lactation¹², but by the afternoon there was no change, and the cub was removed for examination. The female cub was a healthy weight at 420g (Appendix B), but was dehydrated, and its stomach was empty, indicating that it had not fed. A management decision was made to remove the young for hand-rearing at the zoo nursery. Muffin searched thoroughly for her cub immediately after it was removed, but soon settled down and slept. Keepers reported that she did not appear unduly distressed on the following day, and had a normal appetite. The cub died of unknown causes on 07 June 1997.

¹² This hormone causes 'let-down' of milk stored in the mammary glands.

2.3.3 Study Group Two: Wellington Zoological Gardens (WZG)

2.3.3.1 Management

The female 'Chomel' (Studbook #607) and male 'Bakti' (Studbook #617) were usually kept together, however, several periods of separation occurred during the study. Management was based primarily on female behaviour believed to impending parturition *e.g.* nesting activity. This section is divided into Periods that define alternative management arrangements *i.e.* location and subject (refer Table 2.1).

Results are presented firstly as a general overview and chronology of events, then as analysis of changes in solitary and interactive behaviours between the bears in relation to the reproductive status of the female (oestrus vs. pregnant). Results are given as weekly means unless otherwise stated.

2.3.3.2 General Activity Budget

The bears spent nearly all their time (female mean 94.7%; male mean 94.0%) in solitary activities, with rest and foraging representing priority behaviours. The two animals had similar mean rates of resting (female 17.8 ± SE 2.8 mins per hour; male 14.9 ± SE 2.3 mins per hour); and on average feeding occupied approximately 30 minutes per hour (female 30.8 ±SE 2.7 mins; male 33.9 SE 2.7 mins).

Foraging occupied most time for both bears, especially the male (female 48.8%; male 83.0%; Figure 2.26). They usually fed immediately on release each morning, and generally other activities were not observed for at least 20 minutes after they entered the exhibit. Approximately 15% of the bears' time was spent in locomotion. For the male, self maintenance, reproduction and miscellaneous were infrequent; totalling less than 5% of active solitary time. For the female, however, self maintenance and reproductive activities occupied about 30% of active solitary time (15.4% and 14.8% respectively) and little time was spent in miscellaneous activities (3.7%).

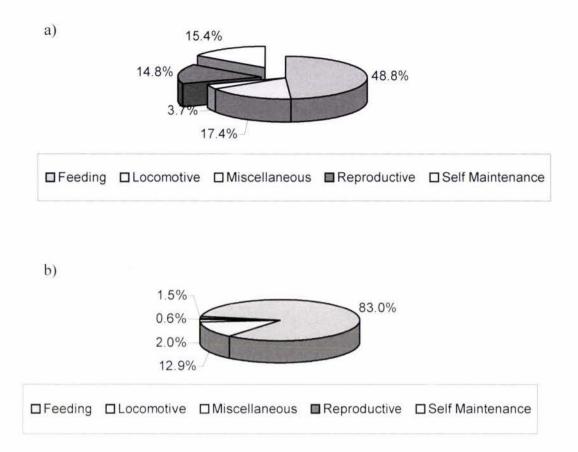


Figure 2.26: Annual time budget showing relative proportion of solitary behaviours over 1997 for a) female Chomel (#607) and b) male Bakti (#617).

2.3.3.3 Period 1 (Weeks 1-5: 01 January 1997 - 31 January 1997)

There was noticeable increase in the frequency of self maintenance behaviour by the female between weeks 1 and 4, rising from ~2 bouts per hour to ~7 bouts per hour. Self-maintenance behaviour was less regularly observed in the male. Grooming and scratching bouts by both sexes were brief, lasting only approximately 30 seconds (mean 39.0 ± SE 5.7 secs), and were infrequent for the male (<1 bout per hour). Rubbing was observed only in the female, and although relatively infrequent, bouts occurred each week for approximately 30 seconds (mean 25.1 ± SE 6.5 secs). Rubbing was often performed at specific sites within the enclosure.

Interactions, though regular, accounted for little of the bears' time budget (<10%), and were relatively brief (<30 seconds). Most interactions were affiliative, but for the female, affiliative behaviour declined sharply after week 2, and was accompanied by a complementary rise in agonism (Figure 2.27a).

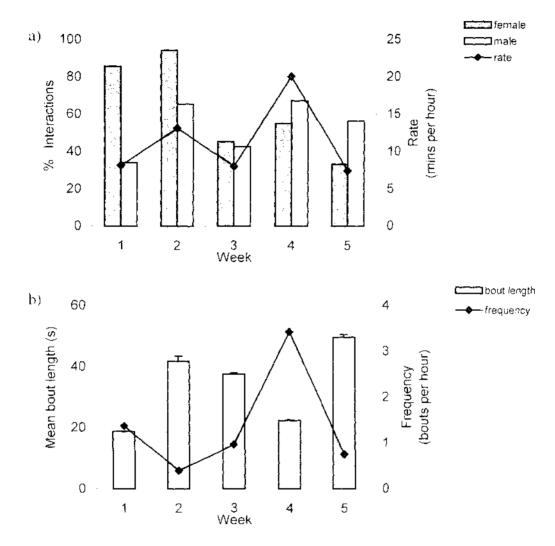


Figure 2.27: a) Proportion and rate of affiliative interactions and b) frequency and duration of wrestling between the male Bakti (*617) and female Chomel (*607) during weeks 1-5.

Bars show I standard error of the mean.

Mutual play behaviour was uncommon, but the bears regularly engaged in bouts of head jockeying and jaw wrestling. Both behaviours were brief, usually lasting \leq 30 seconds (head jockey mean 11.2 \pm SE 4.4 secs; jaw wrestle mean 20.0 \pm SE 6.9 secs), and a consistent increase in the frequency of jaw wrestling was apparent. Bouts of wrestling occurred frequently throughout the five weeks (Figure 2.27b). Typically initiated by the female, wrestling bouts were lively but silent. Most bouts were also terminated by the female after approximately 30 seconds (mean 32.1 \pm SE 5.6 secs), but sometimes lasted

for 3-4 minutes. During week 4 bouts of wrestling became very common (~3 bouts per hour).

The female solicited the male's attention most regularly during weeks 2 and 3, often approaching him and initiating contact. Bodily contact between the bears was brief (mean bout length 42.0 ± SE 17.3 secs) but occurred 1-2 times each hour. Contact between the pair was usually preceded by a brief exchange of mutual sniffing (nasonasal contact), followed by slight jaw gaping and olfactory investigation directed toward the partner's head and shoulders. Sniffing bouts were long (mean 15.6 ± SE 2.6 secs) and performed increasingly often during weeks 1-4 (Figure 2.28a). The increase in sniffing was particularly evident for the male, rising to 12 bouts per hour.

The female exhibited reproductive behaviours associated with oestrus (rolling, masturbation, inguinal presentation and mounting) from the onset of the study. Rolling and masturbation were observed only during week 1 and were relatively infrequent compared to inguinal presentation. Inguinal presentations persisted from weeks 1-5 and on average, lasted for approximately 1 minute (mean 54.5 ± SE 12.5 secs; max 209.2 secs). The duration and frequency of inguinal presentation peaked during week 4, (Figure 2.28b).

The male's behaviour indicated his growing interest in the female between weeks 1-4. He approached Chomel more often, and typically in response to inguinal presentation. Olfactory investigation of the female's anogenital region and her urine/faeces became frequent, occurring up to 8 times each hour. The female usually permitted his attention for short durations (<30 seconds), but his persistence typically invoked mild agonism (jaw gaping) from her. Between weeks 1-4 she demonstrated an increased level of tolerance.

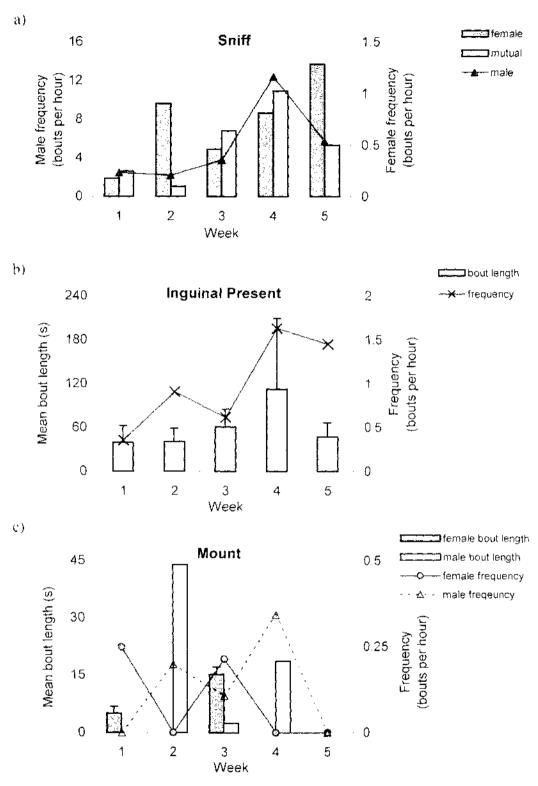


Figure 2.28: Frequency and duration of at sniffing between the male Bakti (#617) and female Chomel (#607), b) inguinal presentation by female and c) mounting behaviour between the male and female during weeks 1-5. Bars show I standard error of the mean.

During week 4 there was a marked rise in the rate of interactions between the pair from ~ 8 mins per hour to 20 mins per hour (Figure 2.27a). The male became increasingly assertive and made repeated attempts to herd the female toward the upper south area of the exhibit, using physical contact (leaning, pushing and dragging), jaw gaping and swiping or biting at her rump and heels. Bakti reinforced his dominance during interactions by rearing and standing upright over the female. He also became notably aggressive toward humans - challenging people with growls, barks and threat postures. On several occasions he charged at staff and visitors.

Chomel was observed mounting the male for brief periods during weeks 1 and 3, and during weeks 2-4 Bakti mounted her more regularly (Figure 2.28c). Pelvic thrusting occurred during the male's mounts, but intromission was not observed. Mounting was relatively brief, lasting only \sim 15 seconds on average (mean bout length male 16.8 \pm SE 7.8 secs; female 13.5 \pm SE 3.6 secs).

In week 5 the male's level of interest in the female appeared to wane. He approached and followed the female much less often, and mounting was not observed. Bodily contact between the bears was less frequent and Chomel was less tolerant of the male. She began actively avoiding Bakti, and used threat behaviours (wide jaw gaping, growling) and swiping to keep him at bay. The overall rate of interactions and proportion of affiliative behaviours between the pair tailed off during week 5 (Figure 2.27a).

2.3.3.4 Period 4 (Weeks 15-33: 06 April 1997 - 16 August 1997)

2.3.3.4.1 Weeks 15-19 (06 April 1997 - 10 May 1997)

In comparison with Period 1, during weeks 15-18 the rate of interactions between Bakti and Chomel was considerably lower (mean <5 minutes per hour). The bears showed reduced interest in each other and mutual avoidance. Approaches and bouts of sniffing were uncommon. Bouts of bodily contact between the pair were less regular, and the frequency of playful interactions such as wrestling and jaw wrestling also declined. The reproductive behaviours rolling and masturbation were still observed for Chomel, but were much less common. Sometimes Bakti followed or attempted to herd the female, but she was able to rebuff him using mild threat behaviour (slight jaw gape). He did not attempt to mount her.

The female's self-maintenance activity declined to baseline levels by week 17, but grooming persisted at a lower rate through weeks 18 and 19 (Figure 2.29a). During weeks 17-19 the female began to focus attentively on grooming her nipples, which were slightly pronounced and reddened. On several occasions she also groomed the male. Bakti rarely tolerated her attention for long, however, and usually terminated the interaction after ~30 seconds with threat behaviour (slight jaw gaping, swiping) or avoidance.

During weeks 16 and 19. Chomel emitted perceptible 'nickering' noises while walking rapidly about the exhibit. Bakti did not usually show any apparent response. On average, bouts of nickering fasted for approximately 5 seconds. The vocalisation was heard several times each hour, and became particularly noticeable during week 19 (Figure 2.29b).

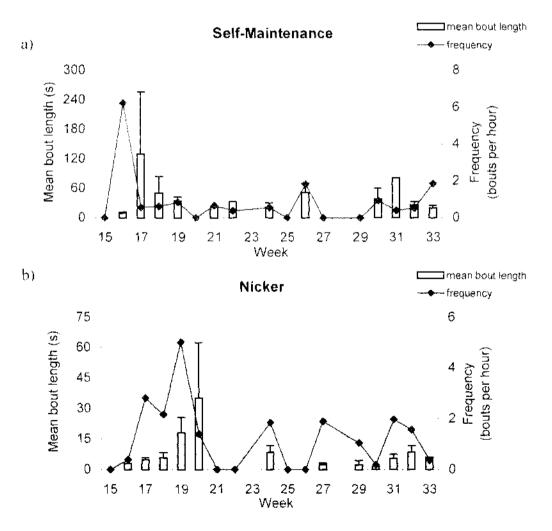


Figure 2.29: Frequency and duration of a) self-maintenance and hinickering vocalisation from female Chomel (#607) during weeks 15-33. Bars show I standard error of the mean.

There was a significant increase in the rate of interactions between the pair during week 19, and heightened levels of agonism (Figure 2.30a). During week 19 bouts of wrestling were frequent (Figure 2.30b). Jaw wrestling and head-jockeying behaviour also increased in frequency and intensity (data not shown), often resulting in superficial scratches and bites to both bears.

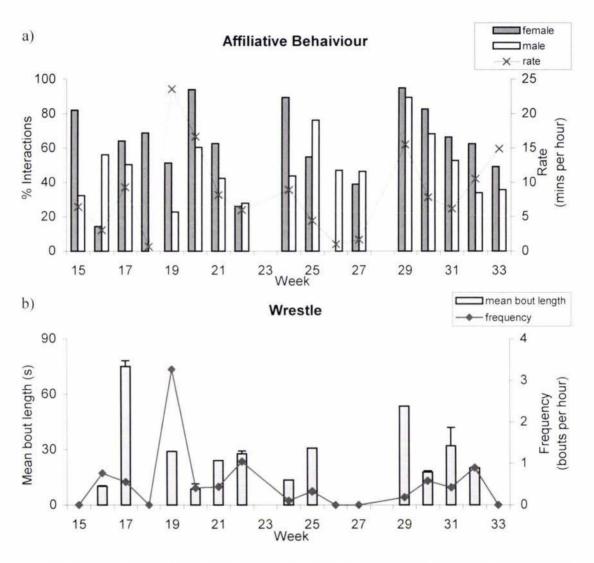


Figure 2.30: a) Proportion of affiliative interactions and b) frequency and duration of wrestling between the male Bakti (#617) and female Chomel (#607) during weeks 15-33. Bars show 1 standard error of the mean.

Under standard management practice the dens were closed during the day and the pair given access to the north dens overnight (see Materials and Methods; Section 2.2.1 for further details). During week 17, as a precaution, the pair were also given access to the south dens overnight because some eucalyptus branches found in the north dens were thought to indicate an increase in nesting activity. On 01 May (week 18) keepers noted the bears spent most of the day near the dens and showed little interest in food. On the

morning of 02 May, a nest was found in the north dens and from 03 May overnight access to the north dens was restricted to facilitate introduction of the female to the adjacent maternity wing under construction.

On 05 May Chomel still had little interest in food and appeared distressed - keeping a close watch on the male, pacing nervously, and startling at slight noises. She made numerous trips to the upper south area of the exhibit, nickering and walking rapidly. Sometimes she carried corn husks and branches to the alcove outside the south dens, and throughout the day remained in the alcove for up to an hour at a time.

During week 19 Bakti showed renewed interest in the female, frequently following her and sniffing at her anogenital region. He also appeared nervous on 05 May, and paced up and down near the south dens when she disappeared from sight. Several times when he cautiously approached the alcove, Chomel left it and dragged him about by his scruff or leg. Bakti usually responded with mild agonism (slight jaw gape) and retreated. On one occasion the female lunged forward, biting him on the rump as he left the area.

On the morning of 06 May, the left rear paw of a cub was discovered beside the entrance to the north dens. On further investigation a dead cub missing a right front paw was found in a nest under the far south den alcove (Plate 2.2). The body of the second cub¹³ was never found, but faeces collected from the female later in the day contained a cub's pelt and numerous claws.

The cub found dead within the nest was male; its body heavily bruised and lacerated with tooth and claw marks (Plate 2.3). The front right paw had been bitten off and there was extensive damage to the torso, partially exposing the intestines. A sizeable portion (~2.5cm diameter) of the skin around the anus had been nibbled off. The cub weighed 352.0 g (within the range for a full-term cub - Appendix B) and appeared fully developed, but a necropsy report showed the lungs had not inflated, indicating that itwas probably stillborn¹⁴. The paw from the second cub indicated that the twin was probably similar in size.

¹⁴During week 24 the female was weighed (85.0 kg) and anaesthetised for a physical examination to check her general condition. Blood tests, vaginal and rectal swabs and a vaginal wall biopsy were performed, but no medical signs of abnormality or infection were found to explain the stillbirth.

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¹³ Although giving birth to more than one cub is unusual in Sun bears, Chomel is herself a twin; and in April 1998 she again, gave birth to twins.



Plate 2.2 Sun bear nest at Wellington Zoo, 06 May 1997. a) Site located under the far south den alcove, with the semicircle of vegetation seen in foreground; b) nest contained a variety of plant material including larger pieces of wood, but no bedding material. The dead cub was found within the nest at left rear (see Plate 2.3).



Plate 2.3: Sun bear cub born at Wellington Zoo, 06 May 1997. Extensive damage was inflicted by dam and/or sire; note the distinctive circle of skin nibbled away from around the anus. The male neonate was within size and weight range of a full-term cub, but necropsy reports indicated it may have been stillborn. (photo; S.Lockwood)

The nest containing the dead cub was poorly formed from pieces of wood and bark, but included other plant material from the exhibit (see 'nesting' Section 2.3.1.1.7 for further details). A well-formed straw nest was found in the south dens, having been built the previous week when the bears still had access to the area. On 06 May, when the pair were given access to the south dens after the discovery of the cub, the female immediately began rearranging the straw on the bunk. Both bears remained in the dens for the rest of that day, and most of the next day.

2.3.3.4.2 Weeks 20-33 (11 May 1997 - 17 August 1997)

During the two weeks after the birth (weeks 20 and 21), Chomel spent varying periods of each day in the area outside the south den, often entering the alcove where the cub had been found. She was very defensive when the male approached, threatening him with wide jaw gaping and whining followed by barking and roaring if he did not leave the area immediately. On occasions she was observed cradling pieces of wood and food items for extended periods (Plate 2.4).



Plate 2.4: Female 'Chomel' (SN# 607) cradling pieces of wood one week after loss of young in May 1997.

The rate of interactions between the pair declined by week 20, but still occupied ~15 mins each hour (see Figure 2.30a; Section 2.3.3.4.1). A large rise in affiliative behaviours was evident for both bears. In comparison with week 19, bodily contact was less frequent during weeks 20 and 21, but the mean duration of bouts was considerably longer (~2 mins compared to 30 secs).

Mutual play and jaw wrestling were observed only during weeks 20 and 21, whereas bouts of head-jockeying continued to occur regularly. Bouts of wrestling were also relatively constant throughout weeks 20-32 (Figure 2.30b), but they became much more intense and agonistic vocalisation was heard during some bouts. In general, the bears appeared less tolerant of each other — frequently threatening each other with jaw gaping; encounters usually ended with swiping or biting rather than avoidance.

For the female, rolling was very noticeable during weeks 21 and 22. Bouts were performed 1-2 times each hour, and on average lasted \sim 30 seconds (mean 27.8 \pm SE 9.4 secs). She still nickered regularly during week 20, but the vocalisation was distinct, being emitted continuously for long periods of time (see Figure 2.29b; Section 2.3.3.4.1).

Reproductive activity was observed between the pair during weeks 20-22 (Plate 2.5). Bakti showed high levels of interest in the female, approaching and following her frequently (up to 5 times per hour), and often sniffing toward her anogenital region. The female tolerated these repeated approaches, and rarely rebuffed him. During week 22, zoo visitors reported seeing the bears copulating. Mounting by the male and female continued to occur intermittently during weeks 25-33 but the behaviour was more frequently associated with agonistic encounters. There was a gradual decline in the rate of interactions between weeks 20-27, dropping from 23 mins per hour to less than 2 mins per hour (see Figure 2.30a; Section 2.3.3.4.1). The proportion of affiliative interactions fell between weeks 24-27.

During week 27 and 29 Chomel was again observed carrying plant material to the south den alcove. She collected large amounts of dried fennel (*Foeniculum vulgare*) from near the den, bending or biting off several stems at a time and carrying them in her mouth. Sticks and grasses were also collected from the south area of the exhibit. The female was hidden from view when she entered the alcove but sometimes was seen manipulating nesting material with her forepaws. Bakti approached Chomel very cautiously when she was nesting, walking slowly toward her with jaws gaped, but he quickly retreated if she responded with threat.

At times when the pair sat in contact, Chomel was regularly observed grooming Bakti, her attention usually directed at his shoulders and sides, but she also focused on an area of alopecia on the male's inner leg¹⁵. Brief bouts (~30 seconds) of allogrooming were observed several times each hour. Bakti terminated each interaction using jaw gaping and swiping, but his mate became particularly persistent, jaw gaping and 'standing over' in an apparent attempt to dominate him.

Between weeks 29 and 33 there was a steady increase in the levels of agonism between the bears (Figure 2.31). The female was observed dragging the male by his lower jaw or nape on several occasions, and bouts of intense wrestling became common (see Figure 2.30b; Section 2.3.3.4.1). Agonistic vocalisation was frequent and both bears sustained minor scratches and bites.

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¹⁵ The skin condition was thought to be mites, and successfully treated with oral doses of ivermectin (0.4% Ivomec for cattle). Because the male frequently scratched at the affected area during the affliction, his self-maintenance data for the period was excluded from analysis. Allogrooming by the female was included in the analysis because the behaviour was exhibited regularly throughout the year.





Plate 2.5: Reproductive behaviour of Sun bears at Wellington Zoo, May 1997. a) Female 'Chomel' (#607 on left) presenting inguinal region to male ('Bakti' #617), b) 'Bakti' (on left) approaching the oestrus female cautiously, with low level jaw gaping. Wounds on the male's upper back were caused by earlier encounters between the pair.

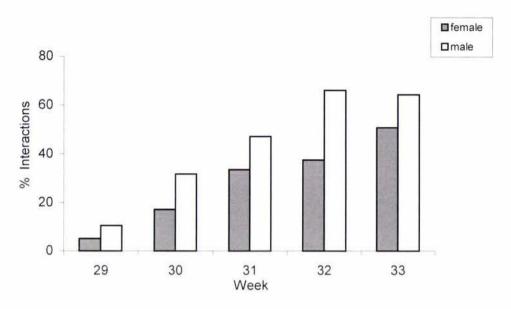


Figure 2.31: Proportion of agonistic interactions between male Bakti (#617) and female Chomel (#607) during weeks 29-33.

On 17 August (week 33) during the public feeding, the bears were acting unusually. Bakti was particularly wary, and Chomel remained out of sight for approximately 5 minutes after being repeatedly called. She eventually appeared from within the south den alcove and walked extremely slowly down the exhibit, stopping periodically to sit down. Her appearance and behaviour suggested that she felt unwell. Her head was hanging down, with ears held low, and several times the she sat and hunched over looking at her stomach. Typically the bears would sit attentively and beg at feeding times, but Chomel remained unresponsive to the keeper and public; Bakti also appeared uninterested in feeding.

Ignoring the food being thrown, Chomel instead picked up a large branch (~1m x 4cm diameter) in her mouth and attempted to carry it toward the south dens. She had obvious difficulty with the size of the branch and placed it on the ground, then promptly began to collect grass and headed toward the dens. She moved slowly and carried the grass only part-way up the path, stopping and looking around uneasily, before depositing it and returning to the lower part of the exhibit. For the next 10 minutes Chomel collected other pieces of vegetation (palm husk, sticks, twigs) and carried them in the same direction, nickering at intervals.

Soon after, the bears were let into the north dens and Chomel immediately began nesting in the straw bedding. The exhibit was inspected and the alcove was found to contain a well-formed nest (~1m diameter) constructed from pieces of wood, grasses, corn husks and other vegetation.

Straw and bamboo were placed in the rear south den for Chomel to use in nesting, and supplemented with material from the nest that had been made outside. The bears were released back onto exhibit, and the wary female eventually entered the den. When Bakti tried to enter she seized him by the nape and dragged him outside. Chomel was isolated in the far south den, but the outer barred door was left uncovered so the pair could still interact. The adjacent south den was set up for observation by fixing a piece of plywood with a hole cut for viewing to the door between the dens. Staff offered food and checked on the female several times during the evening, and reported that she was more settled.

2.3.3.5 Period 5 (Weeks 34 and 35: 19 August 1997 - 31 August 1997)

On the 19 August, a video camera and monitor were set up in the adjacent den to assist with monitoring the female. Data were collected for up to 24hrs per day between 20-30 August. Food was offered several times each day, and although Chomel showed little interest in eating, on several occasions she was observed cradling items of food. She remained very alert within the den and was easily disturbed by any noises; she also became quite defensive and on one occasion barked at a keeper who entered the adjacent den. She acted very aggressively toward the male - charging and barking loudly at him whenever he approached the den door.

After 20 August Chomel exhibited increasing levels of aggression toward her keepers and Bakti. She appeared particularly upset by the male's presence outside the south den, and continued to bark and charge at him, but also began to threaten him through the bars of the door with wide jaw gaping. To increase her privacy, on 23 August the surveillance equipment was relocated to permit monitoring from a remote site, and on 24 August an electric fence was set up to exclude the male from the area. Results of data from observations and video tapes recorded over the two week period are now presented:

After the male had been excluded from the area outside the den, Chomel appeared more relaxed; she became less vigilant and did not appear as easily disturbed. She also began to exhibit solitary play at regular intervals - lying on her back and twirling small

branches with all four feet, or using her mouth to toss and grapple objects in a lively manner. Bouts of solitary play occurred on most days, and usually lasted for approximately 5 minutes but some sessions extended for up to 15 minutes (mean $191 \pm SE 32.0 \text{ secs}$; max 842.1 secs).

The female's level of activity was considerably lower during Period 5, declining from \sim 45 mins per hour to \sim 20 mins per hour. This was partially due to a sharp drop in her rate of feeding. She remained very alert throughout the day and night, and woke at the slightest noises. Episodes of rest were of relatively short duration (mean 15.9 \pm SE 2.4 mins) and she appeared to have difficulty getting comfortable, turning frequently and shuffling about within the nest. Rest was interspersed with bouts of self-maintenance and nesting activity.

During weeks 34 and 35 Chomel's frequency of self-maintenance was elevated (~2 bouts per hour) but remained relatively constant. Self-maintenance behaviours mainly consisted of grooming and scratching. Bouts of rubbing were less common, and the behaviour was site-specific - being performed against the support beams of the nesting platform or the wall near the exit. Grooming bouts increased in length and rose to a peak on 28 August, accompanied by a substantial elevation in her rate of self-maintenance behaviours (Figure 2.32a). During week 34, Chomel changed her pattern of grooming, focusing less on her nipples and attentively grooming her vulva and forepaws (Figure 2.32b).

Chomel's reproductive activity increased during weeks 34 and 35. Behaviours included masturbation, rolling, cradling and nesting. Bouts of masturbation were uncommon, but relatively lengthy ($81.0 \pm SE 31.7 secs$). In comparison, rolling occurred daily (\sim 1 bout per hour), and was particularly noticeable because of the vigorous and lengthy nature of the bouts (mean $104.2 \pm SE 26.9 secs$).

The female had previously been observed cradling an apple several days before her isolation in the den. Cradling of fruit and small pieces of wood was seen more regularly during weeks 34 and 35, bouts usually lasting over a minute (mean $91.5 \pm SE\ 24.6\ secs$) and accompanied by sniffing and intermittent inspection of the item. Afterward the favoured item was either discarded or consumed.

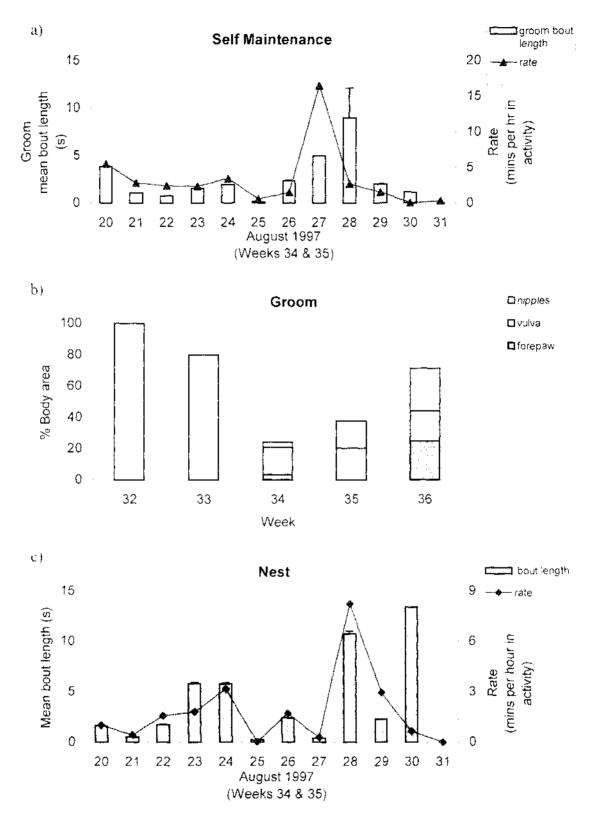


Figure 2.32: Duration and rate of a) self-maintenance and c) nesting activity by female Chomel (#607) during weeks 34 and 35; b) shows grooming of hody area by proportion by female Chomel (#607) during weeks 32-36. Bars show I standard error of the mean.

Nesting was the most prominent reproductive behaviour exhibited during weeks 34 and 35. Although straw and bamboo were provided, Chomel also used her teeth and claws to bite or tear apart timber in the den, collecting the pieces of wood and incorporating them into nests. Structures in the den were considerably damaged by her actions. There was a general increase in the rate of nesting (Figure 2.32c), which increased gradually between 21 and 24 August, and rose markedly on 28 August. A concurrent increase in the duration of bouts was observed. Most nesting bouts lasted $< 5 \text{ mins} (206.1 \pm \text{SE} 35.5 \text{ secs})$, however on 28 August the majority of bouts exceeded 10 minutes in length. Her rate of nesting declined to low levels by 30 August.

On the morning of 26 August Chomel was temporarily moved to the adjacent den to replenish her water supply because she had tipped the container over. Accumulated faecal matter and soiled nesting material were removed from the den and fresh nesting material was provided. She appeared very anxious to return to the den, and immediately began nesting.

The surveillance camera also needed to be reaffixed because the female had interfered with it during the night, causing loss of reception. Work at the camera continued throughout the day and by the afternoon Chomel had became obviously disturbed. She left the nest periodically, and charged toward the adjoining door when a power tool was used. More loud work noises elicited further charging from the bear, and as they continued she repeatedly tried to escape by charging into the outside door. Becoming increasingly fearful and frantic, she paced rapidly beside the exit, head-tossing and tongue-flicking. After approximately 10 minutes, work was abandoned and the camera remained off-line until 28 August, but periodic observations continued.

By 31 August Chomel was very restless and increasingly spent time sitting beside the exit or trying to escape from the den. Because of the change in her behaviour, including the decline in periparturient activities (*i.e.* self-maintenance and nesting; Figure 2.32), she was released from the den and reintroduced to the male later in the day. Keepers reported seeing mutual sniffing and hearing nickering from the female; no agonistic behaviour was observed.

The south den was thoroughly searched but no evidence of birth was found, and the faecal pile did not contain any cub remains. The female's nipples appeared to be slightly reddened and enlarged, but she did not appear to be lactating.

2.3.3.6 Period 6 (Weeks 36-39: 01 September 1997 - 23 September 1997)

On 01 September, Chomel made numerous visits to the area near the south den and repeatedly tried to access the closed den by pulling at the door. In the afternoon the den was reopened and she entered it for brief periods (<15 mins). Although the bears had access to both dens overnight, there was no evidence of further nesting activity.

Chomel continued to appear distressed during weeks 36 and 37; she showed little interest in feeding and was very nervous, startling at slight noises and sounds made during routine maintenance activities. She was exceptionally restless, and spent ~40 minutes of each hour in locomotion - often pacing uncharacteristically up and down the length of the moat. She was observed making numerous attempts to escape the exhibit by wading or swimming out in the moat and trying to scale the enclosure wall. The male appeared to be disturbed by the female's atypical activity and kept a close watch on her.

Self-maintenance behaviour was a prominent part of Chomel's activity during weeks 36-39, and rose to a peak of 15 bouts per hour during week 36, with individual behaviours showing up to a 10-fold increase in frequency (Figure 2.33). A change in the pattern of rubbing was observed, and on several occasions she rubbed her rear end against a wall or other vertical structure. On week 36 bouts of grooming were comparatively longer than during weeks 34 and 35 (79.8 \pm SE 18.1 secs), and the nipples, vulva and forepaws were targeted increasingly often (Figure 2.32b).

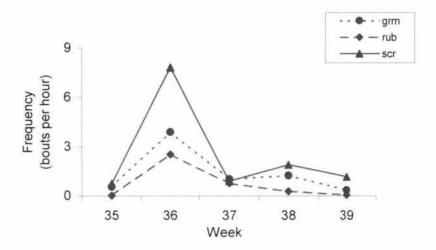


Figure 2.33 Frequency of self-maintenance activity (groom, rub and scratch) by female Chomel (#607) during weeks 35-39.

During week 36 there was a high rate of interactions between the bears, occupying ~18 mins per hour. Although Chomel was less aggressive toward Bakti, he acted somewhat warily around her. Approaches were typically followed by an exchange of mutual jaw gaping and sidling around each other prior to cautious bouts of sniffing. Brief bouts of head-jockeying resulted when the pair were in proximity for over a minute, but bouts of jaw wrestling and wrestling were common. The female was most likely to initiate interactions, but usually avoided the male when he attempted to interact. Sometimes she tried to rebuff him by rearing bipedally, jaw gaping or swiping. At times Bakti also responded aggressively to the female and asserted his dominance by rearing over her and snapping or biting. Bodily contact between the bears was infrequent.

Chomel began to exhibit reproductive behaviours associated with oestrus (backward walking, inguinal presentation, rolling and masturbation) on week 36. Backward walking was first observed during 31 August, on the last day she was in the south den. During week 36 bouts of backward walking were observed regularly (~2 bouts per hour), and on average, lasted approximately 10 seconds (mean 11.2 ± SE 3.4 secs). On several occasions the female deliberately backed into the male or lay in his path and presented her inguinal region. Bouts of inguinal presentation, rolling and masturbation occurred regularly on 04 September, whereas backward walking persisted at a lower frequency (~1 bout per hour) throughout week 37.

Bakti followed Chomel frequently during week 36, but did not approach very often. He was very cautious when he did approach, watching the female closely and moving

slowly forward with slight jaw gaping. He often sniffed toward her with his neck fully extended, and was quick to rear up and push the female away if she responded aggressively. The male frequently sniffed toward her anogenital region when following closely behind, and she occasionally permitted a brief investigation during inguinal presentation.

During week 37 Bakti appeared to lose interest in the female, no longer following her about and approaching less often; bouts of sniffing were also infrequent. The rate of interactions between the bears was considerably lower (~7 mins per hour) with high levels of agonism. Chomel was very intolerant and exhibited a high proportion of agonistic behaviours (>90% of total weekly interactions), at times charging the male for no apparent reason. Charging was often accompanied by loud roaring. She typically responded to any approach by whining, growling and head-down threat; if Bakti continued to advance she reared up and opened her mouth wide with the teeth fully exposed. In general, the male showed less intense agonism but usually reciprocated with similar behaviour.

Chomel began to frequent a platform high in a tree that was rarely used by the bears at other times, but appeared to serve as a means of avoiding the male. If Bakti climbed the tree, she became defensive and threatened him with growls and swipes. Bodily contact between the pair was not observed, and bouts of jaw-wrestling and head jockeying were less frequent. Bouts of wrestling persisted but were comparatively brief (~30 seconds), and usually initiated by the male. Wrestling was intense with less obvious restraint and was typically accompanied by loud growling and roaring.

Between weeks 36-39 the bears had little interest in feeding and were reclusive, spending the majority of time out of sight in the upper south area of the enclosure. They were wary around people and at times exhibited threat behaviour toward their keepers and zoo visitors. Because of their behaviour, during week 37 they were permitted access to the south dens during the day. Bakti became increasingly nervous, and often retreated into the dens if alarmed by a loud noise, or following a serious altercation with the female. He began to spend increasing periods of time in the den between weeks 37-39.

During week 37 Chomel was given access to the completed maternity wing for the first time. Nesting material was provided in the sleeping quarters of the maternity den, and video surveillance was set up to monitor indoor activity. Chomel spent most of the time exploring outdoors and generally appeared relaxed, foraging and rolling about on the bark chip floor. Her pacing declined after introductions to the maternity wing began, but still occurred regularly when she was in the exhibit. She was permitted access to the cubbing area for 1-2 hours on most days, and this period was increased gradually to full days by week 39. At night the pair were kept together in the main enclosure.

In the first week, the crush leading to the maternity wing was left open so the female was able to return to the north dens, and once she repeatedly charged Bakti when he approached outside the north dens. When Chomel was isolated in the maternity wing with the door closed she appeared much more relaxed, and on 15 September was observed building a nest and sleeping within the maternity den. Further nesting activity was observed on 16 and 18 September. Most bouts of nesting were fairly brief (mean $95.6 \pm SE 31.2$; max 231.6 secs), and the female appeared to be easily disrupted from the activity, rapidly exiting the den in response to outdoor noises.

When Chomel was put back onto exhibit each day, the bears usually met with a brief exchange of mutual sniffing and jaw gaping and then parted, however, on some occasions she charged at Bakti within 5 minutes of reintroduction. Altercations between the bears were common and the female became increasingly reluctant to go back onto the exhibit in the afternoon.

2.3.3.7 Period 7 (Weeks 39-42: 24 September 1997 - 27 October 1997)

On 24 September a management decision was made to isolate the female within the maternity wing to give the bears several weeks away from each other. Chomel had *ad libitum* access to the den in the cubbing area, which was under continuous remote video and audio surveillance. Her typical pattern was to enter the den at c.6pm and remain inside, waking and usually exiting soon after sunrise. Overnight, the female left the den for brief periods (< 5 mins), presumably to urinate or defecate as excretion rarely occurred in the den. She did not usually enter the den during the day.

Although the pair were separated for most of the time, each morning Chomel was transferred into the north dens while the maternity wing was serviced. This

maintenance took ~30 mins and included removal of soiled bedding, and the distribution of food and other enrichment items (Appendix A). Fresh nesting material was provided approximately once a week. During servicing, the male usually waited outside the north dens, but at times approached the female and sniffed toward her through the bars. Chomel usually responded aggressively to his presence by whining, barking and charging.

In general, Chomel appeared to be much more relaxed after being transferred to the maternity wing full-time. She stopped pacing, and was less restless. Her pattern of activity was comparable to the time spent in the south den (Section 2.3.3.5). She also regularly exhibited play behaviour again. Chomel's feeding rate remained low during weeks 39-42 (~ 8 mins per hour), and she sometimes declined previously favoured items. Additional rations were provided to increase her nutritional intake during the potential pregnancy, and though appearing to be selective, usually ate most of the food.

Nesting was the most prominent reproductive behaviour exhibited by the female during weeks 39-42, but other behaviours observed included cradling, rolling and masturbation. On numerous occasions she was observed playing with items of food or carrying and cradling them. She also favoured grass sods or pieces of bark and wood and sometimes carried the chosen item into a tree and balanced it against her stomach or chest.

Chomel usually built nests on the platform provided, but sometimes she nested on the floor beside the platform or underneath it. The frequency of nesting activity remained relatively low (~1 bout per hour) but the mean rate of nesting was higher than during weeks 34 and 35 (see Figure 2.32c compared to Figure 2.34). Her rate of nesting fluctuated but rose during weeks 39 and 42. On average, nesting bouts were also comparatively longer, and during week 39 some bouts of nesting lasted 30-60 minutes.

On several days during week 40 and 41 Chomel appeared to be unwell. She was uninterested in food, very slow-moving, but also restless - frequently changing position and rarely remaining still for longer than 10 minutes at a time. She also periodically hunched over and looked at her stomach. By week 42 there were obvious changes in her physical appearance. Chomel appeared to have put on weight because her stomach was noticeably rounded, her loose folds of skin had become thicker, and she had

developed additional folds. Her mammaries and nipples were larger and more prominent.

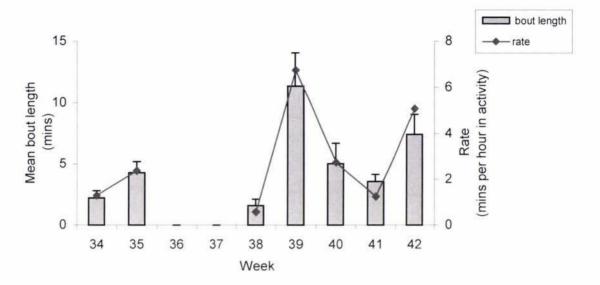


Figure 2.34: Duration and rate of nesting activity by female Chomel (#607) between weeks 34-42. Note that video surveillance of dens was not undertaken on week 36 or 37. Bars show 1 standard error of the mean.

During week 42 Chomel began to enter the den at regular intervals during the day. She usually entered the sleeping quarters, briefly sniffed about the nesting area and left again within several minutes but sometimes remained inside for several hours, nest-building, grooming and resting. When indoors, Chomel was easily disturbed by slight noises. Although she did not seem unduly disturbed when minor renovations began in the adjacent service area soon after her isolation, by week 42 she became increasingly agitated when work was underway, or when there were other loud noises *e.g.* mowing of the nearby wolf pen. During such disturbances the female exited the den swiftly and sometimes paced about anxiously looking toward the source of the noise.

On 26 October keepers noted that Chomel did not appear keen to return to the maternity wing after servicing. Because of the change in her behaviour and uncertainty surrounding the length of gestation in Sun bears (see Chapter 1; Section 1.2.1.3), a decision was made to reintroduce her to the male.

2.3.3.8 Period 8 (Weeks 42-47: 28 October 1997 - 18 November 1997)

From 28-30 October the male was shut in the south dens while Chomel was given free access to the exhibit for approximately 1 hour. When she approached the south den agonistic vocalisation was heard from both bears. On 31 October the male was released

onto the exhibit with her. The following two paragraphs describe their behaviour during the first day of reintroduction:

When Bakti was released, Chomel was busily feeding and did not notice him until he had approached to within 5m. She immediately roared and charged but the male stood his ground, and reared upright with his front paws held stiffly out. The female stopped short, reared upright and snapped at him. Both bears emitted loud agonistic vocalisation (growls, roaring) and circled with wide jaw gaping; they used their front paws to push and keep each other at bay. After several seconds they parted and continued threatening each other from a semi-bipedal stance. When the male stretched out his neck toward the female she growled loudly, turned and retreated. Bakti followed her and attempted to sniff her anogenital region, but Chomel snapped and swiped at him, then ran away down the exhibit roaring loudly.

To distract the pair, keepers provided further food and both bears ate what was offered. Bakti acted warily but remained near Chomel, observing her closely from several metres away. She ignored him as she fed, while he circled around and climbed to an elevated area of the exhibit behind her. He cautiously approached several times, eliciting from her loud whining, head-down threat postures and charging, that caused him to retreat to higher ground. After approximately 1 hour, the female was let back into the maternity wing. Reintroductions were staged each morning and gradually increased to full days by 06 November. Overnight the pair were kept separated.

After the first week Chomel appeared to become more tolerant of Bakti, but aggressive behaviours (charging, swiping) continued to occur at intervals throughout the day (Plate 2.6). When particularly high levels of aggression were observed, the bears were sometimes left apart the following day. Altercations were typically caused by the male making repeated attempts to interact with the female, however, sometimes Chomel attacked him without any apparent provocation. She thwarted his approaches to a certain extent by climbing to the tree platform, and was rarely observed at rest on the ground.





Plate 2.6: Reintroduction of male ('Bakti' #617) and female ('Chomel' #607); Wellington Zoo, October 1997. During pregnancy threat behaviour and aggressive episodes were common, being accompanied by loud growling and roaring from both bears. a) Female (on right) charges toward male, both animals have jaws held wide open and teeth fully exposed in threat; b) note the length of male's canines and extreme mobility of upper lip, with the end of the snout nearly forming a right angle to the muzzle. An intense episode of fighting ensued, but both animals sustained only minor injuries.

Bakti became increasingly nervous, particularly when Chomel was also on exhibit, and sometimes stayed in the south dens all day. He startled easily and either ran from, or charged at, vehicles that passed the exhibit during routine activities. The male was frequently observed pacing up and down the exhibit, and became increasingly aggressive toward people. Most often, he singled out particular zoo visitors, watching them closely and tracking them along the length of the exhibit with a characteristic stiff-legged gait. He also charged and barked at sudden noises and challenged keepers and other staff when they passed the enclosure. To reduce potential causes of stress to the male (and staff!), some personnel used an alternative route.

During the first week of introduction the rate of interactions between Chomel and Bakti was relatively high at ~15 mins per hour, but thereafter it declined to <5 minutes per hour. The majority of their interactions were agonistic. Jaw gaping was regularly exhibited by both bears and took the form of high-intensity threat. The mouth was held open very wide, with the teeth fully exposed and bouts were frequently accompanied by aggressive vocalisation (whining, growling). Jaw gaping was most likely to occur when the distance between the pair was less than 2m. Bodily contact was rare, and the female usually terminated any brief contact by pushing the male away and jaw gaping.

During weeks 42-46 there was little change in the Chomel's self-maintenance activities, but in week 47 there was a noticeable change in her pattern of grooming. She began to focus on her nipples and vulva more often and cat-like face washing was observed. She sometimes sat in her water trough in the maternity wing as if to cool herself. The trough was not large enough to accommodate her entire body, but she climbed the side and turned to immerse her rear end in the water for several minutes at a time.

There were also few changes in the rate or types of reproductive behaviours exhibited by the female between weeks 42-47. Rolling still occurred regularly, and although masturbation remained relatively infrequent (<1 bout per hour), there was a slight increase in the frequency of bouts. She also continued to cradle food and other items. Chomel built nests each evening, and on some days when she had access to the maternity wing. After week 42 her rate of nesting to ~1 min per hour fell (Figure 2.34), and remained fairly constant thereafter.

By week 46 Chomel had become increasingly unwilling to enter the exhibit in the mornings. She could be entired out with food, but began periodically returning and sitting outside the south dens during the day. She spent little time foraging on exhibit, and spent increasing time on the platform high up in the tree.

During week 47 a well-formed nest of twigs and other vegetation was found in the alcove outside the south den. It was uncertain which bear had made the nest, but it was presumed to be the female because she had begun to spend some time in the area. Chomel remained out of sight in this area for most of the day, and in the afternoon was discovered frantically trying to get inside the south den by scratching and pulling at the door. She was also observed hunching over periodically and busily grooming her nipples. The female was immediately transferred back into the maternity wing, and again charged at the male during the change-over.

Because of continued levels of agonism between the bears and their apparent increasing anxiety at being kept together, the female was isolated in the maternity wing full-time, and stayed there for the remainder of the study.

2.3.3.9 Period 9 (Weeks 47-51: 19 November 1997 - 18 December 1997)

As with previous management, the female was permitted *ad libitum* access to the maternity den in the cubbing area. Straw and bamboo were provided in the sleeping quarters, and to ensure the bear had an adequate supply of nesting material, half a bale of straw was placed in the enclosure.

During Period 9 there was limited opportunity for contact between the bears, except when the female was temporarily moved into the north dens during morning servicing of the maternity wing. The male was rarely in sight but on most occasions when he appeared outside the den, she roared and charged at him. Chomel appeared to be much more relaxed when alone; she was less restless and began to actively forage and exhibit solitary play behaviour again. After the bears separation Bakti stopped pacing and began to come out of the south dens more often. He still appeared wary and continued to challenge staff and visitors, but generally was more settled.

During week 48 Chomel was weighed and visually inspected by the vet to check her general condition. She was reported to be in good health, and at 92.0 kg she was considerably heavier than during the immobilisation in June. Since October (Plate 2.7a)

her body had become distinctly pear-shaped with a prominent abdominal bulge and her mammary glands also showed further enlargement (Plate 2.7b).

During weeks 47-51 Chomel began to 'check' the nest site at regular intervals throughout the day (1-2 times each hour). Sometimes she just put her head inside the sleeping quarters and looked about but on other occasions she entered the den and sniffed around the nest site. Chomel also began to habitually enter for several hours each day and was observed in nest-building or self-maintenance activities as well as rest. She often lay upon her back when resting, a posture that previously had been unusual.

On some days, when the female rested inside, the outer door was temporarily closed so her faeces could be collected from outside¹⁶. The procedure was usually completed within <5 minutes, and appeared to cause minimal disturbance to the bear because she often returned to the sleeping quarters after a brief investigation of the closed door. When the door was opened a food reward was provided.

When inside the den, the female remained very alert and responded abruptly to any loud outside noises (e.g. maintenance of the adjacent enclosure); her typical reaction was to rush out of the den and look about to locate the source of the sound. Even when outside, Chomel appeared sensitive to disturbances, which were largely due to major construction work being undertaken <50m away. A service road passed directly above the bear pit, and traffic included numerous vehicles and earth-moving equipment, as well as unfamiliar people. The use of a pneumatic drill to break up concrete <10 metres from the den was a considerable source of disturbance.

Loud noises usually made Chomel flee to the maternity den and crouch inside, but she rarely entered the nesting area. On one occasion when alarmed by a front-end loader as it scraped along the service road, she ran toward the den but misjudged the entrance, banging her head hard against the outside wall. She recovered quickly and ran into the den without any apparent injury.

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¹⁶ Fresh faeces were routinely collected throughout the study to monitor hormone levels for a concurrent project (see Chapter 3).



Plate 2.7: Pregnant Sun bear 'Chomel' (#607); Wellington Zoo, November- December 1997. a) Approximately six weeks prior to birth - lower abdomen was distinctly rounded and additional skin folds had developed; b) approximately three weeks prior to birth - the bear's stomach was distended further and her nipples were swollen and prominent.

During weeks 47-49 Chomel's rate of feeding remained low (~5 mins per hour), and after week 47 she regularly carried food into the den for consumption. Several times during week 50 Chomel left the den at unusual hours (midnight-0300), and returned within 10 mins carrying nesting material or items of food. On one occasion she brought a bone into the den, carried it onto the nesting platform and cradled it for ~10 mins before falling asleep. During week 50 Chomel had little interest in feeding and on several days did not eat at all.

The amount of time the female spent inside the den increased continually. During week 50 she spent an average of ~20 hours inside the den each day, usually leaving it only for brief periods (<15 mins). Chomel became increasingly restless, with an increase in her activity rate on week 50 from 10 mins per hour to 15 mins per hour. This mainly resulted from rising rates of locomotion and nesting. She regularly explored the inside of the den, walking and climbing about, sniffing at the walls and investigating the nest site. Bouts of rest were brief (mean ~15 mins) and frequently interrupted with bouts of self-maintenance and nesting.

Chomel became increasingly restless during weeks 49 and 50. When outside she often wandered about without foraging and appeared nervous, sometimes barking loudly when startled. She made numerous trips to and from the den, and on occasions was seen transporting vegetation (palm fronds, sticks, leafy branches and bamboo) from the outdoor enclosure to inside the den. Her rate of locomotion increased steadily between 7-10 December, and a concurrent increase in the duration of locomotive bouts was observed (Figure 2.35).

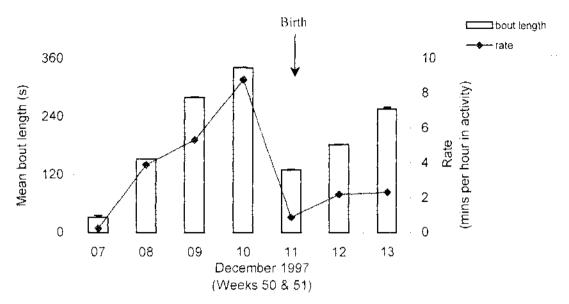


Figure 2.35: Duration and rate of locomotive activity by female Chomel (#607) during weeks 50 and 51. Bars show 1 standard error of the mean.

The frequency of self-maintenance behaviours for the female remained low (~2 bouts per hour) and was relatively constant throughout weeks 47-51. The rate and length of grooming bouts rose, however, and she began to specifically target her forepaws, nipples and vulva (Figure 2.36a). During week 48 and 49 the forepaws were the primary area targeted, but during week 50 the vulva was targeted much more often (Figure 2.36b).

Chomel regularly carried out rolling, masturbation, eradling and nesting with low frequency (<1 bout per hour). There was, however, a noticeable rise in the frequency of masturbation between weeks 45-48 (Figure 2.37a).

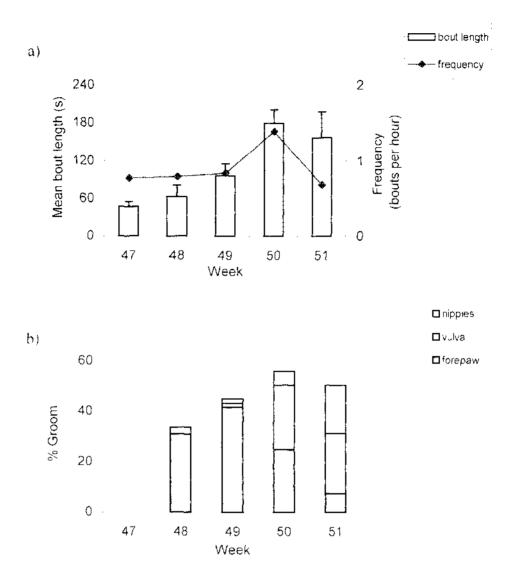


Figure 2.36: Duration and frequency of as self-maintenance and h) proportion of body areas groomed by female Chomel (#607) during weeks 47-51. Birth occurred on week 50, Bars show I standard error of the mean.

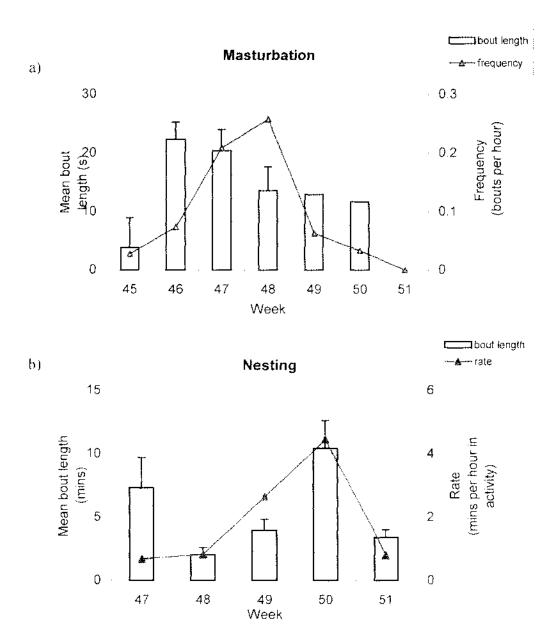


Figure 2.37: Duration and rate of a) masturbation and b) nesting by female Chomel (#60*) during weeks 47-51; birth occurred during week 50. Bars show I standard error of the mean.

During weeks 47-51 nesting was a prominent activity. Chomel built nests from the straw and bamboo provided, and often included vegetation collected from outside, as well as pieces of plywood torn from the den walls. Her rate of nesting rose to a peak during week 50, with a concomitant increase in the length of bouts, from an average of ~ 5 mins (mean $6.4 \pm SE$ 1.0 mins) to ≥ 10 mins (Figure 2.37b).

On 12 December (week 50), faeces collected from the female mid-morning were found to contain numerous cub claws. Tapes recorded during the previous 48hrs revealed that

a birth had occurred on 11 December. Results from an analysis of the tapes are presented below:

The rate of Chomel's nesting activity had increased 10-fold between 07 December and 10 December and remained elevated on 11 December (Figure 2.38a). The average duration of bouts also increased markedly with some lasting 45 minutes-2 hours. On 10 December the female spent a total of 3 hours in nesting activity; leaving the den and returning with copious amounts of vegetation (nikau fronds (*Rhopalostylis sapida*), sticks, straw) throughout the day and night. She also moved the nest from the floor of the den back onto the platform.

Although the female's self-maintenance activity during week 50 increased only a little (Figure 2.36a), grooming frequency rose sharply (Figure 2.38b) and there was a change in its pattern. Prior to the birth the proportion of forepaw grooming increased, and she began to target her nipples; but on the day of the birth (11 December), vulva grooming increased sharply while forepaw grooming ceased (Figure 2.38c).

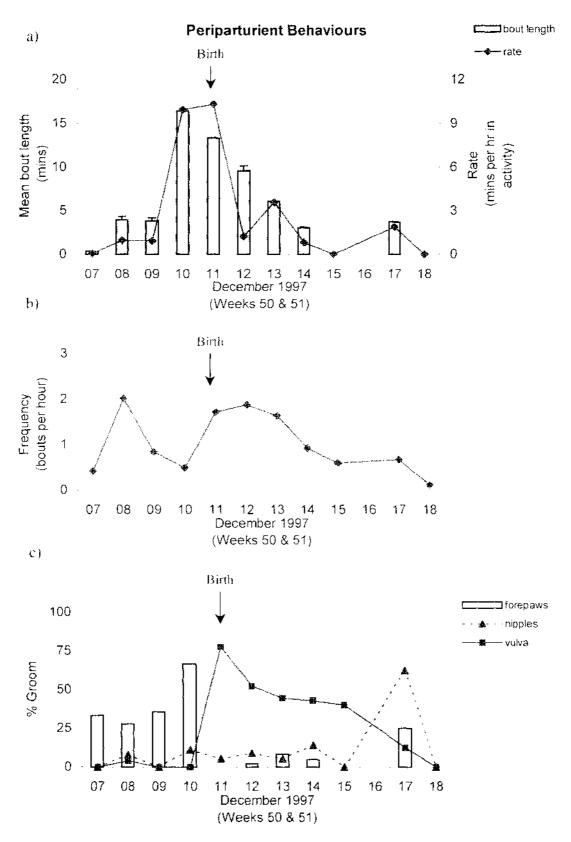


Figure 2.38: Periparturient behaviours by female Chomel (#607) between 07 December - 18 December 1997 (weeks 50 and 51); a) duration and rate of nesting activity, b) frequency of grooming and c) proportion of specific body areas groomed. Bars show I standard error of the mean.

2.3.3.9.1 Periparturient Behaviour and Birth (Week 50)

In the morning of 11 December when the keepers arrived to service the exhibit, Chomel did not leave the den readily, and returned soon after being released from the north den. She continued to exhibit a high rate of nesting activity (Figure 2.38a) and although easily alerted to outside noises, did not exit the den to investigate them as she had previously done. Chomel seemed unable to rest in one position for long, frequently turning about in the nest, rolling onto her back and scratching or kicking at her stomach. At c.13.30 hrs she began to periodically hunch over in response to visible shuddering contractions. She frequently groomed her vulva, and at 13.58 hrs a birth sac became visible. Delivery was rapid, occurring within several minutes and accompanied by high-pitched squealing from the neonate. The cub continued to vocalise and raised its head and moved about as the female sniffed, licked and nosed at it.

For the next 45 minutes Chomel lay curled beside her young, but despite continuing loud vocalisation from the cub, showed minimal interest in it. At 14.50 hrs, the female lay over the cub, which screamed loudly, and appeared to fall asleep. The cub's cries were heard intermittently when she repositioned herself in the nest, and detected for the last time at c.15.15 hrs. No further movement was seen from the female for nearly an hour. At 16.07 hrs Chomel woke and groomed her vulva; the cub was seen briefly, but was flattened, still and appeared to be dead. As the female groomed she changed position and rolled on top of it with her shoulder. After several minutes Chomel curled around her cub and documentation ceased because she had her back to the camera.

At c.20.55 hrs another series of contractions were seen and the female woke, sat up and promptly began to groom her vulva. At 21.13 hrs a cub was briefly seen in the straw between her legs, but there was no way to determine whether it was a second cub, or the first reappearing from beneath the straw. Chomel immediately licked the cub and turned it over with her claws but there was no movement or vocalisation from the neonate. She was attentive to it for ~5 minutes, alternating between sniffing and licking it and grooming herself. At c.21.25 hrs the female left the den and went outside for ~10 minutes leaving the cub lying in the nest.

When Chomel returned to the sleeping quarters she climbed onto the nesting platform, pawed briefly at the straw near the cub, covering it from view, then lay down nearby and slept. The female woke and became active several times in the night but it was

often difficult to determine what she was doing because her back was to the camera. Around midnight she was seen consuming an unidentified item. The following morning (12 December) when the female left the den, no young were visible in the nest.

On 12 December Chomel spent <30 minutes outside the sleeping quarters. She also appeared to be very restless and nervous, startling easily at slight noises coming from outside the den. At around midday contractions were seen and the female woke, hunched over and kicked at her stomach. On 13 December, similar behaviour was observed and female left the den for only ~2hrs in total, on one occasion returning with nesting material. There was no evidence of lactation or any sign of blood around her vulva.

In the early hours of 14 December Chomel appeared to undergo further contractions, and remained in the den for most of the day (~23 hours). She exited briefly at ~2.30pm, moving about very slowly and showed little interest in food provided. In the morning of 15 December several grams of bloody tissue were collected from outside the den. The sample was still tacky when collected and placed into 10% formalin for identification. Laboratory analysis of the sample was inconclusive, but indicated that the tissue was characteristic of placental membranes.

2.3.3.9.2 Postpartum Behaviour

There was a pronounced drop in Chomel's nesting activity after the birth (Figure 2.38a). On 15 December she moved the nest back to the floor of the den, which remained the nesting/sleeping site thereafter. Her rate of grooming remained elevated until after the 14 December, and she continued to primarily target her vulva. (Figure 2.38b and Figure 2.38c).

On 17 December Chomel still had little interest in food, but was seen foraging outside the den in the morning. When she was moved into the north dens during servicing she was reported to enter readily and when she encountered the male through the bars the pair briefly sniffed at each other and nickering was heard from the female. She then climbed into the crush and sat there until the maternity wing had been serviced. On 18 December Chomel was reported to be somewhat reluctant to go back into the cubbing area after it had been serviced.

Because the female appeared to have been in a constant state of reproductive activity for over a year, a management decision was made to keep the pair separated for ~6 months to allow the female time out from breeding.

2.3.3.10 Synopsis of the Reproductive Cycle

In this section, solitary and interactive behaviours of the bears are considered in relation to the reproductive status of the female (*i.e.* oestrus vs. pregnancy). During 1997 Chomel underwent three successive reproductive cycles, beginning with oestrus in January and culminating in birth during December. A reproductive cycle is defined here as the time between the onset of behavioural oestrus and termination of the pregnant/pseudopregnant phase (*i.e.* birth or the cessation of periparturient behaviours respectively). Pregnancy and pseudopregnancy are hereon referred to collectively as 'pregnancy' or 'gestation'.

Because of considerable variability between reports of reproductive parameters for female Sun bears (see Chapter 1; Section 1.2.1.3), timing/duration of oestrus could not be confidently extrapolated from dates of birth. Therefore, grouped weekly means were generated for female reproductive behaviours predominantly associated with oestrus (backward walk, inguinal presentation, roll), and the combined frequencies were aligned by week of birth /end of pseudopregnancy.

Weeks where grouped frequencies consecutively exceeded 1 standard error of the mean were considered to represent oestrus (Figure 2.39). Aligned data from the three reproductive cycles defined oestrus as occurring at least 13 weeks prior to end of gestation and revealed a significant peak in the frequency of oestrus-related behaviours during week -14. The length of the three reproductive cycles varied considerably, from 14 to 19 weeks (Table 2.3).

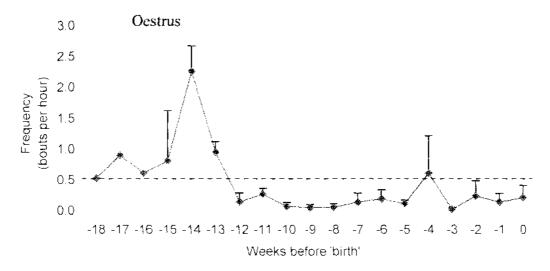


Figure 2.39: Grouped frequency of oestrus-related reproductive behaviours (backward walk, inguinal presentation, rolls aligned by week of 'birth' for end of pseudopregnancy) for female Chomel (#60%) in 199%; n = 3 reproductive cycles. Dashed line shows threshold (grouped mean + 1 SE) and bary show I standard error of individual weekly means

Table 2.5: Characteristics of reproductive cycles for female Channel (§607) during 1997.

Reproductive Cycle No.	Week of 1997	Oestrus Duration (weeks)	Status	Reproductive Cycle Length (weeks)
1	1-19	.5	Pregnant	19
2	20-35	4	Pseudopregnant	15
3	36-50	3	Pregnant	1.4

2.3.3.10.1 Solitary Behaviours

The female's level of activity declined steadily between the onset of oestrus and the end of gestation (Figure 2.40a). Her activity rate dropped significantly (p = 0.017; n for oestrus = 10, pregnancy = 29) from a mean of ~ 45 mins per hour during oestrus to ~ 30 mins per hour during pregnancy (Figure 2.41a). There was little change in the male's overall rate of activity.

For both bears, the decline in activity levels was mainly indicated by decreased rates of feeding, which dropped noticeably during oestrus and were lowest during week -13 (Figure 2.40b). Chomel's mean rate of feeding was considerably lower during pregnancy, however, the male's overall rate of feeding remained relatively constant (Figure 2.41b). The female's mean rate of locomotion was significantly higher (p = 0.001; n for oestrus = 10, pregnancy = 29) when she was in oestrus (Figure 2.41c), and a major peak was observed during weeks -13 and-14 (Figure 2.40c). There was little change in the male's rate of locomotion.

The female's self-maintenance activity was elevated during oestrus and late-stage gestation. Self-maintenance behaviours were a prominent component of her oestrus activity, on average, occurring ~4 times each hour and rising to a clear peak in frequency during week -14 (Figure 2.42a). The second peak increase in self-maintenance was observed during week -3, with levels declining gradually toward the end of gestation. For the male, the frequency of self-maintenance was comparatively lower (~1 bout per hour) and no clear trends were apparent (data not shown).

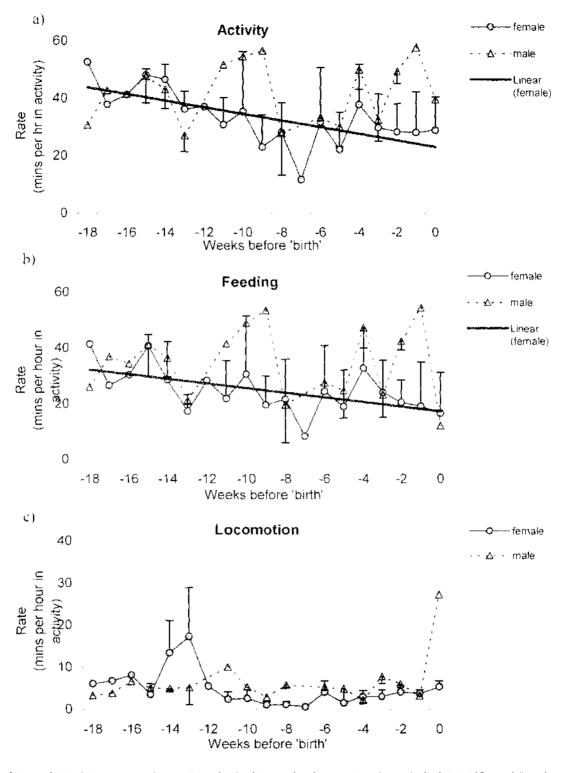


Figure 2.40: Mean rates of a) activity, b) feeding and c) locomotion for male Bakti (#61*) and female Chomel (#60*) during the female's reproductive cycle in 199*. A trendline has been added to a) and b) to depict regression of activity and feeding for female. Bars show I standard error of the mean.

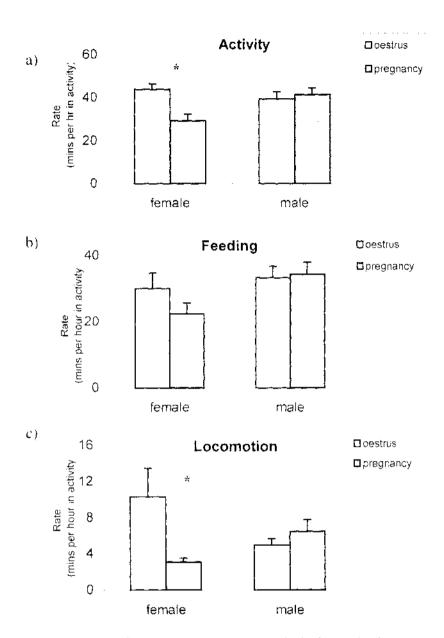


Figure 2.41: Grouped rates comparing at activity, b) feeding and c) locomotion during oestrus and pregnancy for female Chomel (#60°) and male Bakti (#61°) in 1997. Bars show I standard error of the mean. Asterisks indicate a significant difference tp < 0.05; Mann-Whitney test: n for oestrus = 10, pregnancy = 29) between oestrus and pregnancy.

Although grooming, rubbing and scratching were more frequent during oestrus, the duration of bouts were up to five times longer during pregnancy (Figure 2.42b). A steady increase in the duration of grooming was observed during the last 3 weeks of pregnancy, with bouts rising from an average of ~30 seconds to ~2 minutes. Specific body areas (vulva, nipples, forepaws) were groomed more often during pregnancy, and data suggest the vulva was the primary target. Nipple-grooming was associated more with oestrus, whereas an increase in forepaw grooming occurred during pregnancy (Figure 2.42c).

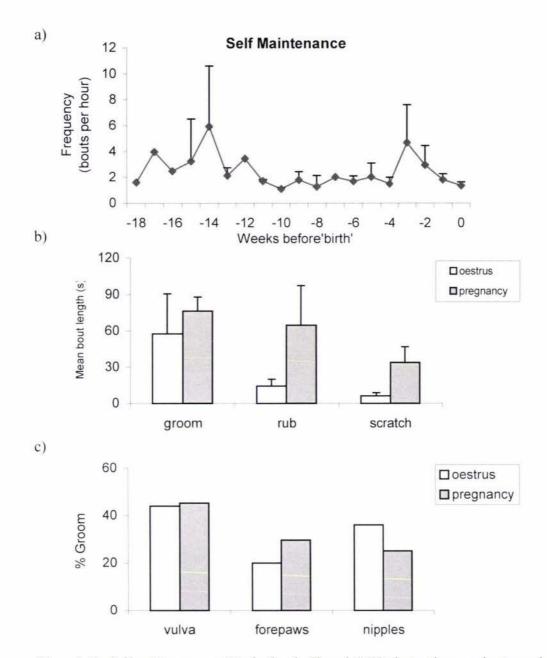


Figure 2.42: Self-maintenance activity for female Chomel (#607) during the reproductive cycle in 1997. a) grouped frequency of self-maintenance aligned by week of 'birth', b) compares duration of self-maintenance behaviours and c) compares proportion of specific area groomed during oestrus and pregnancy. Bars show I standard error of the mean.

Female reproductive activity was predominantly associated with oestrus, but the mean frequency of reproductive behaviours was low (<1 bout per hour). Backward walking, rolling, inguinal presentation and cradling were more common during oestrus, whereas masturbation occurred more frequently during pregnancy (Figure 2.43). Inguinal presentation was exclusively associated with oestrus whereas nesting was only observed during pregnancy. The only reproductive behaviour observed for the male was rolling, and occurrences were rare.

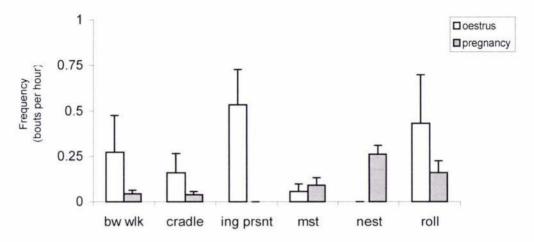


Figure 2.43: Comparison of reproductive behaviours by female Chomel (#607) during oestrus and pregnancy in 1997. Bw wlk = backward walk, ing prsnt = inguinal present, mst = masturbate. Bars show I standard error of the mean.

Backward walking became apparent during week -14, peaking in frequency, but remaining elevated until week -11 (Figure 2.44a). The duration of bouts increased steadily between weeks -14 and -11. Backward walking was less common during pregnancy. Rolling showed a similar pattern to backward walking, however, a second peak occurred during week -4 (Figure 2.44a). Rolling declined in frequency during week -3, and then rose steadily toward the end of gestation. There was a concurrent rise in the duration of bouts between weeks -3 and 0 (data not shown). Inguinal presentation was the most prominent reproductive behaviour (see Figure 2.43) and occurred consistently between weeks -18 to -14 (Figure 2.44b). Although cradling was more frequent during oestrus, the behaviour was especially noticeable during pregnancy because it was exhibited consistently throughout the gestation (Figure 2.44c).

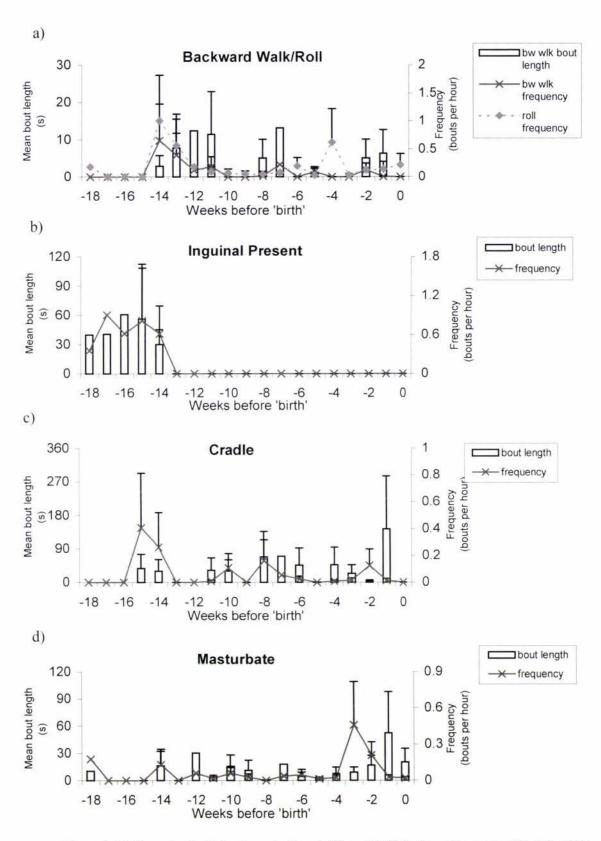


Figure 2.44: Reproductive behaviours for female Chomel (#607) aligned by week of birth in 1997.

a) Duration and frequency of backward walk and frequency of roll, b) duration and frequency of inguinal presentation, c)) duration and frequency of cradle and d) duration and frequency of masturbation. Bars show 1 standard error of the mean.

Masturbation was the least frequent reproductive behaviour (Figure 2.43), but was exhibited fairly regularly throughout oestrus and pregnancy. A slight peak in frequency was observed at oestrus, but a more marked increase occurred near the end of gestation (Figure 2.44d). The rise in frequency was accompanied by a steady increase in bout length. A direct comparison of nesting behaviour over the three reproductive cycles is not possible because the activity was usually performed out of sight within a den, and surveillance equipment was only used regularly during one pregnancy. Data from video tapes obtained during Period 5, however, support the observation that an increase in the rate and duration of nesting occurs at least 2 weeks prior to the end of gestation.

2.3.3.10.2 Interactive Behaviours

The rate of interactions between the bears was higher during oestrus (oestrus $8.9 \pm SE$ 1.2 mins per hour; pregnancy $5.4 \pm SE$ 1.2 mins per hour); and marked by a large peak during week -15 (~15 mins per hour) that declined gradually to baseline levels by week -12 (data not shown). During oestrus the majority of interactions were affiliative, and for the female, heat was also characterised by a high proportion of contact behaviours (see Ethogram; Section 2.3.1.5 for details). For the female, pregnancy was associated with a decrease in the proportion of affiliative behaviours and a complementary increase in agonism (Figure 2.45). A slight rise in agonism was evident for the male.

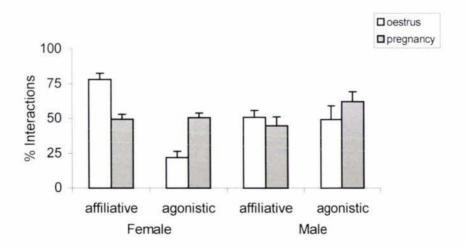


Figure 2.45: Comparison of interactions (affiliative and agonistic) between female Chomel (#607) and male Bakti (#617) during oestrus and pregnancy in 1997. Bars show 1 standard error of the mean.

The onset of oestrus was marked by a conspicuous increase in the male's frequency of approaching, following and olfactory investigation of the female (Figure 2.46). For the female, a similar pattern of approaching and following was apparent. Other modes of olfactory communication including sniffing of the partner and naso-nasal contact were very frequent during oestrus, and occurred up to 10 times each hour.

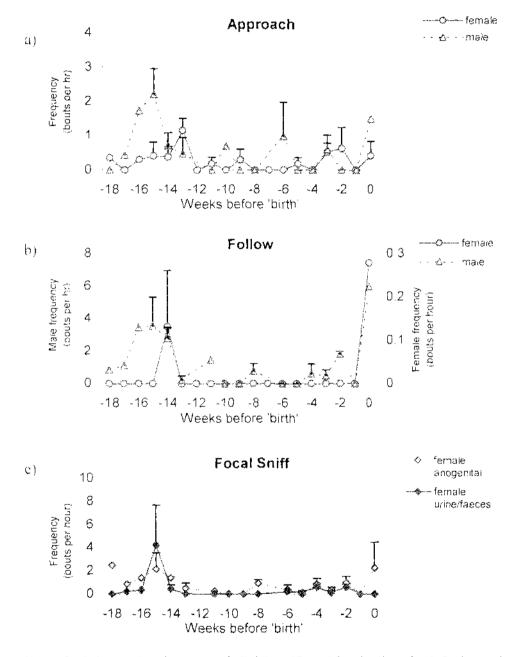


Figure 2.46. Interactions between male Bakti (*617) and female Chomel (*607) during the reproductive cycle in 1997. Frequency and duration of anapproach and b) follow. c) Frequency and focus of olfactory investigation (sniffing) by the male. Bars show I standard error of the mean.

Jaw-wrestling was mainly observed during oestrus (Figure 2.47), when a steady rise in frequency was matched by a significant increase in the duration of bouts (p = 0.035; Figure 2.48). Head-jockeying was less frequent, but a similar pattern was observed (data not shown). After oestrus there was an increase in intensity and reduction in the length of jaw-wrestling bouts.

Jaw gaping showed a clear change in pattern with context. During oestrus, gaping was used to convey low-level threat such as warning off an approach, or terminating an encounter. The signal was brief (<1 sec) and the mouth was held slightly open. At other times the mouth was held open for up to 5 seconds and the behaviour was associated with high-level aggression. The teeth were partially or fully exposed and gaping was sometimes accompanied by whining and growling or snapping of the jaws and biting (see Plate 2.6; Section 2.3.3.8).

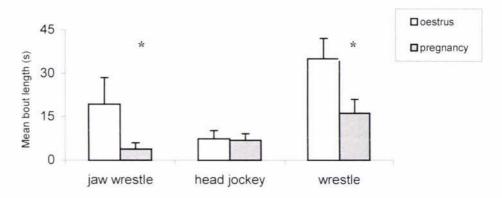


Figure 2.47: Comparison of duration of interactions (jaw wrestle, head jockey and wrestle) between male Bakti (#617) and female Chomel (#607) during oestrus and pregnancy in 1997. Bars show 1 standard error of the mean. Asterisks indicate a significant difference (p < 0.05; Mann-Whitney test; n for oestrus = 10, pregnancy = 29) between oestrus and pregnancy.

Wrestling occurred throughout the year, but was particularly noticeable activity when the female was in heat. Bouts were common (up to 3 times per hour) and lasted for up to a minute in length (Figure 2.48). The frequency of wrestling increased at peak oestrus and declined to mean levels after week -13. The bears were often observed wrestling during the last month of pregnancy, however, the form of the interaction had altered greatly. Bouts were significantly shorter (p = 0.015; Figure 2.47) and were less 'playful'. Aggressive vocalisation (growling and roaring) was often heard during wrestling, and clawing and biting was less restrained, resulting in minor wounding to both bears.

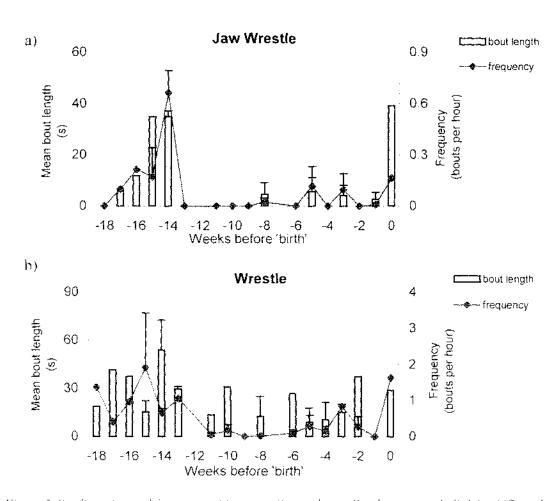


Figure 2.48: Duration and frequency of jaw wrestling and wrestling between male Bakti (#617) and female Chomel (#607) during the reproductive cycle in 1997. Bars show I standard error.

During oestrus episodes of bodily contact were more regular, and the pair remained in contact for longer periods of time (Figure 2.49). Mounting or 'standing over' the partner was infrequent, but could be observed at any time. The behaviour appeared to be used to assert dominance as well as during sexual activity and there were distinct differences in the pattern of mounting between the sexes.

When Chomel was in heat, the male usually mounted from behind and clasped her about the middle, sniffing at her neck and ears; pelvic thrusting and intromission were sometimes observed. During oestrus Bakti mounted more frequently (data not shown), bouts were comparatively longer (Figure 2.49), and he spent a higher proportion (90%) of time on top. Chomel usually mounted the male from the side and showed a tendency to 'stand over' him with her paws upon his back. At times, she approached Bakti when he was seated and draped herself over him from behind (Plate 2.8). During oestrus, her mounts of the male were relatively brief (Figure 2.49) and associated with playful

interactions. During pregnancy, the female spent a higher proportion of time on top (80%) and the behaviour was primarily associated with agonistic encounters.

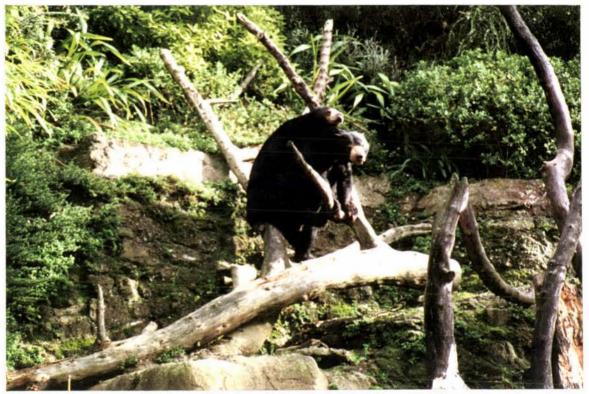


Plate 2.8: Sun bears at Wellington Zoo, May 1997. The female ('Chomel' #607) remained draped over the back of the male ('Bakti' #617) for several minutes, periodically grooming his head and shoulders. Note the degree of sexual dimorphism, particularly the broad head of the male.

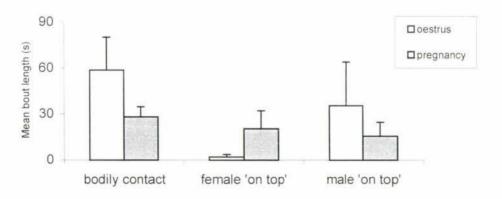


Figure 2.49: Comparison of duration of bodily contact and mounting ('on top') behaviour between female Chomel (#607) and male Bakti (#617) during oestrus and pregnancy in 1997. Bars show 1 standard error.

An interaction that occurred regularly during pregnancy was allogrooming of the male by the female. Bakti usually attempted to shrug Chomel off but she typically persisted by either tightening her grip, or using threat (jaw gaping) and light biting to try to prevent him from moving away. The behaviour became increasingly frequent toward the end of gestation (Figure 2.50a). For the female, another behaviour that was very

noticeable prior to parturition was nickering. The vocalisation was heard during oestrus and pregnancy, but was emitted more regularly and with increasing frequency prior to 'birth' (Figure 2.50b).

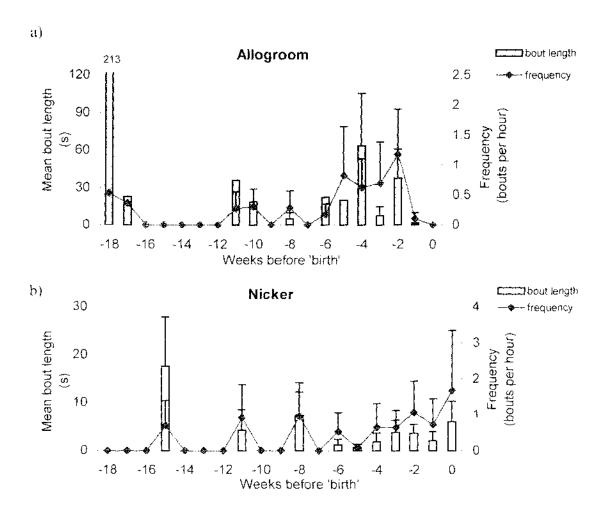


Figure 2.50: Duration and frequency of aiallogrooming and hi nickering by female Chomel (#60°) during the reproductive cycle in 199°. Bars show I standard error.

2.3,3.11 Vulva Characteristics

Size, colour and moisture of the female's vulva were recorded each week as a potential indicator of reproductive status. Characteristics were graded as for female #598 (see Section 2.3.2.2.4). During oestrus and pregnancy swelling of the labia and reddening of the vaginal mucosa was observed, and a clear to pale discharge was often present. Chomel's genitals generally remained red and swollen throughout 1997 in accordance with continuous reproductive activity. Her vulva did. however, tend to be most engorged at peak oestrus and in the week prior to parturition (data not shown).

2.3.3.12 Postscript

The following information covering the period December 1997 - July 1999 was compiled from reports kindly provided by Wellington Zoo.

2.3.3.12.1 December 1997 - December 1998

Behaviours exhibited by the bears suggest that after the birth on December 11 1997 Chomel entered post-partum oestrus within several weeks. The female did not exhibit any aggression toward the male when she encountered him during morning servicing of the maternity wing, and on one occasion nickering vocalisation was heard. Around this time, the bears began pacing about in their separate enclosures, and were described as acting "agitated." In late January oestrus was presumably over, because the female began to show aggression toward the male again.

Reintroduction of the bears occurred during August 1998, and on 04 September they were observed copulating. Approximately 2 weeks later the female began to exhibit aggression toward the male, using high levels of agonistic vocalisation (growls, barks and roaring) during disputes over food or at times when the male was in proximity. Because of the change in their behaviour, the pair were separated temporarily and the female was given access to the north dens and maternity wing. They were reintroduced several days later but continued to avoid close contact and the number of altercations gradually diminished.

In November 1998 Chomel's physical condition was reported to have changed - keepers noted that her nipples were reddened and she had an obvious abdominal bulge. Based on physical and behavioural signs, the female was given access to the maternity wing in the evenings, and was sometimes kept separated from the male during the day. Although the north dens were also left open for her use overnight, she showed a preference for the maternity den.

On 10 December, Chomel was frequently heard nickering and seen trying to interact with the male throughout the day. She was observed following Bakti about the exhibit and nipping him, and bouts of wrestling occurred. The female's behaviour was interpreted by the keepers as "late-stage pregnancy anxiety or cycling/wanting to mate." Because keepers felt that Chomel did not want to be separated from the male, the pair were left together in the exhibit overnight with access to the north and south dens.

On the morning of 11 December cub vocalisation was heard from the south dens. To minimise disturbance servicing of the enclosure was suspended and visits to the area were minimised. The maternity wing was opened, and the male spent most of the day in the cubbing area and north dens. The female did not emerge from the south dens.

On 12 December Bakti was excluded from the exhibit; the female remained in the south den and cub vocalisation was still heard. The female was temporarily shut in while keepers entered the area outside to provide food and nesting material nearby. Food was offered in this manner daily, and was sometimes gone by the following morning.

On 18 December, Chomel was observed in the exhibit during the morning and in the afternoon; the cub(s) was reported to be less vocal. On 19 December cub noises were not heard, but when the female came out to feed swelling of her mammaries appeared to indicate that she had been suckling young. For the next ten days, Chomel remained in the south dens for the majority of each day and typically only emerged to feed. When she encountered the male through the north den door, she showed no apparent aggression.

Due to concerns that cub noises had not been heard for over a week, on 29 December when the female left the south den it was thoroughly searched, but no young were found. It was thought that the cub(s) died on 18 or 19 December, because experienced staff from San Diego Zoo confirmed that Sun bear cubs usually continued to be noisy. Bakti and Chomel were reintroduced without any apparent aggression - nickering was heard from the female and the pair were observed "play-fighting". Behaviour exhibited by the bears suggested that the female came into heat within several days, but by the following week she had begun to show aggression toward the male once more.

2.3.3.12.2 January - April 1999

Throughout January and February Chomel continued to exhibited periodic aggression toward the male. In February she was permitted access to the maternity wing overnight, and in March was isolated in the cubbing area full-time and remote surveillance of the sleeping quarters began. An increase in Chomel's nesting activity and reduction in appetite was apparent near the end of March, and in the first week of April Chomel acted with uncharacteristic aggression toward a keeper. On 09 April she was reported to be somewhat restless and a further increase in nest-building was observed.

On 10 April at c.02.00 hrs the female gave birth to live twins. The keeper that arrived in the morning heard cub vocalisation, and servicing of the area was suspended but to maintain a higher level of privacy, keepers did not enter the area at all. Food was not offered for ~5 days, and a routine for keeper feeding/visits was established for predictability. A routine was implemented because Chomel had become obviously disturbed, and barked aggressively at a member of staff that arrived earlier than usual.

Throughout April Chomel remained in the den most of the time with the cubs, which continued to be vocal. When she left them to feed outside, they usually responded by screaming loudly. She did not show an obvious increase in appetite until May.

The cubs (both male) were first seen clearly during June when they began to leave the den, and both showed quite extensive hair loss. Because the bare patches were thought to be due to a mite infestation, the dam was given oral doses of ivermectin (0.4% Ivomec oral for cattle) so the cubs would ingest the treatment during suckling. Because the skin problem persisted, in July, Chomel was anaesthetised so her cubs could be separated for a general check-up and medical examination. The cause was found to be a double bacterial infection (*Staphylococcus* and *Acinetobacter*), which was successfully remedied with Clavulox.

2.4 DISCUSSION

There is little information about the reproductive behaviour of free-ranging bears. Knowledge mainly concerns mating habits of the Brown bear (*U.arctos*), the American black bear (*U.americanus*), the Polar bear (*U.maritimus*) and the Giant panda (*A.melanoleuca*), but is generally, qualitative and brief (Craighead et al 1969; Jonkel & Cowan 1971; Herrero & Hamer 1977; Herrero 1978; Barber & Lindzey 1983; Schaller et al 1985; Ramsay & Stirling 1986; Hamer & Herrero 1990; Brady & Hamer 1992). Within zoos the Giant panda, because of its conservation status has been the focus of most research. Accordingly, sociosexual and periparturient behaviour of captive Giant pandas has been documented in qualitative and quantitative detail (Kleiman et al 1979; Kleiman 1983), and forms the basis of the comparative literature given here.

This study included preliminary information on all aspects of Sun bear behaviour, however, the following discussion focuses on inter-sexual and reproductive behaviour of *U.malayanus*. Other ursids have a distinct breeding season so that even if copulation is not observed, dates of parturition can still be estimated and preparation for birth made ahead of time. With Sun bears however, copulation and birth can occur at any time of year (Dathe 1970; Kolter 1995; Schwarzenberger et al 1997). It is thereby important to identify a set of behaviours associated with oestrus and impending parturition to assist in detecting reproductive activity.

2.4.1 The Reproductive Cycle

Sun bears have some unique reproductive features that suggest adaptation to tropical conditions. In addition to having no fixed breeding season in captivity, they do not appear to have delayed implantation characteristic of other members of the Ursidae. Gestation is comparatively short, much less variable and more equivalent to the period of foetal growth in other bears (Mead 1989; Schwarzenberger et al 1997; Chapter 3). Furthermore, when cubs die or are removed the dam can undergo postpartum oestrus in one-two weeks (McCusker 1974; Pagel & Kuhme 1992; Kolter 1995). This reproductive strategy coupled with an abbreviated gestation period means that Sun bears are capable of giving birth several times a year (Dathe 1970; McCusker 1974; Kolter 1995).

These features were evident for the female Chomel who underwent three successive reproductive cycles in 1997. Hormone profiles showed that postpartum oestrus also occurred in Moon following the removal of her young in February 1997 (Chapter 3). Although Chomel remained reproductively active throughout 1997, periods of reproductive quiescence lasting for several months can occur in female Sun bears (Schwarzenberger et al 1997).

2.4.1.1 Oestrus

The length of behavioural oestrus in females varied from two-five weeks, with the receptive period apparently limited to approximately one week. This is consistent with published reports for both the Sun bear (Domico 1988; Schaller 1994) and other ursids (*U.arctos*: Meyer-Holzapfel 1957 cited in Ludlow 1974, Dittrich & Kronberger 1962, Hornocker 1962 cited in Barber & Lindzey 1983; Craighead et al 1969; *U. americanus*: Ammons 1974 cited in Barber & Lindzey 1983; Ludlow 1974; Barber & Lindzey 1983; *A. melanoleuca*: Kleiman 1983; Schaller et al 1985; *T.ornatus*: Bloxam 1976, Orejuela 1989).

Female bears typically have a monoestrus cycle, but evidence of a second period of heat in the breeding season suggests that polyoestrus cycling can occur in some species (*U. arctos:* Dittrich & Kronberger 1962; Craighead et al 1969, Tsubota et al 1985 cited in Tsubota & Kanagawa 1986; Tsubota & Kanagawa 1986; *U. americanus:* Barber & Lindzey 1983, Rowlands & Weir 1984; *T. ornatus:* Bloxam 1976). To date, this information has been based on behavioural observations and physical changes (vulva swelling) associated with oestrus. Behavioural observations suggest polyoestrus cycling occurred in the WZG Sun bear, and has been confirmed by hormone profiles (Chapter 3).

2.4.1.2 Pregnancy and Pseudopregnancy

Most reports indicate that gestation length in *U.malayanus* lasts approximately 95-100 days (Dathe 1961, 1963, 1966; 1970; Kuhme 1990; Pagel & Kuhme 1992; Frazier & Hunt 1994; Schaller 1994; Chapter 4), and this has been supported by recent reproductive endocrinology studies (Schwarzenberger et al 1997; Chapter 3). The length of gestation from last observed copulation/end of oestrus to birth was within this range for all study animals. Keeper notes from both zoos indicated that pregnancies were of a similar duration at other times.

Chomel underwent an extremely overt pseudopregnancy between May-September 1997. Pseudopregnancy (also called 'false' or 'phantom' pregnancy) occurs in a variety of carnivores, and is caused when the corpus luteum (the ovarian structure responsible for maintaining pregnancy) continues to function although conception has failed. The length of pseudopregnancy and its hormonal influence was similar to 'true' gestation (Chapter 3), as reported for other ursids (Bretzfelder 1989; Hellgren et al 1991; Tsubota et al 1992; Göritz et al 1997). Because the two states are physiologically similar, they were considered collectively to represent gestation and have been treated as such in the following discussion.

2.4.2 General Observations

The observation of pairs at San Diego Zoo (ZSSD), and the pair at Wellington Zoo (WZG) differed markedly. Data from ZSSD was collected on a daily basis rather than weekly, and for a shorter period (*i.e.* two weeks compared to ten months). Furthermore, management of the bears differed substantially between study sites: the WZG pair had been together on a fairly permanent basis since they were juveniles, whereas Pair B at ZSSD were less familiar with each other and introductions were staged for limited periods each day. This provided the opportunity to examine and compare the development of social behaviours between a cohabiting pair, and a relatively unfamiliar pair, when the female entered oestrus. In addition, alternative management of the bears (between and within study sites), allowed analysis of the effects of different grouping arrangements on captive breeding of Sun bears.

Understanding a species' social requirements is paramount to providing effective captive management strategies for successful breeding (Kleiman 1980). The natural behaviour of Sun bears is unknown, but their social structure is probably shaped by evolutionary pressures similar to those experienced by other ursids (*i.e.* foraging strategies and lack of interspecific predation) (reviewed in Chapter 1). The findings of this study strongly suggest that Sun bears are asocial, as other bears are known to be. Even during mating periods, they spent the majority of their time in solitary behaviours, usually maintaining large 'individual distances' (>10m) by mutual avoidance. Most interactions between males and females were brief and limited to body posture and display, with affiliative behaviours and non-aggressive contact largely restricted to episodes of oestrus. Similar observations are apparent for Sun bears kept at other zoos (Table 2.2; Section 2.2.2.4), and in other ursids amicable interactions between pairs are

rare outside of the mating period (Bledsoe 1975; Henry & Herrero 1974; Kleiman et al 1979; Ames 1992; Forthman 1995).

2.4.3 Solitary and Social Behaviour During Oestrus

2.4.3.1 Activity Pattern

In male and female Sun bears sexual activity was characterised by reduced interest in feeding, general restlessness, and heightened levels of interest and encounters between a pair. Periods of anorexia and restlessness were particularly noticeable with females showing 'anxious' behaviour and sometimes rapid pacing during oestrus. Feng and Wang (1991) report that during oestrus Sun bears are active for eight-ten hours each day.

In other bears oestrus is also associated with low appetite and higher levels of activity including pacing and restlessness (Kleiman 1983; Schaller et al 1985; Rosenthal 1989a; Partridge 1992), but activity may decline when the female becomes receptive (Kleiman 1983). Similar behaviour is described for pairs of free-ranging grizzlies during the mating period (Herrero and Hamer 1977; Stelmock 1981, Hectel 1985, Phillips 1986 cited in Harting 1987a).

Olfactory signals play an important role in ursid communication (Jordan 1974; Colmenares & Rivero 1983; Kleiman 1983; Stirling & Derocher 1993; Swaisgood et al 1999), and were a prevalent interactive behaviour between the Sun bears. Quantitative analysis confirmed that both sexes showed highest levels of interest in their partner's anogenital region and excreta at peak oestrus, illustrating the importance of chemosensory cues during the breeding season.

2.4.3.2 Courtship

Although the WZG Sun bears were housed together most of the time, onset of breeding was characterised by initial agonism, apparently as they adjusted to more frequent encounters. At ZSSD, initial encounters between Pair B were characterised by much higher levels of aggression until the male established dominance. Despite the familiarity between a pair, the development of affiliative behaviours appeared equally important in maintaining a close association during oestrus.

Breeding included a period of courtship established at least one week before copulation. Although there was a greater compatibility between a pair during the mating period, their relationship remained tenuous. During the breeding season, some free-ranging bears form similar, temporary associations (Dean 1976 cited in Harting 1987a; Herrero & Hamer 1977; Murie 1981 cited in Harting 1987a; Barber & Lindzey 1983; Schleyer 1983 cited in Harting 1987a; Schaller et al 1985; Ramsay & Stirling 1986; Orejuela 1989; Brady & Hamer 1992), which is typical of courtship and mating patterns in solitary, dangerous species (Ewer 1985).

The female controlled the development of the relationship using behavioural cues; firstly, to attract the male and maintain his attention, and later to communicate her readiness to mate. This pattern is typical of female mammalian reproductive behaviour, and has been shown to be influenced by hormone levels that signal the optimal time for breeding (Beach 1976). Several researchers have drawn attention to the female's role in controlling interactions and influencing the progression of courtship in other species of bear (A.melanoleuca: Kleiman et al 1979; U.americanus: Barber & Lindzey 1983; U.arctos: Hornocker 1962, Egbert 1978, Murie 1981 cited in Harting 1987a).

Courtship involved extensive and amicable contact and olfactory investigation between a pair. During this stage of their association, pairs spent more time together, briefly engaging in non-aggressive physical contact. The playful context of interactions such as jaw wrestling, head-jockeying and wrestling increased. These courtship activities are typical of Sun bears (Domico 1988; Kuhme 1990) and other ursids (Hornocker 1962 cited in Harting 1987a; Craighead et al 1969; Herrero & Hamer 1977; Kleiman et al 1979; Kleiman 1983; Hamer & Herrero 1990; Kitchener 1992). Mock-fighting is a common courtship behaviour among bears, that may allow individuals to assess the reproductive status of a partner without serious conflict (Ewer 1985) and may also function to assess mate-worthiness.

2.4.3.3 Behaviour of the Male

When the female entered oestrus, olfactory and gustatory investigation of the anogenital region by the male was common. Males often followed close behind the female to sniff or lick her rear end and showed a strong interest in her urine and faeces. Males may be more responsive to conspecific scent than females (Swaisgood et al 1999), and this behaviour is typical as they check the reproductive status of a potential mate (Meyer-Holzapfel 1957 cited in Ewer 1985; Craighead et al 1969; Tschanz et al 1970; Herrero & Hamer 1977; Kleiman et al 1979; Hamer & Herrero 1990).

The male at WZG (Bakti) often exhibited heightened levels of aggression when his partner was in oestrus. He directed threatening behaviour toward staff and members of the public and walked about with a characteristic stiff-legged gait, occasionally charging toward people and barking loudly. In the presence of females, sexually aroused male grizzlies are recognised by a similar stiff-legged or swaggering gait; they may also salivate profusely and urinate on their belly and legs (Harting 1987a). Free-ranging male bears use antagonistic displays and fighting to establish a social dominance hierarchy and gain breeding opportunities (Herrero 1978; Barber & Lindzey 1983; Ramsay & Stirling 1986; Schaller et al 1985; Garshelis & Hellgren 1994), and these behaviours would appear to distinguish the 'rut' caused by rising levels of the hormone testosterone (Lincoln 1981; Nelson 1995).

A seasonal increase in testosterone has been documented for male bears (*U.americanus:* McMillin et al 1976; Palmer et al 1988; *U.maritimus:* Palmer et al 1988; *A. melanoleuca:* Bonney et al 1982; Kubokawa et al 1992; *U.arctos:* Tsubota & Kanagawa 1989), and this may facilitate heightened aggression between males (Garshelis & Hellgren 1994). Although Sun bears are not seasonal breeders increases in testosterone have been associated with mating activity in males, and during this study elevated levels were detected for males at both zoos during episodes of breeding (Chapter 3).

During Chomel's oestrus, Bakti frequently herded her to a secluded area in the exhibit, and prevented her frequent attempts to leave the area. The mating system of free-ranging bears depends on the density and distribution of the population, and in more remote areas males may herd or 'sequester' females during the breeding period (reviewed in Chapter 1). A potential function of this mate-guarding is that isolation of the female from other adult males can ensure paternity of a litter (Bunnell & Tait 1981; Ramsay & Stirling 1986; Hamer & Herrero 1990), and Hamer & Herrero (1990) suggest that female 'mock' attempts to escape may test male vigour.

2.4.3.4 Behaviour of the Female

Female Sun bears showed a characteristic increase in self-maintenance and reproductive behaviours when they were in 'heat'. Oestrus appeared to be associated with general body surface irritability causing frequent scratching, rubbing and rolling. During grooming females focused on their nipples and vulva, and swelling and reddening of these areas was obvious. During oestrus, progressive changes of the vulva are also apparent for the Giant panda (Knight et al 1985; Murata et al 1986), and swelling and reddening of the vulva is reported to accompany the mating period in other bears (*U.americanus*: Erickson et al 1964, Eiler et al 1989; *U.arctos*: Hensel et al 1969; Harting 1987a; *T.ornatus*: Bloxham 1976; Orejuela 1989, Rosenthal 1988, Weinhardt 1988). Morphological changes to these 'target tissues' are commonly associated with mammalian oestrus and result from underlying hormonal influences (Beach 1976; Beach et al 1982; Feldman & Nelson 1996). In agreement with this, for female #598 progressive changes of the vulva were associated with increasing levels of oestradiol at oestrus (see Chapter 3; Section 3.3.1.1). It is also likely that physical stimulation of the nipples and vulva may contribute to swelling and reddening.

Female Sun bears exhibited reproductive behaviours one-two weeks before becoming receptive. The range of reproductive behaviours were common to both females¹⁷, and included rolling, backward walking, masturbation and inguinal presentation. A similar range of reproductive behaviours have been described for the Giant panda in which oestrus is also characterised by conspicuous vocal communication (Kleiman et al 1979, Kleiman 1983, Schaller et al 1985). Generally, affiliative vocalisation is not commonly associated with breeding activity in other bears (Kleiman 1983), but during oestrus female Sun bears emitted frequent 'nickering' calls. The vocalisation often occurred in association with reproductive behaviours such as backward walking or masturbation, and may assist in advertising to males. Keeper log books from various zoos (see Table 2.2; Section 2.2.2.4) indicate that vocalisation is a common component of oestrus behaviour for female Sun bears.

Vocal signals may be important for communication between forest-dwelling bears according to Herrero (1980) and Stirling & Derocher (1993), and vocalisation also accompanies breeding activity in Spectacled bears (Rosenthal 1989b; Weinhardt 1988). Sun bears and Spectacled bears are the most arboreal ursids (Stirling 1993a), which may explain why females of these two species emit conspicuous calls during oestrus.

When females became receptive, they behaved submissively when the male approached, often lying down and presenting the inguinal region. Submissive posturing and

¹⁷ Cradling behaviour seen exclusively in the Wellington Zoo bear, is considered later in the discussion.

anogenital presentation are also used by female Brown bears to communicate their readiness to mate (Hornocker 1962 cited in Harting 1987a; Herrero & Hamer 1977) and the Giant panda female may present by lifting her tail (Kleiman et al 1979; Kleiman 1983). Inguinal presentation was the most prominent reproductive behaviour for both female Sun bears during oestrus and appeared to combine submissive posturing with exposure of the genitalia. Although the tail of Sun bears is shorter than that of the Giant panda it still covers the anogenital area. Raising of the tail, however, was not observed in Sun bears, and when a male inspected a female from behind he sometimes held her tail aside for closer scrutiny.

The relative proportion of time each sex spent mounted or 'on top' varied but appeared to indicate that male bears were dominant. Although both sexes 'stood over' their partner, during oestrus males often mounted the female from behind and clasped around her middle - the typical copulation pattern shown by bears and other carnivores (Kleiman 1983). Male mounting of the female was much more frequent and often accompanied by pelvic thrusting. Although pelvic thrusting was not observed in females, it has been reported for other female bears during sexual activity (Henry & Herrero 1974; Bloxam 1976; Kleiman 1983; Kuhme 1990). Mounting by females was more common during the proceptive period, as has been noted for the Giant panda (Kleiman et al 1979). This behaviour is thought to incite males to reciprocate and backing into the male or crouching also encourages the male to mount (Beach 1976).

Increasing compliance by the female, particularly when being mounted, signalled the onset of receptivity and her readiness to mate. The transition was more evident for the San Diego pair, with the previously uncooperative female standing during all mounting attempts after she entered 'peak' oestrus. This assists the male to achieve intromission (Beach 1976), and copulation was not observed prior to this time.

2.4.3.5 Copulation

As noted for other bears, males often used neckbites and holds, during mounting and copulation (Mundy & Flook 1963, Herrero & Hamer 1977; Ludlow 1974; Kleiman 1979; Schaller et al 1985; Tsubota & Kanagawa 1986; Kuhme 1990). The copulatory postures of Sun bears were similar to those in other ursids (Mundy & Flook 1963; Sparrowe 1968; Ludlow 1974), and was also performed with the female half-seated and the male squatting behind, as reported for the Giant panda (Kleiman et al 1979; Schaller

et al 1985). Davis (1964 cited in Schaller et al 1985) suggests this unusual position may be necessary for the Giant panda because of its comparatively short penis. The baculum, or penis bone, of the Sun bear is relatively short compared to other ursids (Dixson 1995), which may explain why they sometimes copulate in this position.

The general pattern of copulation was analogous to that reported for other ursids: Mounting of the female and periodic thrusting movements by the male were followed by quivering of the male's hindlegs, which is thought to indicate ejaculation (Meyer-Holzapfel 1957 cited in Ludlow 1968; Tsubota & Kanagawa 1986). Immediately after, the female terminated contact using aggressive vocalisation and threat behaviour, or lurching out from under the male and running away. This post-copulatory response is commonly reported for ursids, with the period of avoidance between pairs often lasting for several hours afterward (Ludlow 1974; Bloxam 1976; Herrero & Hamer 1977; Kleiman 1979; Schaller et al 1985).

Male mounting varied in length, those lasting less than five minutes were generally not associated with intromission or completion of copulation. The baculum length has been related to copulatory behaviour of carnivores, and based on this Dixson (1995) predicted intromission would be briefer in the Sun bear. Bouts of copulation, however, lasted 5-30 minutes which is consistent with records for other species of bear (Mundy & Flook 1963; Ludlow 1974; Schaller et al 1985; Tsubota & Kanagawa 1986). For most ursids a single ejaculation is followed by a prolonged quiescent period of ten hours or more (Kleiman 1983), but in Sun bears the interlude between copulations was sometimes as brief as an hour.

Some carnivores, like canids, ovulate spontaneously (Milligan 1982; Rowlands & Weir 1984) but copulation or a similar stimulus is necessary to induce ovulation in other species. Induced, or 'reflex' ovulation has been confirmed for American black bears (Boone et al 1998) and is suspected to occur in other ursids (Ewer 1973 cited in Schaller et al 1985; Kleiman 1983) with the possible exception of the Giant panda (Kleiman 1983; Schaller et al 1985). Physical stimulation by the baculum may play a role in inducing ovulation (Dixson 1995). The pattern of frequent mounting and copulation is characteristic of species with induced ovulation (Kleiman 1983), lending further credence to the presence of this reproductive mechanism in bears.

When male and female Sun bears were housed together permanently, copulation was often missed. This is a potential problem associated with permanent grouping of pairs because if mating is unobserved it is difficult to predict when parturition will occur (Kuhme 1990; Pagel & Kuhme 1992; Schaller 1995). Pagel & Kuhme (1992) have suggested that in Sun bears copulation takes place at night, but although pairs sometimes acted secretively during mating (e.g. semi-hidden behind structures), copulation occurred during the day and in the vicinity of crowds (i.e. during public feeding). At San Diego Zoo encounters between Pair B were only staged for limited periods during the day when the female was in oestrus. Copulation occurred regularly and the breeding episode was successful, indicating that grouping pairs permanently may not be necessary to ensure fertilisation occurs.

When the female was no longer receptive reproductive behaviours became uncommon and episodes of mounting were rare. The end of 'heat' was characterised by waning interest, and mutual avoidance signalled the dissolution of their breeding association. Encounters soon after were marked by low-moderate levels of aggression. For other captive bears, a reduction in sociability and affiliative behaviour similarly occurs after oestrus (Kleiman 1985; Rosenthal 1989a; Ames 1992). In a free-ranging situation bears are likely to go separate ways after the breeding season (Bunnell & Tait 1981).

2.4.4 Solitary and Social Behaviours During Pregnancy and Pseudopregnancy

Management of the Sun bears at WZG varied during 1997, but in general the pair were housed together for most of the year. Although periods of oestrus activity and copulation were documented, separation was not usually initiated until female behaviours indicating late-stage pregnancy, *i.e.* nesting activity, became evident. The following section deals mainly with the behaviour of the WZG bears; because data collected for Pair A at San Diego Zoo were limited to observations conducted over the two days prior to the female giving birth. Nonetheless, this provided the opportunity for a comparison of periparturient behaviours, and has been augmented with keeper records of subsequent births in the study animals.

2.4.4.1 Solitary Behaviour of the Female

During pregnancy Chomel sometimes cradled inanimate objects including 'cub-sized' food items and pieces of wood or bark. This behaviour is considered a maternal care pattern because it resembles the way a mother bear supports her young cub during

grooming and nursing (Kleiman 1983). Periparturient Giant pandas have also been reported to cradle food items (apples and carrots), and the persistence of this behaviour in the absence of young indicates the strength of the maternal instinct (Kleiman 1985; Chadhuri et al 1988). For Chomel, cradling was also observed during postpartum oestruses. The absence of young following stillbirth and pseudopregnancy may explain why cradling occurred during oestrus in this particular individual.

Approximately one month before the end of gestation, Chomel showed signs of general discomfort; scratching, rubbing and rolling were frequent, and at times she appeared unwell, periodically hunching over her stomach. Ultrasound studies of Brown bears have demonstrated accelerated foetal growth in the last month of gestation (Tsubota et al 1987; Göritz et al 1997), and it is possible that discomfort was experienced from foetal movement. This does not, however, explain the similarity in symptoms exhibited during pseudopregnancy, but suggests there may be a contributing hormonal influence, similar to the restlessness exhibited at oestrus.

2.4.4.2 Social Behaviour

After oestrus encounters were much less common. Social interactions involved similar ritualised body posturing (jaw-wrestling, head-jockeying and wrestling) but were distinctly less playful with bouts often ending abruptly in threat and aggression. Altercations sometimes occurred during feeding, and unlike at oestrus, theft was not tolerated. Food-related aggression is commonly reported among Sun bears at other zoos (Schaller 1995; Table 2.2; Section 2.2.2.4), but it is interesting that this was rare during oestrus. This may be reflect the bears' reduced interest in food at this time or the higher level of compatibility between pairs.

At times affiliative interactions occurred, and when the pair sat together the female briefly groomed the male. Allogrooming by the female was common during her first and second pregnancy, but was performed in a domineering manner. Female allogrooming became increasingly frequent and persistent prior to the end of each pregnancy, and was also exhibited by Moon at San Diego Zoo the day before she gave birth. Allogrooming may facilitate bonding between a pair, but was uncommon during oestrus, and its high frequency during late-gestation was surprising given the female's aggressive manner at this stage of pregnancy and during the interaction. Possibly allogrooming serves as an outlet for the female's growing maternal tendencies.

At WZG altercations between the bears became more common with each successive pregnancy. The female's hostility toward the male increased noticeably approximately one month before the end of gestation. She began to threaten and challenge the male frequently and tried to dominate the male. Bakti responded quickly to any challenge and maintained his dominance over the female. When the female was separated she was highly defensive of the maternity area prior to the birth. A marked rise in aggression was also documented for the San Diego Zoo female Moon, a day before she gave birth. Altercations were reported between the same pair prior to a subsequent birth (Log books ZSSD), and other zoos that maintain Sun bears (Table 2.2; Section 2.2.2.4) have similarly noted more disputes around the time parturition is expected.

Management policies differ between zoos with regard to separation of pairs after mating; but when bears are housed together during pregnancy or prior to parturition, signs of avoidance and increased aggression are common (Bastien et al 1985; Villares et al 1985; Reed 1989; Rosenthal 1989a; Weinhardt 1988). The females' increasingly hostile nature appears to represent her strong desire to be alone prior to the birth. In free-ranging bears segregation of sexes occurs and is related to the avoidance of males by females (Bunnell & Tait 1981; Derocher & Stirling 1990; Weilgus & Bunnel 1994; Joshi et al 1995). Males are competitive and aggressive, so this strategy improves the chance that a female can rear young by reducing the possibility of infanticide (reviewed in Chapter 1).

In captivity, separating potentially pregnant female bears from conspecifics prior to birth has been crucial to improving breeding success. Clearly the level of compatibility varies between pairs, however, separation of a potentially pregnant female should occur early enough for her to get accustomed to the maternity facility, and isolation allows her to build a sense of security prior to the birth (Rosenthal 1989b; Linke 1998).

2.4.4.3 Physical Signs Associated with Pregnancy

Physical signs of pregnancy can be difficult to detect in bears (Linke 1998), however, for Chomel there was a noticeable change in appearance one-two months before the end of gestation ¹⁸. She appeared to put on weight, showed mammary development, and her

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¹⁸ Slight mammary development was observed for Moon (SN#608), the periparturient female at San Diego Zoo, but due to this observer's unfamiliarity with the individual, comment on other changes was not possible.

stomach became distinctly rounded. A month before birth in December 1997 Chomel was substantially heavier than during the first month of gestation in a previous pregnancy. The onset and extent of change in the female's appearance varied between pregnancies, but weight gain appeared to occur whether or not additional food was provided.

Because bear cubs are relatively tiny at birth (Appendix B), increase of the dam's girth, even in late gestation, may not be obvious, particularly in species with longer coats. Given the irregular feeding habits of the pregnant bear and the lack of supplemental feeding during two of the gestations, her apparent weight gain was unexpected, particularly in the absence of a foetus. In female mammals increased levels of progesterone associated with pregnancy (and pseudopregnancy) influence the rate of weight gain, body composition and distribution of fat stores (Hervey & Hervey 1981 cited in Ramsay & Stirling 1988), which may explain her appearance at this stage of pregnancy.

Vulva swelling and colouration were evident throughout pregnancy, and has been observed in other prepartal bears (Reed 1989; Weinhardt 1988; Knight et al 1985; Schaller et al 1985). As noted previously (Section 2.4.3.4), this is primarily caused by underlying hormonal influences. Because vulva changes are associated with both oestrus and pregnancy in bears, and data showed little qualitative difference between the two states, this feature cannot be used as an independent measure of reproductive status.

2.4.4.4 Periparturient Behaviour of the Female

Two-three weeks before to the end of gestation Chomel's behaviour changed characteristically. She had a poor appetite and became restless and sensitive to disturbances, startling easily at loud or unfamiliar noises. Moon exhibited similar behaviours during the two days prior to giving birth. When the females were shut out on exhibit at the end of gestation, they showed heightened levels of anxiety and paced about rapidly, periodically waiting near the exit or outside the den.

Frequent and prolonged nickering was heard from Chomel as she paced up and down, and the vocalisation commonly occurred prior to subsequent births (Keeper log books WZG). At oestrus nickering attracted male attention but it also appears to be given in conjunction with anxiety behaviour. Female Sun bears at other zoos (Table 2.2; Section

2.2.2.4) have been heard making similar noises in association with periparturient behaviours, whether or not a birth occurred. Villares et al (1985) interpreted vocalisation from a preparturient Giant panda as calling to the male, although she had recently chased him from the den. Given the situation, and similarly aggressive behaviour by Chomel beforehand, it appears unlikely that she was trying to attract the male at this time.

At the end of gestation, when Chomel was in the exhibit, she became reclusive and spent increasing time out of sight near the south dens. In May 1997, despite having access to the north dens, she appeared to have given birth in a crude nest outside the south dens. These dens may have been favoured by the female because they were located furthest from the public and the regular servicing area. When Chomel was given free access to a den during a later pregnancy, several weeks before the birth she began to spend more time inside, resting and preparing the nesting site. Reclusive and 'broody' behaviour is often reported for female bears up to a month before delivery (Bloxam 1976; Peel et al 1979; Kleiman 1985; Villares et al 1985; McDonald 1989; Schaller 1994). Even in species that do not undergo seasonal torpor, pregnant bears enter dens before giving birth and remain inside with their young for several months¹⁹, presumably, this behaviour is essential for supporting and raising altricial young (Stirling 1993a).

At WZG, nesting by the female increased at least two weeks before the end of each pregnancy with a marked rise several days prior to birth. Nesting behaviour is commonly reported for periparturient Sun bears, and can be used as a cue to separate the female (Dathe 1963; Kuhme 1990; Pagel & Kuhme 1992; Schaller 1994). Kleiman (1985) found in the Giant panda, the onset of nesting activity may occur between several weeks or as late as one day before parturition. An increase in nest-building prior to birth has also been documented for Spectacled bears (Peel et al 1979; Rosenthal 1989a; Weinhardt 1988).

Nesting helps to reduce loss of body heat to the ground, which is important for the altricial young. Without access to nesting material before giving birth, one female compensated by sitting on a heating pad in the concrete den with the cub between her

¹⁹ The Giant panda does not remain in the den, but carries the young as she forages nearby (Schaller et al 1985).

legs. Nest-building behaviour can occur in the absence of nesting materials, and is strongly influenced by the release of prostaglandin F2-alpha during late gestation (Blackshaw 1983). The day before a later birth the same bear was observed making "digging motions" on the concrete floor, and in both cases she immediately utilised nesting material when provided (Keeper log books ZSSD). The female's attempt to nest in the absence of any materials demonstrates the strength of the tendency during the periparturient period, and the necessity for providing vegetative material that permits a female to express this need²⁰.

Increasing restlessness signalled the end of gestation, and a similar pattern of events have been described for other bears prior to birth-giving (Peel 1979; Kleiman 1985; Villares et al 1985; Rosenthal 1989a). Signs of discomfort included frequent turning and repetitive scratching of the body. During grooming females focused on their nipples and vulva, but also licked their forepaws. Licking of the forearms and chest has been described for a periparturient Giant panda, and may keep the area clean or humid for the neonate when it is cradled against the body (Knight et al 1985).

During pseudopregnancy Chomel exhibited similar physical and behavioural signs of 'true' pregnancy. Similarly overt signs, including lactation have been reported for the Giant panda (Chadhuri et al 1988; Bretzfelder 1989). The Giant panda may undergo obligate pseudopregnancy when conception fails (Monfort et al 1989; Mainka et al 1991 cited in Monfort & Johnston 1993), and this may be the case for other bears. There are published (Schaller 1995) and unpublished (Table 2.2; Section 2.2.2.4) accounts of similar behaviour in Sun bears, with females showing prepartum behaviour being shut into a den, but failing to produce young. Without surveillance there is no way of determining whether the females were actually pregnant. If they had given birth to dead young, cub sounds would not be apparent, and the dam is likely to consume any evidence of birth.

2.4.4.5 Maternal behaviour

Failure of female bears to rear cubs in captivity is often the result of disturbed maternal behaviour. *U.malayanus* is considered to be a 'sensitive' species of bear (Linke 1998)

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²⁰ Although nesting may be more obvious in females during late gestation, it is a component of natural Sun bear behaviour exhibited by both sexes in captivity (Section 2.3.1.1.7). As such, it can be considered a basic welfare need to provide materials that enable Sun bears to perform nesting activity (Appendix B).

and as with other animals, periparturient females are particularly susceptible to stress which may affect normal maternal behaviours (Craighead & Craighead 1967 cited in Stokes 1970). There are several reports of Sun bears neglecting or harming apparently healthy cubs, and numerous accounts of maternal infanticide and cannibalism in this species (reviewed in Chapter 4). In most cases failure to provide an appropriate level of privacy for the female was suspected to be the predisposing factor.

The reason Sun bears at San Diego Zoo and Wellington Zoo did not rear their young was attributed to two main factors: inadequate privacy and failure to produce milk. Inexperience may also have played a role. In cases where video surveillance was not used, failure of the female at WZG to rear live young can only be speculated at because she usually ate the cubs.

In 1996 failure to rear her first young may have been due to a combination of inexperience and inadequate privacy. In May 1997 it was difficult to ascertain which bear was responsible for the extensive damage to the stillborn cub but bruising and scratching may have been caused by the dam trying to evoke a response from the young. Excessive grooming could have accounted for the distinctive circle of skin nibbled from around the cub's anus (Plate 2.1; Section 2.3.3.4.1). Although it is not unusual for carnivorous species to dispose of dead young by eating them, injuries to the cub's body were also consistent with signs of 'maternal aggression' (Linke 1998).

In December 1997 video monitoring allowed an assessment of Chomel's maternal behaviour. She cleaned the young, but not attempt to hold or nurse it. Another sign of neglect was her unresponsiveness to the cub, later resulting in it being smothered or crushed as she slept. This presumably accidental behaviour resulting in cub death has been reported at other zoos (Aquilina 1982; Bastien et al 1985; Blurton 1991) and can occur due to exhaustion (Bastien et al 1985). This is a possible explanation considering the continual disturbance and extensive nesting activity during the days prior to the birth.

Most ursids including Sun bears (Kuhme 1990; Keeper log books ZSSD, WZG) usually nurse their young while sitting upright or curled around their cubs (Schaller et al 1985). Spectacled bears, however, may nurse while lying over their young, safe in the depression of the nest (Aquilina 1982). It is uncertain whether Sun bears also nurse in

this position, but this may be an alternative explanation for the female lying over the cub.

When efforts were made to reduce disturbances following her next birth Chomel reared young for approximately one week. Without surveillance there was no way to determine cause of death because, once again, the female ate the young. In retrospect, zoo management felt that privacy may have been disrupted by evening tours held during this time, or by keepers entering the area daily to leave food for the female.

Maternal infanticide by bears may occur if a female feels her young are threatened, or result during redirected aggression in a frustrating situation (Jonkel 1970). Post-natal care is energetically expensive for a mother because the neonate has increased nutritional and thermoregulatory requirements. Infanticide may provide a mechanism for females experiencing stress to defer energetic expense to later broods (Hayssen 1984).

Breeding by the Sun bears under varying husbandry regimes at WZG demonstrated the importance of providing an appropriate environment for the female prior to birth. When the criteria outlined above were satisfied she successfully reared young. In addition to separation from the male well in advance of the birth, it is important to ensure a high level of isolation is maintained. This was achieved by reducing disturbances and intervention through use of remote surveillance, and by adapting servicing routines accordingly.

2.4.4.5.1 The role of hormones

Onset of maternal behaviours is related to a late-gestational shift in the hormonal status of the female. As parturition nears, levels of progesterone fall and the neurohormone oxytocin is released from the posterior pituitary. Oxytocin promotes milk secretion and may also be involved in increased maternal aggression and reduced fearfulness (Pedersen et al 1992), accounting for the highly defensive behaviour of periparturient female bears.

Although the bears at ZSSD were primiparous they showed good maternal tendencies prior to the young being removed. Failure to produce milk (agalactia) could have also occurred in the WZG female and has been reported for other ursids (Knight et al 1985; Linke 1998). The cause of agalactia is unknown but it may be stress-related

(Herrenkohl & Whitney 1976) and more common in primiparous females. Two of the Sun bears lactated and reared young successfully since this study, in one case lactation was noted the day before the birth²¹ (Keeper log books ZSSD).

The failure of the two ZSSD females to lactate obviously did not inhibit the release of maternal behaviour. Chomel's inattentiveness could not, therefore, be primarily caused by her apparent failure to lactate. In addition, throughout the pregnancy she had consistently exhibited cradling behaviour, indicative of a strong maternal instinct, and apparently not under the exclusive control of hormone changes at late-gestation.

2.4.4.6 Requirements for Successful Captive Breeding

Understanding a species' needs is essential to provide an environment conducive to successful rearing of the young (Kleiman 1975), and in the past problems breeding bears have been overcome by adapting conventional approaches to husbandry, based on a better understanding of ursid behaviour. The major factors identified as contributing to improved captive breeding success in bears are 1) separation from conspecifics, 2) provision of a suitable maternity area and 3) maintenance of a high level of privacy during the periparturient period (Rosenthal 1989b; Partridge 1992; Linke 1998).

A husbandry guideline for bears has recently been published by the EEP, and includes recommendations for management of females during reproduction (Linke 1998). Standardising approaches to husbandry may improve captive breeding of Sun bears. For example, Linke (1998) notes that although potentially pregnant females of other species should be separated well in advance of giving birth, Sun bears can remain together until several days prior to anticipated parturition. Presumably this is based on the compatibility reported between some pairs (Kuhme 1990).

Regardless of the level of compatibility, the present study suggests that separation from conspecifics and access to a recluse be provided one-two weeks in advance of parturition. This allows the female time to get accustomed to the maternity area,

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²¹ On this occasion, the female was also observed "allowing and encouraging" the male to lick her nipples. There are unpublished reports of similar behaviour in Sun bears at Oakland Zoo and Woodland Park Zoo (Keeper log books). Based on prior observations of breeding activity, this occurred around the time that parturition could be expected. Lactation was confirmed for one female, however birth was not reported for either of the bears so it is uncertain whether they were, in fact pregnant.

prepare a nesting site and develop a sense of security prior to the birth. Whether mating is observed or not, separation should proceed based on behaviour cues from the female.

Keulen-kromhout (1978) drew attention to the importance of the design of enclosures in improving breeding success of bears in captivity, and recommendations for suitable maternity areas are given in Linke (1998). Ideally, a female should be completely isolated from conspecifics both spatially and acoustically; reducing olfactory stimuli is also likely to be important. Free and exclusive access to a separate maternity area that includes denning facilities should be available. To reduce disturbances, particularly during the periparturient period, remote surveillance should be implemented and keeper routines adapted to minimise noise and maximise predictability. Enough nesting material should be provided so that the female can replenish it herself and after the birth suspension of all routines, including feeding and drinking is recommended.

In temperate bear species that undergo winter torpor, pregnant females enter dens in autumn after a period of hyperphagia during which they deposit fat stores, and fasting occurs throughout gestation and early rearing of the young (Palmer et al 1988). Simulating natural nutritional conditions in captivity by providing supplemental food or withholding it in the appropriate season is a common practice (Kolter 1998c), and females may remain in the den for several months without eating or drinking (Linke 1998).

As noted previously all pregnant bears enter dens prior to giving birth, and zoos often report a reduced interest in food by females during the periparturient period. Because this behaviour also occurs in ursids that do not undergo winter torpor, it is possible that this is related to the dam's need to remain in the den and provide the high level of maternal care essential for raising altricial young. Reducing food intake during the periparturient period to simulate these conditions has improved rearing in several species, including the Sun bear, and suspension of feeding for the first three weeks after birth is recommended (Linke 1998). Installation of an automatic drinker ensures access to a supply of water if it is needed.

2.5 CONCLUSIONS

While research on free-ranging Sun bear populations is required, this study has provided preliminary information on their solitary and inter-sexual behaviour in captivity. Although the natural social structure of *U.malayanus* is unknown, their predominantly solitary nature and temporary mating association is typical of behaviour reported for other bears. Recurring sexual interest throughout the year may account for reports of higher levels of compatibility among some captive pairs. Reduced tolerance and increased aggression during the non-breeding period however, suggests separate enclosures should be available, particularly prior to birth.

Sun bears can undergo postpartum oestrus soon after loss of young or following pseudopregnancy. Because of some similarities at oestrus and prior to parturition/end of pseudopregnancy (nickering, reduced interest in food, increased self-maintenance, masturbation and swelling of the vulva), it is essential to assess the overall context of events to ensure appropriate management. The presence of distinct behaviours *i.e.* nesting and the female's behaviour toward the male may be the best measures of reproductive status.

Oestrus was characterised by the female actively soliciting the male and an increase in affiliative interactions between a pair. Male behaviours associated with breeding were subtler, but included extensive olfactory investigations of his mate, and rut-like behaviour (herding, increased aggression) was also obvious for one individual. Interactive behaviours were similar to those exhibited during non-breeding encounters (head jockeying, wrestling) but episodes were much more common and distinctly playful. Mounting was more frequent during oestrus, and the females' receptive phase was recognised by her permitting copulation.

Pregnancy and pseudopregnancy lasted an equivalent period (~14 weeks), and were characterised by similar physical and behavioural changes of the female during late-stage 'gestation'. Reclusive behaviour and nesting occurred up to several weeks before term as the female prepared to give birth. Providing a potentially pregnant female with access to an isolated area and nesting material is a basic welfare consideration, and also assists to detect impending parturition.

The three key steps for successful rearing of bears in zoos are known to be a) separation of potentially pregnant females, b) a high level of isolation and c) maintenance of privacy during the periparturient period. An appropriate environment proved to be critical for Sun bears to rear their young. Separation well in advance of parturition alleviated opportunities for conflict, and allowed the female to become familiar with the maternity area and prepare for birth. In addition to ensuring complete privacy from the male, reduction of other disturbances during the periparturient period was necessary. Remote surveillance was essential to monitor without disturbance and helped determine the course of events and assess maternal care.

This study has demonstrated that when these husbandry considerations are not attended to, management proceeds on a trial-and-error basis and can result in loss of valuable breeding potential. Recognition of effective strategies and implementation of appropriate husbandry is crucial to improve the chances of successful rearing in captivity. A higher level of commitment by zoos is necessary for more effective management of Sun bear breeding programs.

Chapter 3

Reproductive Endocrinology and Hormone -Behaviour Relationships in the Malayan Sun bear (*Ursus malayanus*)

3.1 INTRODUCTION

The Sun bear (*Ursus malayanus*) is an endangered tropical mammal inhabiting the rainforests of South East Asia. Rapid loss of habitat through deforestation coupled with poaching for the illicit trade in bear parts is placing increasing pressure on this species in the wild. There are no estimates of the distribution or number of Sun bears that remain, but populations in Malaysia and Indonesia are believed to be in serious decline (Mills & Servheen 1991; Santiapillai & Santiapillai 1996). Although *U.malayanus* has been present in zoological parks around the world since the 1930's, there is now growing concern for the status of captive populations. Their breeding record has remained inconsistent and poor, and currently only approximately 120 individuals remain in western zoos.

There is little information about the reproductive biology or behaviour of the Sun bear but an improved understanding is fundamental to future conservation attempts in both wild and captive populations. Most ursids mate during spring and summer and cubs are born during winter following a variable period of embryonic diapause. Usually parturition occurs in alternate years or after a three year breeding interval (Herrero 1980; Schaller et al 1985; Stirling 1993). Compared to other ursids the tropical Sun bear is known to have a number of unique features of their reproductive cycle. These include the lack of a restricted breeding season in captivity, a less variable and relatively abbreviated gestation period suggesting the absence of delayed implantation, and the ability to give birth several times a year if young die or are removed (Dathe 1970; McCusker 1974; Kolter 1995).

In general, the endocrinology of reproduction in ursids has not been well studied, due partly to constraints imposed by the impracticality of regular blood sampling. Reproductive steroids have been measured in serum of the American black bear (*U.americanus*: McMillin et al 1976; Foresman & Daniel 1983; Palmer et al 1988; Hellgren et al 1991; Garshelis & Hellgren 1994; Tsubota et al 1997; Tsubota et al 1998), the Brown bear (*U.arctos*: Tsubota et al 1987; Tsubota & Kanagawa 1989; Tsubota et al 1992) and the Polar bear (*U.maritimus*: Palmer et al 1988; Ramsay & Stirling 1988; Derocher et al 1992).

In zoos, the Giant panda (*A. melanoleuca*) has been the focus of most research because of its conservation status, and researchers have applied urinary steroid monitoring to develop an extensive reproductive database for the species and monitor individuals during assisted reproductive techniques (Bonney et al 1982; Hodges et al 1984; Murata et al 1986; Chadhuri et al 1988; Monfort et al 1989). Non-invasive monitoring of other captive populations was recently proposed as a means of developing a reproductive database to improve understanding of reproduction in lesser-known species including the Sun bear (Monfort & Johnston 1993). A major benefit of these techniques is the ability to conduct long-term studies without the potential stress and risk associated with repeated chemical and physical restraint (Lasley & Kirkpatrick 1991).

Non-invasive monitoring is applicable to a wide range of species due to the conservation of steroid hormone molecular structure across taxa and the stability of metabolites in excreta (Lasley & Kirkpatrick 1991). Steroids are metabolised by the liver before being excreted into the urine or with bile into the gut; hormones are also present in milk and saliva but at lower concentrations (Schwarzenberger et al 1996b). Although the excretion route of steroid metabolites varies within and between species, studies of canids, felids and mustelids indicate that in these carnivores, hormones are predominantly excreted in the faeces (Shille et al 1984; Shille et al 1990 cited in Schwarzenberger et al 1996a; Gross 1992; Brown et al 1994; Monfort et al 1997; Velloso et al 1998). Faecal steroids mimic the pattern of circulating hormone levels in plasma, however, the concentration of metabolites in faeces is generally much higher and their passage through the gut incurs a lag time of up to several days (Lasley & Kirkpatrick 1991; Schwarzenberger et al 1996a).

Faecal steroid monitoring has proven useful for characterising ovarian cycles, investigating endocrine-behaviour correlates, determining events such as ovulation and implantation, diagnosing pregnancy, monitoring foetal status, and detecting impending parturition in a diverse number of captive and free-ranging species (reviews in Lasley & Kirkpatrick 1991; Schwarzenberger et al 1996a). These methods have been successfully used to monitor ovarian activity in a range of carnivores including non-domestic canids and felids (Gross 1992; Brown et al 1994; Czekala et al 1994; Brown et al 1995; Wasser et al 1995; Graham et al 1995; Brown et al 1996a,b; Morais et al 1996; Monfort et al 1997; Velloso et al 1998). Faecal steroid monitoring has also been

applied to monitor reproduction in the Nepalese Red panda (Spanner et al 1998) and the Giant panda (Kubokawa et al 1992).

Sex steroid monitoring has traditionally been applied to study reproduction in females because male germ cell production is less tightly coupled with hormone secretion (Lasley & Kirkpatrick 1991). Studies of faecal androgen excretion appear to be becoming increasingly popular, and have already provided information on testicular cycles, seasonality, social dominance and sex determination in a range of carnivores including the Giant panda (Kubokawa et al 1992), African wild dog (Monfort et al 1997), black-footed ferret (Brown 1997), maned wolf (Velloso et al 1998) and a variety of felid species (Brown et al 1996c; Morais et al 1996).

Recently, several researchers have used faecal steroid monitoring to study the ovarian cycle in captive Sun bears (Brown et al 1996a; Schwarzenberger et al 1997). Schwarzenberger et al's (1997) documented luteal phases of an equivalent length to the reported Sun bear gestation period of approximately 95-100 days (Dathe 1961, 1963, 1966; 1970; Kuhme 1990; Pagel & Kuhme 1992; Schaller 1994), but birth was not detected. Non-conceptive phases are difficult to verify given that foetal resorption/abortion and postpartum infanticide may occur, but in the absence of birth these may have represented pseudopregnancy.

Pseudopregnancy is a feature of reproduction common to a number of carnivores including canids and felids (Feldman & Nelson 1996) and occurs when the corpus luteum continues to function independently of fertilisation. The Giant panda is thought to undergo obligate pseudopregnancy when conception fails (Monfort et al 1989; Mainka et al 1991 cited in Monfort & Johnston 1993), and evidence suggests that pseudopregnancy also occurs in other ursids (*U. americanus*: Hellgren et al 1991, Tsubota et al 1998; *U.arctos*: Tsubota et al 1992, Göritz et al 1997; *U.ursinus*: Brown et al 1996a). In bears, because pseudopregnancy appears to last a similar length and have a similar pattern of steroid excretion to 'true' gestation, this presents a major challenge for accurate pregnancy diagnosis.

Further information is clearly necessary to improve our understanding of the Sun bear toward more effective management of captive populations. It is difficult to assess the factors limiting reproduction of the Sun bear in captivity without an improved understanding of female reproductive physiology and gaining insight into testicular function in males. The aim of the present study was to extend the current reproductive database by using faecal sex steroid assays to monitor gonadal function in male and female Sun bears, explore potential effects of seasonality and examine breeding synchrony between the sexes. Oestradiol and progesterone metabolites were monitored in females and testosterone was measured in males. Behaviour data were collected in conjunction with faecal sampling to investigate endocrine-behaviour relationships during breeding. Information was collected from captive Sun bears housed at various zoological institutions in North America and New Zealand, for periods of up to 27 months. Samples from seven of the North American males were contributed from a research project co-ordinated through the Sun and Sloth bear Species Survival Plan 1997 – 2001 (Ball 1996a).

3.2 MATERIALS AND METHODS

3.2.1 Animals and Faecal Collection Protocol

Thirteen Sun bears (nine male: four female) from nine zoological institutions were included in the faecal hormone collection (Table 3.1). All animals were of breeding age (>6 years) and with the exception of two females included in the pilot study (Studbook #528 and #608), maintained in male:female pairs. Housing varied between zoos, but all bears had access to outdoor enclosures so were exposed to natural fluctuations in photoperiod. Information on the animal's diets has been included where available.

The month-long pilot study conducted at San Diego Zoological Gardens, U.S.A (ZSSD; 32°48' N) from 14 February - 02 March 1997 included one male (Studbook #606) and three females (Studbook #528, #598 and #608). The bears were maintained on individually tailored diets consisting of protein in the form of dog biscuits (Zu Preem Omnivore Diet, Premium Nutritional Products, Inc. Kansas, U.S.A.)), and a selection of vegetables and fruit; water was available *ad libitum*. Faeces were collected <7 days per week during morning servicing (0700-0900 hrs). Samples were collected as freshly voided, which ensured identity where two animals were housed together. The faecal pile was stirred well with a spatula to homogenise before removal of ~20 grams. The sample was stored in a plastic container at -18°C and later sent on ice to the Centre Wildlife Conservation (CWC), Woodland Park Zoo, Seattle and stored frozen (-18°C). They were shipped to Massey University, New Zealand on dry ice and transferred into a freezer (-18°C).

A longitudinal study of one male (Studbook #617) and one female (Studbook #607) Sun bear was conducted at Wellington Zoological Gardens, New Zealand (WZG; 41°15′ S) from December 1996 - December 1997. The animals were maintained on a diet of various forms of protein (frozen fish, fresh poultry, eggs, dog biscuits (Hill's Science Diet, Canine Maintenance Formula; Hills Pet Nutrition, Kansas, USA) and a selection of fruit and vegetables; water was available *ad libitum*. Faeces were usually collected 2-3 days per week from the female and 1-2 days per week from the male. Recently voided samples were collected opportunistically during the day. The faecal pile was stirred well with a spatula to homogenise before removal of ~20 grams. The sample was placed in a cryotube and stored at -20°C. Approximately once a month, samples were shipped to Massey University on dry ice and transferred into a freezer (-18°C).

Table 3.1: Summary of captive Sun bears (n = 13) included in faecal steroid analysis listed by site, studbook number, sex, age and breeding status at close of study.

Site	Animal Studbook #	Birth origin	Sex	Date of birth/ age at collection onset	Proven breeder	Collection duration (~ months)
Jackson Zoological Park, MS (JZP)	554	captive	Male	17 Apr 1983 (13 yrs)	no	8
Metro Washington Park Zoo, OR (MWPZ)	586	captive	Male	04 Jul 1986 (10 yrs)	no	5
Miami Metrozoo, FL (MMZ)	470†	wild	Male	~1974 (~21 yrs)	yes	16
Minnesota Zoo, MN (MZG)	618	captive	Male	19 Oct 1989 (6 yrs)	no	14
Oakland Zoo, CA (OZ)	516	captive	Male	16 Jul 1979 (17 yrs)	no	12
San Diego Zoo, CA (ZSSD)	528 598 606 608	captive	Female Female Male Female	14 Nov 1980 (16 yrs) 07 Oct 1987 (9 yrs) 02 Aug 1988 (8 yrs) 18 Oct 1988 (8 yrs)	multiparous parous yes multiparous	1 0.5 1 1
St Louis Zoo, MO (StLZ)	420†	wild	Male	~1970 (~25 yrs)	yes	27
Wellington Zoo, New Zealand (WZG)	607 617	captive	Female Male	02 Aug 1988 (8 yrs) 17 Sep 1989 (7 yrs)	multiparous yes	13 13
Woodland Park Zoo, WA (WPZ)	409†	captive	Male	~1969 (~26 yrs)	yes	13

[†] since deceased

Samples from the seven other male Sun bears were collected from various North American zoos (30-45° N) between May 1995 - July 1997, as part of an *ex situ* project co-ordinated by the Sun and Sloth Bear SSP. Faecal samples were collected 1-2 days per week for periods of up to 27 months. When animals were housed together, small plastic beads, unshelled eggs or food dye were added to the diet of one individual to assist in identifying scats. Faeces were placed into zip-lock plastic bags and stored in a freezer at -18°C. They were later sent on ice to the Centre for Wildlife Conservation (CWC), Woodland Park Zoo, Seattle and stored frozen (-18°C). Samples were shipped on dry ice to Massey University, New Zealand and transferred into a freezer (-18°C) until processing.

3.2.2 Behavioural Observations

Behavioural data were collected at ZSSD between 18 February and 02 March 1997. The male (Studbook #606) and female (Studbook #598) were observed for 5-6 days each week between 8.30am - 4.30pm for a total of 49 hours over 2 weeks. The occurrence and length of observation sessions were chiefly determined by management changes to husbandry routines and procedures. Periods of observation were also affected by separation of the male and a newly introduced female following episodes of serious aggression. Solitary and social behaviours were recorded by continuous focal sampling (Martin & Bateson 1993), using a stopwatch to time the onset of each behaviour. Each animal was observed in 30 minute blocks, and additional information including uncoded behaviours of interest were noted qualitatively. Behavioural data were collected at WZG from 02 January to 18 December 1997 using the same methods described above. The pair (Studbook #617 and #607) were observed for 2-6 days each week between 8.00am - 5.00pm for a total of 1005 hours over 10 months. At both zoos, supplementary notes of events that occurred outside sampling periods were compiled from keeper records.

3.2.3 Hormone - Behaviour Analyses

For daily analyses at ZSSD, faecal hormone data were displaced to account for the potential lag time between behaviour and endocrine events. A 24-hr lag period was assumed to correspond with the approximate rate of passage of food (Schwarzenberger et al 1996), based on the appearance of food indicators (chicken feathers, seeds) in Sun

bear faeces²² (unpublished observations). To determine the relationship between endocrine levels and behaviour events, the frequency of selected behaviours associated with mating in this species (see Chapter 2) was compared prior to and during oestrus. For females this included backward walking, inguinal presentation and rolling; intersexual behaviours included olfactory investigation and mounting. For a complete description of these behaviours see Sun bear Ethogram (Chapter 2; Section 2.3.1).

Qualitative behaviour notes documenting episodes of breeding activity were provided for the Sun bears housed in pairs at other North American zoos.

3.2.3.1 Sample Preparation and Analysis

3.2.3.1.1 Faecal Extraction

Faecal samples were prepared by a modification of the method of Wasser et al (1994). Entire samples were lyophilised (Cuddon Freeze Drier, Marlborough Engineering, Blenheim, N.Z.) and any undigested or fibrous matter removed by screening through 2mm gauge plastic mesh²³. 0.1g of the dried sample was weighed out into 13 x 120mm test tubes and suspended in 5 mL of 90% ethanol (AnalaR BDH, Poole, England). To monitor procedural losses 100µL (~5000 cpm) of the appropriate tracer (either ³Hoestradiol (TRK.322 Amersham, UK); ³H-progesterone (TRK.413 Amersham, UK) or ³H-testosterone (TRK.406 Amersham, UK) was added before boiling the suspension for 20 minutes. Samples were centrifuged for 20 minutes (2000g at room temperature), and the supernatant pipetted into 13 x 100mm test tubes. The pellet was rinsed with 2.5mL 90% ethanol, vortexed for 30 seconds and re-centrifuged for a further 15 minutes. The supernatants were combined and the ethanol completely evaporated by placing tubes in a heating block at 37°C and blowing a stream of air over them. 1mL phosphate buffered saline gel (PBSG 0.1M pH 7.0; 0.1% gelatin) was added to the dried extract and the samples refrigerated (4°C) and left to dissolve overnight. The reconstituted extracts were then vortexed briefly (~15 seconds) to remove adhered organic particles, and agitated on an orbital shaker for 20 minutes to facilitate the dissolving process. To ensure a homogenous solution for assay, any remaining particles were removed by

²² A comparable range has been reported for captive Spectacled bears maintained on a similar diet (Graffe 1995 cited in Kolter 1998c).

²³ Lyophilisation has been shown to improve correspondence between faecal and serum values and may minimise effects of dietary fibre on excreted steroid levels (Wasser et al 1988).

transferring the extract into 1mL eppendorf tubes and centrifuging for 15 minutes (21 000g at room temperature). The aqueous phase was recovered and stored at -18°C.

3.2.3.1.2 Radioimmunoassay

Samples were thawed and diluted (1:10 oestradiol; 1:5 progesterone; 1:15 – 1:65 testosterone) in PBSG and assayed in duplicate following the same procedure for oestradiol 17- β , progesterone and testosterone. Briefly, 100 μ L of respective antibody (dilutions in ethanol = oestradiol 1:140; progesterone 1:40; testosterone 1:130) and 100 μ L of tracer (~5000 cpm) were added to samples and standards (9.8-5000 pg/mL for oestradiol and testosterone, 19.5-10 000 pg/mL for progesterone; source of standards: Sigma-Aldrich Pty, Ltd, Missouri, U.S.A.) and then incubated by refrigerating (4°C) overnight. Unbound steroid was separated by addition of 500 μ L dextran-coated charcoal (2.5g/L charcoal (Sigma-Aldrich Pty, Ltd, Missouri, U.S.A.), 0.25g/L dextran (Dextran T70 Amersham Parmacia, Buckinghamshire, England) in PBSG) and incubation for 15 minutes at 4°C, before centrifuging tubes for 15 minutes (4500g at 4°C). The supernatant was recovered and counted in 3 mL scintillation fluid (5 g/L PPO (2,5-diphenyl-oxazole, Sigma), 0.3 g/L dimethyl POPOP (1,4-bis-[4-methyl-5-phenyl-2-oxazoly]-benzene, Sigma)) in toluene for 5 minutes in a Wallac 1409-411 Liquid Scintillation Counter.

The oestradiol antiserum (41-12; Etches, Canada) was raised in sheep, and cross-reactivity with other steroids as provided by Etches et al (1981) were 17α -oestradiol (<1.0%), oestriol (<1.0%) and oestrone (4.3%). Sensitivity of the oestradiol assay was defined as the minimal level of steroid distinguished from the blank at 95% of maximum binding was 0.25 ± 0.05 ng/tube (1.46 ng/mL) (n = 4 assays). The progesterone antiserum (GBTB; Etches, Canada) was raised in rabbits and cross-reactivities with other steroids as reported in Etches and Croze (1983) of 5 β -pregnane-3,20-dione (15.6%), 5 β -pregnane-3,20-dione (6.7%), 11 β -hydroxyprogesterone (5.4%), cholesterol, testosterone, 17 β -oestradiol, cortisol, corticosterone, deoxycorticosterone, 17 α -hydroxyprogesterone, pregnenolone, 5 α -pregnan-3 α -ol-20-one, 4-pregnene-20 β -ol-3-one, 5 β -pregnan-3 α -ol-20-one (<1%). Assay sensitivity for progesterone determined as 95% maximum binding was 0.13 \pm 0.03 ng/tube (1.11 ng/mL) (n = 3 assays). The testosterone antiserum (T3-125; Endocrine Sciences, USA) was raised in rabbits and cross-reactivities with other steroids reported in the product literature were: dihydrotestosterone (20%),

corticosterone (<0.01%), oestradiol (0.14%), Δ -l-testosterone (52%), 4-androsten-3 β -17 β -diol (3%), 5 α -adrostan-3 β -17 β -diol (1.8%), Δ -4-androstenedione (0.5%) and others (<0.5%). Testosterone assay sensitivity determined as 95% maximum binding was 0.09 \pm 0.01 ng per tube (0.89 ng/mL) (n = 8 assays).

The intra- and inter-assay coefficients of variation were determined by including quality control samples in each assay. Preparations contained low, medium and high concentrations of oestradiol, progesterone or testosterone (in PBSG) that approximated 20%, 50% and 80% binding on the standard curve. Female faecal samples (n = 144, in duplicate) were analysed for oestradiol in four assays and progesterone in three assays, male samples (n = 410, in duplicate) were analysed for testosterone in eight assays. Intra-assay coefficients of variation were 14.5, 8.5, 11.8% for oestradiol (n = 20), 16.3, 8.8, 8.4 % for progesterone (n = 20) and 19.3, 7.8, 5.5% for testosterone (n = 20) for low, medium and high samples, respectively. Inter-assay coefficients of variation were <15% for all assays.

3.2.3.1.3 *Validation*

Extraction recoveries were estimated by counting a $100\mu L$ aliquot of the radiolabelled extract in 3mL scintillation fluid (5 g/L PPO (2,5-diphenyl-oxazole, Sigma), 0.3 g/L dimethyl POPOP (1,4-bis-[4-methyl-5-phenyl-2-oxazoly]-benzene, Sigma) in toluene) for 5 minutes on the scintillation counter. Because extraction efficiencies varied considerably within and between triplicates of pooled faecal samples (mean \pm SE = $79.1\% \pm 4.1$ for oestradiol, $71.0\% \pm 5.0$ for progesterone and $81.1\% \pm 4.1$ for testosterone) individual recoveries were calculated for each sample. Parallelism was demonstrated by serially diluting pooled samples five times (1:10-1:160), assaying and plotting binding percentage against their respective standard curve. Recovery of added steroid was determined by spiking faecal samples with oestradiol, progesterone or testosterone (9.8, 19.5, 39.0, 78.0, 156.0, 312.5, 625.0, 1250, 2500, 5000 pg/mL) which yielded a mean recovery of 81.9 ± 4.7 and 89.9 ± 4.6 for oestradiol (n=2), 95.1 ± 3.1 , 98.4 ± 3.0 and 87.9 ± 3.8 for progesterone (n=3), 93.8 ± 2.4 and 96.3 ± 4.4 for testosterone (n=3).

3.2.4 Data Analyses

3.2.4.1 Female Cycle Characteristics

Characterisation of the female reproductive cycle was based on the longitudinal study of steroid excretion in female #607 ('Chomel') between December 1996-December 1997. Increases in oestradiol considered representative of heightened follicular activity at oestrus were values that exceeded the mean + 1.0 SD, and when progesterone was below mean levels. Oestrus duration was estimated based on the number of days oestradiol levels remained elevated above baseline. Inter-oestrus intervals were determined as periods when oestradiol remained below the mean for at least two weeks between significant surges. Mean progesterone levels within one week preceding the preovulatory oestradiol surge were considered representative of baseline values. Onset of the luteal phase²⁴ was determined when progesterone levels exceeded the baseline by 50% and remained elevated for at least 30 days. Gestation length was based on the length of time from the onset of the luteal phase (ovulation) to parturition for conceptive cycles; during pseudopregnancy the end of the luteal phase was based on a sharp decline in activities associated with parturition (e.g. nest-building) concurrent with decreasing progesterone metabolites.

3.2.4.2 Statistical Analysis

For seasonal analysis of testosterone concentration in males, the year was divided into four periods: December-February (winter), March-May (spring), June-August (summer) and September-November (autumn). To generate a comparable format, data from the New Zealand male were displaced by six months. Analysis of variance was used to detect seasonal differences in androgen excretion. Grouped male data is presented as the mean \pm SE. Other data was not analysed statistically due to small sample sizes.

²⁴ The term 'luteal' rather than pregnant phase is typically used for carnivores because characteristic of their form of placentation, circulating levels of progesterone during pregnancy are shown to be primarily luteal in origin (Levasseur 1983 cited in Ramsay & Stirling 1988; Hodges et al 1984).

3.3 RESULTS

3.3.1 Pilot Study: San Diego Zoo (ZSSD)

3.3.1.1 Breeding pair ("Muffin" #598 and 'Ringo' #606)

For approximately eight months prior to the study Muffin was housed with another female (#528), and at the study onset appeared to be in an anoestrus condition *i.e.* exhibiting no behavioural or physical (vulva swelling) signs of oestrus. Muffin was introduced to Ringo on 17 February 1997 with encounters staged on a daily basis during the study period. The pair were permitted the opportunity for physical contact during encounters, but maintained in separate enclosures overnight.

Muffin's faecal oestradiol levels were relatively low (~25 ng/g) on 14 and 15 February, with a major increase accompanying the onset of behavioural oestrus following introduction to the male (Figure 3.1a). Oestradiol rose steadily from 18 February and following a transient decline on 25 February, peaked at approximately 160 ng/g on 28 February, representing a level 9-fold higher than measured at onset of sampling. A similar pattern in faecal androgen level excretion was evident for the male, with testosterone increasing markedly after introduction to the female, and rising from approximately 200 ng/g between 17-20 February to a peak of >450 ng/g on 27 February (Figure 3.1b).

During the first few days encounters between the bears were characterised by high levels of agonism, with the female using threat behaviour and aggressive vocalisation to try to keep the male at bay. Threat often escalated into loud and intense bouts of wrestling. The level of interactions varied over the two week period but a steady rise in affiliative behaviour and a complementary reduction in agonism was evident, with encounters becoming silent and distinctly playful. Behavioural signs of oestrus became apparent on 19 February when rolling and inguinal presentation by the female commenced, and backward walking was first observed on 20 February (Figure 3.2a). Her frequency of inguinal presentation increased steadily between 18 - 20 February, concurrent with rising oestradiol levels, and reached a high peak on 23 February. The other two reproductive behaviours showed a less obvious pattern, varying in frequency, but a common increase was observed on 23 February.

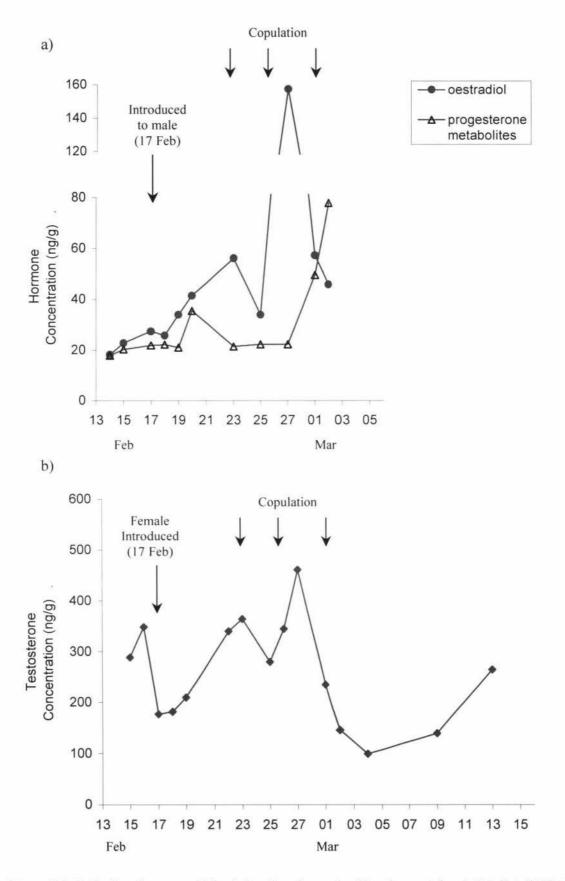


Figure 3.1: Daily faecal sex steroid levels in a breeding pair of Sun bears a) female 'Muffin' (#598) 14 February - 02 March 1997 and b) male 'Ringo' (#606) 15 February - 13 March 1997.

On 23 February Muffin began to actively solicit Ringo, approaching and following him about and often initiating contact. Both bears showed heightened olfactory interest in each other on this date, and investigation of the partner's anogenital region and excreta was more frequent (Chapter 2; Figure 2.8). Changes to the female's vulva were evident several days after introduction to the male. As oestradiol levels rose her vulva became increasingly engorged and red with the highest levels of size, colouration and moisture being recorded at peak oestrus (Chapter 2; Table 2.4).

Brief bouts of mounting (<30 secs) were seen regularly from the time the bears were first introduced, however, the behaviour did not occur in exclusively sexual contexts and initially appeared to be used primarily for asserting dominance. At first, mounting attempts by the male met with displays of extreme agonism by the female, but increased compliance and acceptance occurred during the first week. Pelvic thrusting accompanied some mountings of the female but intromission did not occur prior to her becoming receptive. The female's mounting frequency increased from 18 February as her oestradiol rose, and repetitive mounting of the male was obvious on 23 February (Figure 3.2b). At this stage of oestrus faecal oestradiol levels had increased three-fold (~60 ng/g) above initial values, and her readiness to mate was evident. On 23 February she entered 'standing heat', from thereon willingly permitting all mounting attempts by the male.

Copulation occurred for the first time on 23 February when Muffin became receptive. Bouts of copulation occurred 3-5 times each day on 23 and 27 February but only one episode was recorded on 02 March. The female's frequency of inguinal presentation dropped sharply, but she continued to exhibit reproductive behaviours during her receptive period (Figure 3.2a). A common increase in rolling, inguinal presentation and backward walking was observed on 26 February accompanied by increased levels of self-maintenance behaviour (Chapter 2; Figure 2.12). On 27 February the high peak in oestradiol was accompanied by an increase in the frequency of Ringo's mounting (Figure 3.2b) and extended periods of copulation occurred.

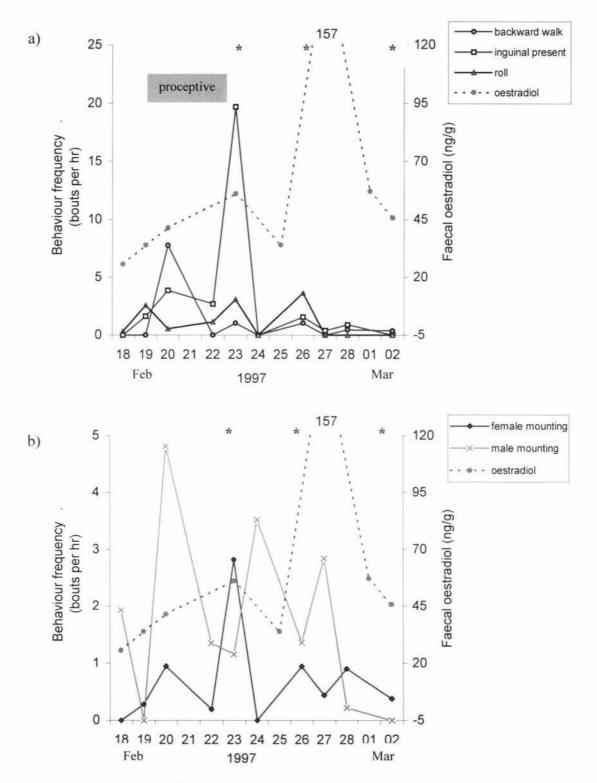


Figure 3.2: Daily behaviour frequencies compared with female faecal oestradiol levels in a breeding pair of Sun bears (female #598 & male #606) between 18 February - 02 March 1997; a) female reproductive behaviours and b) mounting behaviour between the pair. The proceptive phase depicted by shaded area in a) marks the period from the onset of behavioural oestrus to the beginning of the receptive phase when the female permitted copulation. Asterisks denote dates of copulation.

Oestradiol and testosterone levels had fallen sharply by 02 March (Figure 3.1), with a marked decline in the male's mounting behaviour reflecting his waning interest in the female (Figure 3.2b). The female's oestrus phase apparently ended on 02 March, as interactions between the pair tailed off and neither mounting or copulation was observed after this date (Keeper log books ZSSD).

Muffin's faecal progesterone metabolite excretion remained relatively constant at approximately 20 ng/g between 14 February and 27 March (Figure 3.1a). It rose markedly after 27 March, reaching a concentration four-fold higher than apparent baseline values by 02 March. The increase in progestagens was considered indicative of ovulation, thus, marking the onset of the female's luteal phase. The breeding episode was successful resulting in birth of a live cub approximately three months later. Parturition was 103 days from the first mating between the pair, and 96 days had elapsed since the last observed copulation on 02 March.

Female cycle characteristics

Due to the short sampling interval, baseline values for oestradiol were determined from the mean level prior to and on the day of introduction, permitting for a minimum 24-hour lag time of faecal steroids. An increase above the baseline of 50% on 19 February was considered to mark the onset of oestrus. This date was consistent with the onset of reproductive behaviours by the female (Figure 3.2), and is seen to represent the proceptive phase of oestrus, prior to acceptance of mating. Based on these observations, the proceptive phase lasted four days and the receptive period for 8 days, giving a total oestrus period of 12 days.

Because oestradiol levels had not returned to baseline by the final sampling date (02 March) (Figure 3.1), this precluded calculating the definitive length of Muffin's follicular phase from hormone levels. The length of time oestradiol levels remained elevated is, however, consistent with behavioural observations, indicating that oestrus lasted a minimum of 12 days. The length of the luteal phase was 95 days, as calculated from the sharp increase in progesterone on 01 March to parturition on 06 June.

3.3.1.2 Females "Moon "(#608) and 'Dracena' (#528)

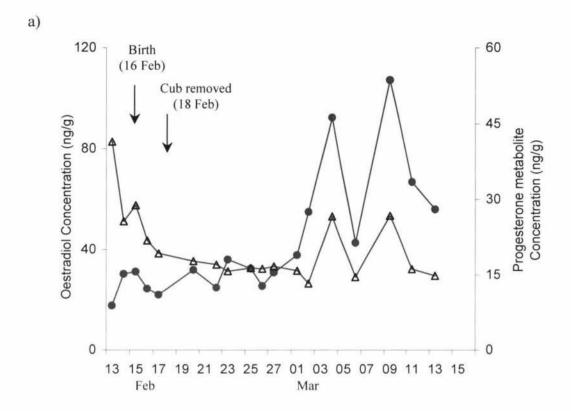
At the onset of the study the female Moon was housed with the male Ringo (#606) on a permanent basis. Following the first date of sampling on 13 February, the female's faecal progesterone metabolite levels dropped sharply from approximately 40 ng/g to 20

ng/g, and on 16 February she gave birth to a live cub (Figure 3.3a). The birth was unexpected because, although the pair had been kept together for nearly 8 months, reproductive activity had never been seen (Keeper log books ZSSD). The male was separated on 16 February, following the birth and on 18 February the cub was removed for hand-rearing due to the dam's failure to lactate. During the following month, on some days Moon was housed with the female Dracena (#528).

Moon's faecal progestagen levels declined very gradually over the week following the birth, but remained around 15 ng/g. Oestradiol levels fluctuated but remained fairly constant at approximately 30 ng/g until 02 March (Figure 3.3a). Faecal oestradiol excretion increased sharply to approximately 90 ng/g by 04 March, and after a transient decline, peaked at approximately 110 ng/g on 09 March. Oestradiol levels declined following this date, and had fallen to approximately 55 ng/g by 13 March. Relatively moderate increases in progesterone metabolites were observed concurrent with the two surges in oestradiol, but progestagens returned to apparent baseline levels by 11 March and remained low on the last two days of sampling.

For Moon, a baseline value for oestradiol was determined as the mean of samples collected up to one week following parturition (17-23 February). An increase above the baseline of 50% was considered representative of significant follicular activity, and marked the onset of postpartum oestrus on 03 March. Oestradiol levels had not reached baseline values by the final sampling date (14 March), which precluded calculating the definitive length for Moon's follicular phase. Based on the length of time oestradiol levels remained elevated above baseline, however, oestrus lasted a minimum of 11 days. No behavioural or physical signs of oestrus were noted during this period (Keeper log books ZSSD). Moon did not have physical contact with the male during postpartum oestrus, and although data are limited, the lack of a marked or sustained progesterone rise during the sampling interval suggests that ovulation did not occur.

Dracena (#528) was not housed with the male during the study. Her hormonal profile revealed fluctuating levels of faecal oestradiol and progesterone metabolites throughout the 26 day sampling interval (Figure 3.3b). There was no coherent pattern of follicular or luteal activity and no behavioural or physical signs of oestrus were noted during this period (Keeper log books ZSSD).



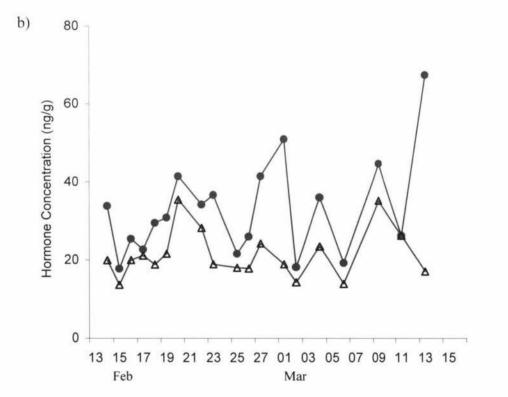


Figure 3.3: Daily faecal oestradiol (•) and progesterone metabolite (Δ) excretion in female Sun bears a) 'Moon' (#608) 13 February - 14 March 1997 and b) 'Dracena' (#528) 14 February - 14 March 1997.

3.3.2 Longitudinal study: Wellington Zoo (WZG)

Grouping of the pair (female # 607 'Chomel' and male #617 'Bakti') varied during the study. In general, they were kept together permanently, but at times, temporary separation and alternative housing was necessary for husbandry purposes (Chapter 2; Table 2.1). Chomel underwent three successive reproductive cycles between December 1996 - December 1997. These were characterised by discrete periods of follicular activity associated with oestrus, followed by a conceptive or non-conceptive luteal phase (Figure 3.4). Oestradiol concentrations ranged from 15 ng/g to 100 ng/g, and progestagens from 10 ng/g to 100 ng/g. The first pregnancy (February - May) resulted in a stillbirth on 06 May, and was followed by a pseudopregnancy ending in August. In September the female became pregnant again and gave birth to a live cub on 11 December.

During oestrus major surges in faecal oestradiol were observed, while progesterone metabolites remained at or near basal levels. Oestradiol rose from a mean of 45.0 ng/g to a peak of between 80-100 ng/g, and increases were accompanied by overt signs of behavioural oestrus in the female, and breeding behaviour between the pair (Section 3.3.2.1). The end of oestrus was characterised by a sharp drop in oestradiol and reduced sexual interest by both partners. Despite having unrestricted access to the male, the female apparently failed to ovulate during two oestrus periods, as evidenced by the lack of a significant or sustained increase in progesterone metabolites following oestrus. In both cases oestrus recurred several weeks to a month later, producing a second distinct peak in oestradiol excretion (Figure 3.4).

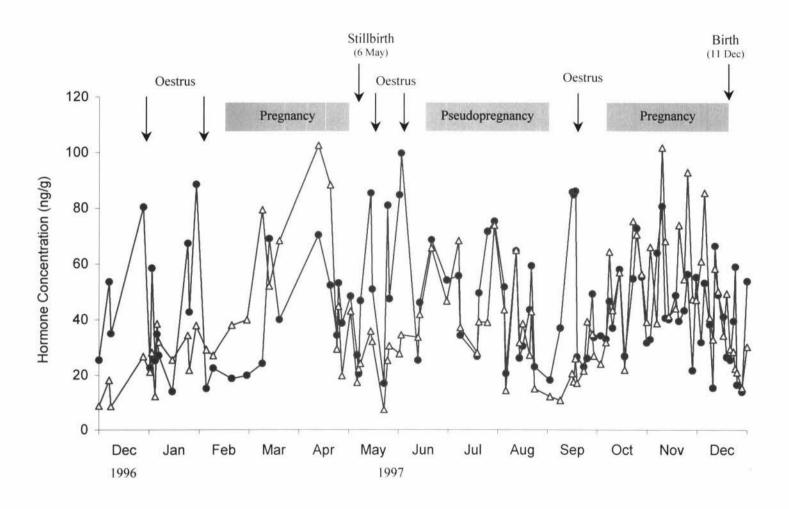


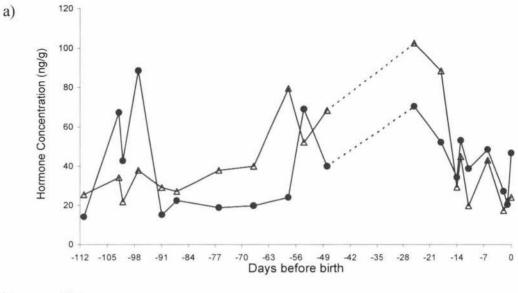
Figure 3.4: Longitudinal profile of faecal oestradiol (•) and progesterone metabolite (Δ) excretion in female Sun bear 'Chomel' (#607) from December 1996 to December 1997. Arrows denote peaks in oestradiol associated with breeding activity.

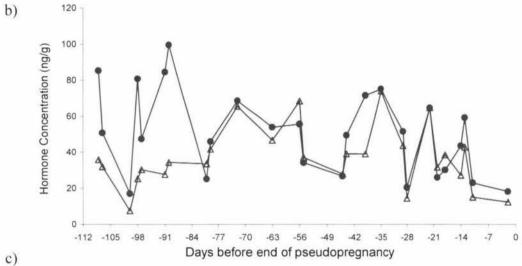
A similar pattern of steroid excretion was observed during the three reproductive cycles (Figure 3.5). After ovulation at oestrus, a gradual increase in oestradiol and progesterone levels occurred. Progestagens were dominant, being excreted in higher amounts than oestradiol which generally remained at levels lower than excreted during oestrus. Faecal progesterone metabolites rose from a mean of 40 ng/g to a peak of approximately 100 ng/g during both pregnancies, whereas peak values during the pseudopregnancy did not exceed 75 ng/g. During the second and third reproductive cycles an increase in both hormones was apparent 2-3 weeks after oestrus (Figure 3.5b and Figure 3.5c respectively). During the first conceptive cycle the pattern of steroid excretion varied, with a less apparent increase until at least a month after oestrus (Figure 3.5a). It is possible that this may have been due to a combination of infrequent sampling and untimely hormone fluctuations.

Faecal progesterone metabolites and oestradiol dropped predictably to near-basal levels by the week prior to birth or end of pseudopregnancy (Figure 3.5). Both births occurred approximately 13 weeks after oestrus (Figure 3.5a and Figure 3.5c). Approximately 11 weeks after postpartum oestrus in May 1997 the female began to exhibit overt behavioural signs of late-stage gestation (nesting, increased grooming) and was separated from the male. She was shut into a maternity den and maintained under remote video surveillance. Two weeks later prepartum behaviours ended abruptly, without her giving birth. The time elapsed from oestrus was approximately 13 weeks equivalent to the length of 'true' gestation (Figure 3.5b).

Oestrus typically recurred within several weeks following birth or the end of pseudopregnancy (Figure 3.4). Although the cub born on 11 December did not survive, increased follicular activity was not detected prior to the end of faecal sampling on 19 December. Behaviour notes from keeper log books suggest that Chomel did enter postpartum oestrus during the following week.

The hormonal profile of the male revealed a recurring pattern of cyclicity in faecal testosterone excretion (Figure 3.6), with concentrations ranging from 13 ng/g to 90 ng/g (Table 3.2). Peaks were observed at two-three month intervals, with androgens rising gradually over a period of approximately one month to reach levels up to four-fold higher than baseline concentrations. Increases in testosterone sometimes coincided with breeding activity, but also occurred prior to and after the female's oestrus (Figure 3.6).





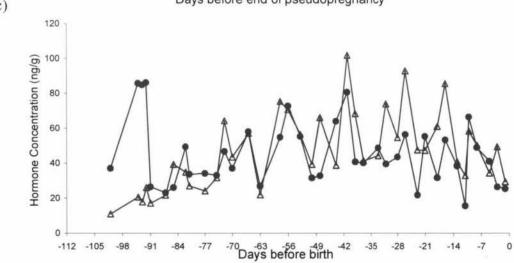


Figure 3.5: Daily faecal oestradiol (•) and progesterone metabolite (Δ) excretion in female Sun bear 'Chomel' (#607) during three successive reproductive cycles January 1996 - December 1997; a) and c) pregnant cycles and b) pseudopregnant cycle.

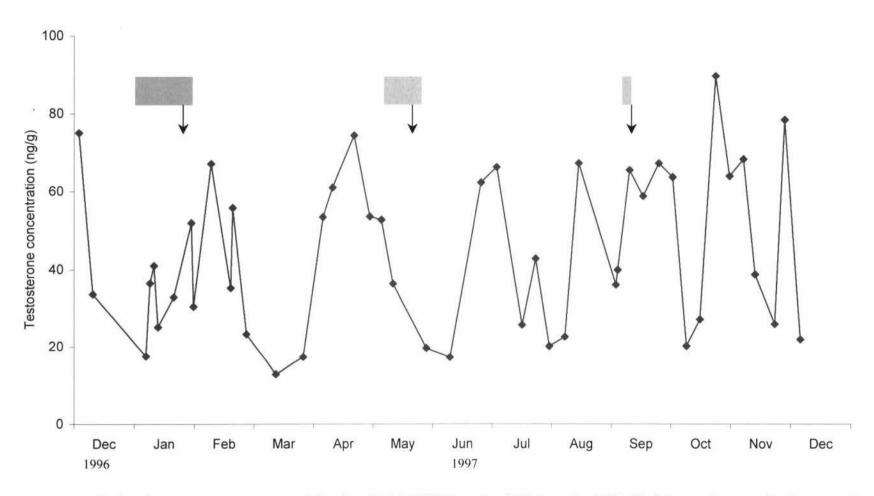


Figure 3.6: Weekly faecal testosterone excretion in male Sun bear 'Bakti' (#617) December 1996-December 1997. Shaded areas show periods of oestrus in his mate (female #607). Arrows indicate episodes of copulation based on behavioural observations and approximate dates of conception.

3.3.2.1 Female cycle characteristics

The length of oestrus varied considerably between Chomel's cycles, resulting in a mean follicular phase duration of 11.0 ± 5.9 days. During polyoestrus cycling (December-Feb, May-June) consecutive waves of follicular activity were separated by an inter-oestrus interval of up to 20 days. The oestrus interval (from the onset of one cycle to the onset of the next) following apparent ovulation, was 141 days and 119 days. The length of conceptive and non-conceptive luteal phases was similar at 94.5 ± 2.5 days and 92.0 ± 0 days, and 84.5 ± 4.5 days, respectively.

3.3.2.2 Behaviour-Endocrine Relationships during Oestrus

The mean daily frequencies of behaviours previously shown to be associated with oestrus in female Sun bears (backward walking, inguinal presentation, rolling, self-maintenance; see Chapter 2) and frequencies of mounting between the sexes, were compared during weeks of high faecal oestradiol (mean >45 ng/g) where progesterone was low (mean <40 ng/g), and during weeks of low faecal oestradiol (mean ≤45 ng/g).

In general, the mean frequencies were low (<1 bout per hour), as previously reported (Chapter 2), however, the sexual behaviours backward walking, inguinal presentation, rolling and mounting were all exhibited at higher frequencies during weeks of elevated oestradiol concentrations (data not shown). Not all behaviours were consistently observed during weeks of high oestradiol, however, several behaviours showed an increase in frequency concurrent with rising oestradiol levels (Figure 3.7). This was most evident during the female's oestrus in January 1997; the sequence of events is described below:

There was a noticeable increase in the female's frequency of self-maintenance between weeks 1-4, rising from approximately 2 bouts per hour to nearly 8 bouts per hour (Figure 3.7a). During weeks 1-5 Chomel regularly solicited Bakti's attention, often approaching him and initiating contact. Rolling was observed only during week 1, but inguinal presentations persisted, steadily increasing in frequency as oestradiol levels rose (Figure 3.7b). Mounting between the sexes was infrequent, but observed regularly between weeks 1-4. Chomel mounted the male for brief periods during weeks 1 and 3 prior to peak oestradiol concentrations, whereas Bakti mounted the female with

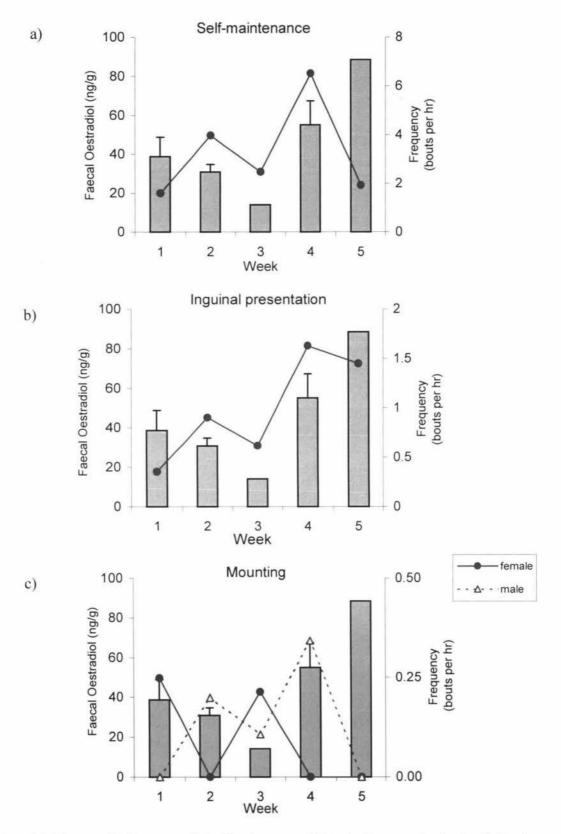


Figure 3.7: Mean weekly frequency of a) self-maintenance, b) inguinal presentation in female Sun bear 'Chomel' (#607) and c) mounting between female and male 'Bakti' (#617), compared with female mean weekly faecal oestradiol concentrations during weeks 1-5. Bars show 1 standard error of the mean for oestradiol.

increasing frequency as oestradiol levels rose between weeks 2-4 (Figure 3.7c). Mounting was relatively brief usually lasting <30 seconds. Pelvic thrusting occurred during some of the male's mounts, but intromission was not observed.

The frequency of other partner-oriented activities associated with heightened sexual interest between Sun bears, similarly tended to increase as the female's oestradiol levels rose (Figure 3.8). During week 4 there was a marked rise in the rate of interactions (Figure 3.8a) including episodes of bodily contact and amicable bouts of head-jockeying and wrestling. The pair's heightened interest in each other was evident between weeks 1-4, with extensive bouts of olfactory investigation often directed toward their partner. Sniffing was performed often during weeks 1-4 and was particularly evident for the male, rising to 12 bouts per hour (Figure 3.8b). The male also frequently sniffed the female's anogenital region and her urine/faeces. Swelling and reddening of her vulva was apparent.

Bakti began to make repeated attempts to herd Chomel to a secluded area in the enclosure and this behaviour became increasingly frequent between weeks 2-4 (Figure 3.8c). The male often exhibited heightened levels of aggression when his mate was in oestrus, and during weeks 1-4 he became notably aggressive toward humans - challenging people with growls, barks and threat postures, and on several occasions charging at staff and visitors.

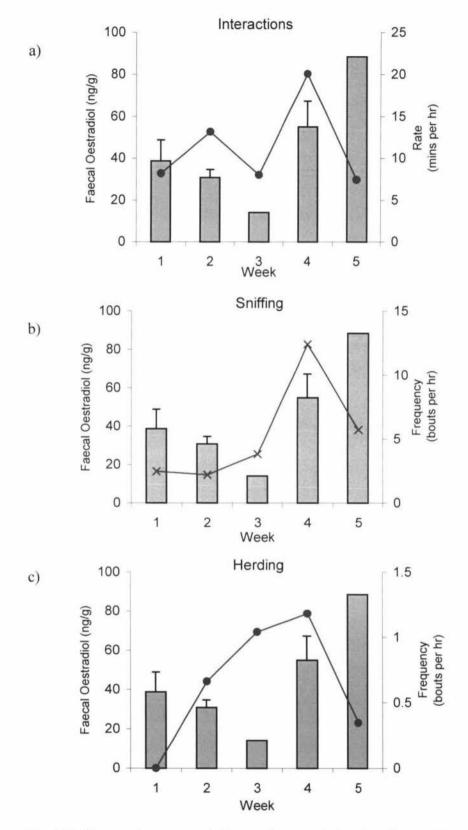


Figure 3.8: a) Weekly rate of interactions behaviours between the Sun bear female 'Chomel' (#607) and male 'Bakti' (#617), b) weekly mean frequency of male sniffing and c) herding female, compared with female weekly mean faecal oestradiol concentrations during weeks 1-5. Bars show 1 standard error of the mean for oestradiol.

In week 5 although the female's oestradiol levels remained elevated, the pair's level of interest in each other appeared to wane. There was a sharp decline in their rate of interactions (Figure 3.8a), and the female was less tolerant of the male. Although Chomel still exhibited inguinal presentation (Figure 3.7b), she began actively avoiding Bakti, and used threat behaviours to keep him at bay. The male's frequency of sniffing and herding her declined markedly (Figure 3.8b and Figure 3.8c), and mounting was not observed (Figure 3.7c). By week 6 the female's oestradiol levels had dropped to <20 ng/g and no further reproductive activity was reported (Keeper log books WZG). Oestradiol levels remained low throughout February during the early stage of pregnancy (Figure 3.4).

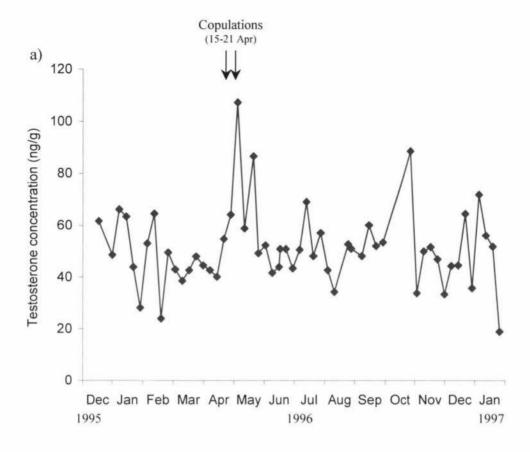
An increase in the male's faecal testosterone levels accompanied the breeding activity during weeks 1-5 (Figure 3.6). Bakti's testosterone continued to rise after the female's oestrus, and peaked the following week. Elevations in testosterone excretion often coincided with breeding behaviour at other times during the year, although testosterone was not necessarily at peak levels during mating (Figure 3.6).

3.3.3 Male Sun bears

3.3.3.1 SSP project: North American zoos

Faecal testosterone profiles for the seven males are shown in Figure 3.9 - Figure 3.11). Longitudinal profiles revealed fluctuating androgen excretion throughout the year, but for most animals sustained increases occurred at four-six month intervals. The pattern of elevated excretion varied within and between males but generally, testosterone rose steadily and remained elevated for up to several months, peaking at levels approximately three-five fold above baseline. Breeding behaviour and copulation was often reported during periods of elevated testosterone excretion, occurring prior to, during or after a peak.

Testosterone profiles for males #586 and #554 over an interval of <12 months were less informative than longitudinal profiles, however, peaks were apparent for both individuals (Figure 3.12). Male #586 showed elevated androgen levels from December 1996 - February 1997, with copulation occurring near the end of this period (Figure 3.12a). Testosterone levels in male #554 fluctuated over the eight-month interval, higher levels were apparent during July 1996 (Figure 3.12b). Behaviour records were unavailable for this individual.



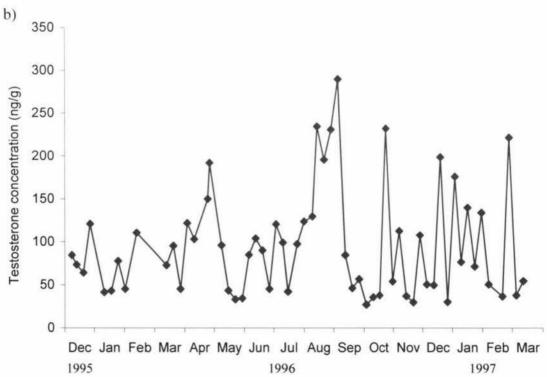
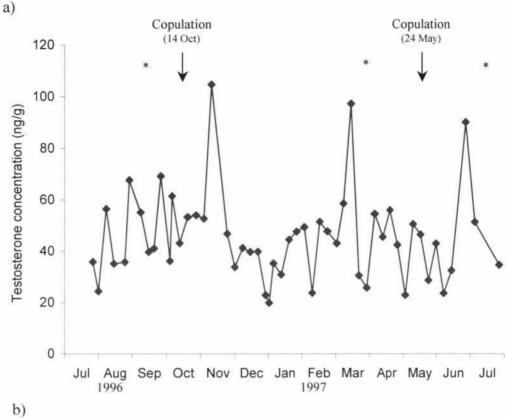


Figure 3.9: Weekly faecal testosterone excretion in male Sun bears a) 'Kuala' (#618) December 1995 - January 1997 and b) 'Yogi' (#470) December 1995 - March 1997.



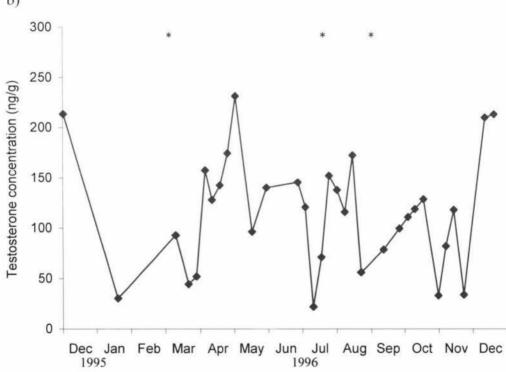


Figure 3.10: Weekly faecal testosterone excretion in male Sun bears a) 'Spike' (#516) July 1996 - July 1997 and b) 'Sunny' (#409) December 1995 - December 1996. Asterisks denote breeding activity in the absence of confirmed copulation.

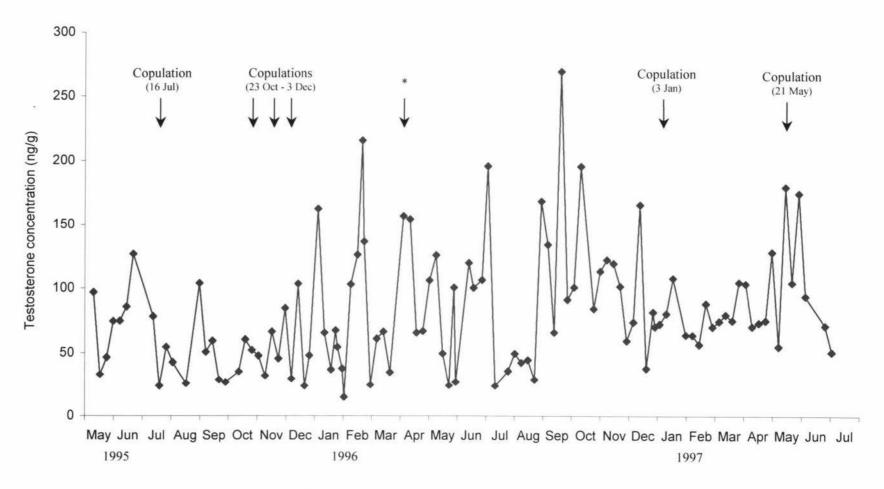
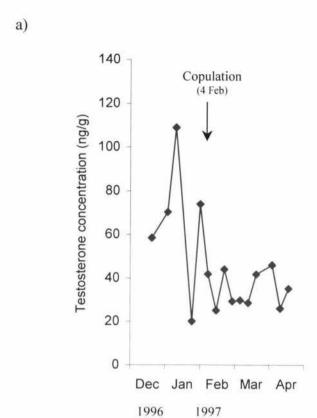


Figure 3.11: Weekly faecal testosterone excretion in male Sun bear 'Buffy' (#420) May 1995 - July 1997. Asterisks denote breeding activity in the absence of confirmed copulation.



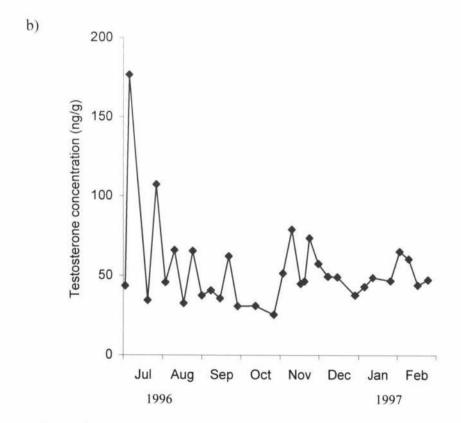


Figure 3.12: Weekly faecal testosterone excretion in male Sun bears a) 'Liberty' (#586) December 1996 - April 1997 and b) 'Boris' (#554) July 1996 - Feb 1997.

3.3.3.2 Grouped Male Data

The mean and range of faecal testosterone concentration for all males is given in Table 3.2, and includes data for the two males studied at Wellington (WZG) and San Diego (ZSSD). There was some individual variation, but the mean testosterone concentration for most animals was between 45-100 ng/g, giving an overall mean of approximately 65 ng/g. Because #606 showed levels substantially higher than the others (mean >250 ng/g) and sampling was limited to one month during breeding activity, his data were not included in the overall mean.

Table 3.2: Mean faecal testosterone concentration and range for captive male Sun bears.

Animal studbook #	Mean faecal testosterone concentration (ng/g)	Faecal testosterone range (ng/g)	Faecal samples
409	116.3 ± 10.1	21.8 - 231.5	32
420	81.9 ± 4.6	15.2 - 269.2	106
470	95.5 ± 8.1 27.0 - 289.9	60	
516	45.4 ± 2.5	45.4 ± 2.5 19.9 - 104.7	
554	54.2 ± 5.1	25.5 - 176.8	31
586	45.3 ± 6.2	20.2 - 109.1	15
606	258.5 ± 26.1	99.8 - 460.7	15
617	44.4 ± 3.1	13.1 - 89.7	45
618	51.2 ± 2.0	18.9 - 107.2	55

There was no significant effect of season in male Sun bears (p>0.05; Table 3.3). A pattern of cyclicity was, however, apparent when data were grouped by week of year (Figure 3.13). Levels generally remained low throughout January before rising to a slight peak during February, with comparatively larger and very consistent increases in testosterone concentration occurring during April-May, June-July and August-September. During each of the latter three cycles, testosterone rose gradually over a month to reach a peak approximately two-fold higher than baseline values, with levels gradually declining over the following month. Brief troughs occurred between the three cycles (during mid-May and mid-July). Between October-December testosterone levels fluctuated, and sustained increases or peaks were not apparent.

Table 3.3: Seasonal variation in faecal testosterone concentration in captive male Sun bears exposed to natural variation in photoperiod.

Season	Faecal testosterone (ng/g)	Range (ng/g)	Faecal samples (n)
Winter	65.1 ± 3.2	52.0 - 86.0	110
Spring	72.9 ± 5.4	46.5 - 110.7	91
Summer 72	72.5 ± 4.7	39.9 - 101.0	88
Autumn	72.9 ± 4.7	52.8 - 103.8	88

Values are means \pm 1 SE; p > 0.05 for all seasons.

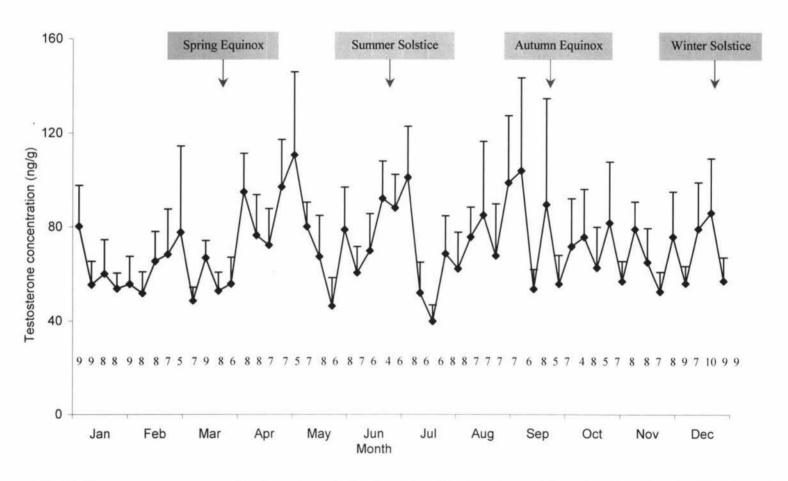


Figure 3.13: Weekly mean testosterone excretion in captive male Sun bears (n = 8) collected over <27 months. Data for male (#617) from the southern hemisphere zoo have been displaced by six months. Numbers below data points represent weekly sample size and bars show 1 SE of the mean.

3.4 DISCUSSION

3.4.1 Female Reproductive Cycle

Although previous studies have measured sex steroids in female Sun bear faeces, this is the first to profile oestradiol-17β and progestagens during confirmed pregnant and pseudopregnant cycles. Although Brown et al (1996a) measured oestradiol-17β in Sun bears, their paper provides only a brief overview of results, while in comparison, Schwarzenberger et al (1997) used faecal androgens to monitor follicular activity. The only reported range of faecal oestradiol in ursids is Kubokawa et al's (1992) study of the Giant panda, but a comparison is not possible because concentrations are reported per wet weight. The range in female Sun bears was, however, comparable to dry weight faecal oestrogen concentrations reported for a variety of non-domestic canid (Wasser et al 1995; Monfort et al 1997; Velloso et al 1998) and felid species (Brown et al 1994; Brown et al 1996b; Wielebnowski & Brown 1998). Unlike oestrogens which are endproducts of steroid metabolism, progesterone is extensively metabolised prior to its excretion in faeces, and for this reason 'group specific' antibodies raised against pregnanes are more suitable for analysis of faecal progesterone metabolites (Schwarzenberger et al 1996b). Differences between assay methods make comparisons of progestagen concentrations between laboratories difficult (Schwarenberger et al 1996b), however, the antibody employed in this study was specific for progesterone rather than being group specific, which is likely to explain why concentrations were up to several thousand times lower than given in the reports cited above.

3.4.1.1 The Follicular Phase

The mean length of the follicular phase for the Sun bears in this study was 11.2 ± 1.3 days, which is lower than the interval of 15.6 ± 1.7 days reported by Schwarzenberger et al (1997). For paired females, marked increases in faecal oestradiol excretion in the absence of a significant or sustained rise in progestagens, were commonly associated with behavioural oestrus and mating. Accordingly, Schwarzenberger et al (1997) noted that mating activity occurred during peaks in faecal androgen excretion. Behavioural oestrus in Sun bears is estimated to last approximately one-two weeks (Domico 1988; Schaller 1994), although Dathe (1963) suggests it may be as short as a single day. Unsystematic observations alone are subject to some error, however, considerable variation in the length of the follicular phase is apparent. Schwarzenberger et al (1997)

reported a range of 10-24 days, which, is higher than the range of 6-19 days reported here. In the WZG female oestrus recurred at intervals of approximately four-five months following a sustained rise in faecal progestagens, which is in agreement with observations by Brown et al (1996a) and Schwarzenberger et al (1997).

Daily sampling coupled with behavioural observations in the ZSSD female permitted a preliminary evaluation of the length of the proceptive and receptive phase of oestrus in the Sun bear, which were 4 days and 8 days, respectively. Urinary steroid monitoring has been applied extensively to characterise the reproductive cycle of the Giant panda. This species has a follicular phase of approximately 10 days, but in contrast the proceptive period endures for approximately one week, with the female's receptive period limited to only several days (Bonney et al 1982; Hodges et al 1984; Chadhuri et al 1988).

In other bears the reported length of behavioural oestrus generally ranges from 5 - 7 days (*U.arctos*: Meyer-Holzapfel 1957 cited in Ludlow 1974, Dittrich & Kronberger 1962, Hornocker 1962 cited in Barber & Lindzey 1983; Craighead et al 1969; Tsubota & Kanagawa 1986; *T.ornatus*: Bloxam 1976, Orejuela 1989; *U. americanus*: Ammons 1974 cited in Barber & Lindzey 1983; Ludlow 1974; Barber & Lindzey 1983), although in the Brown bear oestrus may last for several weeks (Dittrich & Kronberger 1962; Craighead et al 1969; Tsubota et al 1985 cited in Tsubota & Kanagawa 1986). The pattern of steroid excretion during oestrus has not been detailed in other ursids, but an increase in serum oestradiol has been detected in American black bears sampled during the breeding season (Wathen et al 1983 cited in Hellgren et al 1991; Tsubota et al 1998).

Results of this study showed a similar pattern of steroid secretion for female Sun bears #598, #607 and #608 during oestrus, with baseline oestradiol concentrations of approximately 20-30 ng/g, increasing sharply to between 100-150 ng/g. Immunolocalisation of steroidogenic enzymes in the Brown bear suggest that granulosa cells in large follicles may be capable of progesterone biosynthesis (Araki et al 1996), and for Sun bears, slight rises in faecal progestagens were often detected during the follicular phase. These increases may reflect preovulatory luteinisation of follicles, and are similar to the pattern of steroid profiles observed for the domestic bitch (Concannon

et al 1977; Wildt et al 1979; Olson et al 1982) and other canids (*wolf*: Seal et al 1979; Wasser et al 1995; *African wild dog*: Monfort et al 1997).

Induced or 'reflex' ovulation is a feature of reproduction common to a number of carnivores including mustelids and felids (Milligan 1982; Rowlands & Weir 1984). Ursids are thought to be induced ovulators (Wimsatt 1963; Erickson et al 1964; Ewer 1973 cited in Schaller et al 1985) with the possible exception of the Giant panda (Kleiman 1983; Schaller et al 1985), and preliminary findings have recently confirmed this mechanism in the American black bear (Boone et al 1988). In induced ovulators, while cervico-vaginal stimulation during coitus is usually necessary to invoke ovulation, on rare occasions spontaneous ovulation has been reported in solitary or unmated ursids (*U.arctos:* Tsubota et al 1987; *U.americanus:* Boone et al 1998) and felids (domestic: Windle 1939; Dow 1962 cited in Schmidt et al 1983; non-domestic: Schmidt et al 1988; Schramm et al 1994; Brown et al 1995; Brown et al 1996b).

Results of the present study are limited but several observations support the likelihood that the Sun bear is an induced ovulator. In the domestic cat, oestradiol levels decline soon after mating when ovulation occurs, but oestrus may endure for several days if copulatory stimulation is insufficient to elicit ovulation (Wildt et al 1981). This may explain the prolonged period of receptivity noted in female #598 at ZSSD, and why an increase in progestagens was not detected until approximately one week after the initial mating. Female #608 experienced postpartum oestrus following the removal of young, but unlike the females paired with males, an increase in progesterone metabolites was not detected following the fall in oestradiol-17β. Sampling ended too prematurely to allow further comment, but it is tempting to speculate that this may have indicated failure to ovulate at oestrus in this solitary animal.

Despite having unrestricted access to the male at oestrus, profiles suggest that the WZG female apparently failed to ovulate on several occasions. Overt sexual behaviours and mating activity accompanied the period of elevated faecal oestradiol, however, a marked rise in progestagens was not observed, and on both occasions oestrus recurred several weeks to a month later. Female bears typically have a monoestrus cycle, but evidence of a second period of behavioural heat in the breeding season suggests that polyoestrus cycling may occur in some other species (*U. arctos:* Dittrich & Kronberger 1962; Craighead et al 1969, Tsubota et al 1985 cited in Tsubota & Kanagawa 1986;

Tsubota & Kanagawa 1986; T. ornatus: Bloxam 1976; U. americanus: Barber & Lindzey 1983, Rowlands & Weir 1984). Polyoestrus cycling is more typical of domestic (Verhage et al 1976; Shille et al 1979) and non-domestic felids, (Schmidt et al 1979; Bonney et al 1981; Wildt et al 1981; Seal et al 1987; Schmidt et al 1988; Schmidt et al 1993; Czekala et al 1994; Graham et al 1995; Brown et al 1996b), with oestrus recurring at intervals of between one week to a month in the absence of mating or a stimulus sufficient to induce ovulation. Although mating activity was frequently observed between the Sun bears at WZG, the fact that polyoestrus cycling occurred suggests that either the female was unmated or copulatory stimulation was insufficient to evoke ovulation on these occasions. Tsubota et al (1985 cited by Tsubota & Kanagawa 1986) observed polyoestrus activity in the Hokkaido Brown bear, and speculated that the females' failure to ovulate may have been related to the reduced frequency of copulation, associated with lower libido in the 15 year old male. This does not explain the situation at WZG because the male was approximately 7 years old; furthermore he remained in good health throughout the study and in indication of his prime breeding condition, consistently sired young on other occasions.

3.4.1.2 The Luteal Phase

The mean length of the luteal phase for the Sun bear in this study was 93.3 ± 3.0 days, which is comparable with the interval of 94.0 ± 2.3 days reported by Schwarzenberger et al (1997). The pattern of faecal progestagen excretion was similar to profiles published by Schwarzenberger et al (1997). In agreement with Brown et al (1996a), there was little quantitative difference between a pregnant and pseudopregnant state. Following apparent ovulation progestagens increased gradually, peaking 'mid-term' and declining approximately one month prior to the end of the luteal phase. In contrast, other ursids exhibit a modest increase in progesterone after mating that is instead, followed by a characteristically sharp elevation approximately two months prior to parturition (*U.americanus*: Foresman & Daniel 1983; Palmer et al 1988; Hellgren et al 1991; U.arctos: Tsubota et al 1987; Göritz et al 1997; U.maritimus: Palmer et al 1988; A.melanoleuca: Chadhuri et al 1988; Hodges et al 1984). Tsubota et al (1998) suggested that during the delay the corpora lutea secrete lower levels of progesterone because they are incompletely luteinised, and the dramatic increase is associated with formation of fully functional corpora lutea at implantation. As observed for the Sun bear, in other ursids serum progesterone (Tsubota et al 1987; Hellgren et al 1991) or urinary pregnanediol levels (Chadhuri et al 1988; Hodges et al 1984) generally decline several weeks to one month prior to parturition, and reach baseline concentrations within one week postpartum. The pattern and duration of progesterone excretion during the luteal phase is also reported to be similar in both pregnant and non parturient bears (Tsubota et al 1987; Chadhuri et al 1988; Monfort et al 1989; Hellgren et al 1991; Göritz et al 1997).

Compared to progestagen excretion, the pattern of oestrogen excretion during the luteal phase is less understood for bears. Results of the present study showed that the pattern of faecal oestradiol excretion in the Sun bear was similar during pregnancy and pseudopregnancy. Oestradiol levels dropped sharply after oestrus then gradually increased concurrent with rising levels of progestagens. Throughout the luteal phase, oestradiol remained at concentrations lower than at oestrus, and declined simultaneously with progestagens, approximately one month prior to birth/end of pseudopregnancy. In the Giant panda, urinary steroid profiles also showed an increase in oestrogens around the same time as the late-gestational rise in pregnanediol (Monfort et al 1989). Limited findings suggest that there may be a quantitative difference in urinary oestrogen excretion between pregnancy and pseudopregnancy in this species (Bretzfelder 1989).

Information on the pattern of oestrogens in other ursids is limited, but an elevation in serum oestradiol has been noted in pregnant and non-pregnant Polar bears sampled several months prior to implantation (Palmer et al 1988), and a slight rise in serum oestradiol has been reported for the American black bear following implantation (Tsubota et al 1998). Histological studies of the American black bear have shown that follicular growth may continue throughout the luteal phase, but the follicles apparently fail to mature (Wimsatt 1963; Erickson et al 1964). The source of oestrogens during the luteal phase is uncertain, but as Palmer et al (1988) suggested they may represent underlying waves of follicular activity. It is also possible they could be related to placental and/or foetal-maternal production of steroid (Monfort et al 1989).

3.4.1.3 Post-partum Oestrus

In females #607 and #608 postpartum oestrus occurred one-two weeks after the loss or removal of young, in accordance with behavioural observations of Sun bears at other zoos (McCusker 1974; Pagel & Kuhme 1992; Kolter 1995). Lactation was not established in either of the dams, and in all cases loss of young occurred within several

days of birth. Female bears do not usually breed for several years postpartum while rearing cubs, but may breed annually if lactation is interrupted by loss of young (Herrero 1978; Stirling 1993). Studies of felids have shown that suckling during lactation inhibits ovarian follicle development and secretion of gonadal and pituitary hormones (Concannon & Lein 1983; Schmidt et al 1983); however, in these unrestricted breeders as for the Sun bear, ovarian cycling resumes within approximately one week when young are aborted or removed immediately after parturition (Concannon & Lein 1983; Brown et al 1996b).

3.4.1.4 Reproductive Senescence

Female #528 at ZSSD was >16 years old and multiparous, having produced her last cub 5 years previously. She had not been paired with a male since and no signs of oestrus had been noted (Keeper log books ZSSD). Compared to other females in this study her faecal sex steroid concentrations fluctuated erratically over the month long sampling interval. Schwarzenberger et al (1997) noted similarly erratic follicular and luteal activity over a period of approximately six months in an aged (~19 years) multiparous Sun bear. Data from the present study are limited, but it is possible that the pattern of hormone secretion observed in these relatively aged females could be related to irregular ovarian function associated with reproductive senescence. Although bears may remain capable of breeding for most of their life (up to 25 years), (Bunnell & Tait 1981; Palmer et al 1988), a recent study has reported that oocyte number and quality was compromised in Sun bears aged over 20 years (Johnston et al 1994), and data from captive populations has shown that females rarely produce young after they reach 12-15 years (Kolter 1995; Kolter 1998d; Chapter 4).

3.4.2 Male Reproductive Cycle

With the exception of Kubokawa et al's (1992) study of the Giant panda, there are no other published reports documenting faecal testosterone in bears. A comparison of the pattern of testosterone excretion in male Sun bears with those of other bears is presented below, however, a comparison of faecal testosterone concentrations is not possible because those for the Giant panda are given per wet weight faeces. Faecal testosterone has been measured in a variety of other male carnivores (*felids:* Brown et al 1996b; *black-footed ferret:* Brown 1997; *African wild dog:* Monfort et al 1997; *maned wolf:* Velloso et al 1998), but concentrations (dry weight) are highly variable.

Other ursids are seasonal breeders that exhibit a rise in testosterone between spring-summer (*U.americanus*: McMillin et al 1976, Palmer et al 1988; Tsubota et al 1997; *U.maritimus* Palmer et al 1988; *A.melanoleuca*: Bonney et al 1982, Kubokawa et al 1992; *U.arctos*: Tsubota & Kanagawa 1989), with active spermatogenesis usually preceding and succeeding the females' breeding period (*U. americanus*: Erickson et al 1964, Palmer et al 1988, Garshelis & Hellgren 1994; *U. arctos*: Erickson et al 1968; Tsubota et al 1997; *A. melanoleuca*: Platz et al 1983; Masui et al 1985; *U. maritimus*: Palmer et al 1988; *U. thibetanus*: Komatsu et al 1995). The factors that regulate the annual reproductive cycle in these species is unclear, however, photoperiod is considered likely to play the principal role (McMillin et al 1976; Palmer et al 1988; Garshelis & Hellgren 1994; Horan et al 1993).

Results of this study showed that faecal testosterone in individual male Sun bears was often elevated during mating activity, peak concentrations were also observed prior to and following episodes of breeding behaviour and copulation. In other ursids, testosterone generally parallels the duration of the mating season, and similarly, peak concentrations have been observed several months prior to or during the breeding season (*U.arctos*: Tsubota & Kanagawa 1989; *U. americanus*: McMillin et al 1976; Palmer et al 1988; Garshelis & Hellgren 1994). Garshelis & Hellgren (1994) suggest that an early peak may be related to the establishment of social hierarchies prior to mating. A peak in testosterone concentrations or testicular size prior to the breeding season has also been reported for a number of other carnivores including the Siberian tiger (Byers et al 1990), the wolverine (Mead et al 1991) and black-footed ferret (Brown 1997).

The only females that produced cubs during this study, were those housed with males #606 (ZSSD) and #617 (WZG), although it is possible that births at other zoos may have gone undetected. All of the males were considered to be sexually mature (>5 years), and four individuals had previously sired young. While androgens play an essential role in spermatogenesis they do not necessarily provide a measure of fertility (Setchell 1978), but it is of note that in general there were no appreciable differences in faecal testosterone concentrations related to either age or reproductive status of male bears.

The Sun bear has been referred to as being a nonseasonal breeder due to the unrestricted occurrence of births in captivity (Kolter 1995; Schwarzenberger et al 1997). Births are distributed evenly throughout the year in the European population (Kolter 1995), but in North American and New Zealand zoos a significant influence of season on birth is apparent, with the majority (>75%) of young being born during summer and autumn (Chapter 4). Most births took place between June and December²⁵, and pronounced peaks in the birth rate were observed in the months of July and October, with nearly 50% of the cubs being born in these two months alone. Based on the gestation length of approximately three months in the Sun bear, this suggests peaks in oestrus activity occur in April and July (spring-summer) in the Northern Hemisphere, a finding supported by independent data from females in North American zoos (Chapter 4). Although there was no significant effect of season on testosterone in male Sun bears, it is of interest that common peaks were observed between April-May and June-July, the months when peak oestrus activity apparently occurs.

Information is not available on reproductive rhythms of Sun bears in their native habitat, but the lack of a restricted breeding season in captivity suggests that their reproduction is adapted to tropical conditions. A number of other continuous breeders from tropical and equatorial regions including East African carnivores (Seager & Demorst 1986 cited in Briggs et al 1990; reviwed in Bailey 1993) and ungulates (Spinage 1973 cited in Flowerdew 1987) are known to exhibit peaks in reproduction, thought to be related to periods of rainfall or prey abundance. In tropical south east Asia there is little annual change in photoperiod, but the climate is variable and dominated largely by rainfall during the monsoon seasons (Pearson 1988). A correlation between the double pattern of rainfall in this area and season of Sun bear births in captivity suggests that this factor may represent an environmental rhythm involved in timing reproduction in this species (Chapter 4).

Given that female Sun bears are apparently capable of breeding at any time of year, and that a male's energetic expenses of reproduction are primarily behavioural (Bronson 1985), it would be advantageous for males to remain reproductively ready all year long. Seminal characteristics of the Sun bear have not been studied but it seems unlikely that

²⁵ Birth data from the NZ female were displaced by six months.

any effect of season would be apparent. The Clouded leopard (*Neofelis nebulosa*) is a tropical felid from that inhabits the same range as the Sun bear, and similarly young may be born at any time of year in captivity, although peak oestrus activity occurs during autumn and winter (Yamada & Durrant 1989). Wildt et al (1986a, b) observed a significant seasonal effect of testosterone during winter for the male Clouded leopard, but no effect of season on ejaculate quality. Comparable findings are reported for the domestic dog (Amann 1986) and the Siberian tiger (Byers et al 1990), in which testosterone peaks are associated with the breeding period, but sperm production/ejaculate quality are unaffected by season.

There are major gaps in our knowledge of nonphotoperiodic regulation of seasonal breeding in mammals (Bronson 1985). While photoperiod does not appear to play a major role in influencing reproduction in Sun bears, the factors involved in regulation of gonadal activity are uncertain. The potential of a nonphotoperiodic influence on testicular cycles cannot be overlooked, and it is also possible that males may be responding to social cues from females (Section 3.4.3). Other mechanisms known to affect testosterone levels include compromised nutrition, stress and muscular exercise, and endogenous diurnal rhythms (McMillin et al 1976). Nutrition is unlikely to have affected testosterone values because food supply was not restricted in the captive animals, and faecal sampling would have eliminated effects of stress and muscular exercise associated with physical and chemical restraint (Wesson et al 1979; Brown et al 1988; Wildt et al 1988; Garshelis & Hellgren 1994). The existence of a diurnal testosterone rhythm is controversial, but has been reported in various other species (rat: Kinson & Lieu 1972; rhesus monkey: Goodman et al 1974; boar: Ellendorf et al 1975). An added advantage of faecal monitoring is that pooling of steroids dampen typical fluctuations in testosterone that occur in response to pulses in luteinising hormone (Brown et al 1996c), which may have also countered the effects of any diurnal variation in steroid concentrations.

3.4.3 Behaviour-Endocrine Relationships at Oestrus

Behaviour-endocrine correlates of reproduction have been described in a range of non-domestic carnivores including felids (Schmidt et al 1979; Schmidt et al 1983; Seal et al 1987; Schmidt et al 1988; Wielebnowski & Brown 1988; Graham et al 1995), canids (Seal et al 1979; Monfort et al 1997; Osadchuk 1996), and Giant panda (Bonney et al 1982; Murata et al 1986). The reproductive behaviour of ursids is not well documented,

but sexual behaviours of the Sun bear (see Chapter 2) appear similar to those observed in the Giant panda (Kleiman et al 1979; Kleiman 1984). The females' use of behavioural cues to attract the male and maintain his attention, and later to communicate her readiness to mate are typical of female mammalian reproductive behaviour, and have been shown to be influenced by hormone levels that signal the optimal time for breeding (Beach 1976).

In female Sun bears paired with males, the onset of sexual behaviours and active soliciting of the male coincided with rising oestradiol levels, which is in agreement with observations for the Giant panda (Bonney et al 1982; Hodges et al 1984; Murata et al 1986; Chadhuri et al 1988; Monfort et al 1989). As reported by Bonney et al (1982), oestrus was also characterised by a reduction in agonism and increased levels of interest and interactions between pairs. The same sexual behaviours were observed in both female Sun bears, and included inguinal presentation, backward walking, rolling, and mounting of the male. Results showed that in the WZG female these behaviours occurred more frequently at oestrus i.e. under the influence of an oestradiol-dominant state. Grouped data from WZG revealed that the frequency of several behaviours fluctuated in accordance with weekly oestradiol concentrations. Only qualitative data are available for the Giant panda (Bonney et al 1982; Murata et al 1986), however, studies of non-domestic felids similarly report a positive correlation between the frequency of sexual behaviours and elevated oestradiol concentrations (Schmidt et al 1979; Seal et al 1987; Schmidt et al 1988; Schmidt et al 1993; Graham et al 1995; Wielebnowski & Brown 1998).

Daily monitoring of the breeding pair at ZSSD revealed that as female #598's oestradiol levels increased steadily, this was accompanied by a concurrent rise in the frequency of sexual behaviours. Although mounting by the male was observed throughout the proceptive phase, oestradiol concentrations had risen three-fold before the female permitted copulation, with the combined score of all sexual behaviours being highest on the day she became receptive. The most intense period of mating occurred one day prior to peak oestradiol levels, and while copulation was observed again several days later, declining concentrations were marked by a rapid loss of interest between the pair. In contrast, studies indicate that the Giant panda becomes receptive during or after the peak in urinary oestrogens, and sexual activity may continue for several days after

oestrogens have returned to basal concentrations (Bonney et al 1982; Hodges et al 1984; Murata et al 1986; Chadhuri et al 1988; Monfort et al 1989).

In other carnivores proceptive behaviour is also associated with increased oestrogen production, and copulation occurs during, or after peak concentrations are reached (Concannon et al 1975; Schmidt et al 1979; Seal et al 1979; Shille et al 1979; Wildt et al 1979; Schmidt et al 1993; Monfort et al 1998). Falling oestrogen levels and a simultaneous increase in progesterone is responsible for the onset of receptive behaviour in several species, including the domestic bitch (Beach et al 1982), however, in felids there is no preovulatory rise in progesterone, indicating that oestrogens alone are capable of stimulating female sexual behaviour (Wildt et al 1981). Results from the breeding pair at ZSSD showed that copulation occurred nearly a week prior to a detectable increase in faecal progestagens in female #598, suggesting that oestradiol alone was able to evoke receptivity.

Female behaviour played an obvious role in maintaining sexual interest between pairs, when oestradiol concentrations were elevated males demonstrated a high level of olfactory interest in their partner's anogenital area and excreta. This behaviour is typical of male bears as they 'check' the reproductive status of a potential mate (Meyer-Holzapfel 1957 cited in Ewer 1985; Craighead et al 1969; Tschanz et al 1970; Herrero & Hamer 1977; Kleiman et al 1979; Hamer & Herrero 1990). In several species, oestrogens are known to enhance attractivity of the female and their vaginal secretions and urine (Beach et al 1982). For the Sun bears a similar association between elevated oestradiol levels in the female and male olfactory interest was apparent.

In other male mammals a rise in plasma testosterone has been shown to accompany exposure to females and copulatory activity (e.g. rabbit: Haltmeyer & Eik-Nes 1969; bull: Katongole et al 1971; rhesus monkey: Rose et al 1972; rat: Purvis & Haynes 1974; Kamel et al 1975; boar: Liptrap & Raeside 1978; sheep: Gonzales et al 1988; fox: Osadchuk 1996). In this study breeding activity of male Sun bears was often associated with increased or peak faecal testosterone concentrations. For instance, daily sampling of male #606 revealed that testosterone rose steadily following the introduction of female #598, with concentrations reaching a peak when she became receptive. Bonney et al (1982) reported similar findings for the male Giant panda, with urinary androgen excretion increasing during the breeding season and reaching peak concentrations at

copulation. The testosterone profile for male #606 closely tracked the female pattern of oestradiol, as in the Giant panda (Bonney et al 1982); and although copulation was observed several days after the sharp fall in oestradiol and testosterone, continuing decline in concentrations of these hormones was accompanied by rapid loss of interest between the pair and cessation of sexual activity.

Testosterone is also known to facilitate aggressive behaviour in male mammals (Liptrap & Raeside 1978; Lincoln et al 1977; Lincoln 1981; Cooper et al 1990), and in free-ranging bears the seasonal elevation in testosterone is accompanied by characteristic intra-sexual aggression and display (Herrero & Hamer 1977; Herrero 1978; Barber & Lindzey 1983; Ramsay & Stirling 1986; Schaller et al 1985). Garshelis & Hellgren (1994) have reported a correlation between increased plasma testosterone and intra-sexual aggression in the American black bear. For the male Sun bear at WZG, episodes of aggression were often observed during breeding periods, indicating that this behaviour may have been related to increased testosterone levels around that time.

3.4.4 Conclusions and Management Implications

This study has demonstrated the effectiveness of faecal steroid analysis as a noninvasive method for evaluation of gonadal activity in male and female Sun bears. While data should be interpreted cautiously given the small sample size of the study population, it represents the first documentation of testicular-endocrine rhythms in males, and results from females expand on recent findings in other studies. A major benefit of faecal monitoring was that it permitted characterisation of the pattern of sex steroid excretion during the reproductive cycle, which is information previously constrained by traditional sampling techniques. Substantial increases in faecal oestradiol were accompanied by overt sexual behaviour and mating suggesting that concentrations reflect waves of follicular activity at oestrus. A sustained rise in faecal progestagens was apparent only after confirmed mating or during pregnancy, presumably associated with the formation of corpora lutea following ovulation. Recurrent follicular cycles were sometimes observed several weeks to a month apart in the absence of a sustained elevation in progesterone metabolites. Because the nonconceptive phase is not abbreviated in ursids, this pattern of polyoestrous cycling suggests these cycles were anovulatory, lending support to the mechanism of induced ovulation in ursids. The progestagen-dominant luteal phase was accompanied by lower concentrations of faecal oestradiol assumed to represent steroid secretion from immature follicles. No apparent quantitative difference in hormone excretion was noted between conceptive and non-conceptive cycles. The Sun bear is considered unlikely to exhibit delayed implantation, given their relatively short gestation, and that the duration and pattern of progestagen excretion during the luteal phase was similar to post-implantation profiles of other ursids.

In male Sun bears a pattern of continuous cyclicity in annual faecal testosterone was observed. Androgen excretion was often elevated during breeding activity, but copulation also occurred during times of baseline testosterone concentrations. Although this tropical species has an unrestricted breeding season in captivity, the potential of nonphotoperiodic seasonal influences on testicular cycles cannot be ruled out. Grouped data suggest there may be an association between peak testosterone production in captive males and the months of peak reproductive activity. Studies of reproduction in free-ranging populations is required to complement these findings and ensure the effects observed are not artefacts of captivity. Given that females can mate at any time of year, it is likely that males remain reproductively capable year round. Further research is, however, needed to examine seasonal effects on seminal characteristics, and to investigate potential problems such as infertility.

Because Sun bears do not exhibit a fixed breeding season in captivity, identification of behaviours associated with oestrus is important in making pairing decisions, in helping estimate dates of parturition, and promoting more effective management of breeding programs. The onset and maintenance of female sexual behaviours appeared to be influenced by an oestradiol-dominant state and may, therefore, serve as 'key' indicators Pregnancy diagnosis in bears is problematic because of physiological oestrus. pseudopregnant females may exhibit similar physical and behavioural signs of 'true' pregnancy including mammary development, lactation and nest-building activity (Chadhuri et al 1988; Bretzfelder 1989; Chapter 2). Risks associated with traditional methods of pregnancy monitoring such as blood sampling and ultrasound (Ball 1996b) make non-invasive diagnosis a desirable option for these less tractable species. Urinary oestrogen analysis may offer potential in future management of the Giant panda. In the Sun bear, however, the indistinguishable patterns of faecal oestradiol and progestagens during pregnancy and pseudopregnancy, support the assertion that sex steroid monitoring may be of limited use in accurately diagnosing pregnancy in other ursids. The factors limiting breeding success of captive Sun bears are unknown. Further

studies are therefore needed to improve understanding of the reproductive biology of this species, particularly if assisted breeding techniques are to be considered in future management.

Chapter 4

A Review of Captive Breeding and Reproductive Parameters for the Malayan Sun bear (*Ursus malayanus*)

4.1 INTRODUCTION

Sun bears (*Ursus malayanus*) are tropical mammals inhabiting the rainforests of South East Asia. Formerly the species ranged from Malaysia and Indonesia in the east, to as far north as Southern China (Figure 4.1). Rapid loss of habitat through deforestation and poaching for the illicit trade in bear parts is placing increasing pressure on this species in the wild. There are no estimates of the distribution or number of Sun bears that remain, but populations in Malaysia and Indonesia are believed to be in serious decline (Mills & Servheen 1991; Santiapillai & Santiapillai 1996).

U.malayanus has been present in zoological parks around the world since the 1930's, but there is now growing concern for the status of populations in western zoos. To assist with management, regional studbooks were developed in North America and Europe in the early 1990s. A five-year Species Survival Plan (SSP) has also been published actioning both *in situ* and *ex situ* conservation projects for the Sun bear (Ball 1996a). Conservation initiatives include a preliminary field study, genotyping of captive populations and a study of the species' reproductive biology.

The breeding of Sun bears in captivity has been inconsistent and poor, and currently only approximately 120 individuals remain in western zoos. Numbers in North American zoos have been steadily declining since the 1970s, and following recommendations by the Bear Taxonomic Advisory Group (TAG), the importation of potential founders from Malaysia has begun (Frederick 1998). While importations will serve to increase numbers, there is a real need to determine which factors are limiting reproduction in the existing captive population.

Gaining a better understanding of the reproductive biology and behaviour of the species is essential to the implementing of techniques for more successful management. A demographic analysis has been provided for the European Sun bear population (Kolter 1995), but similar research had not been conducted for populations in other regions.

In this thesis, an analysis of breeding records from North America and New Zealand was undertaken to document reproductive parameters and generate a collective database for the species. The findings are presented with a review of the breeding history and

management of the species, and a discussion of potential factors that may be limiting Sun bear reproduction in captivity.



Figure 4.1: Native habitat of the Malayan Sun bear indicated as named countries of SE Asia.

4.2 MATERIALS AND METHODS

Reproductive parameters were determined from analysis of data published in the North American Studbooks for the Sun bear (Ball 1993; Ball 1994; Frederick 1998) and records at Wellington Zoological Gardens, New Zealand (1992-1999). Births in North American zoos were recorded between 1969-April 1998. Data published in the European studbooks (Kolter 1995; Kolter 1998d) were reorganised to permit comparative analysis.

Dates of oestrus can usually be inferred by subtracting the gestation length from the date of parturition. Most studies estimate the length of gestation in Sun bears at ~95 days (Dathe 1961; 1985 cited in Kolter 1995; Schwarzenberger et al 1997; Chapters 2 & 3) but some discrepancies have been reported (McCusker 1974). Because of the variability in observations, oestrus data were compiled from independent behaviour records contributed by 10 zoological institutions (Table 4.1).

The most common behavioural indicator of heat was persistent mounting of the female by the male; intromission was not necessarily observed. In the Sun bear, oestrus lasts \sim 1 - 2 weeks (Domico 1988; Schaller 1994; Schwarzenberger et al 1997; Chapters 2 & 3), and there is an interval of approximately 4 - 5 months between successive cycles (Brown et al 1996a; Schwarzenberger et al 1997; Chapter 3). Although polyoestrus activity can occur (see Chapter 3), most ursids are monoestrus – *i.e.* the female would come into heat only once within this period. Based on these parameters a single score of sexual activity was recorded per individual in any particular month. Data analysis was based on a total of 82 cycles from 12 females.

For seasonal analyses of reproduction the year was divided into four periods: December - February (winter), March - May (spring), June - August (summer) and September - November (autumn). To generate a comparable format with records from northern hemisphere zoos, data from New Zealand were displaced by six months. Chi-square was used for statistical analyses of seasonality.

Table 4.1: Summary of behavioural oestrus data on Sun bears held in 10 zoos. Numbers in parentheses represent oestrus periods when copulation was confirmed.

Site	Animal Studbook #	Date of Birth	No. observed oestrus	Behaviour records
Fortworth Zoo, TX* (FWZ)	346	c.1965	7 (6)	Oct 1969 - Feb 1973
Minnesota Zoo, MN (MZG)	468	11 Jul 1974	7 (0)	Jan 1994 - Jan 1996
Miami Metrozoo, FL (MMZ)	478 640	c.1975 21 Nov 1992	14 (2) 5 (0)	Nov 1989 - May 1997
San Diego Zoo, CA (ZSSD)	528 598 608	14 Nov 1980 07 Oct 1987 18 Oct 1988	3 (3) 2 (2) 3 (3)	Nov 1990 - Feb 1997
Oakland Zoo, CA (OZ)	570	01 Oct 1984	8 (2)	Jun 1996 - Jul 1997
Metro Washington Park Zoo, OR (MWPZ)	586	10 Oct 1985	5 (0)	Apr 1995 - Feb 1997
St Louis Zoo, MO (StLZ)	587	09 Jul 1986	9 (6)	July 1995 - May 1997
Woodland Park Zoo, WA (WPZ) Wellington Zoo,	605	27 Feb 1988	3 (0)	Feb 1996 - Sep 1996
New Zealand (WZG)	607	02 Aug 1988	16 (8)	Jan 1993 - Apr 1999

*Source: McCusker (1974)

4.3 RESULTS

4.3.1 Population Size and Distribution

4.3.1.1 North America (NA)

Between 1992 and 1994, the population consisted of approximately 65 Sun bears distributed among 25 different zoos. Approximately 65% of the population was female, (Dec 31 1993 total = 66 (22 males, 44 females)); Dec 31 1994 total = 66 (23 males, 43 females)) and all animals were older than 5 years. Information on the development and mortality of the population prior to 1992 was not provided. Although the population has continued to diminish over the last 5 years, the importation of 10 potential founders from Malaysia occurred in 1996. One male and nine females ranging in age from ~5 to 15 years old were distributed in pairs among four North American zoos (Frederick 1998)²⁶. A summary of current statistics for the North American population is found in Section 4.3.3.

4.3.1.2 New Zealand (NZ)

Four Sun bears are housed at the Wellington Zoological Gardens (WZG). The male and female were imported from San Diego Zoo in 1993, aged ~ 4 and 5 years respectively. The female is currently rearing twin cubs born in April 1999 (see below).

4.3.2 Births

Thirty-eight Sun bear births were recorded in North American zoos between 1969-April 1998, resulting in an average birth rate of less than two cubs per year. The birth rate has declined further in the last five years with only three births being recorded. Most females had singletons and three sets of twins were born (to different parents), producing a total of 41 cubs. 34% of the cubs born were male (n = 14). Four cases of neonate mortality have been reported since 1992; most deaths occurred within several days of birth but there was one cub death at 4 months of age²⁷.

There were five births (seven cubs) at the New Zealand zoo between 1988 and 1999, with one set of male twins surviving. All cub mortalities also occurred within the week following birth. One cub was male, and four cubs were unsexed. Necropsy reports indicated that a set of twins might have been stillborn.

²⁶ The bears had been taken from the wild when young and kept as pets by Malaysian citizens (Frederick 1998).

²⁷ This cub was one of twins: the first died within 24hrs of birth.

Behaviour records suggest Sun bears become sexually active at 2 - 3 years of age. Twenty two females in NA/NZ zoos are known to have reproduced, and the average age at first birth was 8.5 years. The youngest age at first birth was 4 years and 9 months, and one bear did not have her first cub until 13 years of age. Few females gave birth after 12 years of age, and the oldest to give birth was 19 years. Twelve females were multiparous and several had produced cubs three or four times. Although two females in NA gave birth twice within a year, the mean inter-birth interval for the population was ~2.5 years. The New Zealand female represented the most prolific breeder, having given birth to at least seven young²⁸ (two sets of twins and three singletons) within a period of 3.5 years.

A total of 15 males (including the NZ bear) have sired young. Ages are unknown for the majority of individuals, but a breeding range was calculated based on the estimated ages given in the studbook. The youngest to sire cubs were ~6 years old, which is concurrent with data for the three males of known age. On average, most males did not sire young until they reached ~11 years. The oldest sire of known age was 13 years, but several individuals have continued to reproduce successfully until ~20 years of age.

4.3.3 Breeding Status and Sex Ratio of the North American Population

The following statistics are based on listings from the current regional studbook for the Sun bear (Frederick 1998). As at 30 April 1998 the North American population was 62 individuals (17 males, 45 females) distributed among 24 institutions. More than half (54%) of the females of known ages were ≥15 years old and may be beyond breeding age, and three females were presumably juvenile at ≤ 5 years old. There were 11 proven breeders (*i.e.* had been confirmed to give birth) remaining in the population.

Over half (59%) of the male Sun bears were ≥15 years of age. The youngest male was one of the individuals imported from Malaysia; he was estimated to be 8 years old and likely to be sexually mature. There are four proven sires remaining in the population and a strong sex skew is evident, with females outnumbering males in the population by three to one.

²⁸ On two occasions twins were suspected (audio/video footage), but could not be confirmed.

4.3.4 Seasonality of Reproduction

4.3.4.1 Oestrus

Behaviour records had been collected over a period from 1 - 8 years from various institutions that kept Sun bears (see Table 4.1). Reproductive behaviour indicative of oestrus was observed in any month, and many individuals were reported to come into heat several times a year (Figure 4.2). Although oestrus does not appear to be significantly influenced by season (31% periods were observed during winter, 25% in spring and 29% in summer; 18% in autumn; ($X^2 = 3.8$, d.f. = 3, p>0.05 n.s.), two distinctpeaks in behavioural oestrus were apparent during April and July, and relatively less sexual activity (18%) was reported during autumn.

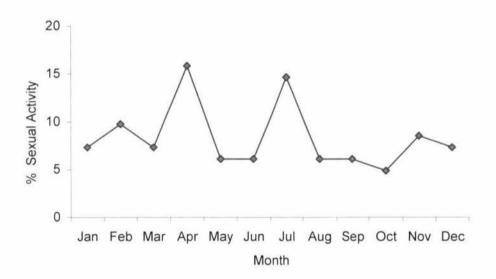
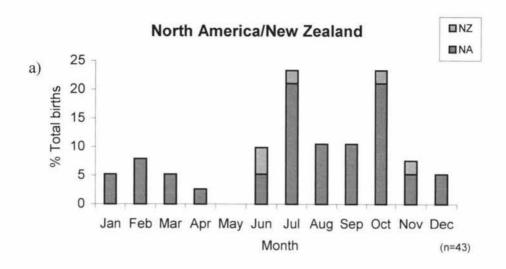


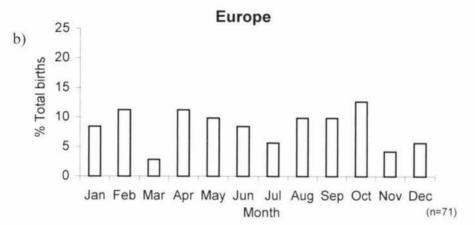
Figure 4.2: Occurrence of behavioural oestrus in Sun bears (North America (NA) and New Zealand (NZ)), grouped by month of year. NA data from Ball (1993, 1994), Frederick (1998). Data for the NZ female (from Wellington Zoo records) have been displaced by 6 months.

4.3.4.2 Birth

An analysis of combined parturition records from NA and NZ (1969-1999) showed that Sun bear births occurred in every month of the year except May. Most births (77%, n = 43) took place between June and December, and pronounced peaks in the birth rate (23%) were observed in both July and October (Figure 4.3a). Nearly half (46%) of the cubs were born in these two months alone. Thus, there was no apparent association between month of birth and the latitude of the zoo (data not shown). Births in Europe were fairly evenly distributed throughout the year (Figure 4.3b). Relatively few cubs were born in March, however, and relatively more in October.

Association of oestrus activity with dates of birth in North American and New Zealand zoos (Figure 4.3c) strongly indicate three-month phase shift between peaks of mating activity in April and July (Figure 4.2), and the peaks in births during July and October.





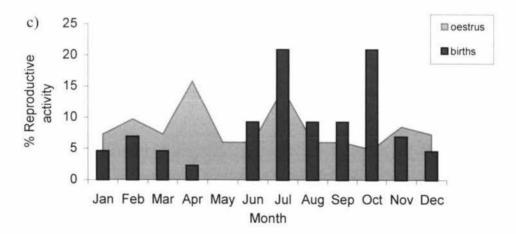


Figure 4.3 Distribution of Sun bear births by month for a) North American (NA) and New Zealand (NZ) zoos (combined; records from 1969-1999) and b) European zoos (1960-1995). 3c) compares behavioural oestrus data (shaded region) with months of birth in NA and NZ. NZ dates have been displaced by 6 months. Data sources - NA Studbooks (Ball 1993, 1994; Frederick 1998), European Studbook (Kolter 1995; Kolter 1998d), and records from Wellington Zoo, N.Z.

The seasonal distribution of Sun bear births in North America and New Zealand was compared with data from the European population (Figure 4.4). There was a significant influence of season on birth in NA and NZ, whether data were combined ($X^2 = 12.8$, d.f. = 3, p<0.005) or analysed separately for North American zoos ($X^2 = 9.0$, d.f. = 3, p<0.05), with the majority of young born during summer and autumn (40% and 37% respectively; 16% in winter and 7% in spring). In European zoos, births were evenly distributed throughout the year (25% winter; 24% spring, 24% summer, 27% autumn; $X^2 = 0.1$, d.f. = 3, p > 0.05 n.s.).

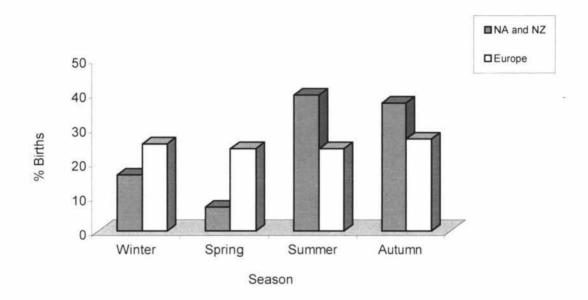


Figure 4.4: Sun bear births grouped by season of year from populations in North America (NA) and New Zealand (NZ) (combined n=43), and Europe (n=68). NZ data have been displaced by 6 months. Sources of data as in Figure 4.3.

4.3.4.3 Timing of Reproduction

The annual change in photoperiod is the environmental cue influencing most temperate mammals in their timing of annual breeding efforts (Bronson 1985). Accordingly, most species of bear mate during summer and give birth during winter (Stirling 1993). At high latitudes ursid populations mate earlier and experience a shorter breeding season (Palmer et al 1988; Garshelis & Hellgren 1994). The semi-tropical Spectacled bear (*T. ornatus*) of South America and the Giant panda (*A.melanoleuca*) of China, however, predictably mate during spring both in the wild and at varying latitudes in captivity (Kleiman 1983; Rosenthal 1989a). The consistent timing of mating in these species, regardless of distribution, suggests the influence of a retained environmental rhythm that may be synchronised, rather than explicitly controlled by photoperiod. For

example, rainfall and relative fruit availability are thought to influence reproduction in free-ranging Spectacled bears (Weinhardt 1993), but in captivity breeding season does not appear to be affected by a differing climate or diet.

If a direct response to photoperiod exists in the Sun bear, it could be expected in the European population that the distribution of births would occur earlier in the year, and be relatively restricted in timing. Significant effects of seasonality observed among Sun bears in North American and New Zealand zoos were not, however, apparent in European zoos (Figure 4.4). This discrepancy may reflect differing management regimes, such as the provision of heating in colder regions (Section 4.4.2.1).

Compared to most temperate zone ursids, heightened mating activity in Sun bears occurred earlier in the year (spring) in North America and New Zealand, and reproduction was more restricted in timing. To determine whether intrinsic cues may also be influencing breeding in the Sun bear, births in North America and New Zealand were considered in relation to climatic conditions in this species' native habitat.

In tropical SE Asia there is little annual change in photoperiod, but the climate is variable and dominated largely by rainfall during the monsoon seasons (Pearson 1988). Rainfall patterns for most regions are similar, being governed by the northern monsoon from November to March/April and the southern monsoon from April/May to September. This dual system results in a typical double rainy season for most regions (Figure 4.5).

Onset of heavy rain in SE Asia usually begins around March or April (the transition period) concurrent with the onset of heightened mating activity observed in Sun bears kept in North American and New Zealand zoos (Figure 4.2). The majority of births in captivity occurred between June and November, falling within the period of increased rainfall in the Sun bears' native habitat. Double peaks in the birth rate during July and October were correlated with the double rainfall peaks in SE Asia.

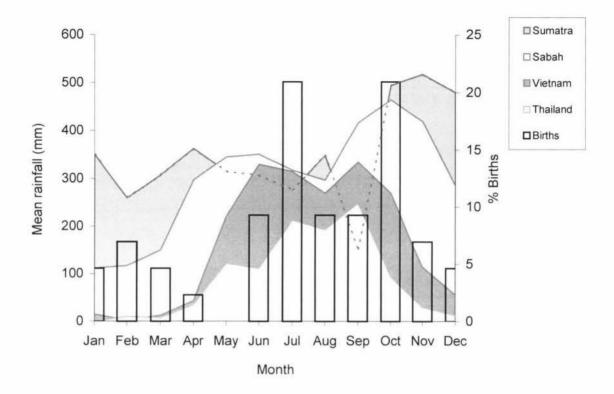


Figure 4.5: Sun bear births in North America (NA) and New Zealand (NZ) zoos (1969-1999) in relation to rainfall during monsoon seasons in SE Asia; dashed line shows concealed values for Sumatra. Data for NZ have been displaced by 6 months. Climatic data derived from tables in Pearson (1998). Sources of birth data as in Figure 4.3.

4.4 DISCUSSION

Sun bear populations in the wild are under serious threat due to rapid loss of habitat through deforestation, and increased poaching for the illicit trade in bear parts in Asia (Mills & Servheen 1991). There is now also growing concern for the status of populations in western zoos (Ball 1996a). In an effort to assist with management, studbooks for the species were developed in North America and Europe in the early 1990's. Fewer than 150 individuals now remain in North American and European zoos, and many individuals in the former population are aged. In both regions imports have contributed more than births to population growth, and birth rates remain inexplicably low (Ball 1993, 1994; Kolter 1995; Frederick 1998; Kolter 1998d). Numbers in North American zoos have been steadily declining since the 1970s (Ball 1994), and following recommendations by the Bear TAG (Taxonomic Advisory Group), the importation of potential founders from SE Asia began in 1996 (Frederick 1998).

There is concern for the preservation of the Sun bear in its natural habitat (Ball 1996a), and a pressing need to more effectively manage captive populations so they become self-sustaining. The species has been maintained in western zoos for over 60 years but has proven notoriously difficult to breed in captivity. At present, because reproduction in North American zoos is insufficient to maintain a genetically viable population, the TAG has recommended further importations, and actively encouraged breeding among the current population (Frederick 1998). Improving our understanding of the reproductive biology and behaviour of the Sun bear is essential to implement management practices that will enhance breeding. The purpose of this study was to generate a collective database of reproductive parameters for the Sun bear and investigate potential causes of the poor breeding record in captivity.

4.4.1 Reproductive Parameters

Demographic analysis of reproductive parameters from North American and New Zealand populations supported many of the observations made for Sun bears in European zoos (Kolter 1995). Because management in captivity influences the reproductive characteristics of animals, these findings should be considered more as guides, than absolute biological values for the species.

Female Sun bears begin to display signs of behavioural oestrus at 2 - 3 years old, but they do not usually conceive before 6 years of age (Dathe 1970; Feng & Wang 1991; Schaller 1994; Kolter 1995). The average age at first birth was 8.5 years, consistent with information for other species of bear (Sloth bear *U.ursinus*: Jacobi 1975; American black bear, Brown bear *U.americanus*, *U.arctos*: Herrero 1978; Giant panda *A. melanoleuca*: Hodges et al 1984; Polar bear *U. maritimus*: Ramsay & Stirling 1986; Spectacled bear *T.ornatus*: Rosenthal 1989a; Asiatic black bear *U.thibetanus*: Reid 1993). Sexual behaviour was also first observed in male Sun bears at 1 - 2 years, but most did not sire young until at least 6 years of age. A similar range for has been reported for the advent of sexual behaviour from the European population (Kolter 1995), captive individuals in China (Feng & Wang 1991) and other male bears (*U. arctos*, *U. maritimus*, *U. americanus* Erickson et al 1968; Palmer et al 1988; Garshelis & Hellgren 1994).

It is thought that bears remain capable of breeding for most of their life (Bunnell & Tait 1981; Palmer et al 1988), which may last up to 25 years in the wild or captivity. Data from this study and the European population (Kolter 1995; Kolter 1998d) indicates that although both sexes can continue to produce young until they are quite aged, breeding does not often occur in individuals after they reach 12 - 15 years. This observation confirms the suspicion that many of the Sun bears in North American zoos may have reached reproductive senescence (Ball 1994).

Only approximately 25% of Sun bears in North American zoos are proven breeders. Many of the older males in NA died between 1992 and 1998 and only four proven sires remain in 1999. The number of males in both European and NA captive populations is also under-represented, with approximately three females to each male. Kolter (1995) has suggested that in Europe this may have resulted from preferential importation of females to support maintenance of the bears in harems. She also suggested that males may have a higher death rate among unsexed neonates. Reasons for the sex bias in North American zoos are uncertain, but no cases of unsexed neonates have been logged in the studbooks. Fewer male cubs are born into the European population (Kolter 1995) suggesting a biased sex ratio at birth.

The mean inter-birth interval for Sun bears in North American zoos is greater than 2 years, compared with an interval of ~ 5 months reported for the European breeding

population (Kolter 1995). This discrepancy may be due to differing survival rates of the young and/or management practices (*e.g.* length of time a cub is permitted to remain with the mother²⁹) in the two populations. *U.malayanus* is unusual among bears because it has no restricted breeding season in captivity and a comparatively abbreviated gestation length. When cubs die or are removed, the dam may undergo a postpartum oestrus and come back into heat within 1 - 2 weeks (McCusker 1974; Pagel & Kuhme 1992; Kolter 1995; Chapters 2 & 3). This reproductive strategy means that Sun bears are capable of giving birth several times within a year (Dathe 1970; McCusker 1974; Kolter 1995; Chapters 2 & 3).

With the exception of McCusker's (1974) report, all other information for *U.malayanus* (Dathe 1961, 1963, 1966; 1970; Kuhme 1990; Pagel & Kuhme 1992; Frazier & Hunt 1994; Schaller 1994; Chapter 2), including recent physiological studies (Schwarzenberger et al 1997; Chapter 3), have indicated that gestation lasts approximately 95-100 days. These observations were supported by data from this study. McCusker (1974) calculated gestation lengths at 174, 228 and 240 days, based on dates of last observed breeding. It has been suggested, however, that these highly variable gestation periods may be due to sub-specific differences (Mead 1989) or faulty observations of mating (Kuhme 1990). Because the male and female were not separated after breeding activity, it is possible that subsequent periods of reproduction went unnoticed. Furthermore, the additional length of gestations reported by McCusker (1974) was approximately 3-6 months, which is a time equivalent for one to two successive reproductive cycles to have occurred.

4.4.2 Evidence of Reproductive Seasonality

Although breeding periods in North America and New Zealand are not tightly restricted reproduction is more likely to occur during particular times of the year, in contrast to breeding in Europe. Sexual activity in North American and New Zealand bears was observed throughout the year but was more frequent during April and July. Although data are limited the behavioural observations of oestrus were supported by corresponding later peaks in births, an interval equivalent to the 95 day gestation length commonly reported for *U.malayanus* (see Section 4.4.1). Most cubs were born between

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²⁹ If management does not occur, Sun bears do not usually wean their young for several years (Kolter 1995).

June - December, and nearly half of Sun bear births in North American zoos occurred during July and October. Births in the Southern Hemisphere were similarly clustered in June/July and October/November when the data were displaced by six months.

An obvious effect of season on reproduction was also apparent in these regions, with the majority of births occurring during summer and autumn. The low number of births in winter and spring suggested that matings earlier in the year are either less successful, or the resulting cubs are less likely to survive. In North America and New Zealand the overall trend indicates a reduced tendency of Sun bears to reproduce all year round.

4.4.2.1 Environmental Regulation of Reproduction

Cues from environmental parameters including climate, food availability, and social signals are of major importance for mammalian reproduction (Sadlier 1969; Bronson 1985). Sun bears in temperate zoos live in an environment that is climatically very different to their natural habitat. In captivity, regulation of other factors such as nutrition and social grouping may influence their natural breeding rhythm. Reproduction in Sun bears kept in temperate zones does not appear to be solely influenced by photoperiod, although many of the animals have either been in a zoo most of their life or were captive-born. The annual pattern of breeding observed in North America and New Zealand indicates that an environmental cue may also be involved in timing reproduction in this species. This cue may be an adapted link to rainfall patterns normally experienced in SE Asia.

The absence of seasonal breeding observed in the European population may be due to differing management regimes in captivity. For example, the latitude of European zoos is ~50° N, and those in North America are distributed between ~30-45° N; consequently, bears in the former population are exposed to cooler climates all year round. Although Sun bears are not known to undergo winter torpor, many zoos provide heating and make available indoor enclosures during inclement weather. Effects of a warm environment are unstudied, but provision of heating during colder periods has been claimed to induce breeding in this species (Dathe 1966) and this could explain the pattern of births shown by European Sun bears.

Information is not available on reproductive rhythms of Sun bears in their native habitat, but the lack of a restricted breeding season in captivity suggests that their reproduction is adapted to tropical conditions. Although not the only ursid to forego winter torpor, the Sun bear is the only species appearing to have lost the characteristic delay in implantation. Their gestation length is comparatively short and more equivalent to the period of actual embryonic growth in other bears (Mead 1989; Schwarzenberger et al 1997; Chapter 3).

Many larger mammals living in the tropics show seasonal breeding that is related to rainfall patterns (Bronson 1985). Studies of rainforest mammals in Africa (reviewed in Delany & Happold 1979), South America (Perret & Atramentowicz 1989), and Asia (Wade 1958; Langham 1983) have shown that reproduction in these regions may be directly or indirectly linked to this environmental factor. Rainfall can affect reproduction by influencing the availability of foods (Bronson 1985), and is the cue thought to time breeding in the Spectacled bear (*T.ornatus*) of South America (Weinhardt 1993). In the wild this semi-tropical species mates from April - June when most fruits ripen, and individuals congregate to feed. Cubs are born during the rainy season (November-February) after a 7 - 8 month gestation, and females emerge with their young the following spring as quantities of fruit begin to ripen once more. Spectacled bears living in temperate zoos (NA and Europe) have retained this annual pattern of breeding (Rosenthal 1989a).

The natural diet of Sun bears is predominantly fruit (Kunkun 1985, Lekagul & McNeely 1977 cited in Joshi et al 1997), but also includes plants, invertebrates, lizards, birds, and small mammals (Domico 1988; Servheen 1993). As opportunistic feeders the bears are probably able to exploit food resources throughout the year, but dietary composition may play a role in regulating their annual reproductive rhythm (Servheen 1993).

The heightened mating activity observed in April among captive North American and New Zealand bears coincides with the onset of the rains in SE Asia, and the majority of births occur during what would be the wettest period of the year. The bimodal peaks in reproduction could result when females that failed to become pregnant or lost cubs during the first breeding period, cycled again in July. Directing less effort toward mating later in the year is a viable strategy because it would mean fewer cubs are born immediately prior to the dry season when food is, presumably, less abundant.

4.4.3 The Captive Breeding Record and Approaches to Husbandry

The importation of more Sun bears to North American zoos has begun (Frederick 1998) and will help increase numbers, but it is important to determine which factors are limiting reproduction in the existing captive population. A consistently low reproductive rate is apparent in North American zoos - fewer than 40 births being recorded in approximately 30 years, and over the last five years only three cubs have been born. Reproduction appears to have been more successful in European zoos, but unlike those in North America the majority of individuals in the former population are considered to be within breeding age (Kolter 1998d). It is unknown whether physiological or behavioural problems are affecting breeding success in the North American population.

The reproductive biology of *U.malayanus* has recently been investigated, providing information on oestrus and gestation in females (Brown et al 1996a; Schwarzenberger et al 1997; Chapter 3) and testicular rhythms in males (see Chapter 3). There is no evidence from these studies to suggest that physiological reasons are responsible for the low reproductive rate, but further work on the reproductive biology of this species is warranted. Problems breeding bears in the past have been overcome by adapting conventional approaches to husbandry, based on a better understanding of the Ursidae. The major factors identified as contributing to improved captive breeding success are separation of potentially pregnant females, provision of a suitable maternity area and maintaining a high level of privacy during the periparturient period (Rosenthal 1989b; Partridge 1992; Linke 1998).

For species that have a distinctive breeding season each year, the date of parturition can be estimated by adding the gestation length to the date of last observed mating activity; thus, preparation for birth can be made ahead of time. It is a substantial challenge to identify pregnant Sun bears because females often come into heat several times each year. Sometimes overt behavioural changes (e.g. increased aggression toward the male, nest-building) and physical signs (e.g. swelling of the vulva and mammaries) during late gestation can be used as cues to detect impending parturition (Rosenthal 1989b; Chapter 3), but successful monitoring depends to a large extent on the ability of staff to observe and assess the behaviour of the animals in their care.

Unfortunately, there are no suitable methods for non-invasive monitoring of pregnancy in bears. Traditional methods such as blood sampling and ultrasound analysis are risky because they require physical or chemical restraint of the animal (Ball et al 1996). Faecal steroid monitoring is a non-invasive technique that has recently been applied to bears (Brown et al 1996a; Göritz et al 1997; Schwarzenberger et al 1997; Chapter 3). As with blood sampling, the limitation of this method is that levels of hormones are similar during pregnancy and pseudopregnancy (see Chapter 3).

Pseudopregnancy (also called 'false' or 'phantom' pregnancy) is known to occur in a variety of carnivores. The condition occurs because in these species the ovarian structure responsible for hormonal support of pregnancy (corpus luteum) continues to function independently of fertilisation (Chapter 3). The Giant panda (A.melanoleuca) is thought to undergo obligate pseudopregnancy when conception fails (Monfort et al 1989; Mainka et al 1991 cited in Monfort & Johnston 1993), and this may be true of other bears. Pseudopregnant females can exhibit similar physical and behavioural signs of 'true' pregnancy including mammary development, lactation and nest-building activity (Chadhuri et al 1988; Bretzfelder 1989; Chapter 2). Without the appropriate technology to unequivocally diagnose pregnancy in ursids, erring on the side of caution may prove the wisest choice.

4.4.3.1 Offspring Mortality

The European regional studbook contains a summary of mortality in the population since 1955. Statistics revealed that nearly 50% cubs died before the age of 12 months and the majority of these deaths occurred less than a week after birth (Kolter 1995). Because information prior to 1992 is not provided in the North American studbook it is difficult to compare offspring mortality rates between the populations. Sun bears are evidently capable of reproducing more frequently than birth rates suggest; which implies either a) there are underlying physiological problems with reproduction, or b) the actual number of births is higher than reported. Behaviour records indicate that the incidence of neonate fatality in captivity could be higher than reported, because births may go unnoticed.

A relatively high rate of offspring mortality among bears can be expected, given the extremely altricial state of the young, and high energy demands placed on the female by her developing cubs (Ramsay & Dunbrack 1986). Foetal death has been linked to

nutritional and captivity stress in bears (Rogers 1976 cited in Herrero 1978; Hellgren et al 1991), and results in either resorption of the embryo or abortion (Herrero 1978; Hellgren et al 1991; Göritz et al 1997). Studies have documented the occurrence of abortion and stillbirth in captive Sun bears (Prator et al 1988; Chapter 2), but the frequency of such events is difficult to determine because the dam may consume any evidence of birth.

The failure of bears to successfully rear cubs in captivity has been related to a variety of factors including inexperience and individual temperament of the female, and social stressors such as failure to separate the male or to obtain an appropriate level of seclusion (Kitchener 1992; Pagel & Kuhme 1992; Schaller 1994; Bastien et al 1985; Rosenthal 1989b; Linke 1998). Provision of a suitable thermal environment in the maternity den has also proven to be important for reducing offspring mortality in bears (Keulen-kromhout 1978; Knight et al 1985; McDonald 1989).

Timing the separation of a potentially pregnant Sun bear is usually based on an estimated gestation period of 95 days since last mating. Sometimes the female's behaviour is the cue to providing her with access to a cubbing den. The most commonly described signs of impending birth in keeper log books (Table 4.1; Section 4.2) have been: female aggression toward conspecifics/staff, nesting activity and a reduced appetite. A number of these reports also indicate that several days after parturition was expected the female's behaviour reverted to normal and, when the bear was released from the cubbing den, no evidence of birth was found. Although surveillance equipment has not been employed in the majority of cases, staff often have assumed that the female was pseudopregnant. Blood spots and smears were sometimes found after an apparently barren female had evacuated the den, and at one zoo unidentified membranous material suspected to be a birth sac was discovered in the exhibit ~95 days after mating.

Without the use remote surveillance, it is difficult to determine when and if a female gave birth, or to document cases of aborted or stillborn young in the event of infanticide. Audio monitoring has limitations but can be useful to confirm the birth of live young. Direct observation of the den during the periparturient stage is not recommended because females are easily disturbed and privacy should be maintained to improve the chance of successful rearing (Rosenthal 1989a; Pagel & Kuhme 1992; Linke 1998; Chapter 2).

Maternal behaviour is sometimes adversely affected in captivity, and carnivorous species including bears may neglect or even kill their newborns. There are several reports of Sun bears neglecting or harming apparently healthy cubs (Dathe 1961, Weber 1969; Dathe 1970; Schaller 1994) and numerous accounts of maternal infanticide and cannibalism in this species (Crandall 1964; Kuhme 1990; Schaller 1994; M.Steffen pers. comm 1997; see also Chapter 2). In most cases failure to provide an appropriate level of privacy for the female was suspected to be the predisposing factor.

U.malayanus is considered to be a 'sensitive' species, prone to disturbances (Schaller 1994; Linke 1999); and as with other animals, periparturient females are particularly susceptible to stress. Sometimes dams fail to produce milk (agalactia) after they have given birth so are unable to feed their young. Agalactia been reported for several species including the Sun bear (Knight et al 1985; Linke 1998; Chapter 2). Whether this condition is stress-related is unknown; but it appears to be more common in primiparous females and does not necessarily present a problem during later births (Knight et al 1985; see Chapter 2).

Neglect is a common cause of death among neonates (Meier 1986; Linke 1998), and video surveillance is also important to assess the level of maternal care. Other signs of inappropriate behaviour include excessive grooming and frequent carrying of the cub(s). Cubs are sometimes removed for hand-rearing when signs of neglect or mistreatment are apparent (Dathe 1961; Weber 1969; Dathe 1970; Schaller 1994; Linke 1998; see Chapter 2). This husbandry practice is controversial (see Appendix B), and policies differ between institutions. Hand-rearing of bears is not recommended by the EEP (Europaisches Erhalturgszocht Program = European Species Survival Program) (Linke 1998).

4.4.3.2 Grouping

Information on the social grouping of *U.malayanus* in the wild is anecdotal. They have been reported to travel in pairs (Fetherstonhaugh 1940 cited in Kuhme 1990; Domico 1988), and associate as 'families' (Domico 1988; Kurt et al 1990). Field studies of other bears indicate that prolonged associations are only formed between mothers and cubs (Bunnell & Tait 1981). Other sightings of two or more individuals are typically either males consorting with a female in heat, or the temporary affiliation of immature siblings (Craighead et al 1969; Laurie & Seidensticker 1977).

The most common breeding scenario for bears is that a male and female meet, copulate and then part (Bunnell & Tait 1981). Most ursids have a polygynous mating system (Stirling 1993) and promiscuous behaviour has been reported for both sexes (Erickson et al 1968; Sparrowe 1968; Craighead et al 1969; Jonkel & Cowan 1971; Ramsay & Stirling 1986). It has been speculated that Sun bears are monogamous "...usually choosing a partner for life" (Erdbrinck 1953 cited in Kolter 1995) but mate preference has not been reported among captive individuals, and data from studbooks shows numerous males have sired young with several females (Ball 1993, 1994; Frederick 1998; Kolter 1995; Kolter 1998d). Whether females will readily mate with different males is less certain, but several cases of alternative siring with the same female are also recorded (Ball 1993; Kolter 1995).

Sometimes in captivity Sun bears are grouped in harems, but this trend has fallen from favour in European zoos (Kolter 1995). High levels of agonism and intrasexual fighting leading to serious or fatal injuries have been reported when the species is managed in this way (Schaller 1995; Kolter 1998b; Steffen 1998). The disruption of matings has also been observed, and reduced breeding success has been associated with this practice (Kolter 1995). These observations support Schaller's (1995) view that a harem is an inappropriate social structure for the species.

There are several unconfirmed reports that in the wild pairs of adult Sun bears have been seen accompanied by cubs (Domico 1988; Fetherston-Laugh cited in Kuhme 1990). In other bears, females with dependent young actively avoid adult males (Bunnell & Tait 1981; Weilgus & Bunnell 1994), presumably because males are known to kill young, which brings the female back into heat and gains the male a breeding opportunity (Weilgus & Bunnell 1994). It is, however, thought unlikely that males would kill their own offspring (Herrero 1978). In zoos isolating the female during the periparturient period greatly reduces the chance of neglect or infanticide by the dam (Rosenthal 1989a; Pagel & Kuhme 1992; Linke 1998; Chapter 2). Behaviour studies of Sun bears have also shown that even among compatible pairs separation of the male and female is necessary for successful rearing of the young (Kuhme 1990; Chapter 2).

Sometimes a female bear with young is reintroduced to the sire after several months, but this depends heavily on the individual temperament of both parents *i.e.* tolerance by the male, and level of protectiveness by the female (Kuhme 1990; Kolter 1998b). Due to

the level of risk, regrouping is not usually attempted until after the young is at least 4-6 months old (Kuhme 1990; Pagel & Kuhme 1992; Kolter 1998b). Postpartum oestrus can occur in Sun bears that are suckling young (Pagel & Kuhme 1992; Kolter 1995; Dathe 1966) and although mating at this time may not result in pregnancy, dams becoming sexually receptive have been known to neglect or mistreat their cubs (Dathe 1963, 1966).

4.4.3.3 Grouping Recommendations

The AZA Bear Advisory Group (1994) has recommended:

"To present bears as conservation ambassadors, they need to be maintained in captivity in ways which reflect the behaviours and social organisation of their free-ranging counterparts."

The natural behaviour of Sun bears is unknown, but their social structure is probably shaped by the same evolutionary pressures (*i.e.* foraging strategies and lack of interspecific predation) as other members of the Ursidae. Anecdotes of the unusually sociable character of this species are speculative and have not been upheld by observations of their behaviour in captivity. In addition to the agonistic behaviour reported among groups (Puschmann 1975 cited in Schaller 1994; Schaller 1990; Steffen 1998; Kolter 1998b), studies have also documented reduced tolerance between malefemale pairs outside of mating periods (Chapter 2). Unlike other ursids, reproduction of the Sun bear in captivity is not strictly seasonal and oestrus can occur three-four times each year. Affiliative associations between a male and female due to recurring sexual interest may account for the amicable nature often reported between pairs.

The AZA Bear Advisory Group (1994) have also recommended that "space must be available (in captivity) for a normal social structure to occur." Zoos usually maintain solitary species (e.g. most felids) separately, and pairing is not attempted outside of oestrus. With the exception of the Giant panda this practice appears to be less frequently extended to bears. Grouping is, instead, often based on available exhibit space and the level of tolerance between conspecifics (Kolter 1998b).

The practice of displaying Sun bears in 'family' groups is based on anecdote and inference rather than fact. Reintroduction of a female with young to the male is a potential source of stress that carries considerable risk. Because there are no obvious advantages to this practice and it appears to be unlikely to represent a natural social situation, it may be more judicious to permit females to rear their cubs alone. Until

behaviour studies in the wild have clarified the natural habits of the Sun bear, management practices could be improved by borrowing from knowledge of other ursids.

4.5 CONCLUSIONS

A demographic analysis of reproductive parameters such as age at onset of sexual maturity, litter size, and age at reproductive senescence, is important to assist with management of captive populations. Data from Sun bears in North America and New Zealand were consistent with information for the European population and knowledge of other species of bear. Sun bear cubs are born throughout the year in captivity and data from the European population have shown no pattern in the continuum of reproduction. Contrary to these reports, this study has shown that breeding in Sun bears in North America and New Zealand zoos is strongly seasonal. Although breeding was also not restricted to particular times of the year, the majority of births occurred during summer and autumn following heightened mating activity in spring. A bimodal pattern of reproduction was observed in the latter half of the year, resulting from sharp peaks in the birth rate during July and October. It is suggested that the lack of seasonality in European zoos might be due to differing management regimes between captive populations.

Because photoperiod does not appear to exclusively involved in the timing of reproduction in Sun bears, an alternative hypothesis of control was investigated. Strong correlations were found between reproductive activity in North American and New Zealand zoos and monsoon patterns in the species' native habitat. Data from this study are limited, but may provide valuable insight to the natural breeding pattern of *U.malayanus*. Research on free-ranging populations is necessary to complement these preliminary findings and ensure the effects observed are not artefacts of captivity. An investigation of wild populations could also assist in determining if differences exist in breeding patterns between mainland and island subspecies of Sun bear.

The causes of poor breeding in captivity are unknown, but a review of breeding records and husbandry practices indicated that reproduction might be improved by implementing more standardised approaches to management. The key to successful captive breeding in bears is providing the female with an appropriate environment in which to give birth and rear young. Diagnosis of pregnancy in bears is difficult, however, and monitoring reproductive activity in captive Sun bears particularly challenging because they exhibit no fixed breeding period. For now, timing of

husbandry protocols will continue to rely on the ability of keepers to monitor the behaviour of the animals in their care.

The difficulties confirming pregnancy coupled with failure of some zoos to separate potentially pregnant females or implement remote surveillance, reduces reliable statistics for birth or neonate mortality in captivity. An investigation of causes of cub fatality and the number of aborted/stillborn young is also not possible. Standardising approaches to husbandry would help to improve our understanding of problems associated with reproduction in this species.

To present bears as "conservation ambassadors" and promote public awareness and education, the AZA Bear Advisory Group (1994) has recommended that in captivity bears should be permitted to maintain a natural social structure. There is no scientific knowledge of the behaviour and habits of free-ranging *U.malayanus*, but studies of individuals in zoos do not support anecdotes suggesting that they are a social species. It is suggested here that until research is undertaken to confirm the natural social structure of Sun bears, grouping should be based, instead, on knowledge of other members of the Ursidae.

Concerns for the status of the Sun bear in North American zoos appear justified in terms of the age structure and low reproductive rate of the current population. The importation of potential founders to North America is a necessary step toward creating a self-sustaining captive population; but more emphasis must be placed on determining which factors continue to limit reproduction in the existing population. While further research on the reproductive biology and behaviour of the Sun bear is needed, a higher level of commitment by zoos is also necessary to ensure the species' continued preservation in captivity.

Appendix A Environmental Enrichment

The main reason for environmental enrichment is to allow captive animals to express naturalistic behaviours such as exploration, foraging and nesting. Environmental enrichment promotes welfare by providing mental stimulation and can prevent or reduce the development of 'purposeless' stereotypic activities such as pacing (Law et al 1990; Carlstead et al 1991; Wechsler 1991; Ames 1992). An effective environmental enrichment program is recognised as being central to ursid husbandry in zoos (Partridge 1992: Management Guidelines for Bears and Racoons; Usher Smith & Kolter 1998: EEP Ursid Husbandry Guidelines) and has been the subject of a recent Taxon Advisory Group Workshop (TAG Bear Essentials Workshop 1999).

The program of enrichment for Sun bears varied between study sites and depended on the location of enclosures (indoors or outdoors). Some animals had unrestricted access to an outdoor environment with opportunity for exploration and browsing. With the exception of maternity dens, indoor enclosures at both zoos often contained few or no enrichment items, however, this practice should be considered especially important where animals are kept indoors for long periods each day. Although implementing an effective enrichment program is central to welfare concerns of captive bears, the type and level of enrichment in outdoor enclosures appeared to be highly dependent on the perception of its importance to individual keepers. Two perceived problems with enrichment commonly cited by zoo staff were a) time constraints and b) creation of additional waste associated with particular practices. Addressing the necessity of this husbandry practice to zoo management and staff through associations such as the TAG and EEP (European Endangered Species Program) may assist in improving conditions for captive bears.

Although a quantitative analysis of the effect of enrichment on behaviour of study animals was not undertaken, main observations were:

- Enclosure design played a large role in the opportunity for exploration and the
 introduction of items. Different types of enclosures required the use of different
 enrichment techniques, for instance, food items could not be hidden in a smooth walled
 concrete enclosure. Addition of temporary furnishings to hide food in such as rotting
 stumps, pieces of wood, a feeding apparatus or cardboard boxes helps to stimulate
 foraging and also promotes exploration and play.
- 2) Provision of enrichment proved to be effective in reducing stereotypic behaviours *i.e.* pacing. Generally, the bears were most motivated to forage when food items were either scattered or hidden in the enclosure, or incorporated in a feeding apparatus (a drilled plastic tube or Boomer ball©). Food 'treats' such as stuffed pinecones/freezicles also prolonged the availability of food. Feeding was also enriched by changing the presentation of the diet to encourage manipulation *i.e.* leaving fruit items whole and unpeeled. As an exemplar of this, at one zoo dead chickens were usually plucked before being fed to the bears. When left unplucked, the bears appeared to enjoy plucking the birds and rolling in the feathers, which were later also consumed.
- 3) The introduction of novel items was important as the bears showed reduced interest in manipulation or exploration after several days, particularly when a food reward was not obtained. They showed a high level of interest in inedible vegetation items (e.g. palm

fronds, coconut husks) and scents distributed in the enclosure (e.g. flavoured sprays, bison wool).

4) Nest-building is known to be a natural behaviour for Sun bears (Domico 1988; D. Middleton pers comm 1997). In zoos, nesting behaviour is often associated with periparturient females, however, both sexes readily make use of material provided for this purpose. Nesting material should be available to all captive Sun bears to allow them to express this natural behaviour. Furthermore, because nesting serves as an important sign of impending parturition, without access to material this behavioural indicator can be overlooked.

List of Environmental Enrichment Items Provided to Sun Bears

Edible Vegetation

Pinus spp.

Hedychium gardnerianum

Yellow ginger

Canna spp.

Ginger

Alpinia zerumbet

Shell ginger

Bambusa spp.

Bamboo

Ficus microcarpa

Small leaf fig tree

Ficus macrocarpa

Morton Bay fig

Ficus rubiginosa

Port Jackson fig

Eugenia spp.

Lilly pilly

Various unidentified grasses

Miscellaneous Edible Items

Beef bones

Raw dead chickens, unplucked

Live crickets, mealworm larvae

Rotting logs containing insect eggs and larvae

Stuffed Pinecones: dipped in honey, filled with seed mix and dried fruits

Freezicles: whole fish or pieces of fruit frozen in blocks of water

Whole coconuts, yams, oranges and apples, unpeeled bananas, corn on the cob

Berries on the branch

In addition to edible items, scents were distributed in the exhibit using pieces of bison wool and commercial fruit or meat flavoured sprays (Feed Flavours, Inc, Wheeling, Illinois).

Nesting Vegetation

Bamboo

Hay

Straw

Bermuda Grass

Nikau palm fronds (Rhopalostylis sapida)

Appendix B Notes on Neonatal Ursids and their Hand Rearing

A major problem with hand-rearing neonates is that bear cubs are born in an altricial state. For most species the gestation length after implantation (excluding embryonic diapause) is only approximately 100 days (reviewed in Ewer 1985). Neonate-maternal weight ratios for ursids are among the lowest for all eutherians; with most cubs weighing a mere 300g at birth³⁰ (Ewer 1985; Rosenthal 1989c; Linke 1998). Newborns are blind and deaf, and have little hair; their physical development is also relatively slow. Their eyes do not open for nearly 1 month, and it is approximately 45 days before they begin to walk. First teeth erupt when a cub reaches approximately 1 month of age, but it may not begin to eat solid food until 2-3 months of age (Rosenthal 1989c; Linke 1998). Most bears complete gestation and begin to rear their young while going without food or water for several months (Ramsay & Dunbrack 1986). Birth of such immature young may be an energy conserving adaptation.

In zoos the decision to remove young for hand raising is often precipitated by maternal neglect, which is a common cause of death among neonates (Meier 1986; Linke 1998). Most ursid species including the Sun bear, have been successfully hand-reared in captivity, and there are a number of publications containing information on this practice (reviewed by Rosenthal 1989c; for Giant panda see Knight et al 1985; Villares et al 1985). Hand-rearing of bears is, however, generally not recommended (EEP Ursid Husbandry Guidelines 1998), and recent findings have confirmed suspicions that human-raised individuals may become socially inept with others of their own species (Schaller 1994; Forthman 1995). The effect of hand-rearing animals is known to have adverse effects on their social, sexual, and maternal behaviour as adults, and has been deemed partially responsible for the reduced breeding success among small exotic felids in captivity (Kleiman 1975; review in Mellen 1992).

A goal of most zoos is to produce individuals that are capable of breeding, and contributing to the captive gene pool. If human-reared animals do indeed become socially maladroit adults, this raises an ethical dilemma when considering rare species. On a positive note, hand-reared individuals can be included in studies to gain insight into the reproductive biology of lesser-known species, and some socialised animals permit sampling without necessitating chemical or manual restraint. Also, recent advances in ART (Assisted Reproductive Techniques) include improved harvesting and storage of sperm and oocytes for artificial insemination (AI). These techniques have been successfully used to assist with captive breeding, including those species in which natural matings are not possible because individuals are often highly incompatible (e.g. clouded leopard (Neofelis nebulosa) (Wildt 1990; Wildt et al 1995).

Any decision to hand-rear bear cubs should be carefully considered in terms of commitment by staff to a relatively intensive and lengthy effort in the short term; and an understanding view of potential management difficulties that may arise when introducing and homing hand-reared individuals in the long term.

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³⁰ Range reported for Sun bear neonates = 255 - 623g (Rosenthal 1989; Linke 1998).

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