# The effects of captivity on display-based communication and social interaction in the captive African wild dog (*Lycaon pictus*)

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By Emily J. Tighe

University of Canterbury

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# ABSTRACT

The obligate cooperative nature of African wild dogs (*Lycaon pictus*), unique among social canids, is thought to be driven by high levels of interspecific competition and intra-guild predation with other large socially-organised predators. Research exploring how wild dogs maintain social bonds through social communication, while avoiding detection from potential competitors, is therefore vital for understanding this species. While olfactory and vocal communications are well represented in the literature concerning *L. pictus*, these channels of communication pose significant risks to wild dog survival, as they are inherently susceptible to eavesdropping by unintended receivers. In comparison, display communication, which requires visual contact between the signaller and receiver, poses comparatively less risk of attracting the attention of eavesdroppers. In spite of this, few studies have explored the use of display communication in wild dogs, leaving its potential significance in maintaining social bonds within packs unexplored. Using video analysis, I investigate how display communication and subsequent social interaction are affected by several pressures of the captive environment. Captivity did not appear to affect the presence of many social display types also used by free-ranging wild dogs. However, sexual behaviour was absent from the study groups, likely due to the use of contraception and pack sex composition. The effects of pack sex composition (single-sex versus mixed-sex) revealed that while the frequencies and durations of many social behaviours were not affected by sex composition, the distribution of social interactions did differ depending on group structure. Here, a highly related, single-sex group was more stable than a highly related, mixed-sex group of the same size. Differences in the captive management strategies, specifically enclosure size and feeding regime, of the two packs, may explain the behavioural differences observed. The death of a pack member permitted investigation of the effects of death on social interactions. While many of the social interactions were unaffected by the death, behaviours relating to the formation and maintenance of social dominance and social hierarchy increased after the dog's death. The distribution of social interactions was non-random, suggesting that individuals were reorganising the social structure of the pack during this period. Finally, a small study into the effects of simultaneously added enrichments in the pack (post death) revealed that enrichment reduced the frequencies of dominance behaviours and allowed for a more even distribution of social interaction within the pack. This demonstrates how enrichment may potentially be used to reduce aggression within captive animals. Overall, this research reveals that display-based communication is important for the maintenance of sociality in captive African wild dogs. To better understand this endangered species, future studies in free-ranging populations should include this channel of communication.

# CHAPTER ONE

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# INTRODUCTION

## *The African wild dog*

First described by Temminck in 1820 and originally thought to be a species of hyena (Family Hyaenidae), African wild dogs (*Lycaon pictus*) are the only extant species in the genus *Lycaon* (Family Canidae) (Woodroffe *et al*., 2004; Bardeleben *et al*., 2005). Slight in build, standing between 65 to 75 cm tall at the withers, and weighing between 18 and 28 kg, African wild dogs are considered to be a large canid (Creel & Creel, 2002; Hartstone-Rose *et al*., 2010). *Lycaon pictus* have large, rounded ears which are thought to maximise auditory reception and possibly reduce heat stress during physical activity (Ewer, 1973). Although males tend to be slightly larger than females, sexual dimorphism is minimal (Creel & Creel, 2002). It is their characteristic patchwork coat of white, browns and black that is most salient, earning them the signature ‘painted dogs’. These patterns are extremely variable and unique (Woodroffe *et al*., 2004), making individual identification from afar relatively straightforward, although the tail and facial colouration is fairly similar between dogs (Creel & Creel, 2002). Despite the similarities in morphology, behaviour and ecology to the Dhole (*Cuon alpinus*), also known as the Asiatic wild dog, the two species have evolved separately, although the evolutionary history of *L. pictus* remains controversial due to a lack of fossil evidence coupled with missing phylogentic information from which to interpret morphological and molecular data (Creel & Creel, 2002; Hartstone-Rose *et al*., 2010). According to Martínez-Navarro and Rook (2003) the extant African wild dog (henceforth: ‘wild dog’) most likely evolved gradually from an ancestor known as *Xenocyon falconeri* that was present during the late Pliocene.

Wild dogs hunt cooperatively and have a high rate of hunting success when compared to other carnivores, such as lions (*Panthera leo*) (Woodroffe *et al*., 2004; Hayward *et al*., 2006; Rasmussen *et al*., 2008). Having a hypercarnivorous diet, *Lycaon pictus* predominantly hunt medium-sized prey, particularly ungulates, but will also hunt smaller prey and, if pack size allows, they may also take larger prey (Creel & Creel, 2002; Hayward *et al*., 2006). Wild dogs rarely scavenge food, although they have been observed stealing prey from other carnivores (Courchamp & Macdonald, 2001; Creel & Creel, 2002). The high level of sociality in wild dogs is thought to be crucial to their being such successful predators (Woodroffe *et al*., 2004; Rasmussen *et al*., 2008). They live in packs typically containing 5 to 15 individuals, although small packs or pairs, as well as some packs containing up to 50 individuals, have been recorded (Ewer, 1973; Maddock & Mills, 1994; Creel & Creel, 1995; Woodroffe *et al*., 2004; McNutt & Silk, 2008).

The pack structure of *L. pictus* is unique, with a separate hierarchy for males and females within a single pack (Creel & Creel, 2002; De Villiers *et al*., 2003). A pack will normally consist of a breeding pair and their offspring (both juvenile and adult), but may also contain unrelated helpers (McCreery & Robbins, 2001; Creel & Creel, 2002). Packs are usually slightly male biased, however, pack sex ratios vary between packs and geographic regions (Derix, 1994; McNutt, 1996; Creel & Creel, 2002; McNutt & Silk, 2008). New packs are often formed when the dispersing female offspring from one pack are joined by a bachelor pack of unrelated males (McNutt, 1996; McCreery, 2000; De Villiers *et al*., 2003). Pack size and relatedness may increase if offspring from the breeding pair are recruited into the pack (De Villiers *et al*., 2003).

*Lycaon pictus* are predominantly nomadic (Woodroffe, 2001; Jackson *et al*., 2012). For much of the year they travel over vast distances in search of prey (Creel & Creel, 2002). It is only during the months where they raise their young that they are relatively sedentary, but even during this period they are mobile when compared to other canids (Ewer, 1973; Creel & Creel, 2002). Reproduction in wild dog packs is dominated by the alpha male and female, although subordinates have also been known to produce offspring (Courchamp & Macdonald, 2001; Creel & Creel, 2002). Most packs produce one large litter per year and all members of the pack will help in rearing the pups, meaning that pack size is important for the successful raising of offspring (Courchamp & Macdonald, 2001). Pups are raised in underground dens until old enough to travel with the pack (Creel & Creel, 2002). Once the pups are weaned, food from kills is brought back to the pups in the stomachs of the pack members and regurgitated to them (Courchamp & Macdonald, 2001). This regurgitation behaviour is continued throughout a wild dog's life, unlike in other canids where this behaviour is only seen in the early stages of development, and even occurs between adult individuals (Fox, 1971).

Compared with other social canids, *L. pictus* experiences severe interspecific competition and predation, as they share their environment with other large predators, some of which also hunt in groups (Derix, 1994; Courchamp & Macdonald, 2001; Creel & Creel, 2002). In fact, natural mortality in wild dogs is primarily due to predation by lions (Woodroffe *et al*., 2004; Webster *et al*., 2012). Additionally, direct competition for prey may be a significant factor contributing to the naturally low densities of wild dog packs throughout Africa (Creel & Creel, 1996; Woodroffe *et al*., 2004; Webster *et al*., 2012). Kleptoparasitism from lions and hyenas (*Crocuta* species) has serious costs for wild dog packs, as they run on tight energy budgets in terms of energy intake and expenditure for hunting (Creel & Creel, 2002; Rasmussen *et al*., 2008; Webster *et al*., 2012). Even small losses can have significant effects, especially in small packs (Courchamp & Macdonald, 2001; Rasmussen *et al*., 2008). Studies have shown that along with remaining at low densities and active avoidance of areas where lion or hyena populations dominate, wild dogs have also adopted different temporal activity patterns to avoid competitors, as well as humans in areas of high human activity (Rasmussen & Macdonald, 2012; Webster *et al*., 2012). These high costs of predation and kleptoparasitism are not experienced to the same degree by other large canids, such as wolves (*Canis lupus*), who do not compete with the other large predators, such as bears (Family Ursidae) in their geographic region. As predation from lions is a major cause of wild dog mortality in the wild (Derix, 1994; Woodroffe *et al*., 2004), it is thought that these costs may be one of the factors leading to the extremely high level of sociality seen in wild dog packs (Rasmussen *et al*., 2008). In nature, it is therefore important that wild dog hunts are successful, and a high level of success can only be achieved if there are tight social bonds within the pack (Rasmussen *et al*., 2008).

Historically, wild dogs were present over much of Africa, being absent only from very dry deserts and lowland forest (Woodroffe *et al*., 2004). Of the 39 range states that once supported wild dog populations, only 14 now remain viable and the majority of wild dog populations are now located in southern Africa and southern parts of East Africa (Woodroffe & Ginsberg, 1999; Courchamp & Macdonald, 2001; Woodroffe *et al*., 2004). Wild dogs have been found in many different habitat types, from desert, open grassland and even in dense upland forest, suggesting that they are an environmentally adaptable species (Woodroffe *et al*., 2004). It appears that human activities and prey abundance may therefore limit the current distribution of *L. pictus* (Woddroffe & Ginsberg, 1999; Woodroffe *et al*., 2004; Rasmussen & Macdonald, 2012), which are now classified as endangered by the IUCN (Gusset *et al*., 2006), with fewer than 7000 individuals remaining in the wild. Conflict with human activities, habitat fragmentation and disease have all contributed to the significant decrease and continued decline of free-ranging wild dogs (Woodroffe *et al*., 2004).

### *Sociality in Canids*

Despite the common perception that canids are highly social, pack living is relatively uncommon. Of the 37 different species in the family Canidae, only three form reproductive units that consist of more than a breeding pair: African wild dogs, wolves (*Canis lupus*) and dholes (*Cuon alpinus*) (Gittleman, 1989; Derix, 1994). Although only distantly related, these species have all developed a group living system which depends on alloparental care, suggesting convergent evolution (Bekoff *et al*., 1981; Derix, 1994). While wild dogs and wolves live in what is commonly understood of as a ‘pack’, where there is a dominant breeding pair and their helpers, dholes live in a more clan-like society, whereby individuals fluctuate more frequently and multiple individuals may breed (Derix, 1994; Venkataraman, 1998). Furthermore, wild dogs, unlike wolves, remain as a pack year round, whereas wolf packs may disband once the breeding season is over (Derix, 1994). This makes the level of sociality present in wild dog packs unique.

There are several life history trade-offs associated with group living. Pack living allows for cooperative hunting, which can increase the efficiency at which individuals are able to obtain food compared to lone animals or pairs (Courchamp & Macdonald, 2001; Rasmussen *et al*., 2008). In wild dog packs, studies have shown a strong correlation between pack size and pack survival and success, with some studies suggesting that optimal foraging success is achieved with a pack size between 10-14 dogs, although variation due to ecological conditions is expected (Creel & Creel, 1995; Courchamp & Macdonald, 2001; Rasmussen *et al*., 2008). Packs are also able to divide other labour intensive activities, such as the protection of offspring, among the members (Courchamp & Macdonald, 2001). This also aids hunting, as some individuals may remain with the young while other members carry out the hunt (Courchamp & Macdonald, 2001; Courchamp *et al*., 2002). However, larger packs require more food to feed more individuals (Carbone *et al*., 1997). The opposite may also be an issue if pack size is too small, as the pack may be unable to hunt successfully or defend successful kills (Rasmussen *et al*., 2008). Both of these scenarios can become problematic in areas where prey abundance is low. Packs are also more conspicuous than pairs or individuals, so may attract the attention of predators or competitors (Creel & Creel, 1996; Rasmussen *et al*., 2008). For the African wild dog this is a very real threat, as they live alongside lions and hyenas which are both predators and competitors of wild dogs (Derix, 1994; Creel & Creel, 1996). However, loss of prey to competitors may be mitigated depending on pack size, as larger packs may be able to defend their kills from competitors (Derix, 1994; Creel & Creel, 1996; Carbone *et al*., 1997).

### *Communication*

Social interaction is inextricably linked to communication (McGregor & Peake, 2000). As *L. pictus* rely on tight social bonds within their groups, communication is exceedingly important (Derix, 1994). Communication typically involves a signaller and one or more receivers. However, the communication network, or the social environment of the signal, is also an important consideration. Communication networks can be thought of as all possible individuals that are able to receive a signaller's signal. The further a signal is intended to travel, the wider the communication network. Consequently, some of the receivers will be those intended to receive the signal, while others may be eavesdroppers on the social interaction (McGregor & Peake, 2000; Webster *et al*., 2010).

Much of the literature available on wild dog communication has focused on vocal and olfactory communication, with display communication receiving comparatively less attention (Derix, 1994; Robbins, 2000; De Villiers *et al*., 2003; Parker, 2010; Webster *et al*., 2010). Although studies on vocal and olfactory communication have proved useful for the conservation of free-ranging wild dog populations, these communication modalities are inherently risky for free-ranging wild dogs, as their use widens the communication network and offers greater opportunities for eavesdropping by competitors (Robbins & McCreery, 2003; Apps *et al*., 2012; Jackson *et al*., 2012). In contrast, display communication requires visual contact, which, especially in visually cluttered environments, reduces the size of the social network (or 'active space' of the signal) and therefore limits the possibilities for eavesdropping (McGregor & Peake, 2000). This suggests that although vocal and olfactory modalities are important forms of communication, display may be an equally important form of communication for wild dogs, as it has less associated risks. In terms of research, display-based communication has the additional benefit that it is relatively easy to observe and does not require specialised equipment to monitor or identify it.

### *Captivity*

While often criticized, captive environments offer some unique opportunities for studying animal behaviour by allowing researchers to closely observe the chosen species in a way that may not be possible in the natural environment (De Villiers *et al*., 2003). This can allow for the identification of subtle behaviours that may be missed due to a lack of visibility which may occur in the field (De Villiers *et al*., 2003). Despite these benefits, any information gathered from studies conducted on captive animals needs to be considered with caution if it is going to be applied to free-ranging populations (McPhee, 2002, 2004).This is because captivity may have significant negative effects on the behaviour of certain species, especially in environments that are not suited to that species' natural foraging requirements (Clubb & Mason, 2003; McPhee, 2004; Mason, 2010). Species that are at particular risk of abnormal behaviours are often those with wide home ranges, such as the African wild dog (Clubb & Mason, 2003; Mason, 2010).

Due to the nomadic behaviour of *L. pictus*, and its' ability to travel vast distances, it has proved virtually impossible to set up areas where they are constantly protected in the wild (Woodroffe *et al*., 2004; Jackson *et al*., 2012). Captive breeding programs and reintroductions of captive and free-ranging wild dogs may therefore prove to be one of the best chances that this species has for survival (Frantzen *et al*., 2001; Graf *et al*., 2006; Gusset *et al*., 2006). Wild dogs are kept in many zoo collections globally, but little is known about how the captive environment affects their behaviour and communication (Woodroffe *et al*., 2004). This knowledge may make the difference between a successful reintroduction and an unsuccessful one. Studies have already shown that reintroductions of packs consisting only of captive bred individuals are not as successful as reintroductions of packs with both captive bred and wild bred individuals (Woodroffe & Ginsberg, 1999; Frantzen *et al*., 2001; Gusset *et al*., 2006). As captive breeding programmes are proving to be an important management tool for the conservation of the endangered wild dogs (Frantzen *et al*., 2001), this study aims to describe wild dog social interactions in a captive environment. This study has the potential to improve management practices for captive wild dogs and may aid in the success of future reintroductions of captive bred individuals into the wild. This study is not intended for application to free-ranging wild dog populations, although comparisons with free-ranging populations will be made to determine how captivity affects social interaction and display-based communication.

*Thesis outline*

This thesis aims to describe the display-based social behaviour of captive African wild dogs to improve our knowledge of the unique social behaviour in this species, with particular focus on the effects of captivity. The main focus of this thesis will be determining the suitability of African wild dogs to a captive environment as there is much debate about keeping large carnivores in zoo facilities.

In Chapter Two I will discuss the display-based behavioural repertoire of captive African wild dogs. Comparisons between other captive and free-ranging populations will be made along with how these behaviours relate to those used by other group living canids.

In Chapter Three I will address the suitability of ‘holding facilities’, which are facilities that have non-breeding packs of wild dogs, particularly in terms of the effects that different pack sex compositions may have on social behaviour. This will focus on the difference between a highly related mixed-sex pack compared to a single-sex pack where individuals were also highly related. I will also discuss these differences in term of the implications they may have on the social structure and stability of captive wild dog packs.

Unfortunately, circumstance allowed for the investigation of how pack member death affects the social display behaviour of the remaining captive wild dogs and will be discussed in Chapter Four. In addition I will determine if other factors such as seasonality and zoo guest numbers affect social display behaviours in captive wild dogs before and after the death of the individual.

Chapter Five explores how the simultaneous addition of three different types of enrichment affects the display behaviour observed in a single-sex wild dog pack. Finally I review the results of my thesis together in a brief final discussion (Chapter Six).

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# CHAPTER TWO

# A DESCRIPTIVE ANALYSIS OF SOCIAL INTERACTION AND DISPLAY-BASED COMMUNICATION IN CAPTIVE AFRICAN WILD DOGS

## ABSTRACT

The obligate social nature of the African wild dog (*Lycaon pictus*) is unique among large terrestrial carnivores. Reproduction and survival are closely linked to social relationships that ensure pack cohesion and behavioural synchrony. Heavy interspecific competition and intra-guild predation reinforce the need for pack cohesion, and highlight the potential importance of communication channels that are less likely to be intercepted by unintended receivers. For wild dogs, very little is known about social interaction, particularly about the use of display-based communication, and even less is known about these behaviours in captivity. I provide a detailed description of the display and social behavioural repertoire of captive wild dogs based on an all female pack. All of the social behaviours observed have been recorded in free-ranging populations. Sexual behaviour was not observed, likely as a result of the single-sex composition of the pack. Bar sexual behaviour, it appears that captivity did not restrict the repertoire of social behaviour previously observed in free-ranging populations, but in the absence of time budget data for free-ranging animals, it is impossible to determine whether frequency of behaviour differed from that of their wild counterparts.

## INTRODUCTION

Classifying behaviour provides a standardised model from which patterns can be observed (Altmann & Altmann, 2003). As such, descriptive studies offer a basis for comparison between species, populations, and even individuals. Unfortunately, these studies are often overlooked, and in recent times have become increasingly undervalued due to being observational, rather than experimental or manipulative in nature (MacNulty *et al*., 2007).

Because behaviour is a complex progression of behavioural units linked together fluidly, one difficulty with descriptive studies is that definitions can be subject to interpretation by the observer (Drews, 1993; MacNulty *et al*., 2007). Additionally, in the field, particular units of behaviour can be difficult to disambiguate if definitions are too specific, or not specific enough. Consequently, descriptions of behaviour need to be clear enough to be observed and identified with accuracy without being oversimplified. Nevertheless, classifications need sufficient description to be distinguished from one another without the need for a multitude of different behavioural categories with negligible differences between them. Consequently, broad, functional, behavioural categories comprised of several tell-tale behavioural units which allow the interaction to be readily identifiable are the best approach for descriptive studies.

Our knowledge of species-specific behaviour is severely lacking for the vast majority of species, even among the relatively overstudied mammals. Of the literature available for the African wild dog (*Lycaon pictus*), vocal and olfactory communication have received moderate attention (Bekoff, 1977; Robbins, 2000; Robbins & McCreery, 2003; Parker, 2010; Webster *et al*., 2012; Jackson *et al*., 2012; Apps *et al*., 2012). Nevertheless, there is a lack of information regarding the display behaviour of *L. pictus*, despite there being a wealth of information on display communication for other social canids (Fox, 1971; Bekoff, 1977; Derix, 1994; Fatjó *et al*., 2007; MacNulty *et al*., 2007). *Lycaon pictus* is a unique species, both phylogentically and socially (Macdonald, 1983; Bardeleben *et al*., 2005), and consequently simply mapping what is known about display behaviour from other canids onto *L. pictus,* without empirical evidence to suggest similarities, is insufficient.

The African wild dog has a somewhat similar social structure to other group living carnivores, such as wolves (*Canis lupus*) and dholes (*Cuon alpinus*), but the competitive environment in which wild dog packs live is quite different to other social canids (McCreery, 2000; Creel & Creel, 2002; Sands & Creel 2004; Woodroffe *et al*., 2004; Fatjó *et al*., 2007; Webster *et al*., 2012). Interspecific competition and intra-guild predation from other large group-hunting predators, such as lions (*Panthera leo*) and hyenas (*Crocuta* species), pose a significant risk to the survival of *L. pictus* (Creel & Creel, 1996; Webster *et al*., 2012). Pack survival for *L. pictus* requires significant cooperation with other members of the group, as many activities, ranging from hunting to pup rearing, require the help of multiple individuals, and consequently strong social cohesion within the pack is vital for survival (Courchamp & Macdonald, 2001). This suggests that communication between pack members is a key aspect of the life-history of *L. pictus,* and that its use may maintain strong social bonds between individuals (Rütten & Fleissner, 2004).

Although there is the potential for all modalities of communication to be eavesdropped by unintended receivers, compared to vocal and olfactory communication (Hauber & Zuk, 2010; Hughes & Banks, 2010), displays, used for short-range communication, may be associated with less risk of eavesdropping from predators or competitors. As wild dogs live within a spatially close pack community, the opportunities for the use of display communication should be relatively high. Additionally, should they be discovered by predators or competitors, the costs to wild dogs are high, suggesting that display communication should be the preferred mode of communication, when possible (Creel & Creel, 1996; Webster *et al*., 2012).

Fox (1971) argued that compared to other social canids, wild dogs lack the complex visual expressions, particularly facial expressions, required for the maintenance of an effective dominance hierarchy. Kleiman (1967), however, found that although wild dogs did not curl their lips and bare their teeth in the first stages of a threat display (as wolves do), as the display escalated wild dogs modified their behaviour and displayed using other means. This difference in the use of particular types of display may be the result of the different selective pressures that each canid faces in its natural environment (Berger *et al*., 2008; Webster *et al*., 2012).

Display communication in canids is not limited to obvious interactions such as lip curling, baring of teeth or exaggerated body postures, such as the play bow (Ewer, 1973; Bekoff, 1977; Fatjó *et al*. 2007). Ear position, tail position and eye contact are other, more subtle, methods of communication used by canids (Derix, 1994; Fatjó *et al*., 2007). *Lycaon pictus* is thought to be a highly visual species which may allow it to identify individuals within the group by colouration. It is even thought that *L. pictus* may be able to identify individuals based on the colouration of their muzzles and tails, allowing the identification of individuals both posteriorly and anteriorly (Ewer, 1973). This level of visual ability would likely enable display-based communication without the requirement for exaggerated forms of display in order to respond appropriately to the social implications of an interaction (Ewer, 1973; Fatjó *et al*., 2007). Evidently, there is room for a more lucid understanding of wild dog social interactions, particularly in terms of display communication.

There are many groups of wild dogs held in zoological collections throughout the world (Woodroffe *et al*., 2004), yet the captive environment poses some unique challenges in terms of the management of such a social predator. Captivity may affect normal behavioural patterns for species which naturally have large range sizes in the wild, such as African wild dogs (Clubb & Mason, 2003), and can impair development or cause stereotypic activities such as pacing, to which carnivorous animals are particularly susceptible (Clubb & Mason, 2003). It is therefore logical to suppose that the captive environment may also impact the way in which animals express themselves socially, and consequently there is a real need for information on the behaviour of captive wild dogs that can be used comparatively with data from free-ranging animals.

As there are no current studies that offer a practical standardised way of identifying behaviours observed for wild dogs, here I describe the behaviours observed in captive groups of *L. pictus*. I discuss my findings in light of what little is known about the display behaviour of this species in the wild to determine if captivity has an effect on social interactions and display-based communication. This study has the potential to improve the management of current and future captive populations, by allowing those responsible for wild dog welfare and care to correctly identify behaviour patterns, permitting group cohesion to be maintained and possibly pre-empting outbreaks of aggression.

## METHODS

### *Study sites and subjects*

The field work for this study was conducted from May 2012 to March 2013. Data were collected using a hand-held camera during peak activity times. Most of this study was conducted at Orana Wildlife Park (43°28’0.17”S, 172°27’46.98”E). The park is situated on 80 hectares of land and is New Zealand’s only open range zoo. It is open to the public from 10:00 h to 17:00 h throughout the year. Subjects at Orana were four female African wild dogs (*Lycaon pictus*). These dogs were all littermates that had been bred in captivity at Hamilton Zoo (37°46’27.69”S, 175°13’0.79”E) in the North Island of New Zealand.

The wild dog exhibit at Orana consists of approximately 0.56 hectares (daftlogic.com), of which 0.55 hectares is natural grassland habitat which has been divided into two enclosures, joined by linkways (Fig. 2.1). The enclosures contain trees, underground dens, water troughs, a play platform, logs and housing dens. The dogs had access to all parts of the enclosure during filming for this study, except around feeding time when the dogs were shut in the rear enclosure for c. 10 min to allow the keepers to enter the front exhibit to place the food. Dogs were mainly fed dead bobby calves (*Bos primigenius*) and goat (*Capra aegagrus hircus*), depending on availability, five days a week. However, they sometimes received whole chickens (*Gallus gallus domesticus*).

One month of data (February 2013) was collected from Wellington Zoo to act as a basis for comparison with the data collected from Orana Wildlife Park (to be discussed in detail in Chapter Three). Wellington Zoo (41°19’10.12”S, 174°47’4.48”E) is situated on 13 hectares of hilly terrain. Wellington Zoo is open to the public from 09:30 h to 17:00 h year round. Here, the subjects were three males and one female that were bred in captivity at Wellington Zoo. All individuals in the pack were related (had the same mother): two of the males were from one litter and the remaining male and the female were from another litter.

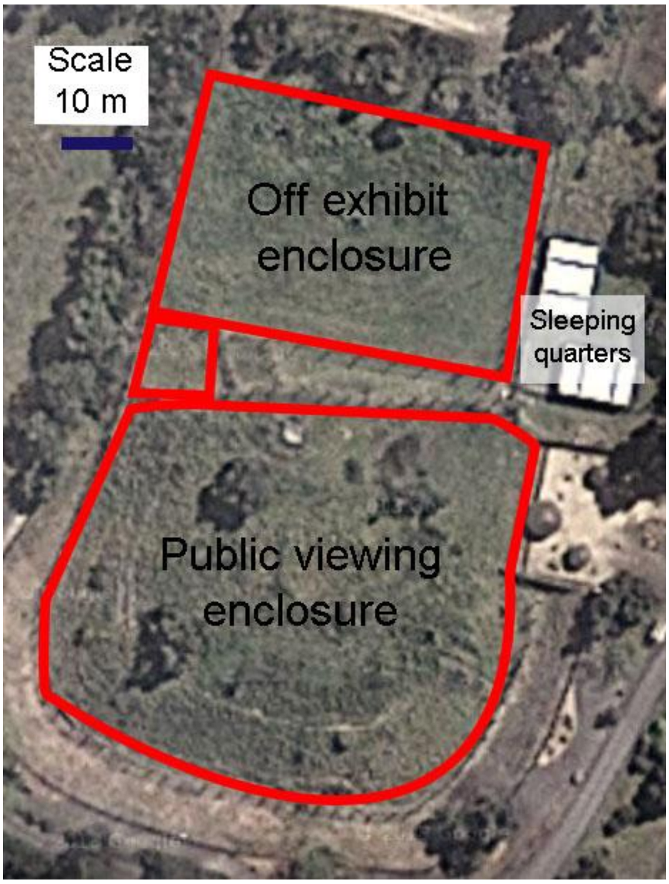

Figure 2.1. Orana Wildlife Park enclosure layout. Area inside the red lines indicates areas accessible to the dogs.

The Wellington Zoo exhibit consists of two enclosures located side by side with a housing building adjoining them (Fig. 2.2). The total area of the enclosure is approximately 0.16 hectares (daftlogic.com). The exhibit is located on a slope with some flat areas at the front of the exhibit and roughly halfway up the slope. The enclosure contains several trees, as well as wooden shelters. The enclosure is covered in grasses and one of the enclosures had a man-made water hole. The dogs were alternated between exhibits on feeding days, allowing the keepers to clean the enclosures before and after the dogs had been moved over. The dogs also had access to the sleeping quarters/housing building unless they were about to be moved or if they were being excluded from this area for management purposes. The dogs did not have a regular feed time, but were usually fed between 13:30 h and 14:00 h three days a week. The dogs were mainly fed partial goat carcasses, whole hare (*Lepus europaeus*) carcasses and/or offal.

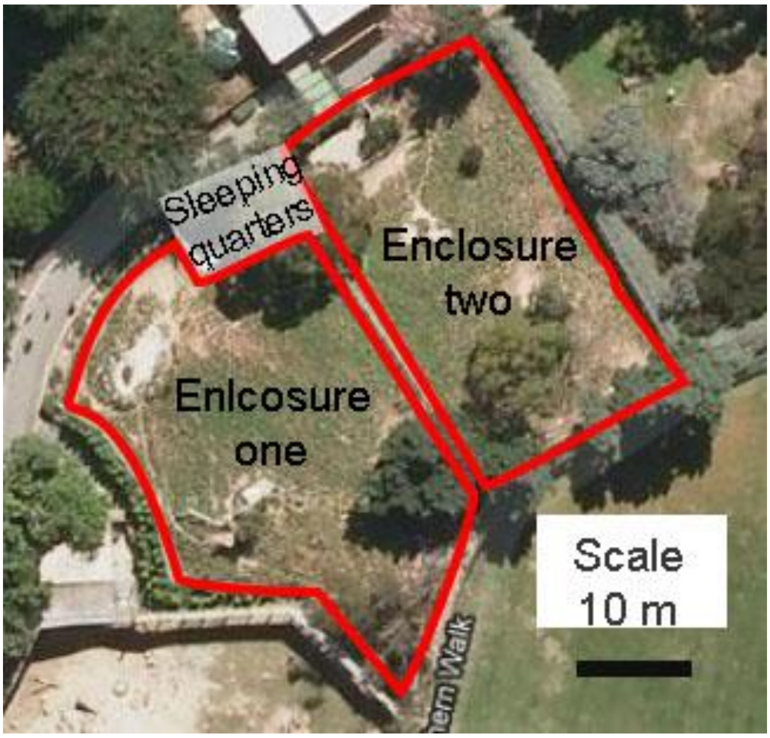

Figure 2.2. Wellington Zoo enclosure layout. Area inside the red lines indicates areas accessible to the dogs.

*Data collection*

Prior to data collection, I familiarised myself with the individual dogs and their behaviour. To ensure that wild dogs were correctly identified, photographs were taken of each dog from both the left and right side, as well as from behind and front-on. In conjunction with these photographs, particular distinguishing physical characteristics (i.e., injuries or obvious coat markings) that could be used for identification during video analysis were noted. In addition to photographic records and notes, behavioural observations with and without a hand-held video recorder were used to identify particular behavioural tendencies of each individual.

Data collection involved filming the wild dogs using a Canon 550 DSLR with a Canon Zoom lens EF 70-300mm 1:4-5.6 USM ø58mm attached to a tripod. The file resolution recorded on 16 GB SD cards was 640 x 480 lines. Footage was then uploaded onto an external hard drive for subsequent scoring. During filming I narrated what was occurring, with dogs both in shot and dogs that were out of view, to provide context for video scoring. Approximately 96 h of footage was collected and scored.

Dogs were given access to all parts of their enclosure during filming, which included both the public viewing and non-viewing areas of their enclosure. During May, July, September, and November 2012, and January and March 2013, video footage was collected at Orana Wildlife Park from 15:00 to 17:00 h every Tuesday, Wednesday and Thursday (all feeding days), weather permitting. Access to staff-only areas of the exhibit was necessary for filming, requiring the presence of a keeper. Keeper presence often excited the dogs, so camera setup began 30 min prior to filming, allowing time to prepare and also allowing the dogs to settle after the keeper had provided access. The Wellington Zoo pack was also filmed on feed days, which were Mondays, Thursdays and Saturdays. Feed times were different from those at Orana, so filming began at 12:30 h and continued until 14:30 h. Other than these differences, all other procedures remained the same as those at Orana Wildlife Park.

### *Behavioural scoring*

Behavioural categories were scored using the video watching software VLC$^{TM}$. Interactions were defined as two or more dogs actively or passively engaging with one another in a social context. Interactions usually occurred consecutively, whereby interactions were separated by time. Some interactions occurred sequentially, whereby the beginning of one interaction ended the previous interaction. Occasionally, interactions occurred simultaneously; for example, a dog might greet another dog that remained resting in close proximity with a third dog. The beginning of an interaction was signalled by a change in the interaction type, rather than by a change in the number or individual dogs present, as this was deemed a progression of the interaction.

Behavioural parameters scored were: the duration of each interaction (s); the number and identities of dogs involved; the body postures of the dogs (both at the start and at the end of each interaction); the identities of the instigators and the receivers of the interaction; whether there was a winner or a loser of the interaction, and any other special notes about the interaction. As identification of each dog was crucial to these data, interactions were only scored if the dogs were individually identifiable.

Body postures were determined by looking at the position of the ears, tail and general body stance of each individual. The starting posture was observed in the first two seconds of an interaction and the end posture was noted for the last two seconds of the interaction. Winning and losing was primarily observed during feeding interactions. Winning and losing were defined in terms of the benefit gained by only one dog. In dyadic interactions if one individual challenged another with food and did not receive any food, the challenger would be the loser. If the challenger managed to get food from the recipient then the challenger would be the winner. Sometimes food interactions resulted in a draw, where both individuals arrived at a food item at the same time and the food was split almost equally between the two. Some interactions, especially when the food item was first placed in the enclosure, involved more than two individuals and these often resulted in all dogs receiving some food, even if they did not take food away with them once the interaction was over. In these cases, winners were considered as those dogs that left the interaction with a piece of food and losers were those that may have received food while all dogs fed together, but did not leave the interaction with their own food. A full list of body postures, behaviours and interaction types are described below.

*Analysis*

An ethogram was constructed based on a total of 474 interactions observed at Orana Wildlife Park between May-November 2012. This timeframe was chosen as it was the largest data set in terms of sampling effort and contained the most varied behavioural data, including all of the main behavioural categories studied. The ethogram is based on the percentage of time dogs spent engaging in the different behavioural categories (see below) per hour of observation.

*Body postures*

**Neutral**

A neutral body posture (Fig. 2.3) was the most commonly used posture when the dogs were relaxed. The head may be above or below the horizontal line of the back. The general body stance is relaxed, meaning that the dog is neither standing high on its toes, crouched, or attempting to appear larger or smaller than other individuals. The tail may be held loosely, hanging down, or it may be wagging slightly. The ears may be relaxed, such that they are not being flattened or pushed forward; however, if the dog is relaxed but alert then the ears may be forward-facing.

Figure 2.3. Dogs in a neutral body posture.

### Submissive

Submission (Fig. 2.4) was exhibited mostly by subordinate individuals. Wild dogs may express active submission, by choosing to submit to higher ranked individuals, or by passive submission, in which the subordinate animal is forced into submission by a more dominant individual. There were varying levels of submission expressed by the wild dogs observed. In extreme displays of submission, a dog may lower its whole body into a crouching position or may even lie down and roll onto its back, exposing the vital organs and genitals. With most displays of submission, regardless of intensity, the submissive dog's ears would be flat and held against its head. The dog's tail is often held low or may even be tucked up between the legs and held flat against the stomach. If the tail is held low, the dog may wag the lower portion of the tail in this position.

Figure 2.4. Dog (left) in a dominant body posture while another dog (bottom right) adopts a submissive body posture.

### Dominant

Dominant body postures are often characterised by a high and forward body stance (Fig. 2.4). Dogs displaying dominance will often stand up on their toes, making themselves appear larger than they would be otherwise. The ears are held in a forward-facing direction. A dominant dog will hold its tail up or out in line with the horizontal line of its back, and it will be held still.

### Defensive

The defensive posture, which was most commonly associated with food defence, often involves the dog crouching over the food item to prevent it from being taken (Fig. 2.5). The head and neck are often held in a straight, horizontal line with the rest of the body in the crouching position. Dogs in this posture will often have their ears flattened back and their tail held down. Dogs may also wag the lower portion of their tail. Dogs that are protecting a food item will often vocalise using high pitched squeals in association with this posture. A defensive dog may also maintain eye contact with any dog that approaches, or may turn its whole body or face away from approaching dogs.

Figure 2.5. Dog (left) in a defensive body posture protecting a piece of food.

**Aggressive**

Aggression was an uncommon behaviour exhibited by wild dogs. The only examples of aggression in this study came from the Orana pack and were usually associated with food (Fig. 2.6). If a dog was unsuccessful at acquiring food from another, it sometimes chased and bit at another individual that had a large food item, in an attempt to take it from them. Aggressive dogs typically had ears held back, mouths open and teeth bared. They also often had lower body postures but did not appear submissive. Often dogs displaying this body posture would bite. Aggressive behaviours were very short (a few seconds) and often occurred at the end of another type of interaction, which is why they have been classified as a body posture, rather than a separate interaction.

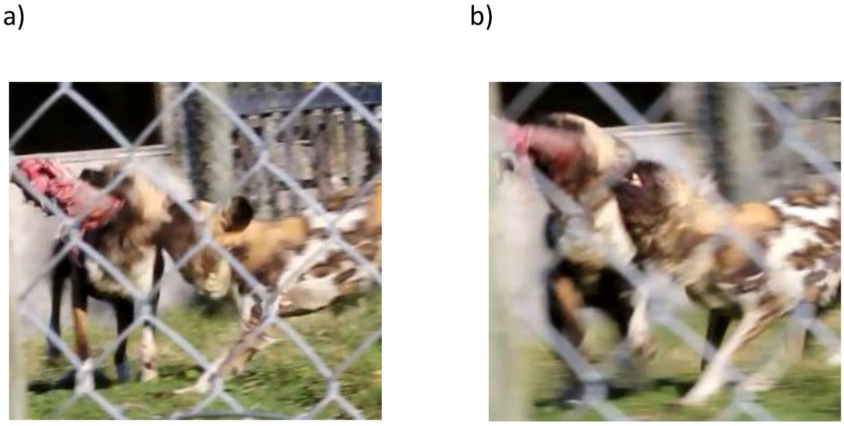

Figure 2.6. Aggression. a) & b) demonstrate aggressive postures, with one dog biting another during a food acquisition interaction.

**Excited**

Wild dogs most commonly exhibited an excited body posture when in pursuit of food items, or in association with play. Dogs that are excited may have a high general body posture or a neutral body posture (Fig. 2.7). A key defining characteristic of an excited dog is that its tail will be held high over its back, usually forming an arc. The tail may also be flared, with that the hairs on the tail extended (piloerect).

Figure 2.7. Dogs moving together in an excited posture with tails flared.

**Stalking**

Stalking often occurred as a precursor to play or, in some cases, when a dominant dog was about to actively express its dominance over another individual. A dog in the stalk posture will typically lower its head below the horizontal line of its back with its ears flattened back but not flat against the head (Fig. 2.8a). Stalking dogs may also, to some extent, lower their whole body, particularly when they are close to their target. They maintain eye contact with the target that they are pursuing. Stalking dogs will often slow down their locomotion and minimise the movement of the rest of their body. For example, they don’t wag their tails or exaggerate any other body movements. In the case of stalking before a dominance display, a dog’s tail will be held out in line with the horizontal line of the back (Fig. 2.8b). During play the tail may be held in a relaxed position.

Prolonged eye-contact

Maintaining eye contact for extended periods of time was observed in several different behavioural contexts. It may occur during play, stalking, some greetings, dominance displays, as well as in food protection or acquisition. Prolonged eye contact requires two dogs to hold each others’ gaze for several seconds without breaking focus. The general body posture of the dogs and the interaction type often gives the clearest indication as to whether the eye contact is friendly or dominant in nature.

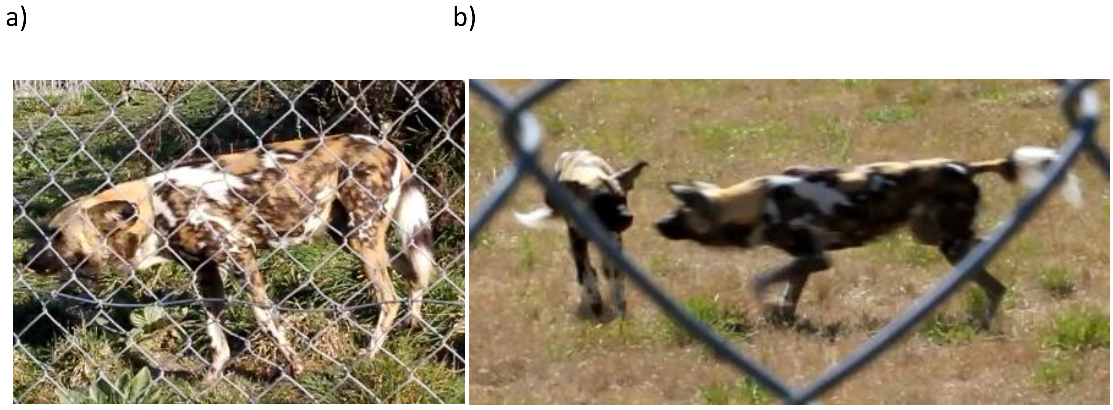

Figure 2.8. Stalking. a) A dog in a stalking posture during play, tail relaxed. b) A dog stalking as part of a dominance interaction with tail held out straight and flared.

**Flight**

The flight body posture (Fig. 2.9) was only observed once, at Wellington Zoo. Two dogs had been lying down together in a heap, but were disturbed by a four-wheeler motorbike with a promotional flag waving off it. The dogs jumped up from the heap and fled further into the enclosure. They had low body postures, tails tucked between their legs, and moved away from the source of distress.

Figure 2.9. Dogs in flight postures after being startled during a heap interaction.

*Interactions*

The interactions observed have been separated into functional groups and the units of which they are comprised. There were 11 main categories of social interaction. There were several behaviours described in the ‘General behaviours’ section that were also observed, but were not included in the ethogram. This was because while at first they appeared social in nature, on closer inspection, it was revealed that the dogs were merely engaging in the same behaviour patterns without interacting socially with one another.

**Greet**

Greetings constitute a large part of wild dog social behaviour. They allow individuals to identify one another, to build social bonds, and to some extent may be used to outline the dominance hierarchy without the need for dominance displays and aggression (Derix, 1994). Here, greetings mainly consisted of dogs sniffing one another or physical contact in the form of nuzzling and open mouth greeting (Fig. 2.10).

Sniff

One dog may sniff any part of another dog as a greeting. Sniffing may be done as dogs walk past one another, or one dog may seek out another to sniff.

Inguinal sniff/lick

This was most often seen during greetings between only two dogs. One dog will sniff or lick the genital region of another dog. This was defined separately from the sniffing of other parts of the dog.

Nuzzle/lick

Dogs often approached each other and engaged in a nuzzling behaviour, whereby a dog(s) used its muzzle (nose and mouth) to nudge and make physical contact with another dog (Fig. 2.10). A dog will usually nuzzle another dog in the neck, chest or facial region, although sometimes dogs were observed nuzzling under the belly and behind the ears. A nuzzling bout may involve a dog nuzzling another dog in several of these regions within a single interaction. Licking may also accompany nuzzling, particularly if a subordinate animal is greeting a more dominant individual. Nuzzling may also result in dogs playfully biting one another if two dogs nuzzle each other’s faces at the same time. This is not aggressive in nature and may help to maintain social order.

Figure 2.10. Nose nuzzling greeting between two dogs.

### Rally

Rally is a ritualised behaviour that is often very difficult to distinguish from play (Fig. 2.11). It is most commonly performed after periods of rest or separation of pack members, or it may be performed before a hunt and, in the case of captive wild dogs, before being fed. It usually begins with at least two dogs greeting each other in an excited manner, although this is not always the case. As the greeting continues, the excitement of the interaction increases and usually more dogs join in. The rally then starts to look more like play as the dogs begin jumping and nuzzling excitedly. Most rallies that were observed involved the mobbing of one of the dogs in the group.

#### Mobbing

Mobbing often occurs when a group of dogs rally or play together, or when excitement levels are high. The group will tend to pick on an individual - hence the term mobbing. Mobbing is not aggressive, although dogs will play-bite, chase and wrestle the individual as if that individual were prey.

#### Biting

Wild dogs often bite one another, although rarely in earnest. Biting normally occurs during play or during mobbing in a rally. Here the bites do not break the skin and are not used to hold on to another individual. There were some instances of biting occurring during aggressive or food related interactions and in these cases the bites often resulted in one individual being able to hold on to the other, even though it was only for a short period of time (Fig. 2.6). These aggressive bites were often targeted around the neck and head area. No serious biting incidents were observed during this study.

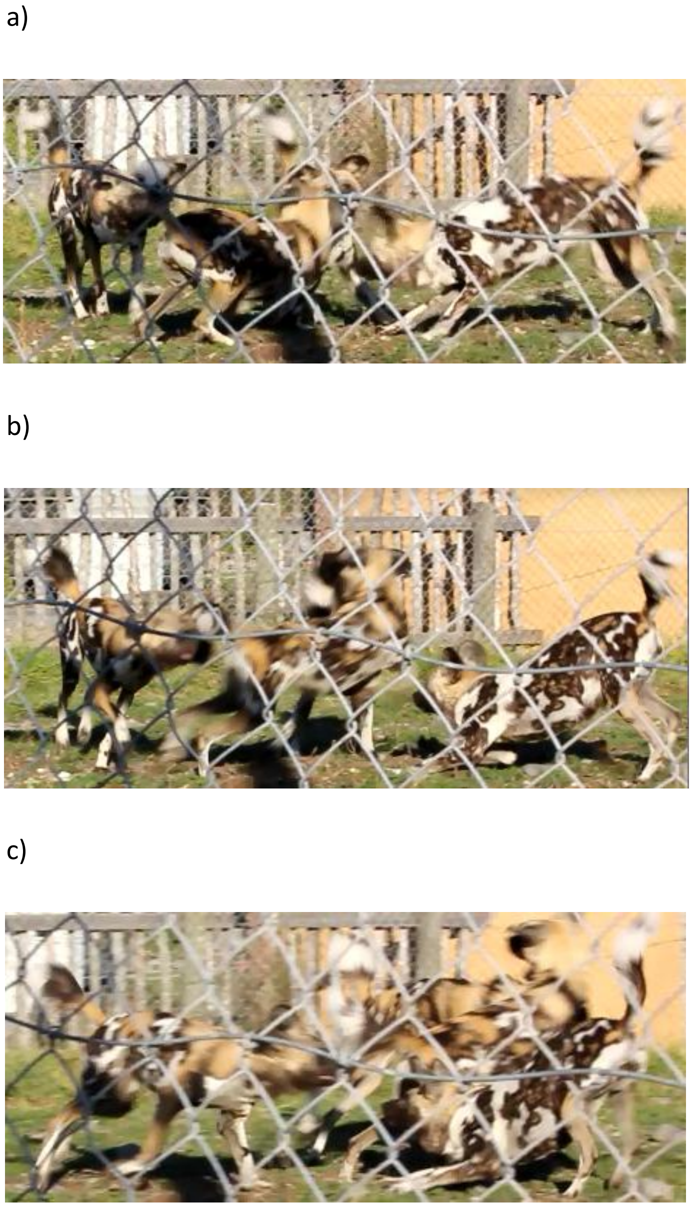

Figure 2.11. Sequence of highly animated interactions between dogs (a rally).

**Play**

Play is an important part of wild dog social behaviour, even as mature adults, as it allows animals to improve the skills they use for hunting, as well as strengthen social bonds within a group. Play was observed in both packs in this study. Play was often initiated by two individuals, although usually the majority of the group joined in.

### Mount

Mounting behaviour was most commonly observed during bouts of play, but it was also observed in other contexts, such as food protection. Mounting occurs when one dog either jumps up or climbs onto the back of another dog from behind. The mounting dog will usually hold onto the other dog by placing its front paws and legs around the stomach of the other dog. Mounting is often thought of primarily as a sexual behaviour, but it may also be used to express dominance or may be performed during periods of high excitement, as in play. The mounting observed in the Orana pack was also accompanied with pelvic thrusting and continued even when the dog being mounted began moving away.

### Wrestle/pounce

Wrestling was defined as a dog(s) jumping up on their hind legs and gripping, boxing or pawing at the face or neck of another dog with their front legs (Fig. 2.12). This typically occurs when dogs face one another. Wrestling may also result in dogs completely jumping or scrambling over top of one another.

Figure 2.12. Two dogs engage in wrestling behaviour during play.

### Bow

The play bow involves a dog lowering the front half of its body by stretching out its front legs and lowering the chest towards the ground. The rear half of the dog remains raised. Play bows are thought to set the play context for the following interactions experienced during play (Bekoff, 1977, 2004), but were rarely observed at the beginning of play in the packs studied. It is possible that other behaviours, such as stalking, may be used to initiate play in wild dogs. In African wild dogs, the play bow was often used during the middle of a play bout. It was sometimes done before the chase aspect of play would begin, but it was also used in conjunction with wrestling behaviours.

### Chase

Chase behaviour is defined as at least two dogs engaging each other so that one dog runs away from another that is in pursuit (Fig. 2.13). This differs from following during locomotion in that it is associated with play behaviour. The dog that is being chased will often adopt an exaggerated run posture whereby the dog will tuck its rear under its body and move its front legs in an almost stiff manner. The dog being chased will often look back, inviting the dog in pursuit to continue the chase. Dogs may also pounce on one another if they are close enough.

Figure 2.13. Dogs engaging in chase behaviour during a play bout.

## Beg

A dog will lick at the mouth of another dog while vocalising with whining sounds (Fig. 2.14). The dog who is begging will often adopt a submissive body posture in which the front half of the body is lowered to the ground with the rear half raised up.

Figure 2.14. Dog on the right adopts a low body posture and licks the face of the dog on the left during a beg interaction.

### Dominance

Displays of dominance closely resemble greetings, but differ in that the instigator often 'greets' in a more intense manner. The dominant dog will approach another dog in a dominant posture (Fig. 2.8b) and then forcefully nuzzles the other dog, often in the groin or neck. The dominant dog may push the other dog to the ground, forcing the other dog into a submissive position, or it may flip and push the other dog by getting its head under the body and lifting.

#### Standing over

Standing over occurs when one dog stands over top of another dog that is usually lying down. Standing over was often seen during dominance displays and food acquisition interactions, when one dog was challenging another dog. During dominance displays a dog may push another dog to the ground and then stand over it. Brief occurrences of standing over may also be seen during heap interactions, just before another dog joins a heap, or as a dog leaves. These examples of standing over are often not deliberate or are done very quickly and these were excluded from this category.

### Active submission

Active submission occurs when a dog, without being forced (as in a dominance display), adopts a submissive posture when in the presence of another dog (Fig. 2.15). If a dog is approached by a more dominant individual, the submissive dog may flop onto its side, exposing its genitals and other sensitive areas.

Figure 2.15. Active submission. The dog on the ground has rolled into a highly submissive posture without being prompted by a more dominant individual.

### Food acquisition

This is when a dog is actively seeking food from another dog (a challenge). This may occur as a group, for instance when the dogs are first presented with a food item at feeding time (Fig. 2.16), or it may occur on an individual level. An individual may try to acquire food from another individual that has a food item by approaching in a dominant or other posture, by approaching and vocalising, or by approaching and nuzzling. The term food acquisition is used when the dog approaching is the dog that is initiating the interaction.

Figure 2.16. Two dogs contest over a piece of food during a food acquisition interaction.

### Food protection

A dog is actively defending a food item. Dogs may simply move away from the dog that is threatening their food item, they may vocalise, they may adopt a defensive posture, or they may lunge at or chase the other dog away. The term food protection is used when the dog protecting the food item is the one that has initiated the interaction.

Lunging

Lunging was often seen in the presence of food. Dogs would lunge at one another to protect food from another individual. Lunging involved a dog leaping towards another dog, usually with its mouth open, ready to bite if necessary.

### Heap

A heap was defined as two or more dogs lying in close proximity (≤ 1.5 m) to one another for the purpose of resting together (Fig. 2.17). Heaps were primarily a passive interaction, meaning that the dogs were not actively engaging one another, but often the dogs would touch. If one dog moved another sometimes sniffed it or briefly actively interacted with it. The differentiation between dogs heaping or lying together is best illustrated with an example. If two dogs were lying in close proximity but one was chewing a bone, this would not classify as a heap because the primary activity of one of the dogs was not resting, but consuming food.

Figure 2.17. Two dogs resting in close proximity to one another, defined as a heap interaction.

**Object interaction**

Dogs may interact with an object together (Fig. 2.18). Here an object is not a piece of food but may be an object containing a piece of food. There may not be direct physical contact or interaction between the individuals, yet the dogs are aware of each other's presence and modify their behaviour accordingly. They may sometimes coordinate their interaction to reach a specific outcome.

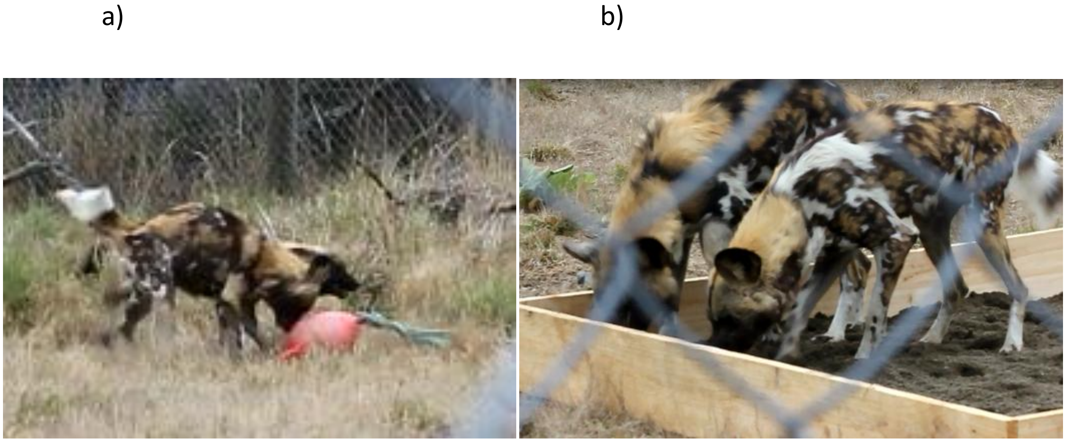

Figure 2.18. Object interaction. a) Two dogs interacting with the buoy enrichment. b) Two dogs interacting together in the sand-pit enrichment.

**Other**

These behaviours have been grouped together in this category because they appear to be forms of social communication and interaction but do not fit into any of the above categories, even though some may be seen in conjunction with other interaction types.

Chin Rest

One dog rests its chin and the weight of its head on the back or body of another dog (Fig. 2.19). The recipient dog may be sitting or standing.

Figure 2.19. One dog rests its chin on another.

Over mark

One dog will urinate or defecate and a second dog will urinate or defecate in the same place (Fig. 2.20). The second dog may approach and sniff the first before it has finished eliminating and in some cases the first dog is pushed out of the way by the second dog.

Figure 2.20. One dog (right) urinates directly over where another dog (left) has previously urinated.

Body rubbing

Body rubbing was an unusual behaviour that was observed in both Orana and Wellington packs. This was usually a solitary activity, but there were a few instances where multiple dogs engaged in this activity together. Dogs would lie down and then roll over onto their backs. They would then writhe about in the grass, often starting at the top of a slope in the exhibit and working their way to the bottom. When multiple dogs were seen body rubbing, they would often touch one another. This may be by wriggling into each other or they may intentionally reach out their paws or mouths and touch each other. Their tails would often be wagging. The purpose of this activity is unclear. It may serve to remove dirt or parasites from the coat or for scent marking (Van Heerden, 1981).

*General behaviour*

**Prey pursuit**

Prey pursuit occurred when the excitement level of the pack was high and was most commonly observed just before the dogs were fed. Prey pursuit behaviour was observed in both packs. Dogs would adopt an excited body posture. They would typically begin to vocalise using high pitched squeaks, and their tails would be raised high and flared, curling over their backs in an arc. The dogs would often begin running together, although they did not touch. This behaviour was observed in both Orana and Wellington packs, but was not included in the ethogram because the dogs were focussing on the food or the keeper and not on each other, and consequently this was not classified as a social interaction.

**Hunting**

Hunting behaviour was observed several times, but only in the Orana pack. At Orana there were a significant number of wild rabbits that frequented the wild dog exhibit and these were occasionally hunted. Hunts usually began by the dogs scenting out the rabbit. They would walk along the perimeter of the enclosure together, stopping to sniff the same objects or places. If they got close enough to a rabbit and it moved the dogs would begin pursuit. Several times the dogs were successful, and although the dog that caught the rabbit was often first challenged by the others, she was always allowed to eat what she caught. During hunting interactions the dogs did not directly interact with one another but they did modify their behaviour due to the presence of the other dogs. For this reason, this behaviour was not considered social behaviour and was excluded from the ethogram.

RESULTS

The dogs at Orana spent only 5% of their time engaging in social interaction (per hour of observation). The most frequent interactions when socially active were heap behaviours (Fig. 2.21). The dogs also engaged in large amounts of food acquisition behaviour compared to the remaining interaction types (Table 2.1). Play behaviour occupied a moderate amount of the time dogs spent socially interacting. Rally, object and greet interactions all constitute a small proportion of the overall social activity of these captive canids while beg, 'other', and food protection behaviours occupy even smaller proportions. The percentage of time dogs engaged in dominance and submissive behaviours was less than 1% of the total time spent engaging in social interaction (Fig. 2.21).

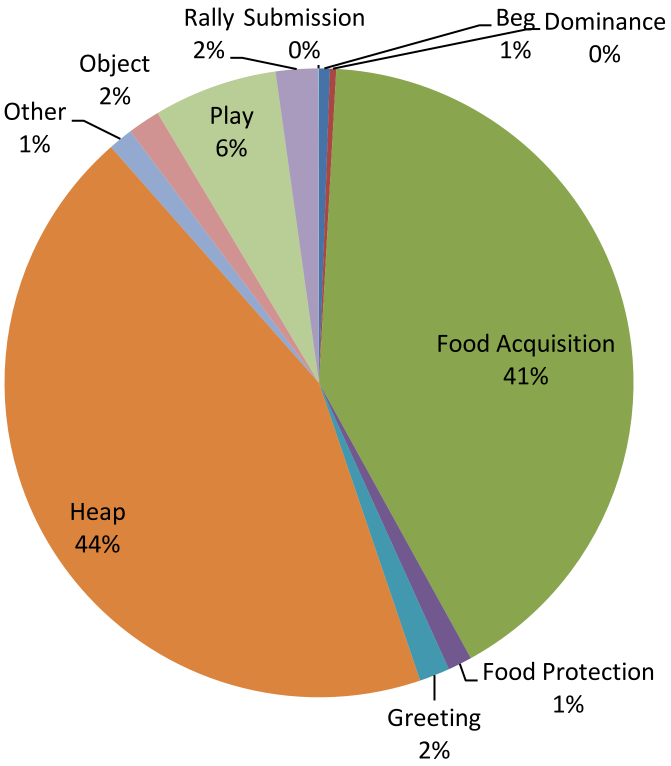

Figure 2.21. Pie chart representing the relative percentage of time spent engaging in each of the 11 main interaction categories out of the 5% of time that the dogs were socially active.

Table 2.1. The percentage of time (per hour of observation) spent engaging in each of the 11 main interaction types.

| **Interaction category** | **Time spent engaging in each interaction (%)** |
|---|---|
| Beg | 0.03 |
| Dominance | 0.02 |
| Food acquisition | 2.15 |
| Food protection | 0.07 |
| Greet | 0.08 |
| Heap | 2.28 |
| Other | 0.07 |
| Object | 0.09 |
| Play | 0.33 |
| Rally | 0.11 |
| Active submission | 0.002 |

## DISCUSSION

The activity of free-ranging African wild dogs is largely bimodal, with dogs typically engaging in socially activities early in the morning and later in the afternoon, coinciding with hunting activity (Fuller & Kat, 1990; Creel & Creel, 1995). This tendency was also seen in the current study, with social activity increasing prior to feeding times in the afternoon. The data used for this description of the repertoire of social behaviour was therefore collected during this high activity time, as the dogs remained relatively inactive during other parts of the day.

The most highly represented forms of social interaction in the all-female Orana pack of captive African wild dogs were heap, food acquisition and play. Greet, beg, object, rally, food protection and ‘other’ (chin resting and over-marking) behaviours were all present in this pack, but were rarely performed. Additionally, the small percentage of dominance and active submission behaviours suggest that these forms of social interaction were uncommon in this captive group, as was found in another captive study by Derix (1994). Although all of the behaviours observed in this pack have also been observed in free-ranging populations or other captive groups (Kühme, 1965; Derix, 1994; Gusset *et al*., 2006; Price, 2010), no studies have explicitly explored the activity budgets of either free-ranging or captive wild dogs in relation to social behaviour, so my discussion will be restricted to a comparison of whether certain behaviours are absent in captive versus free-ranging packs.

Social interaction in the Orana pack of wild dogs appeared to occupy a rather small proportion of the activity budget. Although heap interactions serve a social purpose, by allowing dogs to passively interact through resting associations (De Villiers *et al*., 2003), they also function as rest (McCreery, 2000). This may explain why heap interactions occupy such a large proportion of the social activity budget of captive wild dogs, as a large amount of time is dedicated to resting in this species (Fuller & Kat, 1990; McCreery, 2000). Heaping interactions have been recorded in other captive and free-ranging populations (McCreery, 2000; De Villiers *et al*., 2003; Rasmussen & Macdonald, 2012), indicating that the presence (and perhaps use) of heap behaviour is not significantly affected by the captive environment.

Food acquisition interactions also represented a large proportion of social activity in these dogs, probably because filming was conducted only on feed days. When presented with a large food item, dogs often engaged in lengthy interactions as the dogs set about sharing the food among the pack members, similar to what they do in the wild (Kühme, 1965). If a dog missed out on a food item in the initial stages of the feeding process, it often engaged in persistent food acquisition behaviours with other individuals that did receive food. Despite this, food protection behaviours were not used as frequently as food acquisition behaviours. As such, although the dogs often initiated interactions in which the goal was to displace another from the food, they seldom initiated interactions in which the goal was to protect food. This indicates that dogs were not possessive of food items, as this would likely increase the amount of time spent engaging in food protection behaviours (Carpenter, 1987). Instead, the food sharing behaviour of wild dogs centres on the ability of dogs to openly share food, and challenging others to food appears to be accepted (Ewer, 1973). This is supported by studies of free-ranging populations where dogs feed communally at kills with little to no aggression, and share food through equal access to the carcass, regardless of rank, age or sex (Kühme, 1965; Creel & Creel, 1995).

Another form of food-related social behaviour, begging behaviour, used by wild dogs to solicit food from one another (Courchamp *et al*., 2002), only represented a small proportion of the time spent socially active in this study. This may be due to the fact that these dogs were well fed, or that the dogs engaged in more food acquisition behaviour, thus replacing the need for the dogs to solicit food from one another by begging. Begging behaviour has been observed in free-ranging wild dogs to request food from one another, or as part of the ritualised rally ceremony (Malcolm &

Marten, 1982; Rütten & Fleissner, 2004). Unlike in other canids, where begging behaviour is a strictly juvenile behaviour, begging in African wild dogs continues into adulthood (Fox, 1971).

Although not included in the ethogram, hunting of wild rabbits that ventured into the dog enclosure was observed. Although all dogs were usually present during hunting, they did not work together to catch their quarry, and the pursuit and capture of the prey was usually carried out by a single dog. This markedly differs from the behaviour of free-ranging populations, where wild dogs consistently hunt cooperatively (Macdonald, 1983; Creel & Creel, 2002). Cooperative hunting is thought to be inherently obligate in wild dogs, yet in other canids it is thought to be facultative (Macdonald, 1983). Rather than being an artefact of captivity, this may simply be due to the small size of available prey. In other words, rabbits may not require the combined work effort of the pack when the energetic payoff is small (Rasmussen *et al*., 2008).

Play interactions constituted a relatively large portion of the time spent socially active. Play behaviour provides the opportunity for animals to practice certain physical skills that aid survival and is often used to strengthen social bonds between animals without the need for aggression (Ewer, 1973; Bekoff, 2004). As wild dog survival depends on significant group cohesion and cooperation, it is likely that the latter function of play is very important in this species (Creel & Creel, 2002). Similarly, rally and greet interactions are thought to improve group relationships within wild dog packs and studies have demonstrated that affiliative interactions are often used by wild dogs rather than dominance or aggression (Derix, 1994; Rütten & Fleissner, 2004). However, in this pack the time invested in such interactions was considerably less compared to play. While greetings can serve as affiliative interactions, they may also function to distinguish dominance relationships between individuals (De Villiers *et al*., 2003; Gusset *et al*., 2006; Bonanni *et al*., 2010). Play, on the other hand, often requires the absence of rank distinctions in order for the play to continue, as overly aggressive or dominant interactions are often not tolerated in canid play interactions (Bekoff, 2004). As this was an established pack it may be that play served as an appropriate substitute for greeting and rally interactions, which are more likely to convey dominance and submissive type behaviours.

The negligible amount of time spent engaging in dominance and submissive social interactions suggests that these may not be used to maintain social bonds in wild dogs. Derix (1994) also found that despite the presence of dominance and submission-based interaction in captive populations of both wolves and wild dogs, wild dog interactions were based on affiliative interactions, while wolves used more dominance and aggression. This notion is supported by the initial belief that wild dogs had no social hierarchy (Fox, 1971) due to the apparent absence of any dominance or aggression when observed in hunting situations. It is now realised that the extreme level of sociality among wild dogs requires limited displays of aggression (Ewer, 1973; Creel & Creel, 2002).

While many of the social interactions observed in free-ranging populations were also observed in this captive group, the key aspect of sexual behaviour was not observed, either in the Orana pack or in the Wellington pack. While the Orana pack consisted of all females, the fact that sexual behaviour was absent in the mixed-sex Wellington pack was likely due both to the dogs being highly related (siblings) and to contraception being used as a population management strategy (McNutt, 1996; Asa *et al*., 2010). McNutt (1996) demonstrated that free-ranging wild dogs will avoid mating with closely related individuals, but inbreeding has been recorded in some captive populations where contraception was not used (Frantzen *et al*., 2001). Some mounting behaviour was observed at Orana, but this was not of a sexual nature and was more likely used in play, or perhaps as a technique for asserting dominance within the group.

Negative effects associated with captivity often result in the criticism of behavioural studies conducted in such conditions (McPhee, 2004). While some studies argue that canid behaviour in captive environments is not significantly affected by captivity (Shivik *et al*., 2009), others argue that captivity introduces a new suite of pressures that may negatively affect social behaviour, as demonstrated in wolves, where captivity often increases aggression (Sands & Creel, 2004). Although it is important to keep in mind the limitations of captivity on animals and the possible negative implications on their behaviour, behavioural studies on captive animals are essential. With increasing emphasis on the importance of captive breeding programs, such studies allow for comparisons between captive and free-ranging populations and the associated behaviours to be explored (McNutt, 1996; De Villiers *et al*., 2003). This not only indicates whether the proposed negative effects of the captive environment exist, but also demonstrates how different animals respond to captivity, offering insights into possible ways to improve captive animal welfare and maximise the potential of breeding programs.

With the exception of sexual behaviour, all of the social behaviours present in the captive group at Orana are consistent with what is found in other captive and free-ranging populations (Kühme, 1965; Derix, 1994; McNutt, 1996; De Villiers *et al*., 2003; Rasmussen & Macdonald, 2012). Overall, this study suggests that the presence or absence of different social interaction types is not significantly affected by the limitations of the captive environment, implying that sexual behaviour would likely be observed in unrelated captive groups or if animals were not prescribed contraception (e.g. Frantzen *et al*., 2001). While it was originally believed that wild dogs lacked many forms of social communication used by other large, social canids, recent evidence suggests that many of the behavioural types are present in wild dogs but that the significance of certain behaviours may differ between wild dogs and other canids, such as wolves (Fox, 1971; Derix, 1994; De Villiers *et al*., 2003; Bekoff, 2004). Although captivity may negatively affect many aspects of animal behaviour, including the formation of stereotypic or repetitive behaviours (Price, 2010; Shyne & Block, 2010), overall the types of social communication used by the dogs are representative of natural social behaviours. However, the proportion in which the behaviours are performed in captivity compared with free-ranging populations remains unknown.

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## CHAPTER THREE

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# A FAMILY THAT PREYS TOGETHER STAYS TOGETHER: THE EFFECTS OF PACK COMPOSITION ON SOCIAL INTERACTION IN CAPTIVE AFRICAN WILD DOGS

## ABSTRACT

Although group living species often receive significant attention in relation to how their presence may affect their surrounding ecological systems, few studies have attempted to understand the social mechanisms holding such groups together. Here I aim to identify the differences, in terms of social behaviour and relationships, between two non-breeding packs of African wild dog (*Lycaon pictus*): one all female pack, where all individuals are littermates, and a second pack that contains related males and females from two litters. The results indicate that social interactions were more evenly distributed between individuals in the all female pack, while the effects of group sex composition on the frequency and duration of social interactions appear to be weak. The difference in the frequency of food acquisition, duration of food protection and the frequency and duration of heap (social resting) interactions can be explained by differences in the management of the two populations. This study highlights the importance of understanding social group structure and relationships and suggests that single-sex packs may be more stable than highly related non-breeding mixed-sex packs. This has the potential to change the way that wild dogs are housed in captive situations, particularly if individuals are related and are not intended for breeding programs.

## INTRODUCTION

Group living has evolved as a response to a variety of selective pressures. The ability to better defend resources, whether they be territories, mates, food, or nesting sites, combined with the opportunity for increased individual protection, are just some of the reasons that animals have adopted a group living strategy (Price & Stoinski, 2007; Kutsukake, 2009). As with all life history strategies, there are associated trade-offs. Group living increases the density of individuals in a given area, which may increase the level of intraspecific competition, as well as increasing the likelihood of disease transmission (Kutsukake, 2009). Despite this, many animals, including the African wild dog (*Lycaon pictus*), must live in groups in order to obtain and defend resources, as well as to ensure successful survival of offspring (Courchamp & Macdonald, 2001).

In captivity the requirement for group living appears to be redundant, as many, if not all of the selective pressures that characterise the need for group living are eliminated. It has therefore been suggested that the characteristics of group structure may be more flexible in captive populations because predation and competition for resources are reduced or eliminated (Price & Stoinski, 2007). Additionally, being artificially composed, the structure of animal groups housed in captivity can vary significantly from what is typically found in free-ranging populations, with potentially important concomitant ramifications. Although some species may be flexible regarding group structure in captivity, others suffer greatly if the social structure of groups differs significantly from what is expected in the wild. Examples from the primate family demonstrate this contrast well. While orangutans (*Pongo pygmaeus*) naturally live solitary lives, in captivity they do well in small social groups; in contrast, studies have shown that rhesus macaques (*Macaca mulatta*) experience lower group stability where captive group structure is abnormal (Edwards & Snowdon, 1980; Beisner *et al*., 2011). This is because the captive environment, while removing some selective pressures, introduces a new suite of social selective pressures, thus potentially influencing social groups.

Group structure in captive animals is limited by many factors. The overall group size of captive populations may be smaller or larger than among free-ranging conspecifics, with some animals living in isolation while others experience severe overcrowding. Whilst isolation has been linked to the formation of repetitive abnormal behaviours (stereotypies), overcrowding has been shown to increase stress and aggression (McAfee *et al*., 2002; Li *et al*., 2007; Olsson & Westlund, 2007; Pyykönen *et al*., 2008). Furthermore, the lack of natural dispersal in captive populations increases the level of relatedness within groups and may affect the age or sex composition of groups, especially in species where reproductive sex ratios are biased (Glatston, 1997; Fraust & Thompson, 2000). Lack of dispersal may also alter the dynamics of a group by retaining individuals or cohorts of individuals within the group that would normally leave at sexual maturity, potentially affecting the structure of a group, particularly where rank is governed, at least in part, by age or kinship (Fraust & Thompson, 2000; Beisner *et al*., 2011).

The factors outlined above can drastically alter the social dynamics of a group, by affecting the level of competition between individuals for suitable mates, access to resources, and in some cases by affecting the social hierarchy system. Furthermore, unsuitable group structures may result in unnatural social situations which captive animals may be unable to respond to appropriately, intensifying stress responses and aggression. This, in turn, may have negative impacts on captive animal reproductive success (Beisner *et al*., 2011). It is therefore highly important that captive animal management aims to identify new pressures brought on by captivity that may influence group structure and addresses them appropriately to ensure the success of animals housed in social groups.

There are several captive management strategies aimed at controlling group reproductive dynamics and thus controlling social group structure within captive facilities. Contraception (both reversible and permanent), controlled euthanasia, the movement of individuals between different captive facilities, in addition to housing animals in single-sex groups, are all procedures that captive facilities apply to group-housed animals (Jewgenow *et al*., 2006; Asa *et al*., 2010). While these methods mainly address the issues of relatedness within captive groups, they may also influence the sex ratio of groups, as well as limit population growth. As the management of endangered species, such as African wild dogs, *Lycaon pictus*, often involves breeding programs aimed at increasing global population numbers, the uses of the more permanent population control techniques are often discouraged. This means that contraception or single-sex housing are more accepted methods for controlling reproduction, and thus group structure, in many globally-threatened or endangered species.

Here I consider the suitability of housing *Lycaon pictus* in single-sex groups as an alternative to the use of contraception. My focus will be on determining if there are significant differences in the display and social interaction behaviours of a single-sex pack compared to a non-breeding mixed-sex pack with the same number of individuals. The individuals in both packs were highly related, and can be described as 'holding facilities', because reproduction in these groups was prevented either by contraception or the absence of the opposite sex. Of the many potential implications of housing animals in single-sex groups, most relate to how the social system of the group may be impacted by the absence of both sexes. Another concern is that there may be long-term effects that impact the way that one sex may react to another, especially if the animals housed in single-sex groups were to ever join with members of the opposite sex. This study did not determine the long-term effects of single-sex housing on the ability to appropriately respond to the opposite sex, but instead investigated whether there are differences in the ways that wild dogs communicate with one another when housed in single-sex or mixed-sex groups.

## METHODS

### *General*

Data were collected using the hand-held method (see Chapter Two for details) between May – Nov 2012 at Orana Wildlife Park (43$^{o}$28'0.17"S, 172$^{o}$27'46.98"E). Subjects at Orana were four female

African wild dogs (*Lycaon pictus*) from the same litter, bred in captivity at Hamilton Zoo (37°46’27.69”S, 175°13’0.79”E) in the North Island of New Zealand. Comparative data were collected from Wellington Zoo (41°19’10.12”S, 174°47’4.48”E) in February 2013. The subjects from Wellington Zoo were four related African wild dogs, three males and one female, from two separate litters (same mother). All individuals were bred in captivity at Wellington Zoo.

The wild dog exhibit at Orana Wildlife Park is approximately 0.56 hectares of natural grassland, divided into two enclosures joined by linkways (Fig. 3.1). Features of the enclosure include trees, water troughs, underground dens, a wooden platform, logs and housing dens. Dogs were given free access to all areas of the exhibit, except for feeding time when they were confined for approximately 10 min allowing the keepers to place their food. The dogs were fed dead bobby calves (*Bos primigenius*) and goat (*Capra aegagrus hircus*), depending on availability, and sometimes received whole chickens (*Gallus gallus domesticus*), five times a week.

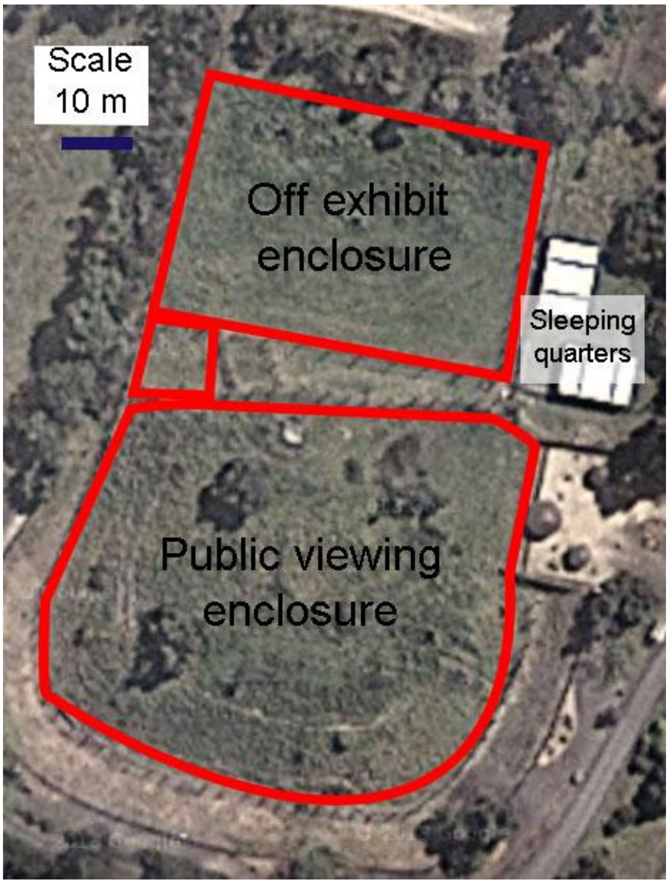


Figure 3.1. Orana Wildlife Park enclosure layout. Area inside the red lines indicates areas accessible to the dogs.

The Wellington Zoo exhibit was approximately 0.16 hectares, which was divided into two enclosures with a housing building adjoining them (Fig. 3.2). The exhibit was on sloping terrain with some small flat areas. It contained trees, grasses, wooden dens and one enclosure had a man-made water hole. Dogs were alternated between exhibits on feeding days, allowing the keepers to clean the enclosures before and after the dogs had been moved over. The dogs had access to the sleeping quarters unless routine management procedures required them to be excluded from this area for a short time. Feed times were irregular, but were typically between 13:30 h and 14:00 h three days a week. The dogs were usually fed partial goat carcasses, whole hare (*Lepus europaeus*) carcasses, and/or offal.

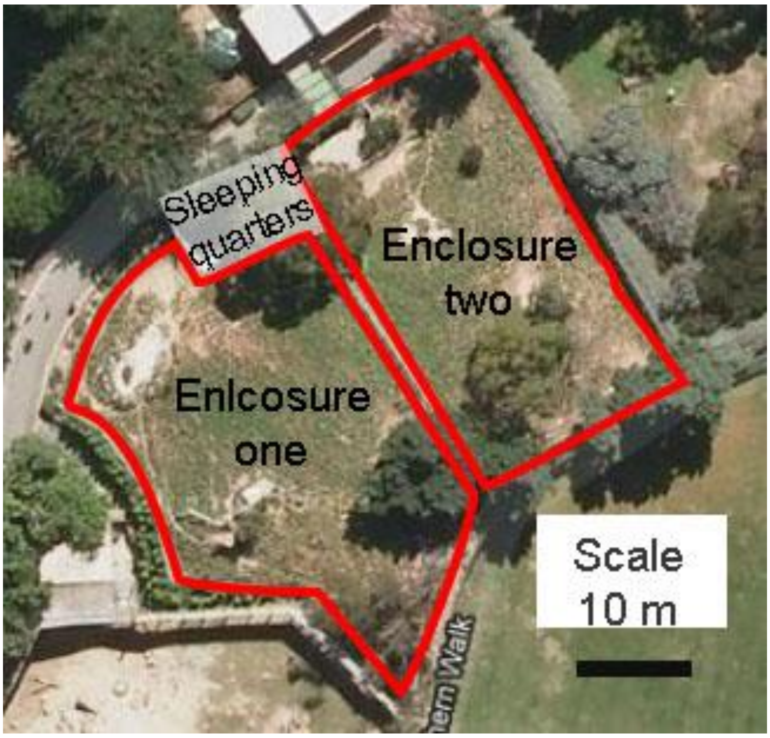


Figure 3.2. Wellington Zoo enclosure layout. Area inside the red lines indicates areas accessible to the dogs.

*Statistical analysis*

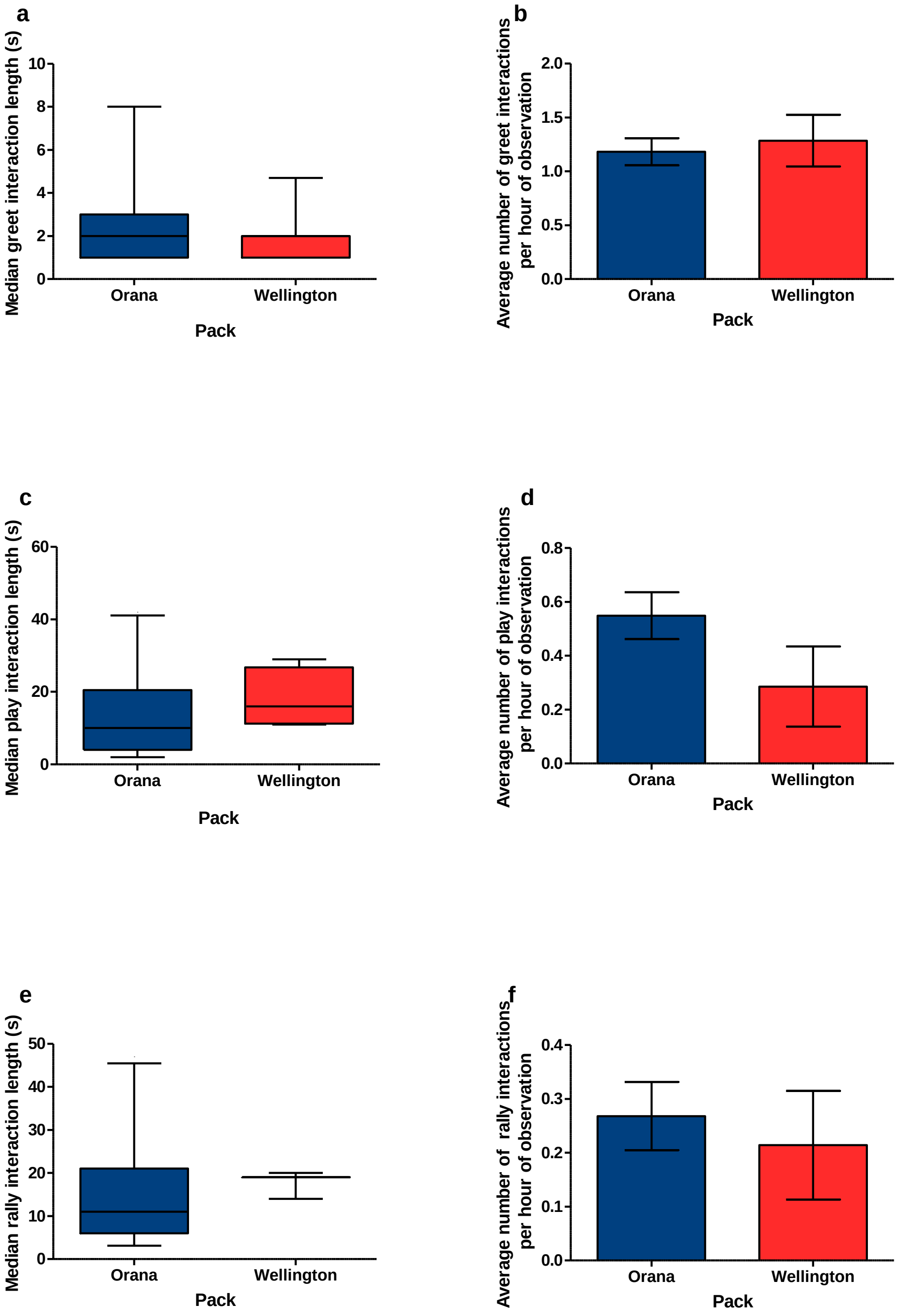
Once scored (see Chapter Two for details), data for behavioural frequencies and duration were analysed using the mixed effects models package in R (lme4). All data collected using the hand-held method for Chapters Three, Four and Five were analysed together in the same analyses, but here I was only interested in the direct comparisons between the all-female related Orana pack (when there were four dogs) and the mixed-sex related Wellington pack of four dogs. Mixed effects models, using ‘day’ as a random factor, were used to account for differences in sampling time between the packs and to account for the unbalanced nature of the data set. Each of the interaction types were analysed separately, although there was insufficient data to analyse three interaction types (active submission, beg and object interaction). Behavioural categories that were compared between the Orana pack and the Wellington pack were greet, play, rally, heap, food acquisition, and food protection (see Chapter Two for descriptions). All data were log transformed. Degrees of freedom are not reported, as there is considerable controversy about the correct way to calculate them for mixed effects models (Hoshino, 2008) and the lmer package used to analyse these data, does not require degrees of freedom to generate accurate p values. P values for duration data were based on using Markov Chain Monte Carlo (MCMC) values, as this is the most appropriate choice when using mixed effects models (Hoshino, 2008); however, conventional p values were used for frequency data.

Data used for the social network analyses were based on all dyadic interactions relating to affiliation behaviours, limiting the analysis to ‘greet’, ‘heap’, ‘play’ and ‘rally’ interactions only. Plotting and descriptions of social networks were graphed using ‘igraph’ in R. Basic social network metrics, such as degree of centrality, reciprocity, vertex connectivity and tie strengths (Wey *et al.*, 2008) were generated based on the number of social interactions per hour of observation.

## RESULTS

There was no difference in either the frequency or the duration of greet interactions (frequency: $z = 0.533$, $p = 0.594$; duration: $t = 0.156$, pMCMC = 0.881; Fig. 3.3, a, b), nor of the relatively infrequent play interactions (frequency: $z = -0.987$, $p = 0.324$; duration: $t = 1.014$, pMCMC = 0.322; Fig. 3.3, c, d), between the Orana pack and the Wellington pack. There was also no difference in either the mean frequency or the median duration of rally behaviour between packs (frequency: $z = -0.214$, $p = 0.831$; duration: $t = 0.764$, pMCMC = 0.450; Fig. 3.3, e, f). However, with the probability of heap behaviour in the Wellington pack being 38%, compared to 2% in the Orana pack, there was a significant difference ($z = 5.017$, $p = < 0.001$) in the mean frequency of heap interactions, and in their median duration ($t = -2.619$, pMCMC = 0.013; Fig. 3.3, g, h), whereby heaps were longer in the Orana pack (mean = 239.1 s) compared to the Wellington pack (mean = 104.2 s). There was also a significant difference in the mean frequency of food acquisition interactions between packs ($z = -2.928$, $p = 0.003$), with the probability of food acquisition behaviours being higher in the Orana pack (33%) than in the Wellington pack (10%). In contrast, the length of food acquisition interactions did not differ significantly between packs (t = -2.139, pMCMC= 0.053; Fig. 3.3, i, j), despite food acquisition interactions being on average nearly 10 s longer in the Orana pack (13.9 seconds) compared to the Wellington pack (3.6 seconds).

The mean difference in the frequency of food protection interactions between the Orana and Wellington packs was non-significant (z = -0.829, p = 0.407), but there was a significant difference in the length of food protection interactions between packs (t = 2.288, pMCMC = 0.02; Fig. 3.3, k, l).



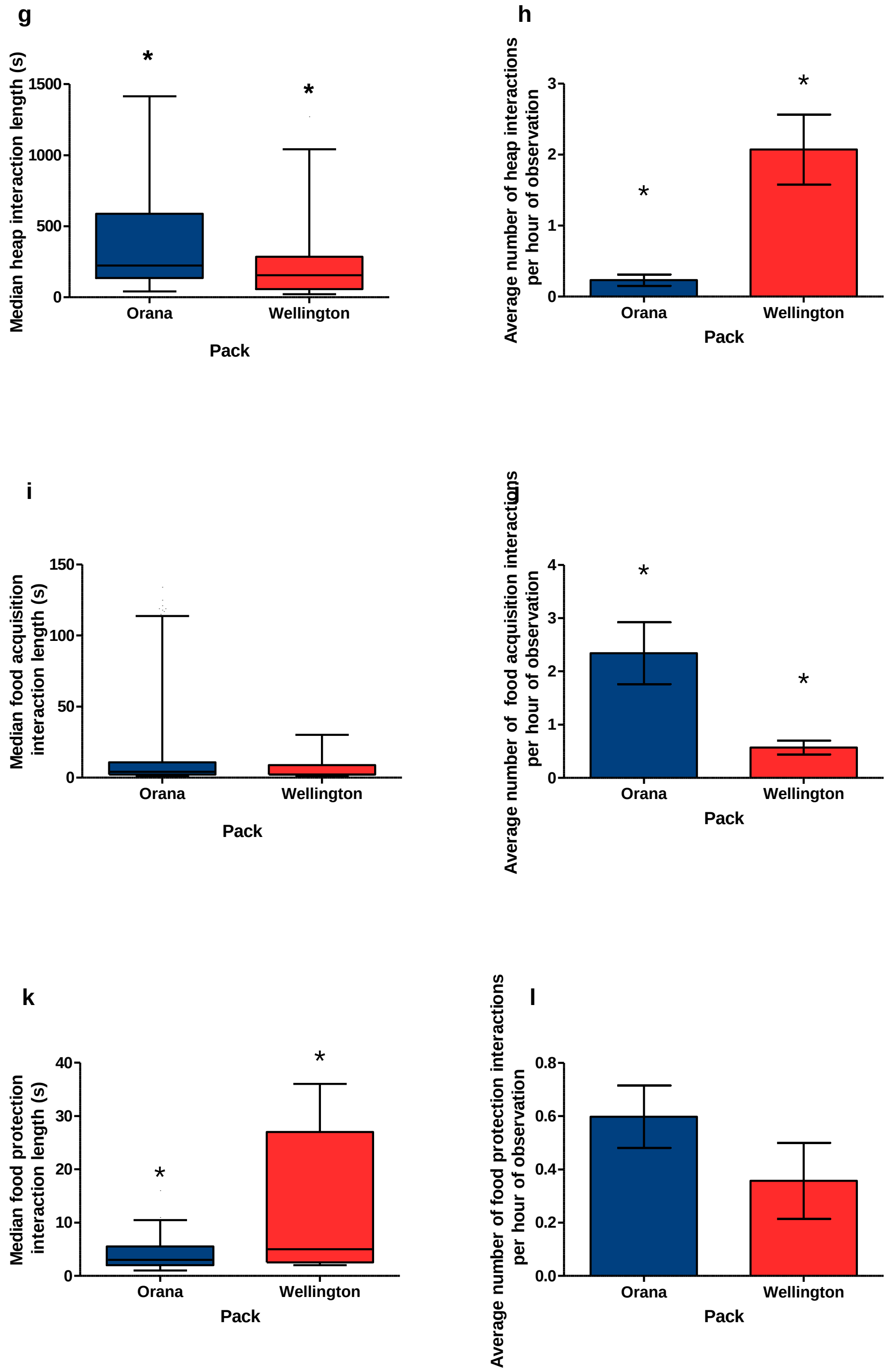


Figure 3.3. Median length (whiskers: 10 and 90 percentiles) of social interaction (boxplots) and average number (±SEM) of social interactions/h (histograms) for each behaviour at Orana Wildlife Park and Wellington Zoo. a) greet length, b) number of greets, c) play length, d) number of plays, e) rally length, f) number of rallies, g) heap length, h) number of heaps, i) food acquisition length, j) number of food acquisition interactions, k) food protection length, l) number of food protection interactions. Asterisk denotes significant difference ($p < 0.05$).

In social network analyses, the degree of centrality describes the number of ties (both incoming and outgoing) an individual has to other individuals. The Orana network (Fig. 3.4) was based on affiliation interactions collected from the all female pack, while that of the Wellington network (Fig. 3.5) was based on affiliation interactions collected from a mixed-sex pack of the same size. In the Orana network all dogs had the same number of ties, both incoming (three ties per dog) and outgoing (three ties per dog), where the total number of ties per dog is six. This suggests that all dogs both initiate and receive interactions with all others in the network. The degree of centrality for each dog was slightly different in the Wellington pack, suggesting that not all dogs were equally connected within the group. Each dog also had different measures for in-degree (receiving ties) and out-degree (initiating ties), further supporting the notion that not all dogs were tied within the network in the same way. Moyo had the highest overall measure of degree (five ties) and he received ties from two dogs (Mongo and Jelani); however, Moyo initiated ties (three ties) with all dogs in the pack. Overall, Mongo had four ties within the pack, receiving ties from all dogs, but only initiating ties with Moyo. Jelani only initiated ties with two individuals (Moyo and Mongo) and only received one tie from Moyo, giving him an overall degree of centrality of three. Layla had the lowest degree of centrality (two ties), receiving one tie from Moyo and initiating one tie with Mongo. If we are only concerned with the number of individuals that each dog is tied to, it is apparent that Mongo was the only dog that received ties form all other dogs and Moyo was the only dog that gives ties to all other dogs.

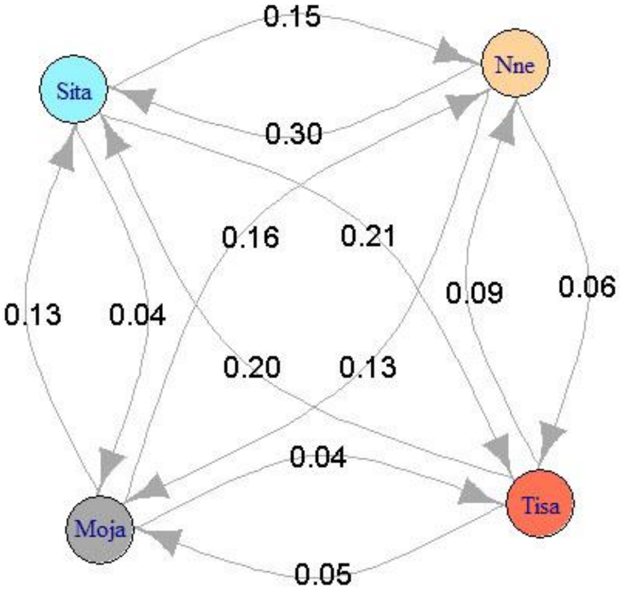


Figure 3.4. The network of affiliation interactions in the Orana pack per hour of observation. Nodes are labelled for each dog (coloured circles) and the size is weighted by degree of centrality, with ties weighted by strength. The strengths of ties are depicted on each tie.

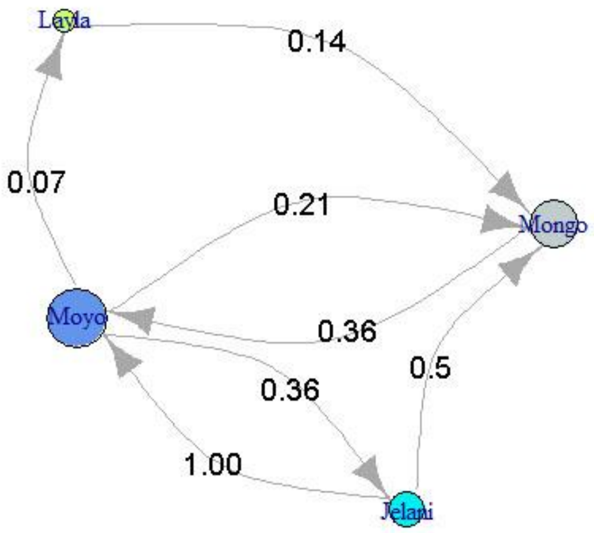


Figure 3.5. The network of affiliation interactions in the Wellington pack per hour of observation. Nodes are labelled for each dog (coloured circles) and the size is weighted by degree of centrality, with ties weighted by strength. The strengths of ties are depicted on each tie.

The measure of reciprocity between all Orana dogs in the network was one, indicating that affiliated social interaction within this pack was bidirectional between all dogs. For the Wellington network, the measure of reciprocity between all dyads (0.57) indicates that only half of the ties between dogs are reciprocated. In this network only Moyo and Jelani, and Moyo and Mongo experienced reciprocated ties with one another.

Measures of vertex connectivity determine the minimum number of individuals that would need to be removed in order for the network to collapse. For the Orana network the measure of connectivity was three, indicating that three dogs would need to be removed for affiliated social interaction within this pack to collapse, clearly indicating the strongly connected nature of this pack. In contrast, the measure of connectivity within the Wellington network suggests that only one individual needs to be removed in order to cause the collapse of the network. From the information gained about this network, it appears that the removal of an individual such as Moyo, who connects all individuals within the network, would significantly affect the stability of this pack.

Tie strengths determine the relative strength of social ties between individuals. In Fig. 3.4 and Fig. 3.5 the ties between individuals have been weighted based on tie strength, where tie width indicates strength, and the actual tie strengths have been labelled on the figure to make patterns clear. The tie strengths between some dyads at Orana, such as between Sita and Tisa, were stronger than others. The tie strengths between Sita and Tisa were reciprocated, while those between Sita and Nne, while strong, were not as equally reciprocated. As all dogs appeared to have relatively weak ties with Moja, this suggests that she was the lowest ranked individual in the pack. In the Wellington pack, there was significant variation in the strength of ties between individuals. The strongest ties were between Moyo and Jelani, who are members of the same age-sex cohort. Following that, the majority of both strong and medium strength ties existed between the three males within the pack, with Layla being weakly connected to other members of the group, suggesting that this dog was the least dominant individual within the pack.

## DISCUSSION

Although this study looked at two packs with different sex compositions it is important to reiterate that all animals within these packs were highly related, both packs were relatively small (a characteristic of many internationally kept wild dog packs), and that although sex ratios were different between the packs, they did not necessarily mimic natural pack sex ratios of free-ranging wild dogs. These factors, combined with the inability to replicate each pack, make drawing conclusions about causality extremely difficult. However, it was possible to identify some patterns within the data collected, and these patterns are all the more interesting because both packs were comprised of the same number of individuals and both packs were related, with differences in housing and maintenance and in sex composition being the primary differences between the packs.

In free-ranging wild dog populations pack sex ratios are often relatively equal, with some studies suggesting that a slight male bias is more common (Maddock & Mills, 1994; Creel & Creel, 1995; Frantzen *et al*., 2001; De Villiers *et al*., 2003). The male: female pack sex ratio of the Orana pack was 0:4, while the Wellington pack was 3:1. As the study packs had ‘unnatural’ sex compositions one might expect differences in the use of social interactions between the groups. However, the observed frequency and duration of many of the social interactions observed were relatively similar. This may seem unusual, but previous studies have identified that two separate hierarchies exist within wild dog packs, one for males and one for females (Creel *et al*., 1997; Creel & Creel, 2002). In addition, free-ranging wild dogs may temporarily form single-sex groups when dispersing from their natal packs at sexual maturity, indicating that single-sex groups, although not permanent in the wild, are feasible (McNutt, 1996; Creel *et al*., 1997). Furthermore, individuals have been shown to have higher levels of association and coalition formation with individuals of the same age-sex cohort, with rank and relatedness also being significant factors (De Villiers *et al*., 2003).

Given that the Orana pack consisted of four related individuals from the same age-sex cohort, it is perhaps not surprising that social interaction between them was high, as shown by the social network analysis which indicated considerable interaction between all individuals, resulting in a stable pack. Similarly, in the Wellington pack all individuals were related, but they were from two separate litters. This means that two individuals were from the same age-sex cohort, three were from the same sex cohort and two were from only the same age cohort. Social interaction within the Wellington pack was dominated by the three males with the lone female, a subordinate individual, having limited social interaction within the group. The strongest social ties within this pack were between the two male individuals from the same litter (age-sex cohort). Albeit based on a limited sample size, these results suggest that the composition of mixed-sex packs should be such that multiple individuals of each sex are present to prevent individuals from becoming socially isolated within social groups. It would therefore seem that group sex composition may not significantly impact the frequency or duration of social interactions within groups, but might affect the distribution of social interaction among individuals within groups.

The similarities in the frequencies and durations of many social interaction types between the packs may suggest that the effects of pack sex composition are minor in determining the ability of captive wild dogs to display appropriate social behaviour, and it may be that relatedness masked any effects of sex composition on social interaction. Despite this, food acquisition and heap interactions were performed at significantly different rates, and the length of heap and food protection interactions differed between packs. However, these observed differences could be explained in terms of differences in the management of both populations, rather than by differences in group sex composition. For example, the higher frequency of food acquisition interactions in the Orana pack may be attributed to the different feeding regime implemented at Orana Wildlife Park compared to that of Wellington Zoo. At Orana, dogs were fed a single half carcass, simulating wild dog hunting and food sharing behaviours in the wild (Kühme, 1965). Although some dogs did not acquire food in the initial stages of feeding, these dogs often engaged in persistent food acquisition behaviours with other dogs later on, making it extremely uncommon for a dog to completely miss out on food on any given day. The dogs at Wellington Zoo were fed portions of meat spread throughout the enclosure to limit aggression. These differences may have resulted in the higher rate of food acquisition interactions in Orana, where food competition would have been higher as a result of dogs having to try and acquire food from each other rather than each receiving their own piece of food.

Food protection interactions may be longer in the Wellington pack due to the lack of food sharing experiences. A study by Fox (1969) discussed how the act of group coordinated activities aid group coordinated hunting behaviours. As the Wellington pack does not experience group coordinated hunting, and food sharing behaviour is relatively uncommon, the amount of food available to each individual is proportional to what they receive in the initial stages of feeding time. If the loss of a food item is likely to incur greater costs to an individual, that individual is likely to increase the time invested in the defence of that item if challenged (Carpenter, 1987). As food intake in the Wellington pack is governed by the food each individual receives initially, dogs may be more possessive than at Orana, as the loss of that food item may mean the dog goes hungry until next time.

The higher frequency and shorter duration of heap interactions in the Wellington pack compared to the Orana pack may also be explained by management differences, particularly in terms of enclosure design. Enclosure design is now recognised as an important factor affecting the behaviour of captive animals. An inappropriately designed enclosure can cause animals to form abnormal repetitive behaviour patterns, such as pacing, which are brought on by psychological stress, brain dysfunction and/or frustration caused by the inability to perform species-specific behaviours (Clubb & Mason, 2003, 2007; Mason *et al.*, 2007). Stereotypic pacing was observed in both packs, but this appeared to be more pronounced in the Wellington pack (personal observation). This could have been linked to anticipatory behaviours related to feeding times, but may also be the consequence of limited space in the Wellington enclosure providing little opportunity to perform species-specific behaviours.

Studies demonstrate that species with large natural ranging tendencies appear to suffer significantly more from abnormal behaviours than species with smaller natural range sizes (Clubb & Mason, 2003, 2007). This illustrates how the inability to perform a species-specific activity, such as roaming, may affect a species' vulnerability to the formation of abnormal behaviours. While some animals under stress from captivity display significant amounts of stereotypic behaviour, others may react by reducing general activity levels (Mason, 2010). Weller & Bennett (2001) found that captive ocelots (*Leopardus pardalis*) were considerably less active than their wild counterparts, demonstrating that lethargy may arise if environments provide little stimulus or appropriate outlets for species-specific behaviour. This may help explain the more frequent but shorter duration of heap behaviour observed in the Wellington Zoo pack compared to the Orana pack, suggesting restlessness, possibly as a result of the inability to perform species-specific roaming behaviour. The area of the wild dog enclosure at Wellington Zoo was 3.5 times smaller than that at Orana, and of this, the Wellington dogs only had access to half of the total area at any given time. For a naturally wide ranging species, such as wild dogs, limited space significantly reduces the ability to perform roaming, hunting and patrolling behaviours and this may have resulted in increased levels of inactivity in the Wellington pack exemplified by an increased rate of heap behaviours.

Within wild dog packs, resting associations (as illustrated in heap interactions) are important not only as rest, but also for the maintenance of social bonds (McCreery, 2000). The Wellington pack may have modified the use of certain behaviour types as a response to a smaller exhibit that may prevent the use of more animated forms of social interaction. Although not significantly different, the more active forms of social interaction, such as play, were observed less in the Wellington pack compared with the Orana pack, which tends to support this hypothesis. Although it is impossible to determine causality, it is important to acknowledge that reductions in more active types of social interaction and increases in more passive forms of social interaction in the Wellington pack indicate that enclosure design may have significant impacts on social interactions.

The tendency of wild dogs to interact closely with kin (De Villiers *et al*., 2003), combined with high levels of pack relatedness in both packs, may have masked any effects of sex on social interaction parameters. It is, however, possible that single-sex groups have more evenly distributed social interactions compared to mixed-sex packs, especially if all individuals are in the same age-sex cohort. This appeared to affect the relative stability of packs, with the single-sex pack appearing more stable than the mixed-sex pack. Factors such as the captive environment and management regime may also have had an impact on certain social interactions. Additionally, as previously explained, both packs can be considered holding facilities. It may be appropriate to look at these results as a comparison between different methods of reproductive preventative housing. More research into the long-term social effects of separate housing based on sex will be needed to determine the suitability of housing wild dogs in single-sex groups, as these results suggest that wild dogs can be kept in relatively stable single-sex groups, without the need for contraception.

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# CHAPTER FOUR

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## HANDING OVER THE REINS: THE EFFECTS OF DEATH ON SOCIAL BEHAVIOUR IN A CAPTIVE AFRICAN WILD DOG PACK

### ABSTRACT

The death of a group member has the potential to significantly alter the social dynamics of pack animals by reducing available mates and altering dominance hierarchies. Here I examine how the death of an adult African wild dog (*Lycaon pictus*) affects the social behaviour of the remaining pack members of a captive group. While the frequency and duration of many social behaviours were not significantly affected by the conspecific's death, there was a higher incidence of dominance, greeting, and 'other' (which included both potentially affiliative and agonistic interactions) behaviour categories after the death. This, combined with the increased variation in the distribution of social interactions after the dog's death, suggests that the hierarchical structure of the pack was undergoing change. Food-based social interaction declined after the dog's death, possibly due to reduced food competition. There were interaction effects of season and zoo guest visitation on the percentage of time the dogs spent engaging in active and passive social interaction before the death but not after the death. These results suggest that the death of an adult conspecific affects social interactions used in the formation of hierarchies and can alter the distribution of social interactions between individuals.

### INTRODUCTION

Sociality has evolved as an evolutionary strategy adopted by many species as a response to various selective pressures (Macdonald, 1983). Sociality provides the opportunity for cooperative foraging, alloparental care and group defence, as well as providing an environment that facilitates social learning (Macdonald, 1983; Courchamp & Macdonald, 2001). Research into the social dynamics of groups frequently focuses on the ecological significance of social groups, in terms of how sociality may affect the ecology of wider biological systems, while failing to address the proximate mechanisms, in terms of dyadic interactions, that are vital for group existence. Free-ranging social groups are often composed of a family unit containing breeding individuals and their offspring, and possibly unrelated helpers (De Villiers *et al*., 2003; Wittemyer & Getz, 2007; Williams *et al*., 2010). This suggests that sociality is not only affected by the benefits that each animal may receive by being part of a group, but may also be linked to varying complex dyadic interactions and kinship between individuals and cohorts within social groups (Lemasson *et al*., 2006).

Highly social species often form tight bonds with individuals within their group. These bonds help to maintain sociality, often by providing a hierarchy from which social order is maintained (De Villiers *et al*., 2003; Wittemyer & Getz, 2007). Many social animals, including the African wild dog (*Lycaon pictus*), have been shown to form coalitions or affiliations with other group members (Holekamp *et al*., 1997; De Villiers *et al*., 2003; Lemasson *et al*., 2006). These coalitions are non-random, with age, sex, relatedness, and rank affecting the formation and maintenance of such relationships (Holekamp *et al*., 1997; De Villiers *et al*., 2003; Lemasson *et al*., 2006). De Villiers and colleagues (2003) demonstrated that in wild dogs these coalitions are often formed between individuals of the same age-sex cohort, illustrating how factors such as age, sex and potentially relatedness (siblings or littermates) may influence social interactions between individuals. It is therefore essential to consider the importance of proximate mechanisms in conjunction with ultimate mechanisms when discussing sociality.

Although the social mechanisms fundamental to sociality have received some attention, there are considerable gaps in our knowledge. For example, the death of an individual within a group has the potential to significantly alter social interactions and behaviour, but very few studies have explored how social behaviour is affected by the death of a pack member, with reports from charismatic species, such as primates and African elephants (*Loxodonta africana*), comprising the majority of literature available (Douglas-Hamilton *et al*., 2006; McComb *et al*., 2006; Fashing *et al*., 2011; Buhl *et al*., 2012; Stewart *et al*., 2012). The scarcity of the literature may in part be due to the inability to predict when a fatality will occur. It is also difficult to determine if the death of a conspecific causes stress in non-human animals, as observational studies have been inconclusive in this regard (Buhl *et al*., 2012).

Many of the reports describing animal responses to death discuss the mother-infant relationship, with few studies describing the death of an adult within a social group (Fashing *et al*., 2011; Cronin *et al*., 2011; Buhl *et al*., 2012). This is not surprising, as infant mortality is typically higher than adult mortality in social groups, resulting in more opportunities for this relationship to be explored. Both elephants and primates, such as chimpanzees (*Pan troglodytes*), also have strong bonds with their offspring, as the period of dependency is relatively long (Cronin *et al*., 2011). Reports also tend to focus on the reactions of group members to the body of the deceased, rather than how social interaction between the remaining members is affected (McComb *et al*., 2006; Fashing *et al*., 2011; Cronin *et al*., 2011; Buhl *et al*., 2012). Although interesting, these reports often discuss animal responses to carcasses in relation to the cognitive abilities of different species, often implying emotional states. Douglas-Hamilton and colleagues (2006) state that caring for sick or dying members of a group is a quality only observed in those species perceived to have higher cognitive abilities. Nevertheless, it may be that sociality, rather than cognitive ability, is a better predictor for ‘caring’ behaviours. African wild dogs have been recorded taking care of ailing members of the pack by tolerating them at kills and have even been recorded regurgitating food for them; however, they are not considered to have exceptional cognitive abilities (Ewer, 1973; Malcolm & Marten, 1982). The literature on animal cognition is controversial, as there is biased sampling of species deemed capable of cognitive ability, and the frequent projection of human emotional states onto study subjects has been deemed ‘unscientific’. Here my focus will be to discuss animal responses to death in terms of empirically testable parameters, specifically as changes in social interaction behaviour.

Some studies have documented animal responses to adult conspecific death with a focus on social interactions. In rhesus macaques (*Macaca mulatta*), the death of an adult not only affected the number of potential mates available but may also have affected coalitions, potentially changing the dominance hierarchy (Buhl *et al*., 2012). Brainerd and colleagues (2008) also illustrate how the loss of a breeding individual often results in the complete collapse of wolf (*Canis lupus*) packs. Here I will discuss how the death of a conspecific affects the types and the duration of social interactions, as well as how social relationships within the group might be altered in an all female pack of captive African wild dogs.

## METHODS

### *Subjects and data collection*

The subjects were four female African wild dogs (*Lycaon pictus*) at Orana Wildlife Park. Unfortunately, one of the dogs died (on the 10th of November 2012) of natural causes during the course of this study, providing the opportunity to explore how pack member loss affects social interaction within a pack. The results of a necropsy revealed that the dog had died from a respiratory infection which was possibly due to barley grass (*Hordeum vulgare*). This particular dog was high up in the hierarchy and was thought to be the alpha individual within the pack (personal comm. with zoo staff). Data collected before the dog’s death (May – November 2012) were then compared to data collected directly after her death, during the month of November 2012, and then in January 2013.

Data were collected using two camera techniques: the hand-held method, involving hand-held camera recording during peak activity times (see Chapter Two for details), and the 'fencecam' (fence camera) technique. I observed a total of 474 social interactions over 82 hours of observation before the death of the pack member and a total of 379 interactions over 40 hours of observation after her death using the hand-held method. A total of 287 h of footage was collected and scored using the fencecam method.

The fencecam technique involved filming the dogs over a 24 h period using security cameras. Two cameras, with overlapping fields of view, were used to get adequate coverage of the rear enclosure at Orana Wildlife Park. This method was originally designed to test the effects of seasonality, zoo guest visitation and time of day on both passive and active forms of social interaction across a whole year. Unfortunately, due to the unexpected death of one of the dogs, the data had to be split into two data sets, one containing data when there were four dogs in the pack and one for when there were only three dogs in the pack. This also made it impossible to accurately test the effect of season (month) on social interactions across the year; however, comparisons were made between the pack of four and the subsequent pack of three, providing a before and after death scenario.

For the fence cameras, a length of 12V DC cable was connected to an existing power source just outside of the wild dog enclosure. I ran the cable around the enclosure perimeter to the location of the two SVAT boxes (a mini portable digital video recorder inside waterproof housing). The DC cable was dug underground in areas where it may have been exposed to the public and was attached to the enclosure fence using standard cable ties. The DC cable was then connected to the SVAT boxes. A CCTV cable (used to connect the SVAT boxes to the security cameras) was cut into two lengths, one 40 m long and the other 60 m long, allowing the cameras to be mounted at different distances along the rear fence of the enclosure and permitting almost full view of the entire enclosure (Fig. 4.1). The CCTV cable was then plugged into the SVAT boxes, attached to the fence using cable ties and then connected to the cameras. A ladder was then used to position the cameras at the top of the wooden poles of the enclosure fence, which were roughly 3 m high. The cameras were secured to the poles using metal L brackets which were screwed onto the side of the camera. The SVAT boxes were set up to run continuously for a 24 h period on both Tuesdays and Saturdays for the months of May, July, and November 2012, and January 2013.

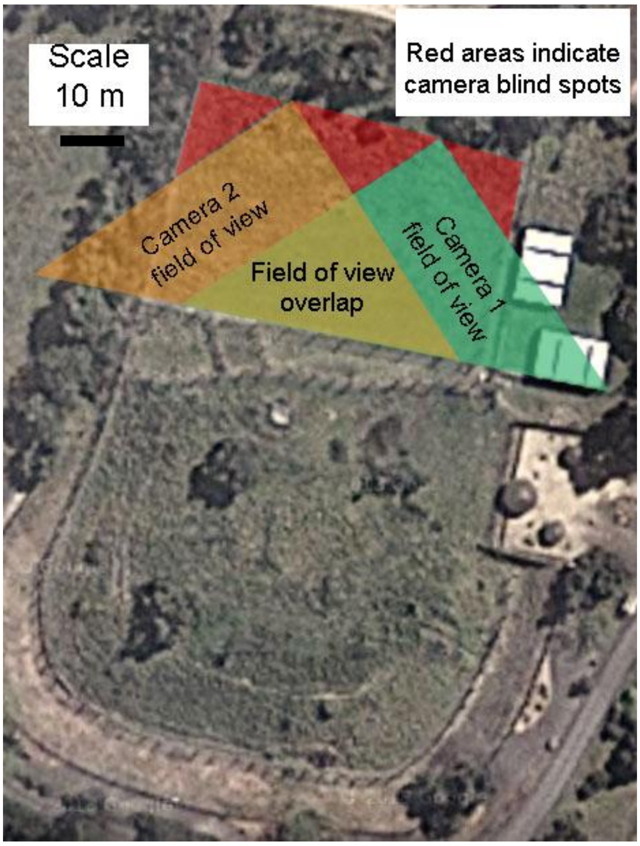

Figure 4.1. Fencecam layout. Red areas indicate camera blind spots, green indicates field of view for camera one, orange indicates field of view of camera two, yellow indicates overlapping field of view for both cameras.

*Behavioural scoring*

The data collected using the hand-held method was scored according to the procedures outlined in Chapter Two. This method was used to score behaviour in which individual identification was necessary for recording the frequencies and durations of social interactions, as well as indentifying the dyadic interactions for the social network analysis. Fence cameras did not provide the resolution required for these analyses, but did provide an overview of dog activity throughout the day.

The fence cameras (cam 1 and cam 2) were set up to record continuously and simultaneously over 24 h. Dogs were said to be 'in view' if at least one dog was visible in either camera and was inside the rear enclosure (see blind spots depicted in Fig. 4.1). The dogs were said to be 'out of sight' if there were no dogs visible in either camera. This occurred if the dogs left the rear enclosure through either the right or left enclosure doors, if the dogs entered the camera blind spots, or if they entered one of three underground dens found in the rear enclosure.

From the fencecam footage obtained, I recorded the amount of time the dogs spent in the rear enclosure and the time they spent interacting with one another whilst in this enclosure. All observations were recorded to the nearest second. As the dogs came and went from view in the rear enclosure throughout the day I calculated the total time the dogs spent in view of the cameras in the rear enclosure. This was done by recording the time a dog came into sight and subtracting that from the time all dogs went out of sight. This was repeated over the course of the day, enabling me to calculate the total amount of time the dogs were 'in view' of the rear enclosure cameras. This allowed for the total and percentage of time that the dogs spent in the rear enclosure to be calculated. In addition, I recorded the number of dogs involved in each interaction, both at the beginning of the interaction and the maximum number of dogs involved throughout, along with the interaction type. As above for time in view, the length of each interaction was recorded, allowing me to calculate the total length of time the dogs spent interacting socially. Due to low sun angles in July, 'whiteouts' occurred through direct sun glare on the camera. The length of whiteouts was also recorded and subtracted from the total time the dogs were 'out of sight'. Additionally, data on the number of visitors to the zoo on each of the recording days was obtained from Orana park records.

Social interaction using the fencecam technique was divided into 'active' and 'passive' interaction. 'Active interaction' was defined as dogs actively engaging one another in a social manner eliciting a response in the other dog. 'Passive interaction' was defined as two or more dogs lying together in close proximity (≤1.5 m). The decision to distinguish between active and passive interaction stems from the difference in activity levels between the two types of social interaction. Active interaction requires dogs to engage one another in relatively high energy level interactions, whereas passive interaction acknowledges that while the dogs appear to only be lying together they are actually passively interacting through spatial associations with one another. If a dog got up and actively interacted with another (e.g., licked another) this constituted an active interaction, but if it got up and lay back down while accidentally touching another in the process, this was considered a passive interaction.

*Statistical analysis*

Mixed effects models were used to analyse the frequencies and durations of the social interactions observed using the hand-held method (see Chapter Three for full details on statistical analyses). Due to insufficient numbers, some interaction categories had to be omitted from the statistical analyses; those omitted were beg, object and submissive interactions. The categories that were analysed were heap, rally, greet, other, food acquisition, food protection, dominance, and play (see Chapter Two for full descriptions). Mixed effects models accounted for the difference in sampling effort between the different pack structures and enabled me to distinguish the fixed effects of pack and interaction type from the random effect of sampling day. All data was log transformed. Even though mixed effects models were not a perfect fit for these data they were the best approximation, given the unbalanced nature of the data set. Degrees of freedom are not reported in the results as their calculation for mixed effects models is considered controversial and the lmer package (R) used to analyse these data does not require them to generate accurate p values (Hoshino, 2008). P values for the data concerning the duration of interactions are given as Markov Chain Monte Carlo (MCMC) p values, as they are the most appropriate choice for these particular models.

A social network analysis based on dyadic affiliative interactions (limited to heap, greet, rally, and play interactions) was conducted for both three-dog and four-dog pack structures. Here, degrees of centrality, vertex connectivity, tie strengths and reciprocity were measured (Wey *et al*., 2008). The data used for these analyses were collected from the hand-held collection method. These data were normalised by the number of observation hours for the three-dog and four-dog situation so that tie strengths could be compared between the pack before and after death.

I also wanted to determine how the interactions between dogs were affected by season, by number of zoo visitors, and by time of day. Here I considered whether the percentage of active and passive interaction types were affected by the factors mentioned above. The fencecam method was unable to observe the interactions in the same level of detail as the hand-held method so I could only distinguish whether the interactions were active or passive using the fencecam method. To answer these questions I developed a general linear model (GLM), and fitted it to two data sets, one using data obtained before, and one after, the death of the dog in the pack. However, the death of the dog made determining the effect of season on behaviour across the whole year impossible. Nevertheless, the effects of season within the two sets of data were analysed separately. Each of the factors in the two models (before and after death) had two levels. Before the dog's death the factor of month consisted of May or July, while after the death it consisted of November or January. The factors of time of day (am or pm) and zoo visitation (busy ≥ 300 guests per day or quiet < 300 guests per day) were defined the same in both before and after models.

The most appropriate model was selected based on Akaike's 'An Information Criterion' (AIC). Although the model selected did not have the lowest AIC score (128.3), the model used had the second lowest AIC score (129.4) and accounted for the factor of time of day, which relates to the specific questions I set out to answer. Diagnostic plots revealed that the residuals of the data were non-normal, so I performed a logit transformation on the proportional data (percentage of time interacting). This, however, did not significantly improve the fit of the model so I used bootstrap simulations on the logit transformed data to resample the data.

## RESULTS

The differences between the durations of all social interaction types studied were non-significant (greet: t = 0.175, pMCMC = 0.855; other: t = -1.783, pMCMC = 0.1034; food acquisition: t = 0.982, pMCMC = 0.139; food protection: t = 1.351, pMCMC = 0.1810; dominance: t = -0.470, pMCMC = 0.679; play: t = -1.435, pMCMC = 0.148), indicating that the durations of all interaction types were similar in both three-dog and four-dog scenarios.

There was no significant difference in either the frequency or duration of heap (frequency: z = 0.368, p = 0.713; duration: t = -1.503, pMCMC = 0.143) and rally (frequency: z = -0.020, p = 0.984; duration: t = 0.665, pMCMC = 0.582) interactions after the death of the pack member. However, the frequencies of the remaining behaviours were significantly different between three-dog and four-dog scenarios. The probability of greet interactions was significantly higher after the death of the individual (33%) compared to the before her death (21%) (z = 2.618, p = 0.009; Fig. 4.2, a). There was also a significant difference in the frequencies of interactions categorised as ‘other’ (defined as either chin resting or over-marking behaviours) (z = 2.851, p=0.004), whereby the probability of ‘other’ interactions was higher after the dog’s death (11%) compared to before (5%; Fig. 4.2, h). Dominance display interactions were also significantly more frequent after the death of the pack member (18%) than before (1%) (z = 6.036, p = <0.001; Fig. 4.2, g).

Food-based social interactions also differed significantly between the three-dog and four-dog scenarios, whereby the probability of both food acquisition (z = -2.680, p = 0.007) and food protection (z = -4.419, p = <0.001) interactions were higher before the dog’s death (33% and 10%, respectively) than after (20% and 2%, respectively). The probability of play interactions was also higher before the death (8%) compared to after (1%) (z = -3.735, p = <0.001).

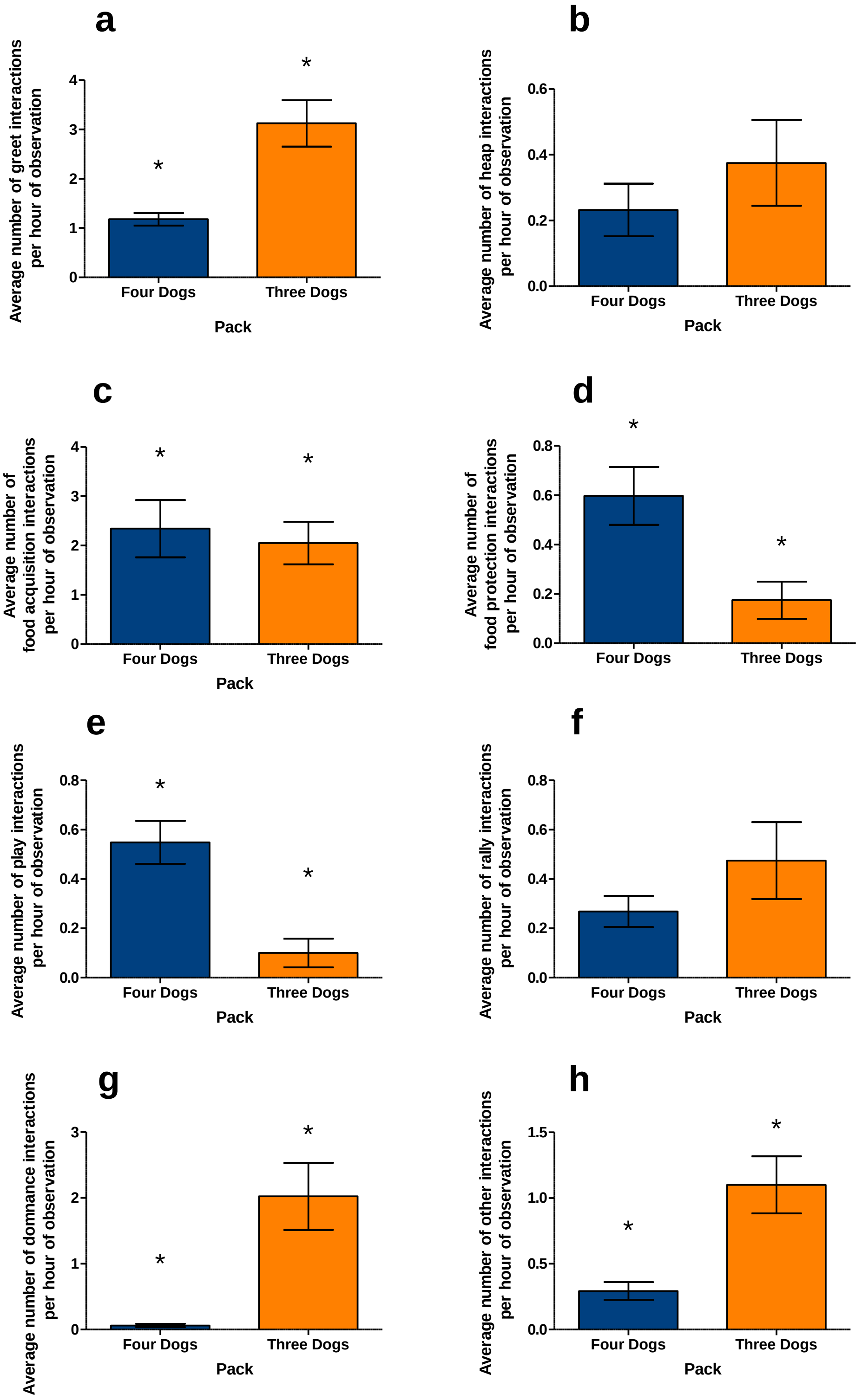

Figure 4.2. Average number (±SEM) of interactions per hour of observation for each of the social interactions analysed. a) greet interactions, b) heap interactions, c) food acquisition interactions, d) food protection interactions, e) play interactions, f) rally interactions, g) dominance interactions, h) ‘other’ interactions (chin resting and over marking). Asterisks indicate statistically significant differences ($p < 0.05$).

Table 4.1. Model coefficients for general linear model based on fencecam data collected before the death of the dog at Orana Wildlife Park.

| **Factor** | **Estimate** | **Std. Error** | **t** | **p** |
|---|---|---|---|---|
| Intercept | -6.9525 | 0.9051 | -7.681 | <0.001 |
| Month (May) | 0.8978 | 1.2730 | 0.705 | 0.2128 |
| Interaction type (Passive) | 0.6436 | 1.1749 | 0.548 | 0.5924 |
| Visitation (Quiet) | 0.3857 | 1.2964 | 0.298 | 0.5742 |
| Time of day (PM) | 0.6553 | 0.7185 | 0.912 | 0.3634 |
| Month (May): Interaction type (Passive) | 4.4965 | 1.8003 | 2.498 | 0.002 |
| Interaction type (Passive): Visitation (Quiet) | -3.4052 | 1.8334 | -1.857 | 0.002 |

Table 4.2. Model coefficients for general linear model based on fencecam data collected after the death of the dog at Orana Wildlife Park.

| **Factor** | **Estimate** | **Std. Error** | **t** | **p** |
|---|---|---|---|---|
| Intercept | -6.0638 | 0.8508 | -7.127 | <0.001 |
| Month (Nov) | -0.5317 | 1.2131 | -0.438 | 0.5898 |
| Interaction type (Passive) | 3.6591 | 1.0753 | 3.403 | 0.002 |
| Visitation (Quiet) | 0.5637 | 1.2556 | 0.449 | 0.664 |
| Time of day (PM) | -0.5151 | 0.7635 | -0.675 | 0.4312 |
| Month (Nov): Interaction type (Passive) | 3.0235 | 1.7155 | 1.762 | 0.1284 |
| Interaction type(Passive): Visitation (Quiet) | -3.8769 | 1.7757 | -2.183 | 0.0842 |

The fencecam data revealed that before the death of the pack member the main effects of month, time of day, or zoo guest visitation do not appear to have a significant effect on social interactions (active or passive). However, there were significant interaction effects between these variables. The model coefficients (Table 4.1 and Table 4.2) are displayed in terms of the difference between the two levels of each of the factors considered, whereby the intercept represents the baseline. Before the dog's death, month appeared to affect the percentage of passive (but not active) social interaction used by the dogs, with significantly more passive interactions observed in the month of May compared to July (Fig. 4.3). The percentage of active interaction was not significantly different between May and July. The number of zoo visitors also affected the percentage of passive and active interaction used by the dogs before the pack member death. Here, passive social interaction was significantly higher on busy days than on quiet days in May and July, while active social interaction was higher on quiet days than on busy days in both May and July (Fig. 4.4, a & b).

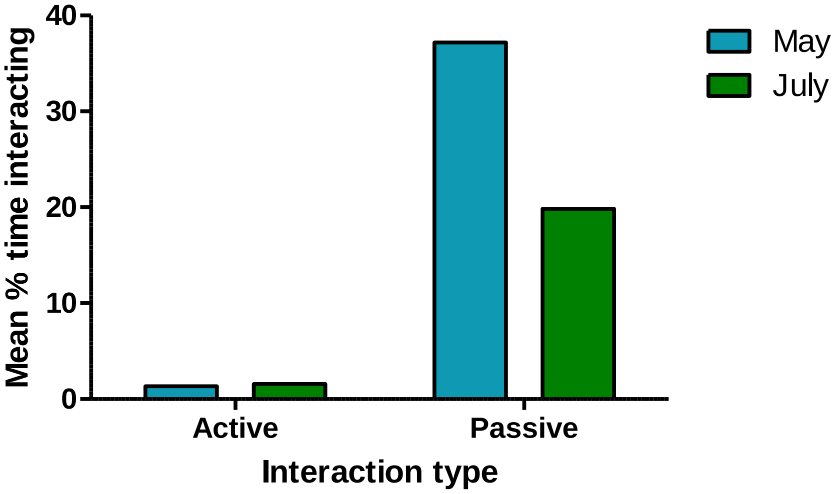

Figure 4.3. Histogram of the interaction effect of month on interaction type before the death of the pack member.

The fencecam also revealed that after the death of the individual, the main effect of passive or active interaction type was significant, with the percentage of time spent engaging in passive interaction being higher than for active interaction in both November and January (Fig. 4.5). All other main effects (time of day and zoo guest visitation) did not have a significant effect on social interactions after the dog's death.

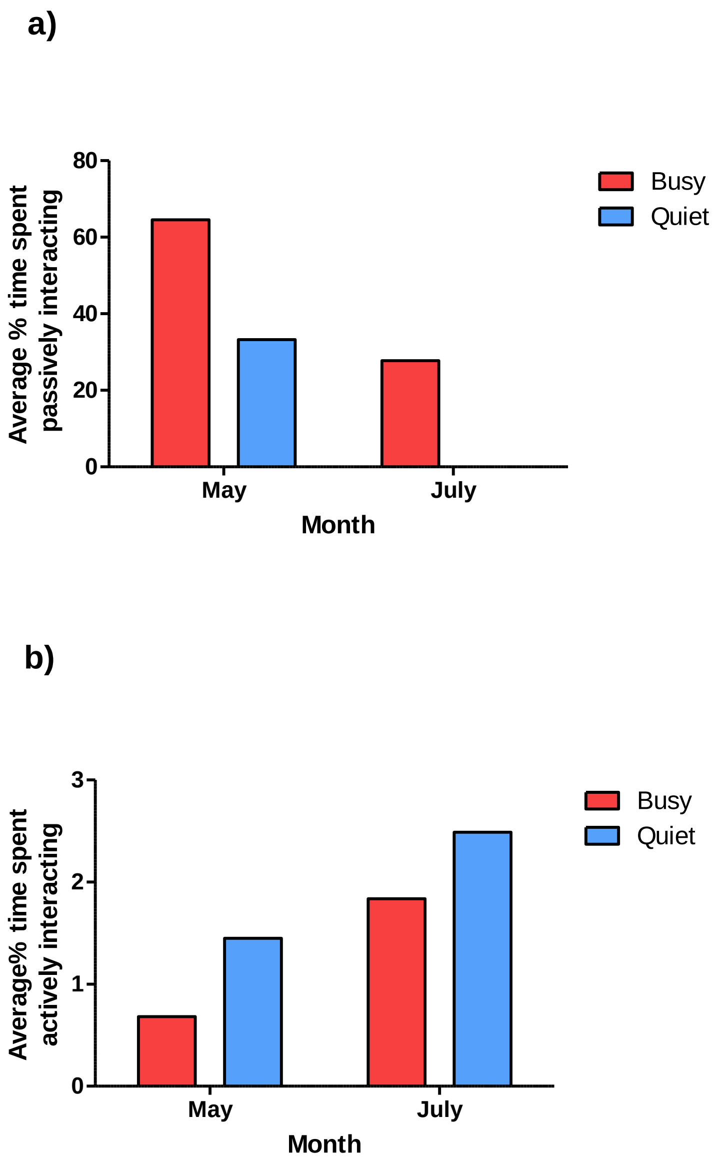

Figure 4.4. Histogram of interaction effect of zoo guest visitation on social behaviour before the death of the pack member a) Passive social behaviour. b) Active social behaviour.

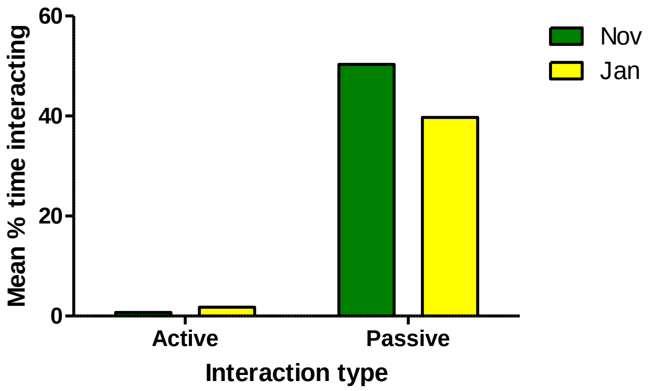

Figure 4.5. Histogram of effect of interaction type after the death of a pack member.

The degree of centrality is a common measure used to describe the relative importance of individuals within a network by calculating the number of links (or ties) an individual has with others in the network, and determines how many of those ties are directed to an individual (received), as well as how many ties are directed from that individual (initiated). Before Tisa's death (Fig. 4.6), all individuals had the same overall measure of degree (six ties per dog) and each dog received and initiated the same number of ties with all other dogs in the network (three ties per dog). Similarly, after Tisa's death (Fig. 4.7), all dogs had the same overall measure of degree (four ties per dog) and all received and initiated the same number or ties (two ties per dog) with all others in the pack. In summary, all individuals in both networks initiated and received interactions from all others in the pack.

The measure of reciprocity between dogs before as well as after the death was one, indicating that all ties between dyads were reciprocated, resulting in a bidirectional network of affiliative social interaction unaffected by the death.

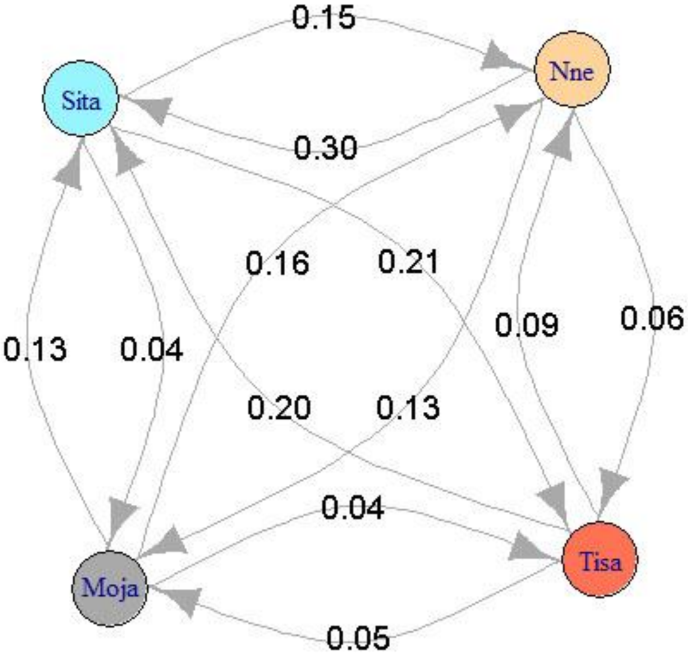

Figure 4.6. Social network of affiliative social interactions per hour of observation at Orana Wildlife Park before the death of the individual (Tisa).

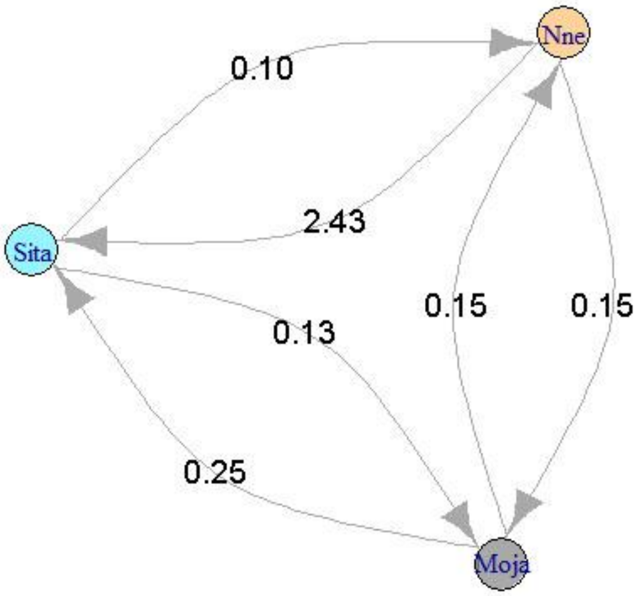

Figure 4.7. Social network of affiliative social interactions per hour of observation at Orana Wildlife Park after the death of the individual (Tisa).

Measures of vertex connectivity determine the minimum number of individuals that would need to be removed from a network to affect pack stability. Before Tisa's death network connectivity was found to be three, suggesting a highly connected network from which three individuals would need to be removed for the network to collapse. After Tisa's death, the connectivity of the network was two, suggesting that two individuals would need to be removed to collapse the network. These results imply that both networks are very stable, as stability is maintained until all but one individual is removed from each network.

Tie strengths were variable in the network prior to the death (Fig. 4.6), demonstrating the different strengths of relationships between individuals in the pack. Tisa and Sita appeared to have a strong reciprocal relationship, whereas the relationship between Sita and Nne appeared to be strong – but mainly initiated by Nne. Moja appeared to have relatively weak ties with all other dogs, suggesting that she was the lowest ranked individual within the pack. The tie strengths in the network after the loss of Tisa were also variable, perhaps more so than prior to her death. The highly skewed relationship between Sita and Nne suggests that Nne had a pivotal role within the pack and may have been initiating more afflilative interactions with Sita to further assert her position in the pack. Although not analysed statistically, all dominance interactions after Tisa's death were initiated by Nne and directed towards Sita, further supporting the notion that Nne was assuming the dominant position in the pack. The tie strengths between Sita and Moja and between Nne and Moja appeared much the same as prior to Tisa's death.

## DISCUSSION

The death of the pack member did not appear to affect the durations of any of the interaction types studied here, but did affect the frequencies of certain behaviours. Specifically, food-based social interaction and play behaviours were significantly lower after the death, while greet, 'other' (chin resting and over-marking), and dominance behaviours were significantly higher after the dog's death. In addition, while the stability of the pack was unaffected by the death, the distribution of social interactions was altered after the death. Broader analyses into other confounding effects that may influence social behaviour revealed that there were complex interaction effects of both season and zoo guest visitation rates. Interestingly, the negative effects of zoo visitation on active behaviour were only present before the death of the dog and not after, while the overall percentage of passive interaction were significantly higher than active interaction after the death of the dog, a trend that was not found before the death.

Although the stability of the pack was not affected by the death, contrary to what has been found in wolves (Brainerd *et al*., 2008), the highly skewed distribution of affiliative (and dominant) interactions from Nne to Sita, after Tisa'a death, demonstrates how the death of an individual can alter dyadic social interactions within a group. This, combined with the lack of change in the strength of social interaction with the third pack member Moja, suggests that this change in distribution is not random, but is potentially based on rank positions within the pack. As sex and age were indistinguishable between individuals, rank is the most likely determinant (De Villiers *et al*., 2003).

The increased frequency of greet and dominance behaviours also suggest that the pack was undergoing social change. Greet behaviours are often used to strengthen social bonds through appeasement signals, reducing the need for aggression or formal dominance (Rütten & Fleissner, 2004). The frequency of dominance behaviours also increased, suggesting that individuals were attempting to assert themselves over others. As shown in previous studies (De Villiers *et al*., 2003), the most dominant individual (Nne) directed all of her dominance behaviour onto the middle ranked individual (Sita), who was most likely her closest rival (Drews, 1993). The skewed distribution of affiliative behaviours and the increased frequency of greet and dominance behaviours show that the death of the pack member significantly altered the social relationships of the remaining individuals in the pack.

The increased frequency of ‘other’ (chin resting and over-marking) behaviours after Tisa’s death may also relate to the formation and strengthening of social relationships. Over-marking behaviour in many species is viewed as an inherently dominant behaviour, as scent marking is often a sign of territoriality or ‘ownership’ (Jackson *et al*., 2012). Typically only the dominant individuals will scent mark, however, if a subordinate does scent an object, a more dominant individual may come and scent over top of the original scent (Jordan *et al*., 2013). Conversely, chin resting behaviour has been described in other species of canid, such as coyotes (*Canis latrans*) (Bekoff, 1972), and is thought to act as a contactual form of social communication that strengthens social bonds without the need for aggression or dominance. This demonstrates that the increase in the behavioural category of ‘other’ may indicate an increase in over-marking behaviour, which could be viewed as a dominant form of social interaction used to assert rank position, and/or an increase is chin resting behaviour that would indicate an increase in affiliative type social interactions aimed at strengthening existing bonds. This, combined with the surge in dominance and greet behaviour, demonstrates that the death of the pack member has the potential to alter the use of social behaviour in order to reinforce rank positions between the remaining members.

Conversely, the frequency of play interactions decreased after the death of the pack member. Play is often used to decrease the social distance between individuals by strengthening social bonds (Bekoff, 2004). It has also been suggested that play does not function to include any form of agonistic or submissive behaviour, suggesting that play would most likely occur between individuals that had an established social relationship (Bekoff, 1972). As the individuals in the study pack were experiencing a period of change in terms of social relationships, it may be that play was not an appropriate form of communication after the death of the individual, while social relationships and ranks were still being contested. In addition, food-based social interactions were likely reduced after the death of the pack member, as food competition would have been reduced in the smaller pack (Courchamp & Macdonald, 2001).

While seasonality, zoo guest visitation and time of day had no significant effect on the percentage of time spent engaging in social interaction before the dog’s death, complex interaction effects of seasonality and zoo visitation were found to significantly affect the use of active and passive social interaction before the dog’s death – effects that, surprisingly, disappeared after the death. Passive social interaction appeared to decrease in July compared to May, while active interaction showed little change. One explanation is that the as the temperature cooled and the weather became less favourable throughout July, the dogs engaged in less heaping behaviour outside (in the rear enclosure). It is also possible, as this was an all female pack, that the effects of seasonality are reduced, as sexual reproduction is inhibited. Studies have shown that animals housed in single-sex groups may fail to display seasonal variation in sexual behaviour in the absence of the opposite sex (Gordon & Bernstein, 1973). In African wild dogs this phenomenon may extend further, as studies have shown differences in other forms of social behaviour that are not sexually-based (e.g., dominance behaviour) in relation to seasonal variation in the presence of the opposite sex (Creel & Creel, 2002).

Similarly, the effect of zoo guest visitation also showed a complex interaction effect on social interaction before the dog's death but not after. Passive interaction was significantly higher on busy days compared to quiet days during both months. Conversely, active interaction was significantly higher on quiet days than on busy days during both months. The notion that captive animal behaviour is negatively affected by high zoo patron numbers has been demonstrated in a variety of species, and is also supported by the findings here (Sellinger & Ha, 2005; Wells, 2005; Davey, 2007). Sampling for this part of the study was collected from the rear enclosure, which, although in view of the public, was a considerable distance from where zoo patrons were permitted. The increase in passive interaction and reduction in active interaction on busy days suggests that the dogs may have preferentially selected the rear enclosure for passive social interactions in an attempt to avoid the high number of zoo guests experienced on busy days. Additionally, the increase in active and reduction of passive social interaction on quiet days compared to busy days also suggests that social behaviour was affected by zoo guests. This suggests that high levels of zoo guest visitation do affect the social interactions used by captive wild dogs. High numbers of visitors encourage dogs to retreat to areas of the enclosure where they may avoid human contact, and engage in social interactions that do not draw attention to themselves, such as heaping, as sleeping dogs are very difficult to see (Sellinger & Ha, 2005). The interaction effects described above were only present before the death and not afterwards, indicating that the packs' response to visitation rates varied before and after the death. This may indicate that the dogs were preoccupied with re-establishing a dominance hierarchy and thus the effects of zoo guest visitation and seasonality appeared to be less important in the months following the death.

The overall percentage of time spent engaging in passive interaction was significantly higher than active interaction for both November and January after the dog's death, a trend not seen before the death. This is possibly the result of uncharacteristically hot weather (+30°C), which may have resulted in inactivity in dogs that are more accustomed to cooler weather (Ismail *et al.*, 2011).

Replication of an event such as the natural death of a pack member is almost impossible. Consequently, these results are based on the observation of a single highly related pack of captive wild dogs with an unusual sex composition, and as such, conclusions drawn from this research should be viewed with some caution. Despite these limitations, these observations imply that the death of an adult African wild dog pack member does affect the social behaviour of the remaining members. These results suggest that behaviours relating to the formation and reinforcement of social bonds and rank are more likely to be affected than behaviours that strengthen existing social bonds, and, perhaps unsurprisingly, that dominant behaviours may increase as social rank positions change. The stability of the pack was relatively unchanged, most likely the result of the highly stable social network before Tisa's death. This information may help captive wild dog management in terms of identifying how social relationships and behaviours may change after pack member death.

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## CHAPTER FIVE

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# KEEPING THE PEACE: THE EFFECTS OF ENRICHMENT ON SOCIAL BEHAVIOUR IN THE CAPTIVE AFRICAN WILD DOG

## ABSTRACT

The implementation of different enrichments in the enclosures of captively housed animals, to prevent or reduce the formation of abnormal behaviour patterns and increase species-specific behaviours, has been studied in a wide variety of species. Few studies, however, have been aimed at how added enrichment affects the social relationships and interactions of social animals housed in groups. Here I discuss how three simultaneously added forms of enrichment affect the social behaviour of a small, single-sex pack of African wild dogs (*Lycaon pictus*) four months after the death of a conspecific. I found that many of the interaction types studied were unaffected by the addition of enrichment; however, added enrichment did reduce the frequency of greeting interactions and the frequency and duration of dominance related behaviours in the group. This demonstrates that enrichment could be used to mediate social interactions, especially in groups where social tension is abnormally high and, if used correctly, could potentially reduce aggression in captive social groups.

## INTRODUCTION

Although for many species captivity has benefits, including reliable sources of food and water, veterinary care and the loss of interspecific competitors and predators, captivity may also place significant restrictions on species in terms of space, group composition affecting social interaction, diet influencing foraging experiences, as well as the inability to disperse naturally (Clubb & Mason, 2007; Morgan & Tromborg, 2007). While some species appear to thrive in captivity, others show extreme physiological and psychological responses to the stressors of the captive environment. Species may manifest stress differently, with some species having reduced fecundity in captivity compared to their counterparts in the wild, others appearing uncharacteristically inactive (lethargic), and yet others engaging in repetitive abnormal behaviours, known as stereotypies (Mason, 2010). Abnormal stereotypic behaviours develop in a variety of species and are thought to be coping mechanisms used by animals when unable to engage in species-appropriate behaviours (Cooper & Albentosa, 2005; Mason *et al*., 2007). Stereotypies have a variety of different symptoms; however, some common forms are pacing in carnivores, self-harm in primates, and swaying or weaving in some herbivores, such as horses or elephants (McAfee *et al*., 2002; Rees, 2004; Honess & Marin, 2006; Szokalski *et al*., 2012; Quirke *et al*., 2012).

The variation among different species in susceptibility to stress in captivity has received considerable recent attention as animal welfare becomes an important area of ethical captive animal management protocols. It is now thought that species suitability to captivity is closely linked to the life history characteristics of that species. Typically, those that are highly adaptable and cope well with disturbance are better suited to living in captive environments, whereas species that are highly specialised in an ecological sense, or those that have life history requirements that are unable to be met in captivity, often struggle in such an environment (Sol *et al*., 2008; Mason, 2010).

Despite these apparent predispositions to failure or success in captivity, animals that are ill-suited to captivity are still housed in many collections worldwide. Reasons for this include captive breeding programs, to act as advocates for their species, or to raise awareness for ecological/bio diversity. One strategy to prevent or lessen the effects and manifestations of stress behaviour in captive animals is to provide animals with enrichment. Enrichment is now widely applied to a diverse range of species (Mason *et al*., 2007) and aims to provide captive animals with opportunities to perform species-specific natural behaviours, thereby preventing the formation of abnormal behaviour patterns. Enrichment typically centres on foraging behaviours; however, sensory and social enrichment, training, enclosure design, and environmental enrichment are also used to minimise the occurrence of abnormal behaviours (Bashaw *et al*., 2003; Honess & Marin, 2006; Birkett & Newton-Fisher, 2011; Baumans &Van Loo, 2013).

Although carnivores are common in captivity, there is significant species variation in their success in captive environments (Clubb & Mason, 2007). The inability to forage naturally is thought to increase the incidence of abnormal behaviours and indicators of physiological stress and, by providing foraging enrichment, abnormal behaviours should be reduced (McPhee, 2002; Bashaw *et al*., 2003). Although this may be an important factor which determines a species' predisposition to the formation of abnormal behaviours and stress in captivity, many studies have found that foraging enrichment only partially reduces the level of stereotyped behaviours or displays of stress (e.g., McPhee, 2002; Price, 2010). This indicates that the inability to forage naturally is only part of the underlying problem. Other studies suggest that species variation in response to captivity may be related to the size of an animal's natural range size, rather than simply the way it hunts. Regardless of the cause, carnivores show a significant vulnerability to the adverse effects of captivity, an issue which is now being further explored. Many studies have shown that enrichment can play an important part in reducing stress and the occurrence of abnormal behaviours (Beattie *et al*., 1996; McPhee, 2002; Bashaw *et al*. 2003), yet the way this works is poorly understood.

Here my focus is on the effect of enrichment on social behaviour within captive animal groups. The presence of abnormal behaviour patterns in captive animals may reduce social interaction in affected animals and impair the social interactions that do occur (Bubier, 1996; Clubb & Mason, 2003). Furthermore, if enrichment is inadequately or inappropriately distributed aggression may increase, subsequently increasing stress in captive animals (Beattie *et al*., 1996; Honess & Marin, 2006; Sha *et al*., 2012).

For highly social species, such as primates and some carnivores, inadequate enrichment has the potential to significantly alter social interactions in captivity. For such species, social activity takes up a considerable proportion of time and is essential for group cohesion (Courchamp & Macdonald, 2001). If unable to interact in a suitable manner, aggression is likely to follow, creating difficulties for those in charge of managing these captive populations (Sha *et al*., 2012). Inappropriate or inadequate enrichment could potentially result in a negative additive effect in social species, whereby a lack of enrichment increases the occurrence of abnormal behaviour, reducing the amount of species-specific social interaction or increasing levels of aggression within groups. Enrichment may then encourage more positive social interactions by reducing the intensity of agonistic social interactions, offering animals alternative outlets for species-specific behaviours, rather than them focussing solely on social behaviours (Sha *et al*., 2012). It is clear that understanding the links between enrichment and social behaviour is fundamental for the management of social species.

Here I compare social interaction within a single-sex pack of African wild dogs, *Lycaon pictus*, before and after the addition of three forms of enrichment to the enclosure. All three forms of enrichment were added simultaneously and involved food, but since they were not applied instead of the main feeding regime in place, these were viewed more as environmental enrichment. The types, number and average length of social interactions were compared to determine if enrichment had any effect on social interaction within the group.

METHODS

*Subjects and study site*

This study was conducted at Orana Wildlife Park (43°28’0.17”S, 172°27’46.98”E). The subjects were three female African wild dogs (*Lycaon pictus*). Enrichment was placed in the rear (off exhibit) enclosure of the wild dog exhibit to maximise visibility and also allow ease of access during instalment and use (Fig. 5.1).

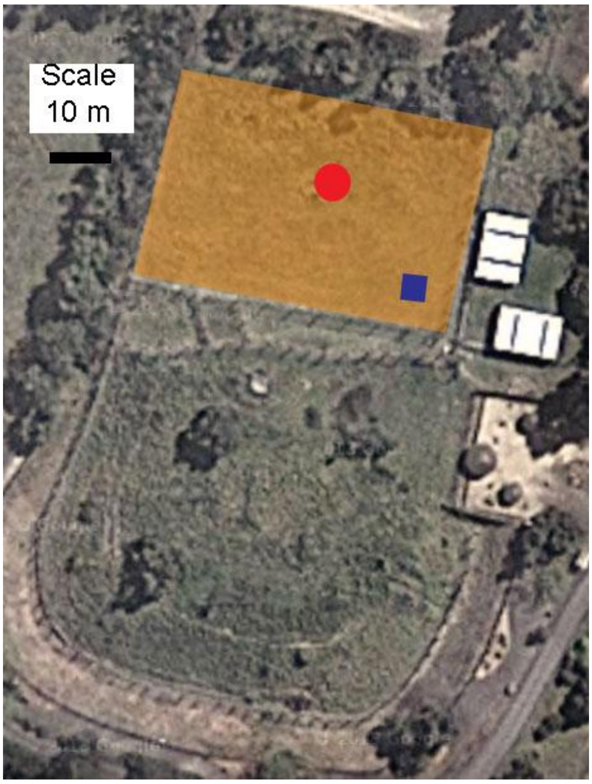


Figure 5.1. Placement of enrichment at Orana Wildlife Park. Orange indicates the area in the rear enclosure where scent trails could be placed, blue square indicates position of sand-pit, red circle indicates placement of buoy.

*Data collection*

Data were collected over six days in two weeks in March 2013 (four months after the death of the pack mate discussed in Chapter Four), between 15:00 h and 17:00 h. Enrichment was set up at 14:00 h, when keepers moved the dogs into the front enclosure of the exhibit, allowing me to access the rear enclosure to set up the enrichment. At 15:00 h the wild dogs were given access to all areas of their exhibit, including the rear enclosure, and filming would commence. These data were compared to data collected prior to the addition of enrichment (November 2012- January 2013), but after the death of the dog described in Chapter Four. All other methods are the same as described in Chapter Three for the hand-held camera data collection method.

*Enrichments*

Three forms of enrichment that differed in spatial scale were simultaneously used to compare social interaction between animals in an 'enriched' and 'non-enriched' environment. The first type of enrichment was a scent trail with a small food/scent reward at the end. Scent trails were made by dragging small pieces of meat (calf meat (*Bos primigenius*)) or ungulate faeces (Giraffe, *Giraffa camelopardalis rothschildi*) over the grass of the enclosure and then placing either food or faeces at the end of the trail. The reward for following the trails was either meat or faeces, which the dog would either sniff or roll in. Between three and five of these trails were laid each enrichment day. Food trails, faeces trails, or both may have been laid on the same day.

The second type of enrichment used was a moulded polyethylene mooring buoy (300 mm diameter) (Fig. 5.2, bottom). A hole of 114 mm diameter was drilled into the buoy using a large electric hole drill. The foam within the buoy was removed for the safety of the dogs and to enable it to be filled with food (two-four pieces of calf meat) which would serve as a challenging foraging experience for the dogs. The foam was removed using a crowbar, and the buoy was then washed out to remove any remaining foam. A rope was tied around one of the plastic loops on the buoy and then tied to an existing fallen tree branch in the wild dog enclosure. Once tests ended the buoy was removed.

The third type of enrichment was a 2x2 $m^2$ sand-pit frame, without a base, constructed from untreated timber (Fig. 5.2, top). The frame was filled to a depth of ~5 cm deep with course sand/fine gravel into which calf meat pieces and giraffe faeces were buried and covered. Approximately four items were buried in the sand-pit each day of enrichment. Each day the surface of the sand was raked over, by hand. As the sand-pit was large, it was unfeasible to move it, so this was left in place (without food or faeces) during non-testing days.

*Statistical analysis*

Although all the hand-held data for all packs studied in this thesis were analysed together, here I am only concerned with comparisons made between the small Orana pack (three dogs) before and after the addition of enrichment. Due to the lack of observations of some social interactions not all interaction categories could be analysed in relation to enrichment.

Data concerning the frequency and duration of interactions before and after the addition of enrichment were analysed using mixed effects models which accounted for the unbalanced experimental design (See Chapter Three for full details). Pack and interaction type were analysed as fixed effects while the effect of day of sampling was a random effect in the models. All data was log transformed to correct issues with normality. Mixed effects models allow p values using Markov Chain Monte Carlo (MCMC) methods to be calculated without the need to calculate degrees of freedom (Hoshino, 2008), and thus degrees of freedom are not reported. Comparisons were made between the behavioural categories of food acquisition, heap, play, rally, greet, 'other' and dominance (for full descriptions see Chapter Two).

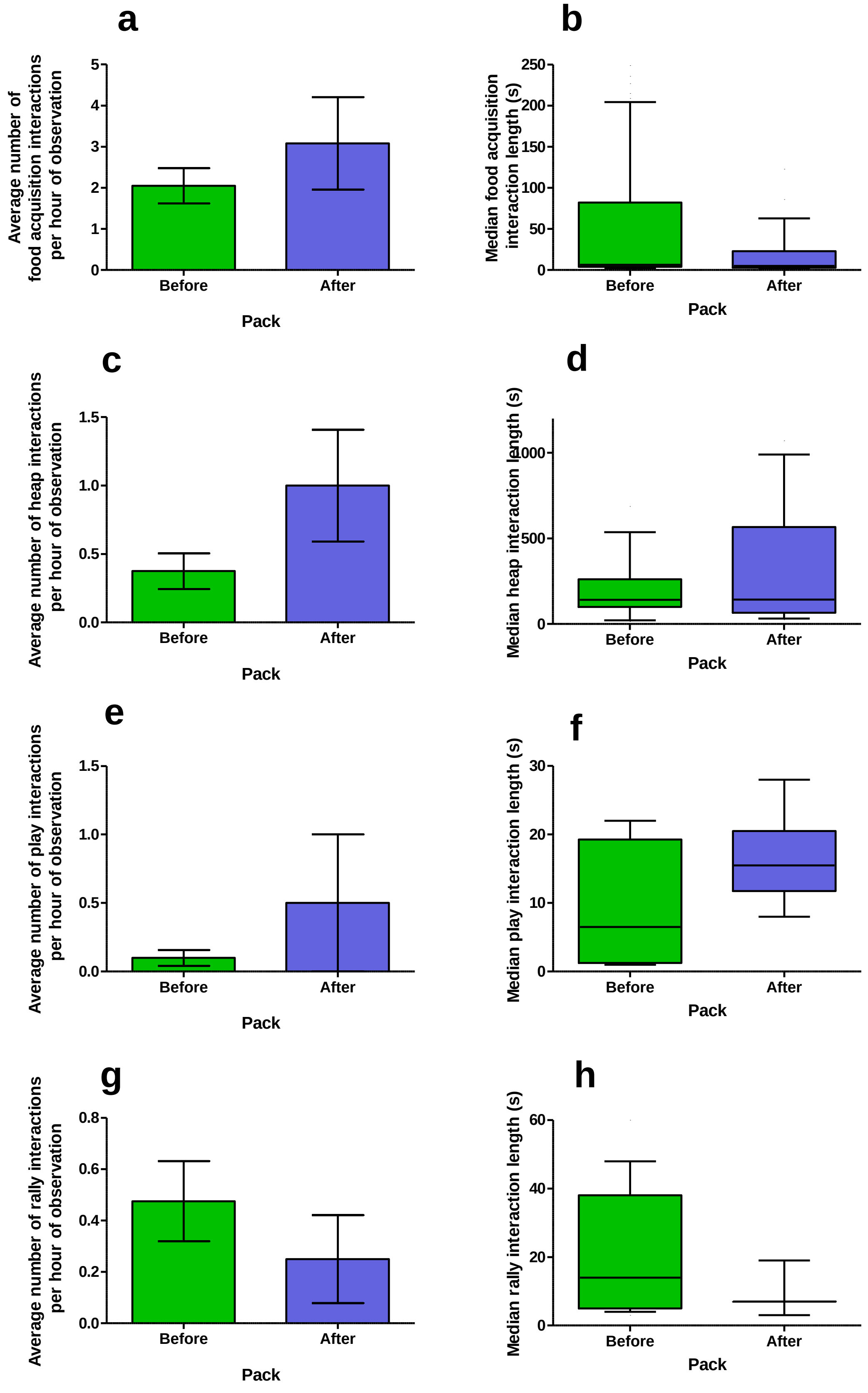
Social network analyses were conducted using information gained on the affiliative dyadic interactions between individuals in each pack. These were normalised for each pack by taking into account the number of hours each pack was sampled for. Affiliative interactions included heap, greet, rally, and play interactions. Information on social network structure, including measures of degree, vertex connectivity, reciprocity of ties and tie strength was acquired using basic social network analysis metrics (Wey *et al*., 2008).

Figure 5.2. Top, sand-pit enrichment. Bottom, Buoy tied to a fallen tree branch in situ.

## RESULTS

A total of 379 interactions were observed over 40 hours of observation before the addition of enrichment and these were compared with a total of 104 observed interactions over 12 hours of observation after enrichment was added to the enclosure. In the 20 days prior to enrichment no object interaction was seen, yet in the six days of observation with enrichment 22 (mean of 3.7 per day) instances of object interaction were seen.

There was no significant difference in the frequency or duration of food acquisition (frequency: $z = 1.813$, $p = 0.07$; duration: $t = -1.012$, pMCMC = 0.25), heap (frequency: $z = 1.879$, $p = 0.06$; duration: $t = 0.518$, pMCMC = 0.61), play (frequency: $z = 1.449$, $p = 0.15$; duration: $t = 1.841$, pMCMC = 0.07), other (frequency: $z = -1.947$, $p = 0.05$; duration: $t = 0.959$, pMCMC = 0.34) or rally (frequency: $z = -0.657$, $p = 0.51$; duration: $t = -1.216$, pMCMC = 0.25) interactions before and after the addition of enrichment (Fig. 5.3). However, there was a significantly higher probability of greet interactions ($z = -3.384$, $p = <0.001$) within the pack before the addition of enrichment (33%) than after enrichment had been added (10%), but the duration of such interactions did not differ ($t = 0.058$, pMCMC = 0.95) (Fig. 5.3, i, j). There was also a significantly higher probability of dominance interactions before enrichment was added (18%) compared to after (6%) ($z = -2.387$, $p = 0.02$), and, the duration of these interactions was significantly longer before the addition of enrichment (mean = 6.0 s) compared to after (mean = 2.7 s) ($t = -2.197$, pMCMC = 0.03) (Fig. 5.3, m, n). Nevertheless, as the results for dominance interactions were only marginally significant they should be viewed with caution, as these data were analysed using multiple tests.


a
Average number of food acquisition interactions per hour of observation
0
1
2
3
4
5
Before
After
Pack
b
Median food acquisition interaction length (s)
0
50
100
150
200
250
Before
After
Pack
c
Average number of heap interactions per hour of observation
0.0
0.5
1.0
1.5
Before
After
Pack
d
Median heap interaction length (s)
0
500
1000
Before
After
Pack
e
Average number of play interactions per hour of observation
0.0
0.5
1.0
1.5
Before
After
Pack
f
Median play interaction length (s)
0
10
20
30
Before
After
Pack
g
Average number of rally interactions per hour of observation
0.0
0.2
0.4
0.6
0.8
Before
After
Pack
h
Median rally interaction length (s)
0
20
40
60
Before
After
Pack

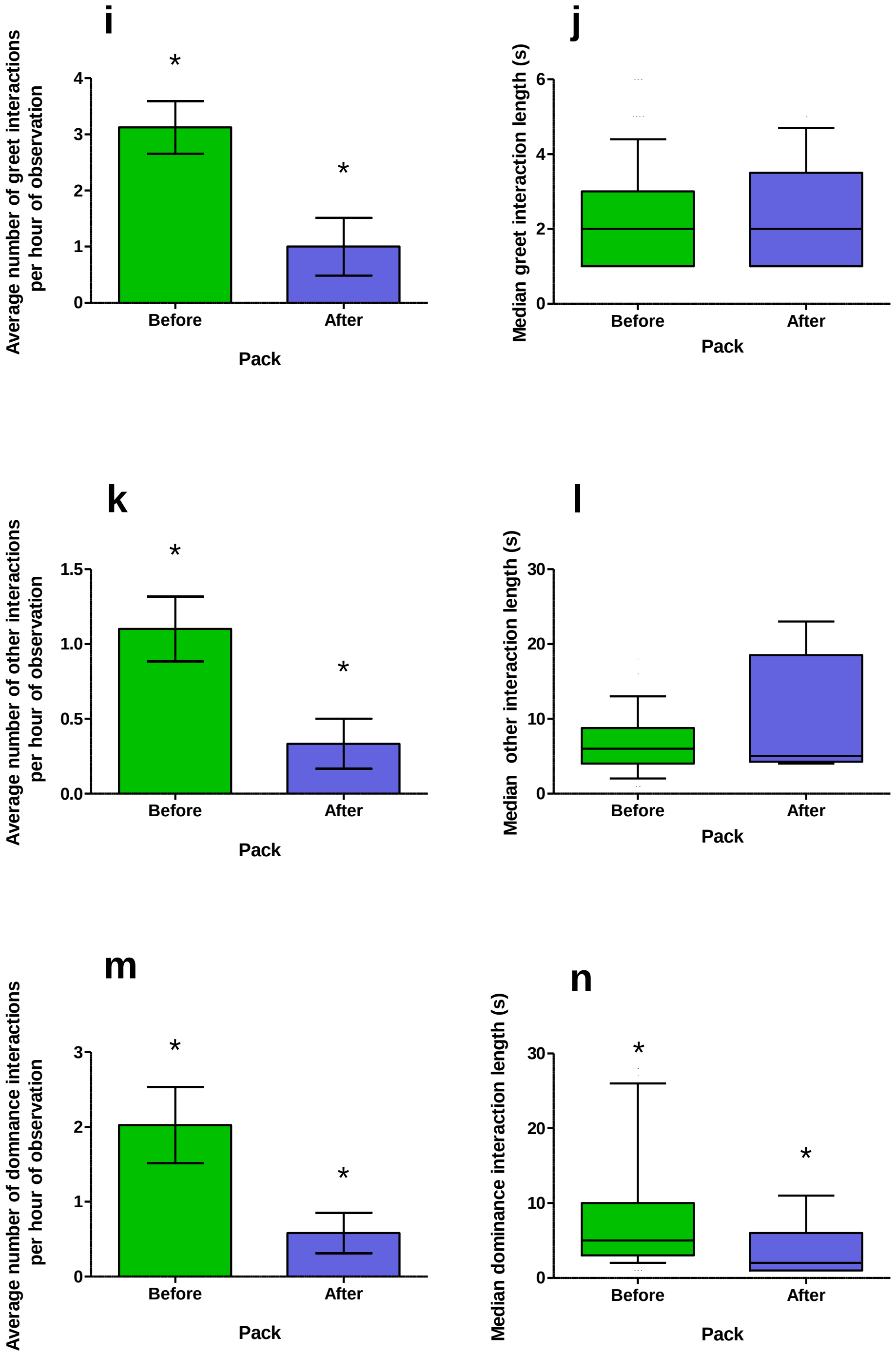


Figure 5.3. Median length (whiskers: 10 and 90 percentiles) of social interaction (boxplots, right) and average number (±SEM) of social interactions/ h observation (histograms, left) for each behaviour at Orana Wildlife Park before and after the addition of enrichment. a) number of food acquisitions, b) food acquisition length, c) number of heaps, d) heap length, e) number of plays, f) play length, g) number of rallies, h) rally length, i) number of greets, j) greet length, k) number of other interactions, l) other interaction length, m) number of dominance interactions, n) dominance interaction length. Asterisk denotes significant difference ($P < 0.05$).

The degree of centrality is a measure of network stability commonly used to determine how individuals within a network are linked. Degree simply measures the number of connections one individual has to other individuals in the network. Here, the number of outgoing ties (out-degree) can be thought of as the number of ties (or relationships) where the individual of interest initiates the relationship with others, while the number of incoming ties (in-degree) can be thought of as the number of ties an individual receives from others in the network. Prior to enrichment, it is apparent that all dogs have the same number of incoming (two ties per dog) and outgoing ties (two ties per dog), giving all dogs an overall measure of degree of four ties per dog (Fig. 5.4). This illustrates that all dogs initiate and receive ties with one another, a characteristic of stable networks. After the addition of enrichment, the degree of centrality for each individual changed (Fig. 5.5). Nne maintained the same overall number of ties (four) with two incoming and two outgoing ties connecting her to both other individuals in the network. The overall measure of degree centrality for Sita and Moja, however, was reduced by one, whereby they both had a total of three ties connecting them to other individuals. Sita received affiliative interactions from both of the other dogs in the pack but she only initiated interactions with Nne. In contrast, Moja initiated interactions with both of the other dogs in the pack but only received interactions from Nne.

The measure of reciprocity prior to enrichment was one, indicating that the all dogs have bidirectional ties with one another. In contrast, the measure of reciprocity in the pack after the addition of enrichment was 0.8, which suggests that only 80% of the ties within this pack were bidirectional.

The measure of vertex connectivity indicates how many individuals would need to be removed from the network to affect stability. In the network prior to enrichment, vertex connectivity was measured as two, indicating that two individuals would need to be removed from the network in order for the network to collapse, suggestive of a relatively stable pack. In contrast, the connectivity of the pack after enrichment was added indicated that only one individual would need to be removed from the pack in order for the pack social structure to collapse. Taking into account all other network measures, it appears that the loss of Nne would result in the collapse of this pack, as Sita and Moja did not share reciprocated ties.

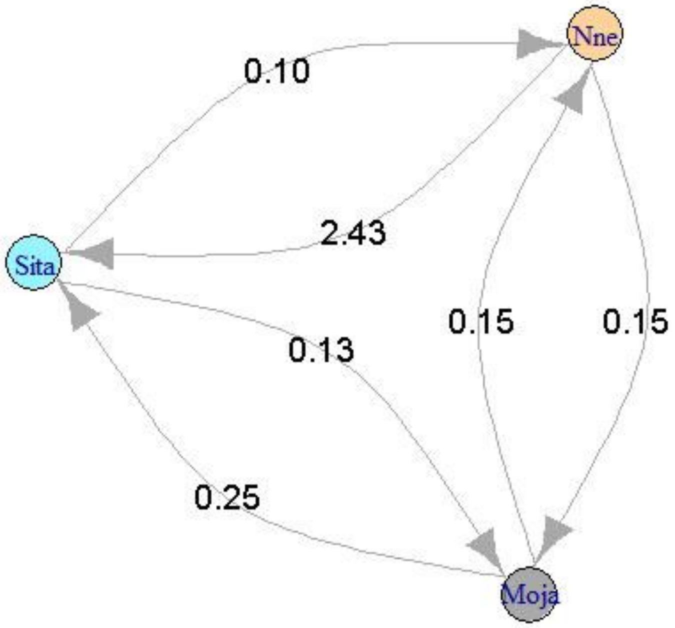


Figure 5.4. Social network of affliliative interactions per hour of observation before the addition of enrichment.

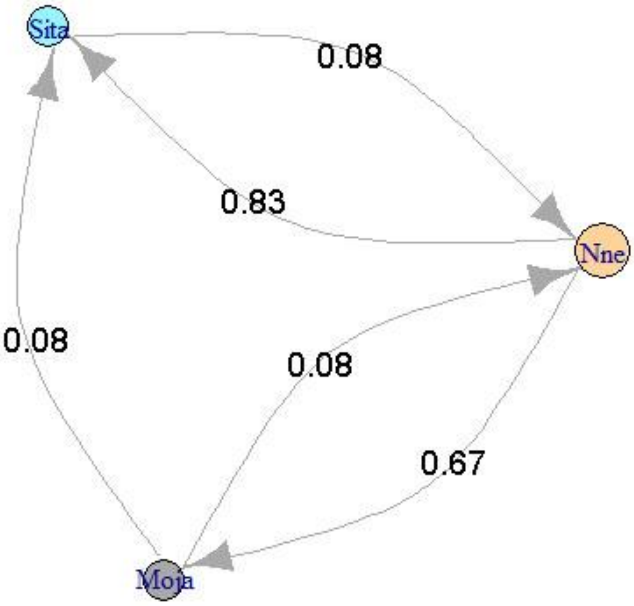


Figure 5.5. Social network of affiliative interactions per hour of observation after the addition of enrichment.

Tie strength measures the number of interactions between individuals, thus describing how individuals interact within the network. Prior to enrichment, the tie from Nne to Sita was extremely strong compared to all other ties in the network, and indicated that a significant portion of affiliative interactions were initiated by Nne (Fig. 5.4). The strength of the tie from Sita to Nne was comparatively weak, possibly indicating that Nne was in a higher position within the group and may have been using affiliative interactions to assert her position over Sita. The strengths of the other ties between the different dyads were similar and reciprocated. After the addition of enrichment, the strength of affiliative interactions between Nne and Sita appear to decrease, whilst the strength of the tie from Nne to Moja increased slightly (Fig. 5.5). The ties from Nne to both other dogs appeared to be more similar in strength, suggesting that the distribution of affiliative interactions, particularly initiated by Nne, are more even after enrichment was added. All other ties within this network appeared to be relatively weak.

## DISCUSSION

These results provide insight into the potential importance of enrichment on social behaviour in captive wild dogs. Notably, the duration and frequency of dominance and the frequency of greeting behaviour was reduced after the addition of enrichment. It is important to note that prior to this study beginning, a pack member had died, but after this death I noticed that the frequency of greet and dominance interactions significantly increased, indicating a change in the social dynamics of the group (see Chapter Four). Consequently, it is possible that the addition of enrichment helped to reduced the frequency of these behaviours to pre-pack member loss levels; perhaps because the added enrichment served as a distraction, whereby the dogs engaged in enrichment-based behaviours rather than focussing on social interactions with one another (Chang *et al*., 1999; Price, 2010). This is likely given the large number of object-based interactions after the enrichment was added. This is not surprising, as the dogs responded well to the novel stimuli provided by the scent trails, sand-pit and buoy, interacting with them readily and enthusiastically. The dogs were also observed engaging in non-social interaction with the enrichment, potentially reducing the time available for social interaction and thus possibly explaining why the frequency and duration of some social interaction categories were lower after the addition of enrichment (Bubier, 1996; Chang *et al*., 1999).

The question then becomes why were only greet and dominance interaction frequencies significantly reduced rather than all social interaction types? The answer to this may lie in the function of these behaviours. As discussed in Chapter Four, it is possible that greet and dominance interactions are used to determine rank positions within the pack, and would therefore be used more frequently when the structure of the pack is undergoing change (Rütten & Fleissner, 2004). In conjunction with altering the activity allocation of the captive wild dogs, the added enrichment may have also reduced some of the social stress created by the changing pack structure (Honess & Marin, 2006). This may have reduced the need for dogs to assert themselves over one another by providing the dogs with other opportunities to engage in species-specific behaviours (Márquez-Arias *et al*., 2010).

The simultaneous use of three different types of enrichment may have reduced conflicts within the group (Honess & Marin, 2006; Sha *et al*., 2012). Scent trails allowed the more subordinate individuals, Moja and Sita, to access enrichment that was spread throughout the enclosure, without the need for them to come into contact with the more dominant individual in the pack. The sand-pit also offered a moderate contact enrichment environment, whereby food was accessible at a medium spatial scale. Finally, the buoy was a high contact enrichment environment whereby the dogs, usually Nne and Sita, worked together in an attempt to obtain the food. The multiple enrichments allowed the dogs to avoid one another spatially, thus reducing competition and potential aggression that may have arisen if only one type of enrichment had been provided (Honess & Marin, 2006; Sha *et al*., 2012).

The social network analysis of the pack after the addition of enrichment supports the reduced social tension hypothesis. It is clear that the strength of the social ties after the enrichment was added are more evenly distributed within the pack, especially when comparing the tie strength from Nne to Sita before the addition of enrichment. Prior to enrichment, Nne was initiating the majority of affiliative interactions within the pack, but she initiated similar numbers with both Sita and Moja after the enrichment was added. This demonstrates that if affiliative interactions were being used to reinforce dominance relationships, they subsided after the addition of enrichment. Nevertheless, it appears that enrichment also destabilised the pack. However, the short timeframe for observation of dog behaviour in the enriched enclosure may not accurately represent the social network after the enrichment was added.

Although not a focus of this study, the addition of multiple forms of enrichment has been shown to reduce abnormal repetitive behaviours in a variety of captive species (McPhee, 2002; Bashaw *et al*., 2003). Whilst only anecdotal, it was noted that the dogs, which previously engaged in stereotypic pacing behaviours prior to feeding times, reduced the amount of pacing behaviour and appeared more relaxed after the addition of enrichment.

There were several limitations with this study, including the limited timeframe preventing replication and, importantly, the fact that this study was conducted on a single, same-sex pack. Nevertheless, these results do suggest that the addition of environmental enrichment helped to reduce social tension within the pack after the death of a conspecific. Added environmental enrichment may have reduced the elevated levels of dominance interactions and directed the attention of the dogs to more appropriate outlets for species-specific behaviour. Consequently, enrichment may aid wild dog captive management in situations where packs are undergoing hierarchical changes. These results suggest interesting avenues for captive management of wild dogs, in particular when faced with a social challenge such as the loss of a pack member, and clearly indicate the need for further research in this area.

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# CHAPTER SIX

# DISCUSSION

The use of display-based communication in social interactions by African wild dogs (*Lycaon pictus*), whose survival largely depends on strong social bonds and group cohesion (McCreery, 2000; Creel & Creel, 2002), has received comparatively little attention to that of other communicative modalities used by this species (Robbins, 2000; Parker, 2010; Jackson *et al*., 2012). The obligate nature of their sociality, combined with the high cost and probability of predation and competitive exclusion, suggest that displays, typically being short-range visual and tactile forms of communication, should be important (Creel & Creel, 1996; Webster *et al*., 2010, 2012). As the associated risks of eavesdropping tend to be larger for olfactory or vocal communication, display communication may offer a ‘safer’ alternative form of communication (McGregor & Peake, 2000). The captive packs used in this study offered the opportunity to explore social display-based interactions in African wild dogs to a degree that would be difficult to achieve in the wild.

Animals in captivity sometimes display signs of compromised psychological health, impaired brain development and function, and species housed in groups can also display increased aggression (Honess & Marin, 2006; Mason, 2010). Although the susceptibility to these issues and to the formation of repetitive abnormal behaviours is often species-specific, some key factors, such as high natural ranging behaviour of a species (how widely it uses its habitat), have been identified as predictors of susceptibility to abnormal behaviour, particularly in carnivores (Clubb & Mason, 2003, 2007; Morgan & Tromborg, 2007). Based on this reasoning, *L. pictus* qualifies as a susceptible species. Coupled with its endangered status (Gusset *et al*., 2006), research is crucial to determine whether captivity affects the social behaviour of this species.

The effects of captivity on social behaviour were explored through identification of the behavioural repertoire of captive wild dogs. Comparisons were made between my observations on captive animals and the available literature from free-ranging populations to determine if captivity affected the presence of different social behaviours. Along with comparisons between different captive pack sex compositions I explore how the social behaviour of a single-sex group varied from a mixed-sex group. Additionally, comparisons before and after the loss of a pack member were used to determine if death affects social behaviour, and finally comparisons between an enriched and a non-enriched environment were used to determine if enrichment affects social interaction in captive wild dogs.

Based on the limited literature available for free-ranging populations, many aspects of display communication among the captive wild dogs studied here were present as they are in the wild; however, sexual behaviour was not observed in these captive groups. This was likely a consequence of the fact that both the Orana pack, consisting of solely female members, and the Wellington pack, consisting of siblings on contraception, were prevented from breeding. Despite this, some play-based mounting behaviour, which was not of a sexual nature, was observed in the Orana pack.

While captivity has the potential to alter the social dynamics of group living by altering many aspects of group structure, such as group size, relatedness and sex composition (Glatston, 1997; Fraust & Thompson, 2000), it appears that these factors do little to affect the presence of species-specific social behaviours in captive wild dogs. Resting associations, also present in free-ranging populations, appeared to be strongly represented in the observed social interactions of the Orana pack, suggesting their importance in maintaining social bonds within both captive and free-ranging packs (McCreery, 2000; De Villiers *et al*., 2003). Similarly, heap interactions were strongly favoured in the mixed-sex Wellington pack, suggesting that although a small enclosure size may have increased their prevalence in this pack, due to the inability to perform other, more active forms of social interaction (Clubb & Mason, 2003, 2007), they are still a very important form of social interaction, regardless of pack sex composition.

Food acquisition behaviours, often observed in free-ranging wild dog packs at the site of a kill (Kühme, 1965), were also strongly represented in the Orana pack, where food was presented in a way that closely replicated the carcass experience of free-ranging wild dogs. This indicates a high level of food-based social interaction within the Orana pack, as might be expected in the wild. Interestingly, this type of behaviour was not as prominent in the mixed-sex pack, where food was individually rationed to each dog, or in the Orana pack after the death of the dog, suggesting a decrease in food competition after the loss of the pack member. Additionally, food protection behaviour was significantly more prevalent in the Wellington pack than the Orana pack. This demonstrates that while food competition in relation to pack size may significantly affect the prevalence of food-based social interaction in captive packs, a feeding regime that allows for species-specific food sharing behaviours may reduce food-based possessiveness in captively housed wild dogs.

While pack sex composition may have little effect on the types of social interaction used by captive wild dogs, or on the frequency or duration of many social interactions, my findings suggest that sex composition is an important factor determining the distribution of social interaction within wild dog packs. My findings support previous research (e.g., McCreery, 2000; De Villiers *et al*., 2003) demonstrating that social interactions in a pack where all individuals belong to the same age-sex cohort were relatively evenly distributed, while social interactions in a mixed-sex pack (consisting of individuals from different age-sex cohorts) had more variation in the distribution of affiliative social interactions. This suggests that sex composition may be integral in determining the distribution of social interactions within captive wild dog packs, whereby individuals of the same age-sex cohort are more likely to interact. My findings were consistent even after the death of a pack member and in the presence of environmental enrichment in the single-sex pack, demonstrating that pack composition is highly important for determining the distribution of dyadic social interactions.

My findings also demonstrate that even within a relatively small, highly related group of captive animals, social isolation can occur if sex compositions are highly skewed from those found in free-ranging populations, as was found in the Wellington pack where the lone female initiated and received few affiliative interactions with other pack members. The relative stability of the packs was also affected by sex composition, whereby the single-sex pack appeared more stable to disturbance compared to the mixed-sex pack, despite both packs being of equal number. While the addition of enrichment appeared to reduce pack stability in the single-sex pack, the death of an individual did not. Captive management of wild dog populations, particularly those not intended for breeding, should therefore aim to reduce the likelihood of individual social isolation by ensuring that multiple individuals of the same approximate age-sex cohort are present within each pack (De Villiers *et al*., 2003).

In group living species, the death of a pack member (especially an adult) has the potential to alter dominance hierarchies, change coalitions and relationships between individuals, and reduce the number of available mates within a group (Brainerd *et al*., 2008; Buhl *et al*., 2012). As a result, death may significantly alter the use and intensity of certain social behaviours within animal groups. The natural death of a study subject is a relatively uncommon and unpredictable event, yet such an event occurred during the course of this study in the Orana pack. This enabled me to examine the effects of death on social interactions and behaviour in this small sibling group. My results suggest that after the death of a pack member social interactions that reinforce the dominance hierarchy, such as greeting, ‘other’ (which may act as dominance behaviours) and dominance behaviours (which increased after death), appear to be favoured over behaviours, such as play, that act to strengthen social bonds but can only operate in the absence of dominance reinforcement (Bekoff, 1972; Gusset *et al*., 2006).

The overall stability of the pack remained unchanged by the dog’s death. The strength of dyadic interactions between individuals did change after the death, but death did not alter the presence of relationships between all dyads in the pack, highlighting the unchanged overall stability of the pack. This was possibly attributed to the fact that all individuals were related and from the same age-sex cohort. The strength (frequency) of affiliative dyadic interactions initiated by Nne and directed to Sita increased after the dog's death. Additionally, all dominance interactions after the death were initiated by Nne and directed towards Sita, suggesting that reinforcement of the dominance hierarchy was taking place between these two individuals. This suggests that due to the high intensity of dominance-based hierarchy reinforcing interactions, play may not have been an appropriate form of social interaction at this time.

The addition of three simultaneously added enrichments appeared to reverse the effects of pack member loss on behaviour, with a significant decrease in the frequency of greeting and dominance-based social behaviours, and a decrease in the duration of dominance behaviours. This indicates that the use of multiple, simultaneous enrichments may function to mitigate social tension in groups, which is congruent with what has been found in other species, such as primates (Honess & Marin, 2006). This shows that enrichment may not only reduce the formation and prevalence of a large suite of repetitive abnormal behaviours but that the simultaneous use of enrichment may also be used to alter social interactions and behaviour in captive animals (Mason *et al*., 2007).

Finally, broader analyses into some unintended associated effects of captivity such as zoo guest visitation and seasonality, on the use of social behaviour found complex interaction effects in the four dog scenario at Orana (before the death of a pack member), while such effects were not present in the three dog scenario (after the death of a pack member). These interaction effects indicate, at least for the limited number of packs observed in this study, that while captivity *per se* may not significantly impact the presence of many of the social behaviours used by African wild dogs, high zoo guest visitation may decrease active forms of social interaction in captive animals. As this is based on a very limited sample size, further research is required to determine if upper limits on enclosure viewing areas should be set to minimise the effects of zoo guests on the animals in such facilities.

This study has merely scratched the surface of a much broader area of research which should be viewed as particularly important for those concerned with captive animal welfare. Although this study investigated a small number of highly related subjects, this is a characteristic feature of many captively held populations, and consequently the trends seen here are most likely applicable to other captive populations elsewhere. Although often implicated as having large negative effects on the behaviour of captively housed animals (Mason, 2010), captivity may have varied effects on the social behaviour of African wild dogs. While many of the behaviours present in free-ranging populations are still present in their captive counterparts, it is evident that pack composition, especially in terms of sex ratio and relatedness, may have significant effects on the distribution, intensity and presence of certain social interactions. The strong dyadic bonds that develop between pack members also need to be considered as important determinants of group structure, especially when pack structure is challenged. Encouragingly, my results suggest that varied and simultaneously presented enrichment may help packs recover normal social behaviour during times of social tension. Overall, this study highlights the need to better understand the behaviour of captive animals as a function of group size, sex distribution, enclosure size, visitation rate, and feeding regimes. This study was unable to look at all of these aspects using the sample sizes required, but it provides the framework for further research in the area. This is especially critical in animals, such as wild dogs, that are endangered and for which there are existing global captive breeding programs.

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