INCREASING CERTAINTY IN AN UNCERTAIN WORLD: THE IMPORTANCE OF SIGNALS AND CUES AMONG WILD MALE VERVET MONKEYS

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ABSTRACT

Too much uncertainty in the world you live in can cause undue stress. Not knowing where to find your next meal or the prospect of being eaten at any moment are two examples. During aggressive encounters, creating uncertainty in your opponent may be the objective, where acts of aggression may be used to test the boundaries of other group members. The primary aim of this thesis was to explore whether the postural displays and aggressive threats used by male vervet monkeys are aggressive in the combative sense or communicative, affording the negotiation of social space. First, the existence of the red-white-and-blue (RWB) and broadside displays was confirmed in a population of wild vervets monkeys, although rarely in the archetypical way as described previously. Through an exploration of male vervet genital displays during the mating season, I found that eye contact played an important role in whether a display escalated into additional threatening, both displays and threats occur within striking distance (equal to or less than one monkey body length apart), and that males were constantly striving to maintain a stable face-to-face perception of their opponent. These overt signals are likely also accompanied by cues, some of which may indicate dominance rank. Two samples of observers, undergraduates and experts, were able to detect the relative dominance of male vervets in a non-social setting. These cues could be important in a variety of contexts, both during and outside of postural displays.

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CHAPTER ONE: INTRODUCTION

Successful navigation of the world, metaphorically speaking, requires the ability to understand and prepare for future events. In autumn, preparations are made for the upcoming winter. Our social umwelt and the systems within our bodies facilitate preparation for reliable changes in order to increase our overall evolutionary fitness. Knowing that it always snows on Halloween in Edmonton, Alberta, ensures that the winter tires are on the car before October 31st every year. However, not all aspects of life are as reliable as the changing seasons, particularly for a social species where the subsequent actions of other agents can rapidly change in response to your own actions. Most often, individuals that live in groups reduce uncertainty through communicative signals, which have evolved because they benefit the signaller and the perceiver. In this way, signals and cues have been of interest across psychology and ethology. The present thesis will explore the communicative and combative nature of postural signals and cues used by male vervet monkeys, specifically with regard to the high degree of variability within postural displays, the reliability of the perceiver's response and the effect of external elements that are relevant to understanding the nature of these conspicuous behaviours.

If the world were completely predictable, as simple in every respect as the sun rising and setting each day, all creatures within it would not need to move or engage with the world, and might behave as plants do (Barrett, 2011). Plants are able to satisfy all their needs by remaining relatively stationary, whereas mammals cannot. A mammal must move and get involved with its environment in order to satisfy its basic needs. The world of an mammal is full of uncertainty with respect to access to resources, mates and avoiding predation. One strategy that some animals have employed to alleviate these issues is group living, which gives rise to a host of new problems related to uncertainty. Predicting the behaviour of others on whom you rely to improve your own fitness (e.g., receptivity to mating attempts, sharing a restricted food resource, avoiding predation) requires some means of communication. Communication through signals and cues can lead to fitness benefits for each group member. Having clear rules, within stable and relatively predictable environments, for instance with individually recognizable group members and a stable dominance hierarchy, is associated with the optimization of food resources and imitators of contests were more likely win among sea trout (*Salmo trutta)* (Hõjesjõ, Johnsson, Petersson, & Jãrvi, 1998). In this case, a predictable environment was directly associated with increased fitness. However, from the perspective of a dominant animal it may serve to behave unpredictably. Randomly timed attacks on random subordinates has been argued to be a strategy that lowers the the cost to the aggressor and maximize the effect on the victim (Silk, 2002). In species with dominance hierarchies, subordinates have been shown to have higher levels of stress related hormones (specifically glucocorticoid) relative to more dominant animals. This suggests that creating uncertainty among fellow group members may be a strategy employed by particular individuals.

With communication favouring increased certainty and predictability in future events, and dominant animals enforcing their position through random acts of violence, the role of postural displays is unclear. Postural displays are thought to function as communicative signals, but with an aggressive or threatening nature. Signalling generally and visual threat displays specifically are one way to increase behavioural predictability, namely playing a central role in conflict resolution. Given that group life involves the costs of simultaneous resource exploitation, making competition probable, it is logical to expect a natural phenomena to maintain a group's association and the benefits for each group member (de Waal & Aureli, 2000). Perhaps the function of threat displays is to facilitate negotiation between partners, where the threat of aggression can be used as a bargaining tool. In this way, aggression is not an adverse social instrument per se, aggression is not the absence or breakdown of cooperation, but a necessary force required to maintain the benefits of group life for each group member (de Waal, 1996). The intention of threat displays, the desired outcome and indications of underlying motivations, relies in part on the information that comprises them.

Displays can use a variety of modalities: visual (e.g., colouration), auditory (e.g., shrieking), postural (e.g., standing on hind legs), movements (e.g., rapid glancing), or any of these in concert. Multiple signals can be produced through one modality, and one signal may incorporate multiple modalities (Hebets & Papaj, 2005). A complex signal is one that uses multiple modalities, where any one modality alone is not sufficient to elicit a response from the receiver. The postural displays of male vervet monkeys are complex signals, and can involve all sensory modalities to some degree. One hypothesis to explain the concurrence of modalities is the “multiple messages” hypothesis which, in its standard form, posits that several bits of information are conveyed within the same signal, where each bit may refer to something different such as: health, fertility, resource holding potential (RHP), (e.g. Doake & Elwood, 2011) dominance, species and/or sex recognition, etc. (Hebets & Papaj, 2005). Another hypothesis for complex signalling is redundancy, where each modality comprising the signal sends the same message (Hebets & Papaj, 2005). Redundancy ensures that the message is more likely to be understood, because in the event that one modality fails, at least one other might have the desired effect. All of these assume, however, that the perceiver of the signal has the ability to witness and understand the signal.

Receiver psychology focuses on the perceiver’s ability to recognize and understand the signal put forward into the world. The abilities of the perceiver of a signal are as important as the properties of the signal itself. Three central elements constitute receiver psychology; can the receiver detect, discriminate and remember what the signal is associated with (Guilford & Dawkins, 1991)? Detectability of signal is based on the perceiver’s perceptual systems, including the brain and processing networks beyond the sensory organs themselves. Discriminating a signal from other surrounding information in the environment, which may distort a signal, requires that the context in which the signal is produced also be considered. Being able to remember the signal, or relate it with some other pertinent stimulus, is the least studied and arguably the most important element of signal properties. Each component of the receiver’s psychology contributes to the evolution of signals; what they look like, how they sound, when they are produced, and the function of complex multi-modal signals is likely in part to address these key considerations. Based on their body morphology, vervet monkeys have the opportunity to display a number of multi-modal signals.

Vervets will expose the white ring around their eyes during threats which contrasts drastically with their black faces. Males especially have a brightly coloured genitalia, with a sky-blue scrotum and scarlet red penis, which is described as frequently used during numerous displays. These features afford male vervets the ability to utilize visual signals in conjunction with other auditory or postural signals. As a result, vervet monkeys have evolved more visual displays than any other guenon (Bolwig, 1978).

1.1 Description of male vervet displays

Struhsaker (1967a, b), Wickler (1967) and Henzi (1982, 1985) provide the only descriptions available of male vervet displays. Two of the displays identified as formalized interactions between males were the “broadside” and “red-white-and-blue” (RWB) display. A broadside occurs when one male (the actor) approaches another (the recipient), and positions himself orthogonally to the recipient, so that the recipient’s face is next to the the actor’s body. Imagine a capital ’T’ where the actor is the top and the recipient is the length of the T. The actor then moves past the recipient and pauses, giving the recipient a full view of the actor’s scrotum and extended penis, at which point the recipient will typically glance towards the actor’s genitals.

The RWB is similar to the broadside, but in this case the actor walks "confidently" around the recipient who maintains a hunched posture, and coordinates the turning of his body with the circling movements of the actor. Struhsaker (1967a) defines a confident walk as a monkey who is alert but relaxed, as indicated by the absence of extreme muscle tonus and the absence of quick sideways glances of the head. The posture adopted by the actor during the display facilitates a full presentation of his genitalia in front of the recipient, while the recipient shields and often abducts his own genitals. Struhsaker (1967a) also describes a vertically erect tail posture and occasionally a hand placed on the head of the recipient. The recipient's response is reliably one of subordination: he is typically hunched, with testicles abducted, submissively vocalizing and rapidly glancing at the actor (Henzi, 1985). The interaction ends either when the recipient backs away and/or the actor moves off.

The males involved in such displays tend to have a clear rank differential: the actor is high-ranking and the recipient low-ranking. When two similarly ranked males begin either of these two postural displays, a different overall pattern of responding follows, although this is described to happen less frequently (e.g., a penis extension resulted in the reactor developing a penis extension as well, after which the displayer solicited grooming) (Henzi, 1985). Occasionally the RWB and broadside displays occur in conjunction with threats. In such situations, however, the recipient of the display typically moves away first, departing from the actor's vicinity. When a RWB or broadside happens in isolation, the actor or reactor may be equally likely to move off. Although both displays are described to be quite separate and unique, there are some postural orientation similarities, which is one reason they have been the target of the present investigation. Both displays emphasize the brightly coloured genitalia, where the penis is erect, and the length of the actor's body is presented. Might it be possible that these two displays are variations or continuations of one another?

Male vervets have never been observed to attack other males who that perform a submissive display after a RWB display (Henzi, 1985). Such a reaction to these displays suggests that the RWB and broadside displays may be a means of mediating or pre-empting higher levels of aggression. More broadly, postural displays may allow males to negotiate and manage aggression during a particularly tumultuous time of year. The extent that displays produced by vervet monkeys are formalized has yet to be established. More generally, the function of displays in the broader range of aggressive actions available to males has yet to be considered.

As is apparent, the RWB and broadside displays emphasize a male's brightly coloured genitalia. Importantly, the frequency of these displays increases during the breeding season, thus their function is thought to help manage rank hierarchy and to "assert rank at a time when [...] [it] is critical" (Henzi, 1985, p. 130; Struhsaker, 1967a). This represents an excellent hypothesis for why RWB and broadside displays occur. The association between these displays and their increased prevalence during the breeding season, which is also a time of intense instability in the male dominance hierarchy, and their occurrence only between males has linked them causally to acts of aggression. But other than their high likelihood of eliciting a fearful response from the reactor, is there any evidence to suggest that such postural displays are actually aggressive? To understand the function of the broadside and RWB displays, I will use predictions drawn from competing combative and communicative signalling hypotheses (Pellis et al., 2013). A purely combative manoeuvre arises from combat tactics, where two animals jockey for the best tactical position from which to launch an attack. In its strongest form, the postures are not signals at all, but derailed attempts at striking a blow or physically attacking the opponent. Alternatively, a communicative signal serves to discourage high intensity acts of aggression by indicating a willingness to fight or superior resource holding potential (RHP, e.g. increased access to resources, superior physical condition). Each of these has specific implications for how a threat display will manifest, but first a foundation in the literature on signalling theory and empirical findings may prove fruitful.

1.2 Virtue as a signal

Signals are behaviours or traits that influence the behaviour of other organisms, and have evolved because they play a particular role in communication (Maynard Smith & Harper, 2003; Hebets & Papaj, 2005). They have been the target of natural selection, the result of which is that these acts or traits influence the behaviour of a potential receiver because such a response is adaptive for either one or both parties. The crux of signalling theory, and the topic of longstanding debate, is what prevents signallers from cheating receivers and reaping the benefits? In order for a signal to benefit both parties, the signal must be honest in an evolutionary sense. An honest signal indicates a true quality that exists within the signaller or the environment, whereas a dishonest signal is the opposite, the signal indicates some quality that does not exist within the signaller or environment (Donath, 2011). Further, the proportion of instances that a signal is honest or dishonest affects the signal's reliability. A signal is said to be reliable if it always indicates a quality that is present, thus such a signal would be reliably honest. Zahavi (1975) initially described the possibility that a signal's honesty is maintained by a high cost, in the evolutionary sense, and termed this the handicap principle. For example, the number of eyespots on peacock's tail is an honest indicator of a male's health (Layau, Jalme, Cagniant & Sorci, 2005) and is associated with energetic costs to grow and maintain (Fitzpatrick, 1998), as well as the potential cost of predation. In this way, inferior males can not afford the same array of feathers because it is too costly to their health and survival. A signal is less likely to be dishonest if it is difficult to produce or associated with a costly penalty for dishonest signallers. The handicap principle is thought to keep dishonest signals to a minimum, ensuring that honest signals are reliably linked with the associated trait or behaviour.

For threat displays, a signal may function to prevent intense agonism, where a weaker male may avoid an encounter with a stronger male to whom he would likely lose and suffer wounds. If a weaker male could use the same signal dishonestly, allowing a weak male to falsely signal higher RHP over a stronger male, the weaker male might be able to reap the benefits of fighting without suffering the cost of a fight or wounds. What prevents this from happening is punishment. Although not typical to most displays, what keeps threat displays honest is the potential cost of cheating, rather than the actual cost of signal production (Számadó, 2011). Thus an important element keeping threat displays reliable is the proximity between males, evidence for which was recently shown with vervet monkeys, where the number of threats significantly declined as the proximity grew between individuals (Takahashi, 2012). This finding illustrates that being within striking range is important for a threat display to be considered honest, whereby questionable signal honesty can be readily challenged. Furthermore, increasing the distance between individuals also decreases the detectability of a threat display, and makes it harder to indicate exactly who is the target of the threat, which in turn might also be costly for signallers. For instance, should a high-ranking male see the threat and respond, thus threats need to be more precisely targeted and proximity is a means of ensuring that as well.

There are two main types of costs for signals, and that is in their production and ensuring they are received (efficacy cost) and additional effort that ensures a signal's honesty (strategic cost) (Guilford & Dawkins, 1991). Given that not all signals have equal costs affords a classification of signals into one of three categories: 1) minimal-cost signals, which have efficacy cost only; 2) handicaps, which have efficacy and strategic costs; and 3) cost-free signals, which have no strategic cost and the cost of efficacy is inconsequential (Számadó, 2011). With these three categories, it is possible to predict when cheating will occur. When prospective cheaters have the option to perform unreliable signals, they will do so unless the cost of cheating is higher than the possible benefits of successful deception (Számadó, 2011). A cost-free signal, the third type, is typically referred to as an index signal, related absolutely to some trait of the animal. For example, an animal's height is a reliable index of its reach. Standing in front of another male, passively demonstrating height, is a free signal that is honest.

Signals are not the only pieces of information available to guide subsequent behaviours when deciding how to behave. A cue is any feature of the world that can be used to guide future action (Hasson, 1994), such as a mosquito detecting carbon dioxide to guide itself towards mammals. Cues, like index signals, cannot be faked. A major difference between signals and cues is that a cue will continue to exist regardless of whether a perceiver is available to interpret the information, whereas a signal exists because of its advantageous relationship with perceivers. Thus, while signals are maintained by natural selection, cues are not (Donath, 2011). A mammal does not stop producing carbon dioxide if there are no mosquitos. Similarly, a cue is inadvertent, and indeed the individual producing the cue may not wish others to know the information the cue relays, in this case the mammal who suffers a mosquito bite. As such, cues can be used to infer information about internal states (e.g., nervousness), location in the environment (e.g., carbon dioxide) or a host of other features.

Cues are not completely separate from signals, however, as a cue could be a component of a signal, or even the precursor of a signal. Cues become signals through the evolutionary process referred to as ritualization (Tinbergen, 1952). Although the process of ritualization is not well understood, the product has clear components. Ritualization, in short, “is schematizing” (Tinbergen, 1952, p. 24). Cues are important to consider because they may function as a component of a signal and/or be the evolutionary precursor to a later more complex signal. Using the broadside display as an example for male vervets, one component of the display is showcasing the length of the body. This could have initially functioned as a cue or index of the physical size of a male. Through the process of ritualization, exaggerating this cue and combining it with other features associated with male dominance has led to the overt broadside display as it exists currently. Furthermore, a cue could also be a signal from another individual’s perspective. In the case of the mosquito searching for an animal, while carbon dioxide is a cue from the perspective of the animal, it is a signal from the perspective of the mosquito. The ability to use carbon dioxide to find animals is maintained by natural selection. With this background in mind, the function of vervet postural displays will considered.

Movement motivated by combat arise from combat tactics, animals jockeying for an ideal tactical position based on both offensive and defensive manoeuvres. Such jockeying makes sustained postures unlikely (Pellis et al., 2013). The combat hypothesis predicts that several small movements will be more likely (think 1/32 turns to rotate full circle), where the animals manoeuvre themselves for the best position, rather than fewer big movements. Withdrawals should be attacked, not abided, as they present an easy opportunity to attack (Geist, 1978). Flourishes, such as unnecessary tail movements, would also be absent, as would any other emphasis of honest predictors of RHP, such as size, speed and endurance. A communicative signal predicts almost the opposite, where flourishes, such as added tail movements or vocalizations, would be present to amplify the signal, as would sustained postures, to facilitate the clarity of the signal. An actor would not attack a reactor who signalled submission because the function of the signal is communication and the goal is attained when one animal submits. The reactor would also likely make fewer large movements (think 1/4 turns to rotate full circle), keeping the actor in sight, but not to gain a positional advantage.

All of the above are predictions might indicate stable behavioural patterns, but what about perception? Inferring elements of the animals' perception can indicate further aspects of their behaviour. Where either animal is looking, and if eye contact is established or avoided, can also be important to understand the intention of the display. In order to understand aspects of the animals' perception, Perceptual Control Theory (PCT) offers an insightful addition to the this currently behaviour focused expedition. PCT takes the premise that behaviour should be considered as a continuous phenomenon and that it is perception that individuals in the system aim to control, and not behaviour (Powers, 1973). Since behaviour is highly variable, and this variability makes pattern-seeking challenging, the focus shifts from controlling behaviour to controlling perception. There are five main steps to explain how this works. Initially, the control system (here the vervet) receives input from the environment through its perceptual capabilities. This input is a combined function of the environmental effect and the perceived effect of the controllers own actions. The input is then compared to a reference state. The difference between the input and the reference state drives the output, which is the behaviour witnessed. Said output is immediately and continuously perceived, along with the effect or lack of effect on the environment. The output varies in order to reduce the difference between the input and reference states. Essentially the receivers of signals are controlling their own perceptions, which are being influenced by the activities of the signallers. In this way, it may be possible to predict additional elements of either animal's behaviour.

For vervet postural displays, rather than examining only the actions of the display, I will also infer elements of the animal's perception. In particular I will try to understand the role of eye contact, defined as when both animal's orient their heads towards one-another at the same time. Vervet monkeys find eye contact threatening, but eye contact also affords an aggressive threat to take place. There is no point in threatening unless eye contact is established first. In this way, eye contact allows threatening to occur, and as such it will likely play an important role in aggressive interactions. When eye contact is made, both animals are aware that they have each seen the signal. In this way, avoiding eye contact may also be a useful strategy. The role of eye contact and threat displays more generally can be understood through lived experience.

A relatively new field of research called embodied cognition advocates that the actions themselves are informative and afford certain responses, thus both animals involved are probing their environment and each other for information about what to do next (Griffiths & Scarantino, 2009). Outside of the interaction between the two individuals performing a display, an audience member who witnesses the actions and outcome of the display both gains information and interprets those actions based on their own previously lived experiences in the same situation. Previous research has shown that onlookers can affect the actions of actors. For instance, Western scrub jays will selectively cache food in more obvious locations when conspecifics witness where the food was hidden (Clayton, Dally & Emery, 2007). While a younger male watching a display may not affect how the display develops, an adult male might. That is to say that a younger male may benefit from watching two adult males engage in postural displays because he may will likely increase his own social knowledge through social facilitation, while the older males involved in the display, may not be affected in any way by the presence of the younger male. The presence of another adult male, however, may facilitate their own knowledge of the two individuals engaged in the display. For example, if two similarly matched males begin to interact and one reliably submits, the on-looker benefits from the knowledge that he too may solicit a submission from that same male. It is for this reason that I will try to investigate the effect of the audience on male-male interactions.

1.3 Aims of this thesis

Too much uncertainty in the world you live in can cause undue stress. Not knowing where to find your next meal or the prospect of being eaten at any moment are two examples. Both group living and communicative signals help to alleviate some of this stress. The primary aim of this thesis is to explore whether the postural displays used by male vervet monkeys are aggressive in the combative sense or communicative, affording the negotiation of social space, suggesting that postural displays are a bargaining tool of social negotiation and not a strictly negative social force (de Wall & Aureli, 2000).

The first data chapter addresses vervet male aggressive threats and postural displays, which is primarily exploratory. I initially describe vervet aggression generally using observational data and then postural displays specifically using video data. In order to understand whether postural displays are aggressive, a general understanding of vervet aggression is required. What are the targets and tactics during physical fights that result in wounds, how do threats typically manifest and progress, and what effect does the audience of aggressive threats have on the progression of aggression? This work is intended to situate the subsequent section on male vervet postural displays. I coded for elements of the RWB, broadside and submission displays based on previous descriptions by Struhsaker (1967a) and Henzi (1985) to verify that they occur in a separate population of wild vervets and whether the elements of these displays happen in an archetypical way, or if they also occurred in isolation. Should the components of the display regularly be observed in isolation, it suggests that these displays may be some emergent property of an ongoing interaction, as opposed to a canonical and highly formalized display that happens in the same way every time. Lastly, I will compare displays in isolation to interactions that contained displays and threats. This contrast is to explore the extent to which displays are in fact aggressive, if they reliably function to avoid higher level threatening, and what might predict when a display will escalate into additional threatening or cause one male to back-down, using the prevalence of proximity, eye contact, and sustained postures as predictor variables. The second data chapter uses an experimental paradigm with two samples of human observers to test if relative dominance rank is detectable using subtle non-social cues. I predict that vervet males are using a variety of cues during postural displays that can allow them to make decisions about what to do next. It could be that each of the components of an actor's display functions on a continuum of aggression, and that all of these behaviours, displays and threats, are used as a way to navigate their social environment.

GENERAL METHODOLOGY

2.1 Study Animals

2.1.1 Taxonomic affiliation and distribution

Vervet monkeys are a medium-sized, sub-Saharan species of primate who are a part of the sub-family *Cercopithecinae.* They are semi-terrestrial living throughout Ethiopia, East Africa and to the southernmost tip of South Africa (Tappen, 1960). Although they were originally classified as *Cercopithecus aethiops,* a part of the genus of guenons, this classification has become a topic of recent debate. Since guenons are forest dwellers typically, vervets seem like an outlier because they are typically semi-arboreal, semi-terrestrial (Fedigan & Fedigan, 1988). Vervets are classified as *Chlorocebus*, however, the literature often misidentifies the six main species of vervet and the eight sub-species as one uniform taxon under the name *Chlorocebus pygerythrus.* The status of this taxonomic classification is currently being debated and may be modified in the future.

2.1.2 Ecology

Vervets are found in greater density in areas of riparian vegetation, but can make use of less prolific environments, including karoo semi-desert, riverine forest, and urban areas (Struhsaker, 1967b), precluding rain-forests and desert habitats (Chapman & Fedigan, 1984). These primates require access to two major resources to thrive: water and sleeping trees (Wrangham, 1980). At night, predators are a major risk and large sleeping trees provide safety (Chapman & Fedigan, 1984; Fedigan & Fedigan, 1988). Common predators include: felines (lion, cheetah, leopard, caracal, African wild cat), jackals, hyenas, baboons and humans (Enstam & Isbell, 2002). As opportunistic omnivores, vervets eat: fruits, flowers, grasses, shoots, fungi, tree sap, and leaves, opportunistically eating eggs and chicks (Struhsaker, 1967a). They adjust their diet according to seasonal availability, but demonstrate a preference for plants and flowers (Fedigan & Fedigan, 1988). Acacia (*Acacia karoo)* is a primary and important food source.

Vervets are territorial, but the degree to which they defend their territory fluctuates with the season and associated resource availability. Inter-troop encounters happened frequently at our field site, roughly once or twice a day, however, the intensity of these encounters also ranged from intensely aggressive to mildly affiliative. Their territory size also varies, for example vervet troops on the island of St. Kitts occupy ~ 0.32 km^2 (Chapman & Fedigan, 1984), compared to those in Senegal who occupy 1.78 km^2 (Harrison, 1983). The size of the territory relies heavily on the quality of habitat and vegetation type (De Moor & Steffen, 1972; Struhsaker, 1967c).

2.1.3 Physical description and reproduction

Vervets have a silver-grey coat with a white band of fur across their brow and surrounding their black face. Their feet and hands are black, and the skin on their abdomen is blue and covered in white fur. Males have brightly coloured genitalia, with a blue scrotum and red penis. They are mildly sexually dimorphic in size, where females are two thirds the size of males. Reports of average mass and body length vary across the literature, likely as a result of the abundance of available resources. For females, average mass ranges between 2.5 - 4.1 kg and an average body length of 37 cm, while males are larger with an average mass between 4.1 - 8.5 kg, and an average body length of 41 cm (Bolter & Zihlman, 2006; Cawthon Lang, 2006; Turner, Anapol & Jolly, 1994, 1997). Our population is comparable where the males weighed an average of 4.7 kg and the females weighed an average of 3.3 kg, well within other cited population averages.

Sexual maturation occurs with slightly different timing between the sexes, males are sexually mature around 36 months, and females a year later around 48 months (Turner, Anapol & Jolly, 1997). Vervets are seasonal breeders, typically copulating from April to June in South Africa. Gestation is approximately 163 days (Melnick, 1987) and the birthing season thus occurs from September to December. Births are single offspring and inter-birth intervals are between 11 to 24 months (Melnick, 1987). Infanticide is not observed, likely because males are not able to reproductively coerce females (Seyfarth, 1980).

2.1.4 Social Organization

The average troop size is 20 members, although the mean size can oscillate, which is commonly reported across the literature (Cheney & Seyfarth, 1983; Wilems & Hill, 2009). Vervets live in a multi-male/multi-female group, usually consisting of an adult sex ratio of 1 M: 1.5 F (Fedigan & Fedigan, 1988). Groups are considered female-bonded, meaning females maintain affiliative bonds with one-another through grooming, huddling and resource defense (Wrangham, 1980). Dominance relationships are linear, although acquired differently between males and females. Females are philopatric, residing in their natal groups their entire lives, and inherit a rank that is similar to their mother's rank; typically directly beneath her (Wrangham, 1980). The outcome of such a system is a relatively stable hierarchy where change or instability only happens when females with an established rank dies (Fairbanks & McGuire, 1985).

In contrast, natal males emigrate when they reach sexual maturity to join neighbouring troops and will typically continue to transfer between troops roughly every three years throughout adulthood (Henzi & Lucas, 1980). This occurs at a higher rate during the mating season and is how inter-breeding is prevented (Henzi, 1982). Because of this emigration among males, maternal rank has little bearing on an adult male's dominance rank, and thus is established through the outcomes of agonistic interactions with other males. The outcome from this is an unstable and even tenuous male hierarchy, particularly during the mating season which is a period of high fluctuations. As such, dominance is perpetually tested and re-negotiated (Henzi & Lucas, 1980). This aspect of vervet social organization means that fighting ability, when tested, is important.

Although aggression is frequently witnessed (Freeman, 2012), low ranking males also utilize "self-initiated submissive interactions" to higher ranking males (Henzi, 1985, p. 133). Referred to as paying 'homage,' such self-initiated displays likely serve to decrease aggression from higher ranking males. In general, males are tolerant of one another, and are occasionally observed grooming one-another (personal observations). Grooming between two males seems to also to transfer to a willingness to form coalitions, where rare grooming pairs become fighting partners against other aggressors (Freeman, 2012).

2.2 Study Site

The present study took place on the Samara Private Game Reserve, Eastern Cape, South Africa (32° 22’S, 24° 52’E) as apart of an ongoing study that began in September 2008. Samara is 34,000ha of mountains and karoo grassland, located on the Plains of Camdeboo south-east of the town of Graaff-Reinet. The reserve is semi-arid karoo land, with a riverine forest of Acacia karoo trees along the Milk River and its tributaries. The river has not been dammed and the monkeys have no access to artificial water sources. Over the many years spent on this field site, we have observed that the river has clear seasonal variability, with flooding in the summer and becoming completely dry in the winter. During the present study, the river was never dry.

Rain and temperatures fluctuate widely with the seasons. Summer is October to April and winter is May to September, with the most rainfall happening between October and March. The average yearly rainfall is 330 mm per annum. The coldest month is July where snow typically falls in the surrounding mountains (mean minimum temperature is 4 °C), and the hottest months are December and January (mean maximum temperature is 34 °C). I collected the data presented here from January to June 2013, during which time the mean monthly precipitation was approximately 26.5mm, with the most rainfall during the month of March. The average monthly temperature was 20.1°C (provided by the South African Weather Service) with monthly average, maximums and minimums for all of 2013 are displayed in Figure 2.1. Daylight hours peaked in December at 14.1 hours and were reduced to 9.6 hours in June.

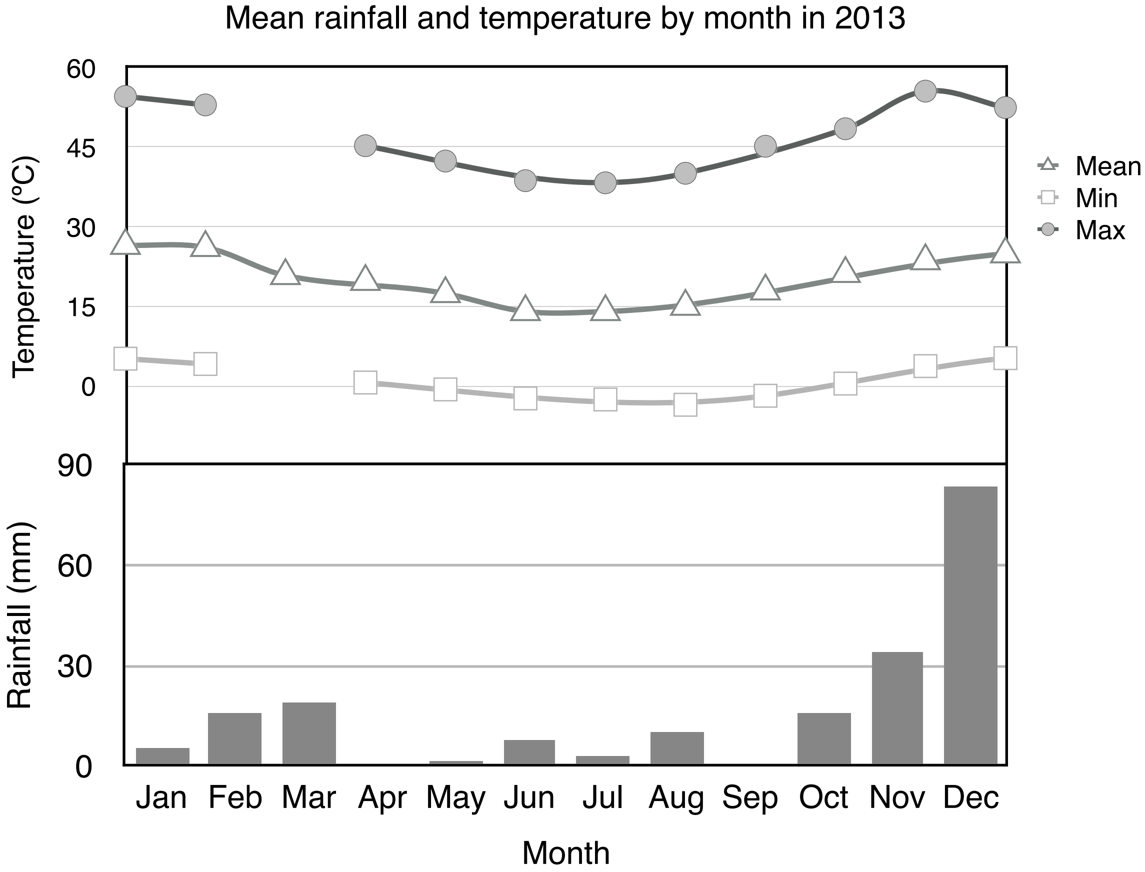


Figure 2.1. Mean rainfall and temperature by month in 2013. The gap in March for the minimum and maximum temperature values reflects that the data were not recorded for that month.

Many animals other than vervets flourish in this highly temperature variant habitat, including a variety of ungulates (i.e., eland (*Aurotragus oryx*), kudu (*Ragelaphus strepsiceros*), and gemsbok (*Oryx gazella*), to name a few). The primary predators of our study animals include cheetah (*Acinonyx jubatus* Brookes),caracal (*Caracal caracal* Schreber), black-backed jackal (*Canis mesomelas* Schreber), Verreaux's eagle (*Aquila verreauxii* Less.), martial eagle (*Polemaetus bellicosus* Daudin), giant owl (Bubo lacteus Temminck), Cape eagle owl (Bubo capensis Smith) and various venomous snakes.

2.3 Study Troops

I collected data on males from two average size troops, River Bend Mob (RBM; N = 20 adults) and Picnic Troop (PT; N = 20 adults) leading up to and during the mating season of 2013 (January to June). The troops are established in neighbouring territories along the Milk River. Both troops have been fully habituated to human observation since 2008. Because this project is ongoing, some of the data is from the larger project sample, from May 2012 to February 2014. Each troop had two regular sleeping sites, where neither troop slept in the others site.

Table 2.1. Troop size and composition at the beginning and end of the study period for both study troops.

Troop Sizes Across the Study Period (January - June 2013)

Troop	January 2013	June 2013
PT		
Males	9	7
Females	9	9
Juveniles	4	4
Infants	1	0
Total	23	20
RBM		
Males	6	11
Females	10	10
Juveniles	8	8
Infants	0	0
Total	24	29

2.3.1 Demographics

When the study started in January, RBM consisted of 16 adults (6 males and 10 females) and PT consisted of 18 adults (9 males and 9 females). This is comparable to the average of about 25 individuals (Fedigan & Fedigan, 1988). In June when the study period was complete these numbers were similar, RBM consisting of 21 adults (11 males, 10 females) and PT 16 adults (7 males, 9 females). The sex ratios of males to females in January 2013 are as follows: RBM (0.6M:1 F); PT (1M:1F), which is lower than the average which is typically 1M:1.5F (Fedigan & Fedigan, 1988). Table 2.1 shows general stability in troop numbers across the study period.

The bulk of the present study represents behaviour during the mating season (April - June) when males are migrating between groups. This makes things difficult because changes in group size and troop membership directly effects both the the calculation of dominance rank and sampling numbers. Table 2.2 shows the number of migrations and deaths that occurred during the study period. PT lost 3 males who emigrated and gained one male who immigrated from a neighbouring troop. RBM lost 3 males to emigration gained 6 males from neighbouring troops. Other extra-group males were seen with these troops for a short time, but since they were not habituated to the presence of humans, they rarely stayed longer than a few days. The one exception is the male Fang who did not seem habituated but stayed and was eventually fully habituated. The male Max is identified as flexible in Table 2.2 because he would frequent and sleep with both troops regularly. He was frequently seen with both RBM and PT in a given day after April 22, 2013 when this first started.

Dominance scores were calculated based on a summary of all agonistic interactions witnessed in the field, recorded ad libitum by all researchers at the site (Richard McFarland, Derek Murphy, Jonathan David Jarrett, Kira Roberts, Karen Lucas and myself from January to June 2013). I used the procedure outlined for Normalized David Scores (de Vries, Stevens & Vervaecke, 2006), which controls for group size. All aggressive interactions that were filmed were also included in this calculation. David scores are also given in Table 2.2 for both May and June. These calculations are done for each month because as males migrate between troops, the scores will shift in as little as one months time (Freeman, 2012).

2.4 Data Collection

I utilized 3 behavioural sampling methods: focal sampling, ad libitum (Altman, 1974) and video recording. Ad libitum data was used to examine observable wound locations and to establish the dominance hierarchy. The focal sampling technique was used to investigate how aggression happens more broadly, specifically how it begins, escalates and ends. Next, I split these interactions based on audience size. Lastly, to understand how displays may escalate into higher levels of aggression, I filmed displays and threats in concert, and evaluated the role of proximity, eye contact, maintaining a face-to-face orientation and sustained movements.

Table 2.2. Migration of males and David scores as an index of dominance rank

Migration of Males and David Scores as Index of Dominance					
Troop	**Male ID**	**May David Score**	**June David Score**	**Immigrate, Emigrate, Death (I, E, D)**	**I/E/D Date**
PT	Arby	5.28	4.79	D	2013/6/18
	Keit	3.55	3.43		
	Leit	3.43	2.97		
	Max	3.91	3.89	Flexible*	2013/4/22
	Mick	-	-	E	2013/4/26
	Nige	2.93	2.69		
	Oliv	5.15	-	E	2013/5/6
	Tren	3.82	3.57		
	Uthe	3.94	3.47		
	King	4	3.2	I	2013/6/13
	Ralp	-	-	E	2013/1/14
RBM	Mori	-	4.53	I	2013/5/23
	Panc	-	5	I	2013/5/23
	Bern	-	4.83	I	2013/6/10
	Chew	-	4.81	I	2013/6/6
	King	4.57	5.52	E	2013/6/13
	Zool	4.74	5.23		
	Larr	3.55	5.11		
	Rasp	3.54	-	E	2013/4/26
	Tyle	4.12	5.23		
	Max	3.5	4.76	Flexible*	2013/4/26
	Oliv	4.78	5.59	I	2013/5/6
	Fang	3.32	4.3	I	2013/2/28
	Ralp	3.87		E	2013/5/27

While I was with the animals from January to June 2013, not all methods of data collection began immediately. Ad libitum data and video sampling began at the end of January, whereas focal sessions began March 15th. Although video-focals began in January I had very little success filming anything useful until the mating season began in April. Adult monkeys were individually identifiable using physical characteristics, such as body size, tail length, facial features (i.e., brow shape or colour pattern typically around the eyes and chin) and distinguishing wounds or scars (see Figure 2.2 for examples).

During the summer months (here January to March) when daylight exceeded 12 hours per day, animals were followed on foot for 12 hours a day, 4 days a week, alternating early and late starts. During the winter months (here April to June) average daylight was 9.5 hours and the animals were followed from dawn to dusk 5 days a week. An average of 7.9 days were spent with each troop per month. For all sampling methods the animals were followed at a distance of 3 to 5 meters, contingent on how comfortable the animal was with being followed. If the focal animal demonstrated increased awareness towards the observers, distance was increased to the point where normal behaviour resumed.

2.4.1. Ad libitum data collection

A multitude of behaviours were recorded in an ad libitum fashion including wounds, aggression and copulations (Altmann, 1974). Wounding data, collected from September 2011 to February 2014 is used to illustrate how males and

Figure 2.2. Examples of face markings on vervet monkeys, making identification possible

females may differ in body location wound frequency. Aggression witnessed, collected from May 2012 to February 2014, was used to examine the highest level of aggression typically observed. This same ad libitum sample was reduced (January to June 2013) to construct the dominance hierarchies. Ad libitum and focal data was collected using Trimble Nomad handheld data loggers, with the software Pendragon Forms Manager 5.1.

2.4.2. Focal animal sampling

Focal males were followed continuously for a 20 minute period by one observer, myself. All males were sampled if they met 2 basic criteria: they had been a resident of the troop for at least one week straight, and had joined the troop prior to the final two weeks of data collection. An ethogram was developed (see Appendix A) defining all relevant behaviours recorded based on Struhsaker (1967a) and Henzi (1982). The order in which males were focal sampled was a balance between random and opportunistic. Each male was assigned a numeral from 1 to n (where n is the total males in the group). An order was created, typically the morning of data collection, using a random number generator. Once in the field, I would look for one of the first three animals on the list. After that focal session was complete, I would look for one of the two not found originally or the fourth on the list. Since focal sampling each male in the troop once typically took half a day, I would alternate whether I would focal or video sample the males in the morning or afternoon so as to get an adequate representation of the males across the day. The data was checked weekly to make sure that completed focal and video sampling sessions were evenly distributed across individuals and time blocks (morning and afternoon).

At the beginning of each focal session the animal's ID, date and time was recorded. The animal's behaviour was continuously recorded for the duration of the focal session. Each time the individual switched to a new behaviour for more than 5 seconds, the change in state was recorded. Whenever an activity involved another animal, such as threatening or grooming, the partner and direction of the activity was noted. Single instance behaviours, such as scratching or eye threatening, were also recorded. At every 5 minute interval, including the start and end, the nearest neighbours at 0, 2 and 5 meters were recorded, for a total of 5 records in a 20 minute period. A note was made if the focal animal went out of sight for more than 5 seconds. If the animal was out of sight for more than 2 minutes within the first 10 minutes of the focal sample, the session was abandoned and not used in the analysis.

2.4.3. Video protocol

Male-male aggression and vervet typical displays were filmed in the field by three observers (Kira Roberts, Jonathan David Jarrett and myself) using a

Canon PowerShot SX50 HS. The order that males were video-recorded was the same as that for continuous focal sampling. Once selected and located, male vervets were followed for 20 minutes. The video session was abandoned if the animal went out of sight for more than 2 minutes in the first 10 minutes. Throughout the video-focal session, the camera was held in the ready position, with the lens cap off and camera turned on. Recording began when two males were within 5 meters of one another or it seemed as though an aggressive interaction between two males might begin. Although this latter criterion is difficult to describe, it was clear, through both the quality and number of useable videos, that with experience a sense of potential aggression between two males became more refined with time. Additionally, if two males, neither of which were the focal animal, began fighting or presenting a postural display, we opportunistically recorded such interactions. The males were video-recorded until they were further than 5 meters apart or an ongoing agonistic interaction ended.

As soon as the record button was pushed, the observer would verbally note the date, time, if the interaction was seen from the start, the ID of both males involved and where they were in the frame, as well as all other visible monkeys in the area. If there was some relevant context to the interaction, such as a prior copulation or previous aggressive encounter, this was also verbally stated.

Before the analysis could begin, all videos collected (300 GB in size) were viewed and categorized as containing an aggressive interaction or display between two males or none of the former. Of those videos containing aggression or displays (97.9 GB) a database was generated with all relevant information that was verbally stated, as well as relevant clip information, such as the clip number and start time. Using my operationalization of the terms threat and display, further categorization took place. I defined a threat as aggressive social behaviours that were also used to calculating the dominance hierarchy and have been expressly described as threats in previous literature (e.g., Struhsaker, 1967a; Henzi, 1982) and in the ethogram used for the present study. A display is a more subtle behaviour where a) the focal animal maintains a posture showcasing his genitalia, and b) the other male shows clear signs of agitation (i.e., vocalizing, fidgeting, etc.). Using these definitions the videos were further classified into one of three categories depending on the videos contents, specifically if it was of: a display only, a threat only or a display and threat. Videos were viewed and categorized in Final Cut Pro X (version 10.0.9).

2.4.4. Video analysis

Once the videos had been split into three groups, I did a detailed frame-by-frame analysis using the Eshkol-Wachmann movement notation (EWMN) on 20% of the display only and display and threat categories of videos (see Eshkol & Wachmann, 1958; Moran, Fentress & Golani, 1981; Pellis, 1982; Pellis et al., 2013; Pellis, Pellis, Barrett & Henzi, 2014). EWMN was chosen because it allows for predictions regarding the intention of behaviour to be suspended until after the interaction is scored (Moran, Fentress & Golani, 1981; Pellis & Pellis, 2011). The two categories, display only and display and threat, were the only ones evaluated due to time constraints on the project. In order to understand the nature of aggression and the function of displays in the broader context of male-male interactions, these are the best two comparison groups.

EWMN is a coding system that uses coordinates on a globographic sphere to reflect the positions of limbs and their movement. The notation itself has each relevant body part as a row in a large table, while each column represents one frame of video. Each video was watched one frame at a time to describe one body part (e.g., the tail) for one individual in the interaction. This was repeated for all relevant body parts and for both individuals. In addition to the movements and positions of limbs, EWMN has 3 types of measures are used to notate the relationship between partners, which are the; point of opposition, distance, and partner-wise notation. Point of opposition is an indication of which parts of the body are nearest to each other, for example head to head, or posterior to head. The distance between animals is notated in monkey body lengths, which maintains consistency regardless of how far the observer is from the animals while filming. Partner-wise notation requires that we first lay a theoretical compass over each animal's body when viewed topographically. 0 would be the animal's head, 1 its right shoulder and so on until 7 its left shoulder and 0 is back to the head again. Using this compass system, animal A is overlaid onto animal B's body. The number that B's head is pointing to on A's body is recorded in curved quotations. For example, if A is standing orthogonal to B, this would be notated as { 6 }. It is possible for a third party, trained in the interpretation of EWMN to read and act out the original behaviour, having never seen the video clip.

From the 20% of coded videos I developed a system that would translate into frequency counts for statistical purposes. The following was coded for each video clip:

- Aggressor identity
- The individual driving the interaction for: the approach, during the aggression, and the depart. Driving an interaction is who moves first, forcing the other individual to react
- The points of opposition during these segments
- The distance (in monkey body lengths) between the two individuals during the display and, when applicable, during the threat. Also the closest two animals reach during an interaction
- If monkeys make eye contact, defined as both heads orienting towards one-another at the same time
- If monkeys strive to maintain an anterior-anterior orientation
- If circling happens (this is described fully in the description of the RWB display), where one animal may walk around the other who pivots in place, or both animals may circle each-other. Whether the circle was a half or complete circle
- Previously, penis extensions and tail posture have been described as a part of both the RWB and broadside displays (see Struhsaker, 1967a and Henzi, 1985). When visible, the state of the penis (extended or not) and height of the tail (approach, during, depart)
- If the postures in a display are sustained, dynamic or both

This is my general method. Other specific methods were used and are described when relevant.

CHAPTER 3: THREATS AND POSTURAL DISPLAYS

3.1. Introduction

Vervet postural displays fit the description of complex signals extremely well, as they involve “complex behavioural routines, incorporat[e] […] more than one signal or related component, often serially and overlapping, frequently across multiple sensory modalities” (Hebets & Papaj, 2005, p. 197). There are a striking number of animal displays that are both multimodal and complex, suggesting that there may be some advantage in incorporating multiple sensory modalities regardless of the ultimate purpose of the display (Hebets & Papaj, 2005). Vervet postural displays are complex because they incorporate the bright colouration of the genitalia, a relative posture and proximity that facilitates a view of the genitalia and the recipient of the display will frequently audibly lip smack. Given that these displays are complex, what is the best method of understanding their function? This chapter is exploratory, where I will describe male vervet genital displays and how they function within the broader framework of more overt aggressive threats.

As described in chapter one, there are two leading hypotheses: the combat and communicative hypotheses. Each predicts different features within the display itself, where the communicative hypothesis favours sustained postures and flourishing or unnecessary behaviours, the combative hypothesis predicts the opposite, where flourishing and sustained behaviours would be attacked, not abided for communicative purposes. I predict that male vervets use postural displays to test the boundaries of other males, meaning that these postures are more communicative than combative. Sustained postures will be frequent, as will striving to maintain a stable perception of the opponent and displays will likely occur within striking distance so as to maintain the honesty of both displays and threats.

When attempting to understand the motivation of combative movements, it helps to first identify a possible target area. Given a known target, the range of bodily actions and responses males use to both reach the target and protect their own target area can potentially be inferred. To make sense of vervet aggression more generally, with the goal of placing postural displays in a situated context, I will look at the frequency, process and context of more overt threats. To do this, I will first establish that aggressive threats (as described by Struhsaker, 1967a) fall naturally into three categories based on their level of intensity. Given that high intensity threats involve the most risk for animals, because they have the highest cost, I will show how threats of different intensity affect their frequency. Subsequently, I will explore how aggression progresses and the transitional likelihood that aggressive threats advance from one intensity to another. If aggressive threats are used to negotiate social space, these transitional probabilities should indicate an overall hierarchical pattern. For instance, if low level threats frequently precede higher intensity threats, they may function as a warning, or a willingness to escalate. I will then examine how the size of the audience might influence how aggression manifests. Context could have an important effect on either the highest threat observed or the way in which threats tend to progress, as dictated by the theory of embodied cognition as discussed previously.

After this foundation has been laid, I will describe the postural displays recorded during the 2013 mating season based on an Eshkol-Wachmann Movement Notation (EWMN) and analysis. I will describe postural signals alone, and then show where threats are inserted within such interactions. Aggressive displays are thought to preempt higher levels of aggression (Számadó, 2003), which suggests that they are more communicative than combative. By contrasting displays in isolation with those that also contain threats it might be possible to tease out when displays fail to avoid higher levels of aggression, or if they are more so the product of combative tactics. Subsequently, when displays and threats happen within the same interaction, I will show how the overall pattern of the exchange becomes more variable. The goal is to understand what aspects of postural signals are stable, and which are variable, with respect to movements, perception and an element of the external environment, namely the audience. I predict that male postural displays are not formalized, and work in a fluid and dynamic manner depending on the situation at hand, and that in general they function as a communicative means of negotiating social space with other males.

3.2 Wounding patterns

Examining what parts of the body are frequently wounded allows for predictions regarding the body areas potentially targeted for aggressive attacks, and the tactics used to protect body regions from such attacks. It’s important to keep in mind that wounds may indicate one of three outcomes: an obtained target, a defensive tactic in an attempt to protect the target, or that there is no target. The best possible outcome is that wounds indicate a targeted body location, but wounds also suggest defensive tactics, whether they be fighting, fleeing, or producing some other display which facilitates assessment of relative RHP. Using wound frequency by body location assumes that areas that are wounded more frequently are most likely to be actively pursued by opponents (e.g., Pellis, 1997; Geist, 1978). An issue with this assumption is that targets are not always reached as a result of successful counter-tactics. Regardless, looking at wounding patterns facilitates the possible identification of offensive and defensive tactics, but discerning what the actual target is, is difficult to do from wounding data alone.

Comparing wounds across the sexes provides a sense of the relative differences of targets and defensive tactics across sexes, which is useful because males and females have the same weapons and defences, so a comparison makes it possible to infer how these can be differentially deployed. There are three possible interpretations of both high and low wound frequencies in a given body location: a high frequency might suggest a target that is frequently reached, whereas a low frequency might indicate a target that is well guarded, or that in general, there is no target. In order to decide which is the case, wounding needs to be integrated with behavioural data. The objective in this case is to examine whether any stable pattern of wounding exists for male vervets.

3.2.1 Wounds - method

Ad libitum sampling of three groups over two time periods (2009-2010 and 2011-2014) were compared. The earlier time period is from a thesis recently completed (Takahashi, 2012) examining the same vervet population. In order to look for overall stability in wounding patterns, I will look for similarities across the two samples. Then using the later larger sample only, I will test for any sex differences which might reflect sex-specific targets and defensive tactics.

3.2.2. Wounds - results

Wound data for 2011-2014 are presented in Figure 3.2, with earlier data (2009-2010) from Takahashi (2012) presented for comparison (Figure 3.1). The only noticeable shift here are fewer wounds on the head-neck-shoulder region in the later time period, but overall the pattern has been preserved suggesting that among vervets, the target for approximately 40% of hits are the torso and tail region, and that this is a relatively stable finding across time within this study population. After dividing the wound frequency by sex, for the more recent time period only, it is possible to see that a sex-dependent difference in targets and/or tactics are employed (Figure 3.3). Females are likely to target the tail most of all, consistent with previous findings (Takahashi, 2012), whereas males are more likely to receive wounds on the fore parts of their body, namely their head-neck-shoulders and forelimbs.

A goodness of fit test comparing where males are most likely to be wounded indicates that there are statistically significant differences between targeted body regions ($X^2 = 30.22$, df = 4, $p < 0.0001$, where expected proportions were calculated based on surface area for each body part). The trend visible for male wounding in Figure 3.3 suggests that males are more likely to contract wounds on the anterior regions of the body (head, neck, shoulders, and

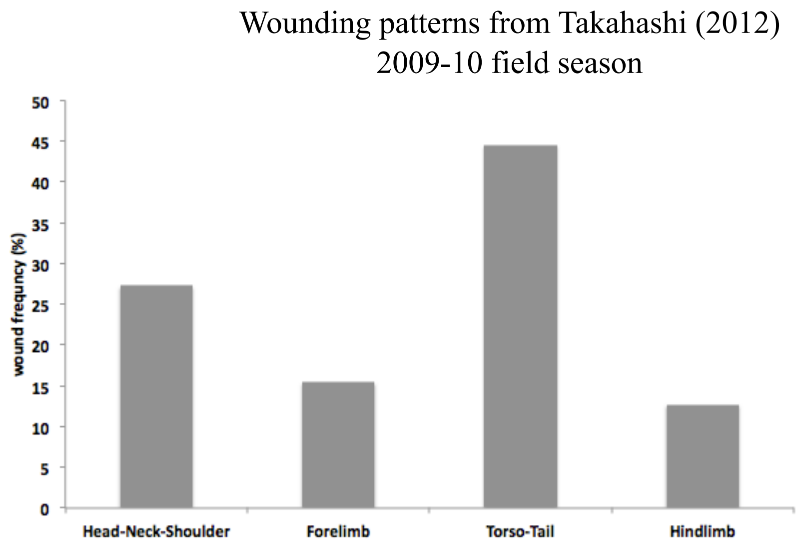

Wounding patterns from Takahashi (2012)
2009-10 field season

Figure 3.1. Wound frequency by body location for Samara vervets (N = 110).

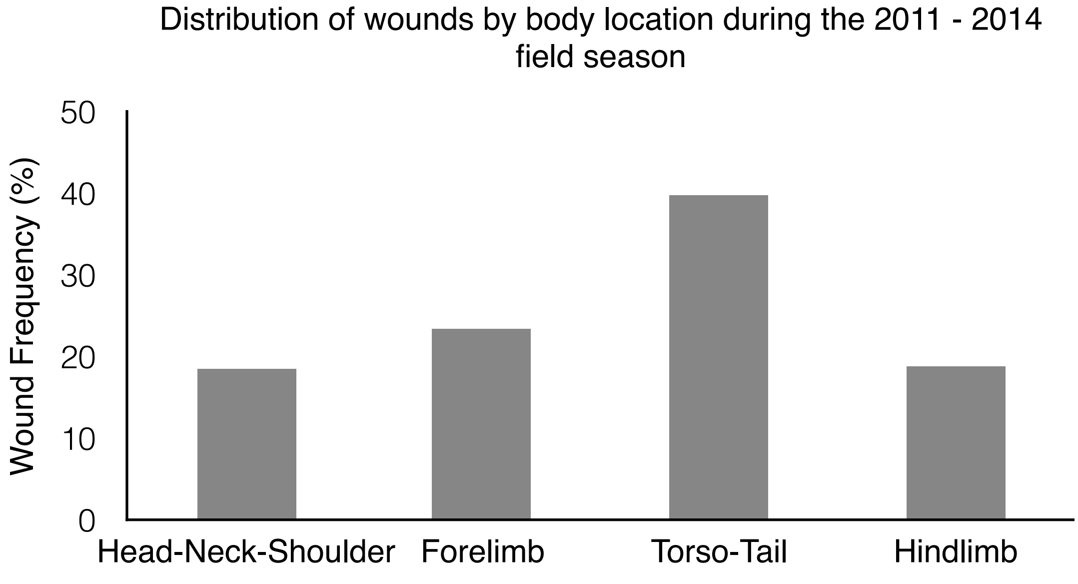

Distribution of wounds by body location during the 2011 - 2014 field season

Figure 3.2 Wound frequency by body location during the 2011 - 2014 field season (N = 245).

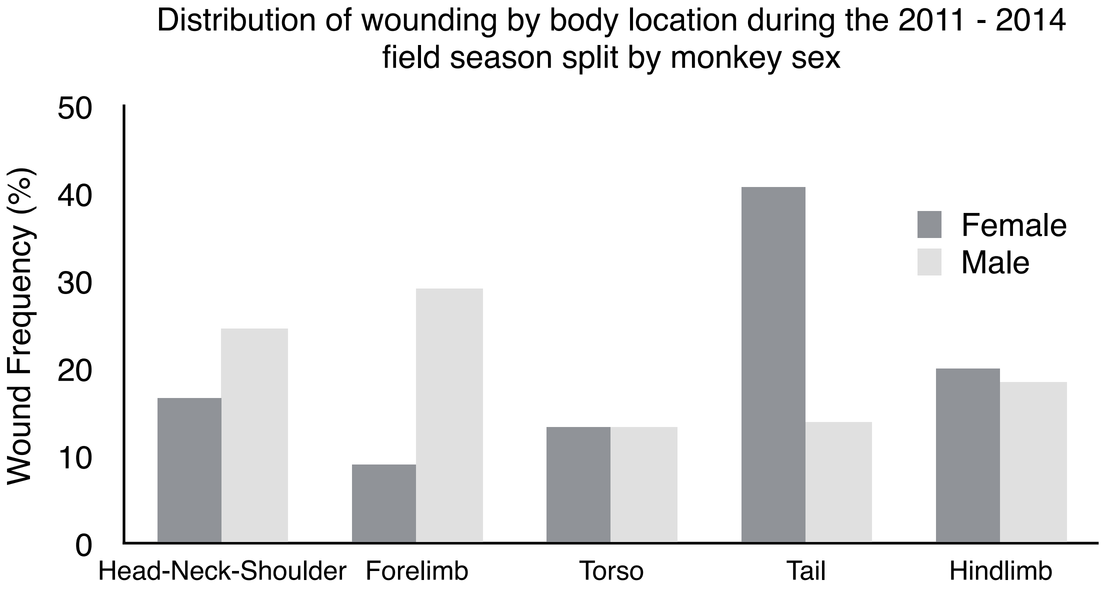


Figure 3.3 Wound frequency (%) by body location for male and female vervets during the 2011 - 2014 field season (N_{males} = 114; $N_{females}$ = 121).

forelimbs) compared to the torso and hind-parts (tail and hind-legs). The higher frequency of wounds on the forelimbs in males suggests that they are more likely to turn and face a fight, rather than flee in situations where wounds are received.

3.3 Threat frequency and intensity

The next important step is understanding the nature of, and frequency with which, vervets typically express their aggression. Extending work that has fully described what threats look like (e.g., Struhsaker, 1967a, b), I will consider the level of intensity and effort that goes into a threat. Understanding the nature of vervet aggression, and how higher intensity threats are used less frequently because they are associated with a higher cost, situates the subsequent analysis of postural displays, and the extent to which they are also aggressive signals.

3.3.1 Threats - method

Threats were split into three levels: low, medium and high (see Table 3.1 for the list of behaviours in each category). A low intensity threat looks like an avoidance tactic, where behaviours in this category require, relatively speaking, the least amount of energy compared to the other two categories. They involve one individual approaching and taking the place of another submitting and departing individual. Relatively low energy here is considered equivalent to the amount of energy needed to move from one location to another, two meters away, along with some added stress from the encounter. This is compared to high intensity, which requires enough energy to sprint away, and relatively speaking more stress for both individuals involved. A medium or mid-level intensity threat is specific to vervets and requires relatively more energy than low intensity aggression, but does not reliably elicit a response as seen in the high level intensity. The highest intensity level requires the highest degree of energy on the part of the aggressor, whereby the aggressor initiates his/her movements very quickly, typically eliciting a response from the reactor, e.g., running away.

Using this new classification of threat intensity I will first look at which level happens the most frequently using the ad libitum data from 2011 to 2014. This

Table 3.1. Behaviours split by level of intensity

Low	Medium	High
Displace	Lunge	Chase
Supplant	Eye threat	Charge
	Head bob	Physical contact
	Vocal threat	

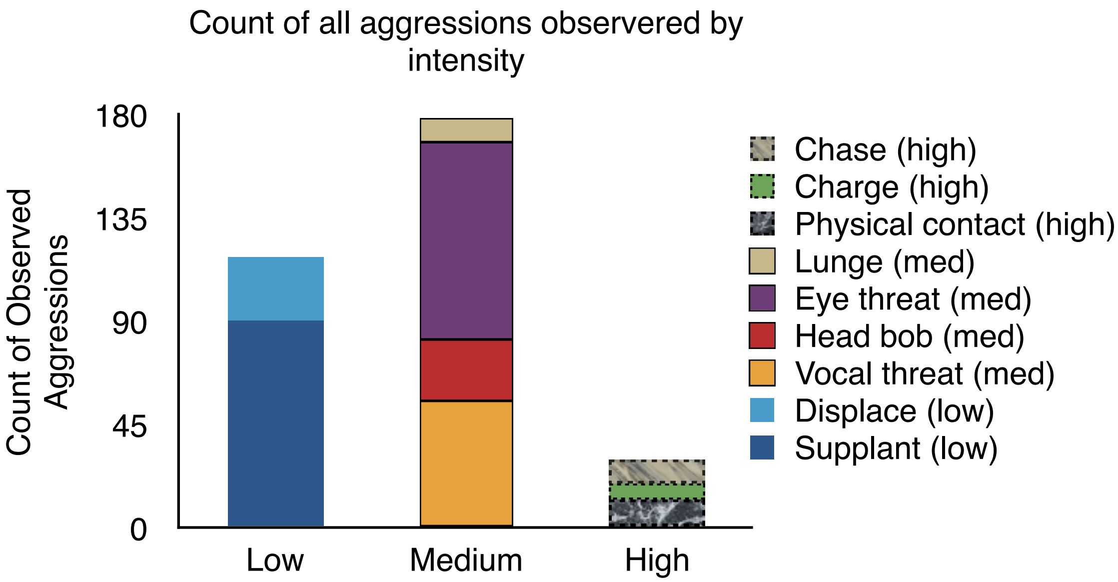


Figure 3.4 Highest aggression witnessed split by intensity (low, medium, high) from ad libitum observations between 2011 - 2014 (N = 328).

data reflects the highest level of aggression witnessed during an encounter between a male and any other partner (e.g., another male, female, juvenile, etc.).

3.3.2 Threats - results

Figure 3.4 shows that medium level intensity threats are observed most frequently, followed by low with high level intensity aggression the least likely to be observed. Controlling for the number of threats that contribute to the intensity category, this pattern is not random (goodness of fit: $X^2 = 94.33$, df = 2, $p < 0.0001$). This evidence is in agreement with previous remarks that high level aggression is avoided whenever possible, and is sought as a last resort (Geist, 1978). It also supports the general idea that lower levels of aggression, and vervet specific threats (defined by Struhsaker, 1967a) like head-bobs and eye threats, may serve as a means of communication in establishing boundaries among vervets, and when those boundaries have been crossed. If that were the case, it would follow that aggression should flow in an orderly fashion, where aggression would begin with a low level warning shot and increase in intensity from there.

3.4 Progression of aggression

By simplifying the numerous threats available in the repertoire into three levels of intensity I will be able to see if the aggressive system is hierarchical, where an interaction would tend to progress from low to medium and then finally high intensity. In such a system, low level threats may function as a warning that higher level aggression may subsequently occur. Based on interactions that were observed, I calculated the transitional probabilities from one level of intensity to another. If high intensity threats are exhibited on their own, with no precursor, it is unlikely that vervets use aggression as a means to negotiate their social space, which a hierarchical pattern would support. Furthermore, if audience has an effect on how aggression might be exhibited, where the make-up of the audience may affect the overall level of aggression exhibited. For instance, given that males were the least likely to show high level aggression towards other males, perhaps this is also the case when there is another adult male nearby. The presence of other males might deter high level aggression in general, since males could be recruited to support during an aggressive encounter. In this case, I would predict that high level aggression would be exceedingly rare in the presence of other males.

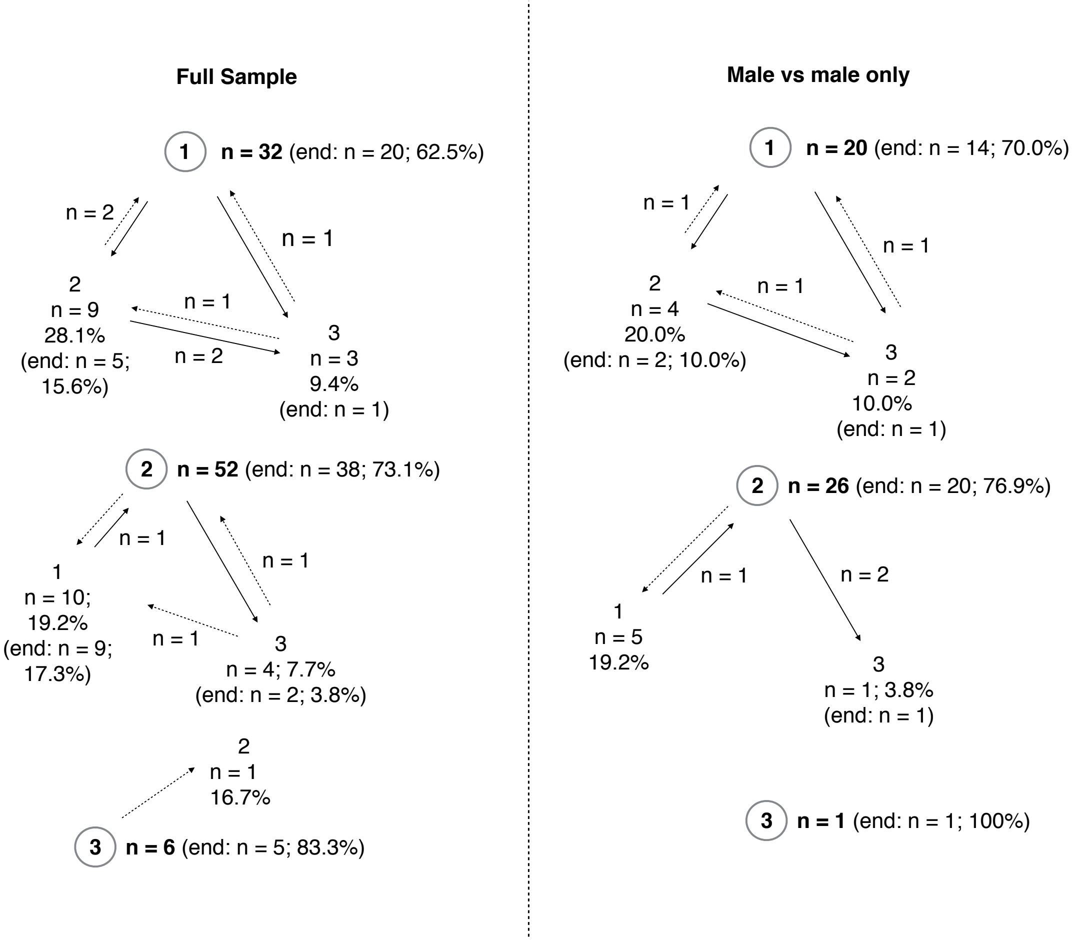


Figure 3.5. Mapping out the progression of observed aggressions and the probability of how aggression escalates during continuous focal sampling of males. The left column is males aggressing towards other males, females and juveniles (n = 90), the right column is a reduced sample of males aggressing towards other males only (n = 47).

3.4.1 Progression of aggression - method

I built two escalation charts using data from the continuous focal sampling of males during the 2013 mating season. The charts map the transitional probability that a threat of a certain intensity would either progress or remain at the same intensity level. The first escalation chart (Figure 3.5) uses the full sample (n = 90, left side), which reflects any time a male aggressed towards any other animal (e.g., female, juvenile, other male), as well as a reduced sample (n

= 47, right side), which shows when one male aggressed towards another male. The second escalation chart (Figure 3.6) splits the reduced sample (n = 47) based on the other audience members around witnessing the aggression. I was not able to show the influence of other males in the audience because the sample was too small, so instead I used audience size. Beginning from the top, where no audience, one, two or more than three audience members are present. When reading these charts, always begin with the number that is circled, which indicates the first threat's intensity in the sequence. The bolded number next to the circled starting point is the total sample that begins at that level. In brackets, next to the bolded sample size, is the number and proportion of interactions that both began and ended at that level of intensity. A solid arrow reflects an escalation in threat intensity, whereas a dotted arrow reflects a de-escalation in threat intensity. Using the first escalation chart, in the top left of Figure 3.5 as an example, this would read that of the 32 interactions that began with a low intensity threat, 20 ended there, 9 progressed to medium level of intensity, and 3 progressed directly to a high level intensity threat. Of the 9 that progressed from low to medium intensity, 2 proceeded to another low intensity threat and ended there. A line with two smaller lines crossing it (as seen in Figure 3.6) indicates that that progression was not observed. For example, in Figure 3.6, with no audience, a low intensity threat never escalated to a medium level threat.

3.4.2 Progression of aggression - results

Looking first at Figure 3.5, where males aggressed towards any other troop member (full sample on the left) or towards other males only (reduced

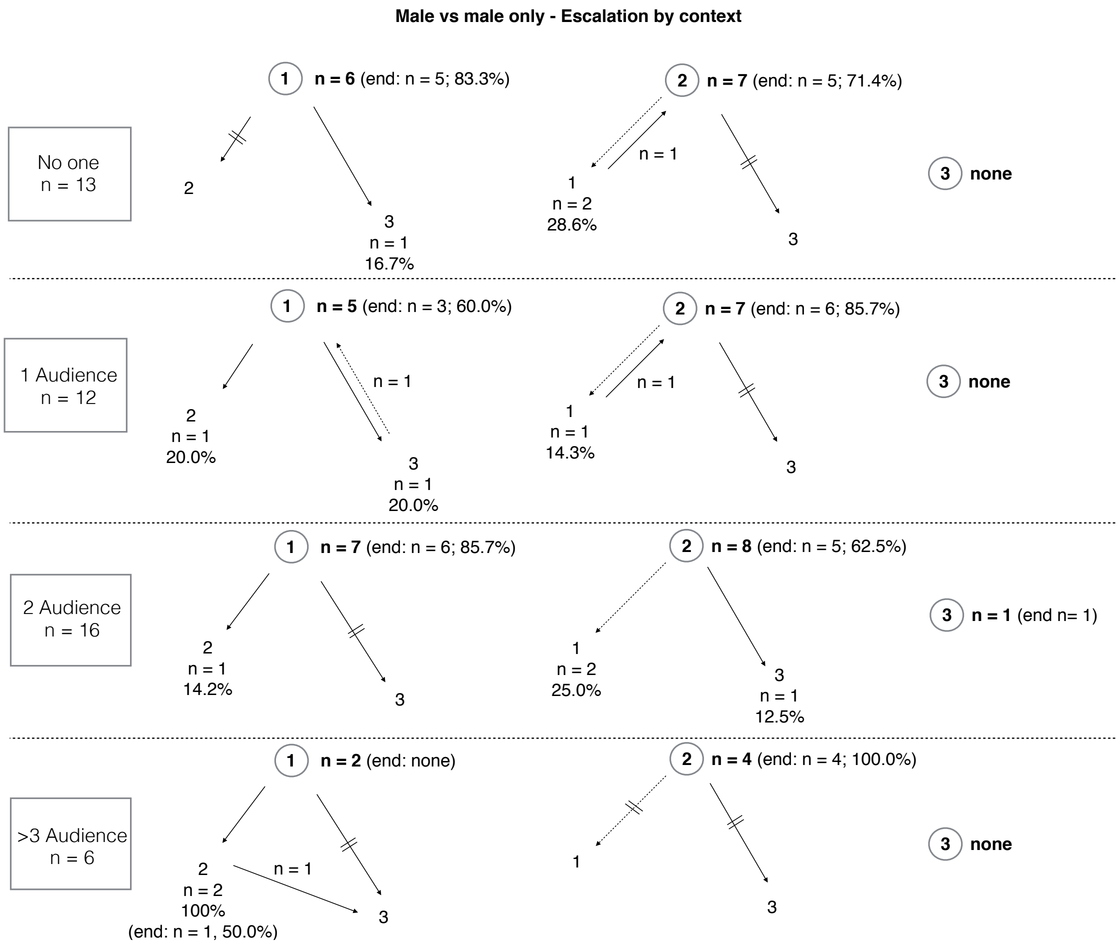


Figure 3.6. Mapping out the progression of observed aggressions and the probability of how they will escalate during continuous focal sampling of males. The top row is the full sample of males aggressing towards other males (n = 47). Each subsequent row represents a different audience size witnessing an aggression between two males, from no one (second row) to three or more audience members (last row).

sample on the right), the overall pattern between the two samples is similar. Unsurprisingly, medium intensity threats were the most frequently observed (full sample n = 52, 57.8%, male sample n = 26, 55.3%). When medium intensity threats were observed, it was frequently a single instance, that did not escalate or deescalate (full sample end: n = 38, 73.1%, male sample n = 20, 76.9%). The same can be said of both low and high intensity threats, where they were unlikely to progress at all (full level 1 end: n = 20, 62.5%, level 3 end: n = 5, 83.3%). Both samples indicate that high-intensity aggression is rare (n = 6), but this is vanishingly so for male-male interactions (n = 1). Although the intensity of an interaction may escalate gradually, from low to medium to high, this happens infrequently (~10% of the time). Also threat intensity does not typically make drastic leaps between levels, thus an animal rarely starts with a low intensity threat that progresses immediately to a high intensity threat (~ 10% in both samples).

Figure 3.6 maps escalation among males onto audience size. Generally the pattern is similar to before, where threats tend to begin and end at the same level of intensity with the exception of the largest audience size (>3), where all low level threats progressed into mid-level threats (n = 2). The low sample size here makes any claims about the effect of audience on the progression of an interactions intensity tenuous at best.

3.5 Description of postural displays

Shifting now from threats to observed display, and then how threats and display work in concert. The extent that postural displays, specifically the RWB, broadside and highly submissive displays, are formalized, and occur in the same way every time will be the first point. The next objective is to understand the variable and stable aspects of vervet postural displays.

3.5.1 Postural displays - method

Videos were considered to contain a display if: a) one animal exposed his genitalia to another animal who b) reacted in an agitated manner. Using the videos that contained a display only (no other threats, n = 54), I evaluated the

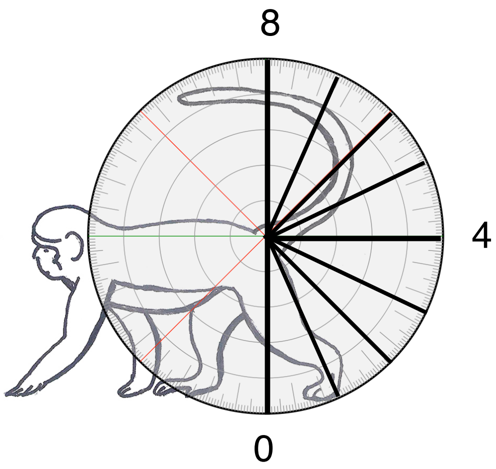


Figure 3.7. How monkey tail posture was measured, using the base of the tail only. The above drawing would receive a value of 5.

frequency of the RWB and broadside displays as they have been described by Struhsaker (1967a) and Henzi (1985) as well as a highly submissive display, compared to the ‘homage’ display described by Henzi (1981). The proportion that each component of each display occurs out of all possible displays in the dataset is reported, along with the concurrence of any two or three other elements.

A RWB display has been reported to contain the following: circling, extended penis, and an erect tail. Circling is when the actor walks around the recipient of the display, who may move to turn and maintain an anterior orientation with the displayer, or sit still in the centre as the displayer walks around him. A penis extension was when the penis was visibly erect or became erect during the interaction. The height of the tail was measured using 16th units around a circle representing the vertical plane of possible tail positions, depicted in Figure 3.7. The tail’s position in space was measured from the point that it left the body, nearest the posterior, and thus does not capture the shape of the tail at the centre or near the end of the tail. The tail was considered erect if it was in position of 4 or higher, in line with Struhsaker (1967a) description. He justifies this minimum tail position because it is the lowest possible position that still allows the actor's genitals to be viewed by the reactor. Tail posture is reported at the time of the display.

A broadside display is described as containing the following components: the actor male presents his side to the reactor (side presented), he then steps past the reactor a few steps pausing to give a full view of the actor's scrotum (posterior view pause) and extended penis. A male presented his side, meaning the length of his body, if the actor stood orthogonally to the recipient, showing the full length of his body. A posterior pause was recorded if the actor paused with his posterior nearest the recipient's face for at least one second (30 frames).

The final display I examined was the highly submissive display, based on the 'homage' display (Henzi, 1981, 1985). The components of the homage display are: a hunched posture, lip smacking and abducting the testicles into the body. A hunched posture is when the animal lowers his head parallel to or below his shoulders, resulting in a hunched back. A lip smack is an audible submissive gesture that vervets do by rapidly opening and closing their lips.

Subsequently, I will describe how postural displays occurred using the simplified results from the Eshkol-Wachmann Movement Notation (EWMN). A subset (20%) of the videos were subject to the full notation process. The notation was evaluated for patterns, which allowed me to make predictions about what factors might be relevant, simplify subsequent coding and generate a dataset

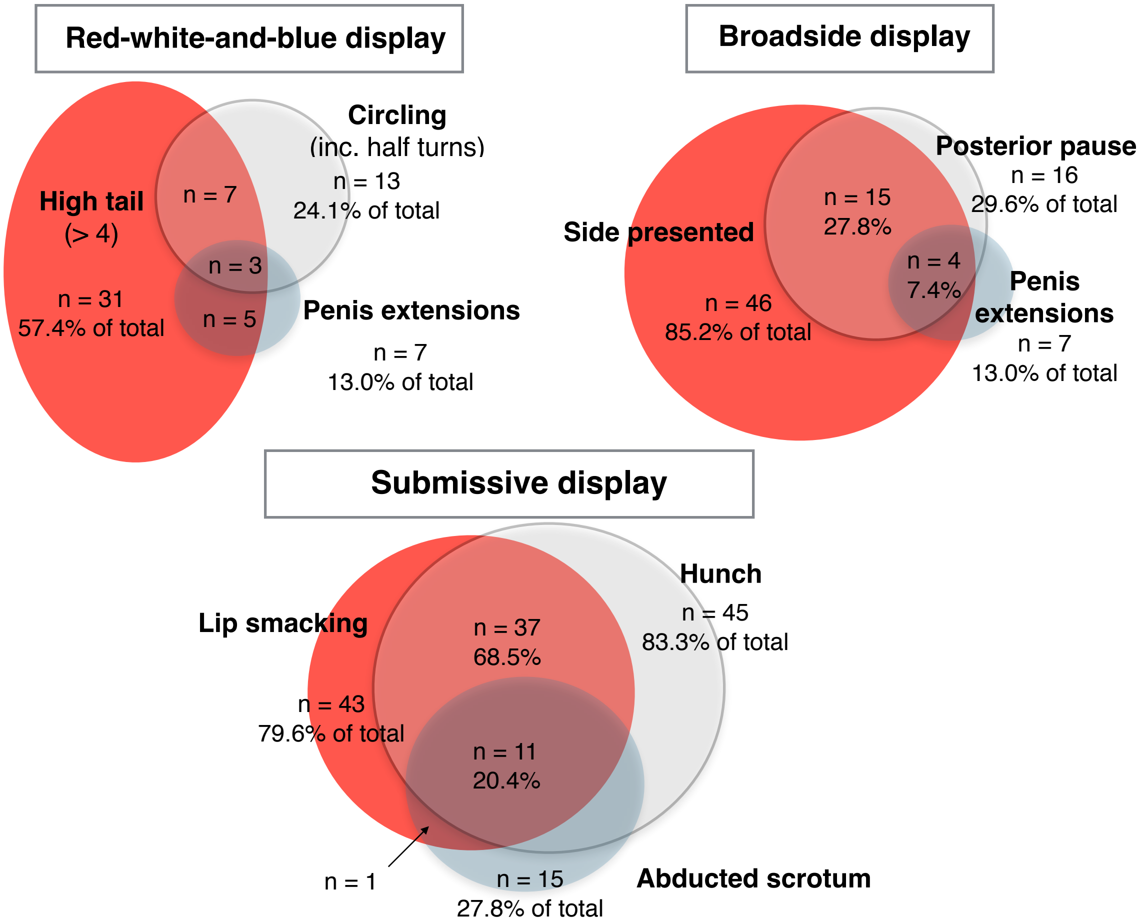


Figure 3.8. Venn diagrams of the RWB, broadside and submission displays. Circles are proportional representations of the observed behaviours.

suitable for statistical analysis. Specifically, 9 relative body orientations (described below) emerged as reoccurring and sufficient to describe the interactions. Each relative body orientation was recorded as a sequence along with which animal (the displayer or recipient) initiated that segment of the interaction.

3.5.2 Postural displays - results

The frequency of components in the RWB display are represented in Figure 3.8. The circles here are ratio of total display observed, giving a visual representation how frequently each component occurred and occurred in concert. Of the 54 total videos, 31 (57.4%) contained a tail held in relatively high position, 13 (24.1%) had animals circling and 7 (13.0%) had penis extensions. Of these, 3 (5.6%) occurred concurrently, which suggests that although these elements are components of a display, that a RWB was not regularly observed as a whole package in its archetypical form. It is worth noting that the height of the tail was not always possible to see (n = 20) nor the state of the penis (n = 20).

For most broadside displays (Figure 3.8, top right), the side presented was often observed (n = 46, 85.2%), whereas posterior pauses were relatively less frequent (n = 16, 29.6%) and penis extensions remains the same as previously described (n = 7, 13.0%). The instances of these three elements observed in concert is comparable to that for the RWB, with 4 instances (7.4%). Note that whenever there was a pause for the perceiver to view the actor's posterior, it was almost always preceded by the actor's side being presented (concurrence rate 93.8%), with only one exception.

Figure 3.8 (bottom row) shows the overlap and frequency of each of submission display behaviours. Maintaining a hunched posture (n = 45, 83.3%) and lip smacking (n = 43, 79.6%) were frequently observed, and frequently observed together (n = 37, 68.5%). The scrotum being abducted into the body was relatively more rare (n = 15, 27.8%) but this is largely a result of the scrotum not always being visible (not visible n = 34, 63.0%). From this it appears that the submissive display is more stable than either of the aggressor's displays.

From the above descriptions, it appears that the aggressor's displays are not as stable as they have been previously described to be. I will now describe the videos containing displays using the 9 postures that emerged as sufficient to describe an interaction that contained a display. The frequency of each posture at the beginning, middle and end of the interaction is shown in Figure 3.9. First I will describe each posture, how to interpret the lettering system, and finally I will describe the frequency graph. It is worth noting, that although from the drawings it appears as though the direction is stable, meaning for example for posture 1 that the standing animal always approaches from the front, and this is not the case. I will elaborate on the directionality of these postures when comparing the display only interactions to those interactions that contain a display and threat in the next section.

Refer to the drawings in Figure 3.9 as I describe each posture. Posture 1 is when one animal is standing with his face nearest the sitting animal's face. Posture 2 is when one animal is sitting and the other stands orthogonal to him, with his feet positioned on either side of the sitting animal. Posture 3 is when both animals stand facing each other and their faces are the nearest body parts. Posture 4 has one sitting animal facing the posterior of the second standing animal. Posture 5 is when one standing animal is standing behind another standing animal, where the face of one animal is nearest the posterior of the second animal. Posture 6 is when both animals face the same direction while standing side-by-side, where their sides are the nearest body parts. Posture 7 is similar, but the animals are facing opposite directions. Posture 8 has both animals standing orthogonal to each other, where one animal faces the other's side. Finally, posture 9 is when both monkeys are sitting. There are two elements worth highlighting across the postures. Posture 1, 2, 4 each have one animal sitting while the second animal stands, and postures 2, 4, 5, 7 and 8 facilitate a view of the animal's genitalia.

Next to the number associated with each posture in Figure 3.9 is a letter that indicates who moved first and initiated the relative orientation, forcing the other animal to react and adjust his own movements. 'A' means that the aggressor initiated, 'V' means the victim or submitting animal initiated, and 'M' represents both animals moving at the same time or mutually initiating. The interaction is broken into three time sections, the approach, during the interaction, and the depart from the interaction.

Next to the drawings of relative body orientations in Figure 3.9 are the frequencies for a particular time segment of the interaction. From this it is apparent that the most common postures are 1 (n = 35 total), 2 (n = 39 total) and 4 (n = 44 total), for the approach, during and depart respectively, during which the aggressor is most likely to initiate and drive the interaction. Other postures do occur, but none with any particularly high regularity (next highest is position 7, n = 8 total). When these positions are put together into a sequence, unsurprisingly this exact pattern emerges. The primary postures 1, 2 and 4 occurred in sequence, with the actor initiating all movements, in 38% of the videos. No other pattern was observed more than twice (for all other patterns observed refer to Appendix B).

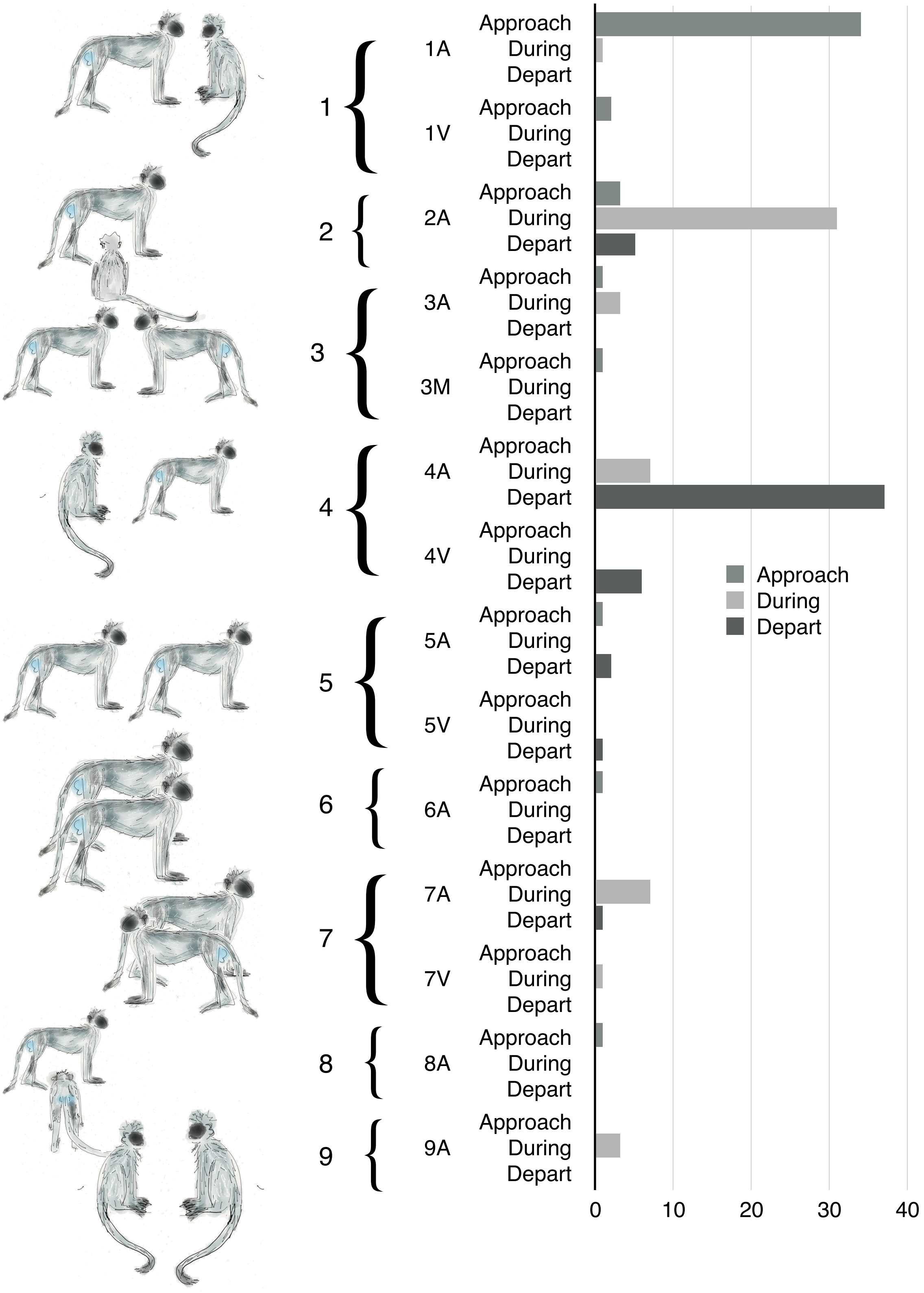


Figure 3.9. Images of the relative postural orientations that emerged the EWMN and the frequency with which they were adopted as the two animals approached, during the interaction and departed from one another.

3.6 Postural displays with and without threats

Given that postural displays elicit a fearful response from the recipient, they are thought to be genuinely aggressive in nature. It has been reported that these displays occasionally occur in conjunction with threats, but not specifically what kind of threats or in what way this may change the outcome or course of the interaction. I will contrast displays that occur in isolation as presented in the previous section, with interactions that contain both postural displays as well as conventional threats. Of particular interest is whether the sequences of behaviour become more or less stable, and what the role of directionality, proximity, eye contact, and sustained versus dynamic movement help to infer about the function of these behaviours within the broader context of aggressive behaviours available to vervet monkeys.

The direction of approach in particular may shed some insight onto the intended outcome of these displays. Vervet monkeys are easily startled, and occasionally a startle response can manifest into aggression (personal observations). An approach from behind would be more likely to startle the recipient, whereas an approach from the front would be the least likely to startle. Proximity is of particular importance for threat displays because threats should be displayed within striking distance in order to be both honest and inherently threatening. Dishonest or unreliable threat displays that occur within striking distance can be readily challenged or punished. Eye contact may allow me to infer small elements of the animal's perception. I hypothesize that vervets will attempt to keep their perception of each other stable, through eye contact and maintaing an anterior-anterior or face-to-face view of one-another. By maintaining a stable perception of the opponent, vervets also manage to keep their opponent's weaponry in view, while also reading yourself to react quickly should an attack be launched at close range. It is possible these perceptual elements are what vervets attempt to keep stable, rather than their relative postures.

One component of the broadside display is when the actor walks past the recipient and pauses to facilitate the full view of his genitalia. In general, a communicative gesture would incorporate pauses to facilitate delivering a clear message, whereas a combative gesture would likely not contain static such poses, because they could be easily challenged and attacked. The last element of this section tests how frequently movements in vervet postural displays are dynamic, static, or both.

3.6.1 Postural displays with and without threats - method

Using the same method described in the the previous section, 20% of the 29 videos recorded as containing both a display and a threat, were subject to the full EWMN, from which the same 9 relative body postures as described previously emerged. When examining the sequence of postures, I removed the threats from the sequence, to simplify the interaction slightly. Lastly, I examined the type, frequency and timing of threats.

Because posture 1, 2 and 4 happened the most frequently, I will focus on their directional components only. For each posture, it is possible for the animals to be in the same relative body orientations but not in the same absolute position, whereby the standing animal could approach from directly head-on (front), from the side (side), from behind (behind) or a 45 degree angle (always side / behind). Interactions that contained both a threat and display were typically longer than the three segments used previously. Sequences with threats were in general more variable than those that consisted of a display in isolation. In order to apply the same sequence logic to sequences that were longer, I only examined the direction of the the first (approach), second (during) and last (depart) positions in the sequence.

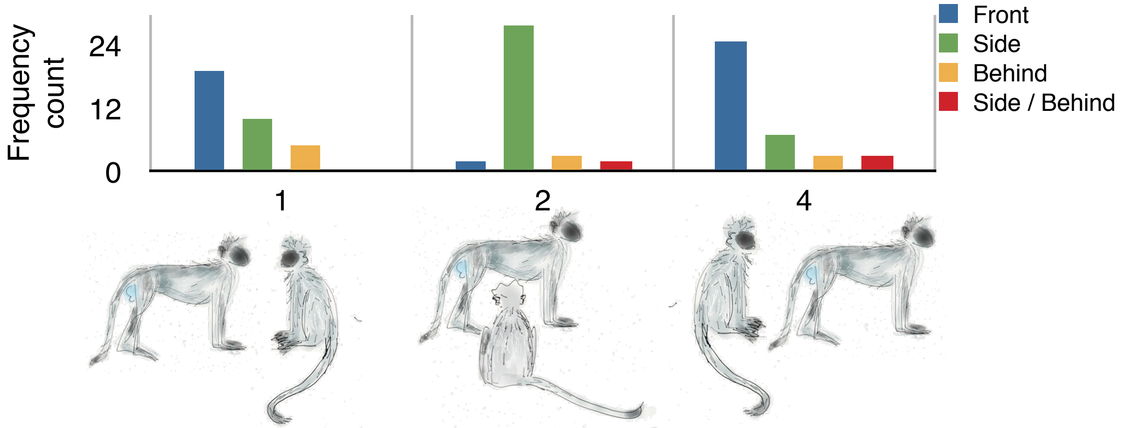
Proximity was measured in units of one or one-half monkey body lengths. The distance between the videographer and the interaction was variable, as was the amount of zoom employed while videoing, and using the monkey's body as a unit of measurement that exists within the frame controlled for all of these other factors. A distance of 0 indicates that the animals made contact, and >0 is almost touching. For the display-only condition, two measures of proximity are examined, the closest point that two males reach during the interaction, and the distance between them at the time of the display. For the display and threat condition, these are also reported as well as the distance at the time of the threat. Eye contact was defined as when both monkeys oriented their heads towards each other at the same time. The presence or absence of eye contact was recorded as occurring during the approach, during the interaction or while departing. Note that in order to make eye contact while departing, the withdrawing animal must look back over his shoulder. I also recorded if the animals were shifting to maintain an anterior-anterior orientation with one-another, despite not making eye contact directly, but still trying to keep their opponent in sight. A movement was recorded as sustained if it was held for at least one second (30 frames), and dynamic if it was never held. Each of these is compared across conditions, where videos contained threats and displays or displays only.

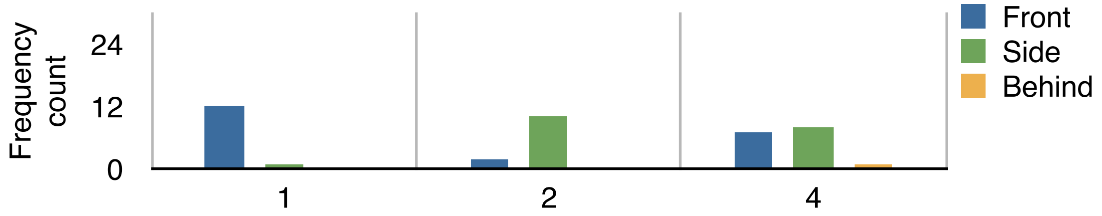
3.6.2 Postural displays with and without threats - results

The frequency with which certain postures occurred was the same as presented in the previous section, where postures 1, 2 and 4 were the most common for the approach, during the interaction and depart respectively. The sequence of postures in a given interaction, however, was not preserved, where no one pattern emerged above any other (see Appendix B for table showing all possible sequences). The most common sequence was 1-2-4 but only in 4 cases (13.8%). In general, this is a result of the fact that sequences were typically longer (33% had more than 3 postures), and thus had more relative body orientations during the interaction, compared to those observed in the display only condition. This suggests that the introduction of threats coincides with longer and more variable interactions.

Threats were equally likely to occur on approach (n = 10) or during the interaction (n = 16), with a few occasions where there were multiple threats, that occurred as the animals approach and during the interaction (n = 3). Most often, there was only a single threat during the interaction (n = 16), although occasionally multiple threats occurred (2 threats n = 3; 3 threats n = 1). The type of threat was likely to be of a medium level of intensity (n = 22: eye threatening n

Figure 3.10. The direction with which relative body orientations occur


Direction of relavitve body orientation most frequently observed during male vervet displays


Direction of relavitve body orientation most frequently observed during male vervet displays where a threat also occurred

= 11, head bobbing n = 2, vocal threat n = 9), with some high intensity threats (n = 5: chasing n = 2, physical contact n = 3).

The direction of the postures most frequently observed (1, 2 and 4) are illustrated in Figure 3.10, where the display only condition is on the top and the display and threat condition is on the bottom. Within the display-only videos, there is a relatively high degree of variability within the first posture, where approaching from the front (n = 19) happens most frequently, occasionally from the side (n = 10), and finally a few from behind (n = 5). The same is not found in the display and threat condition, where the approaching animal nearly always approached from the front (n = 12; side n = 1). This difference between groups is

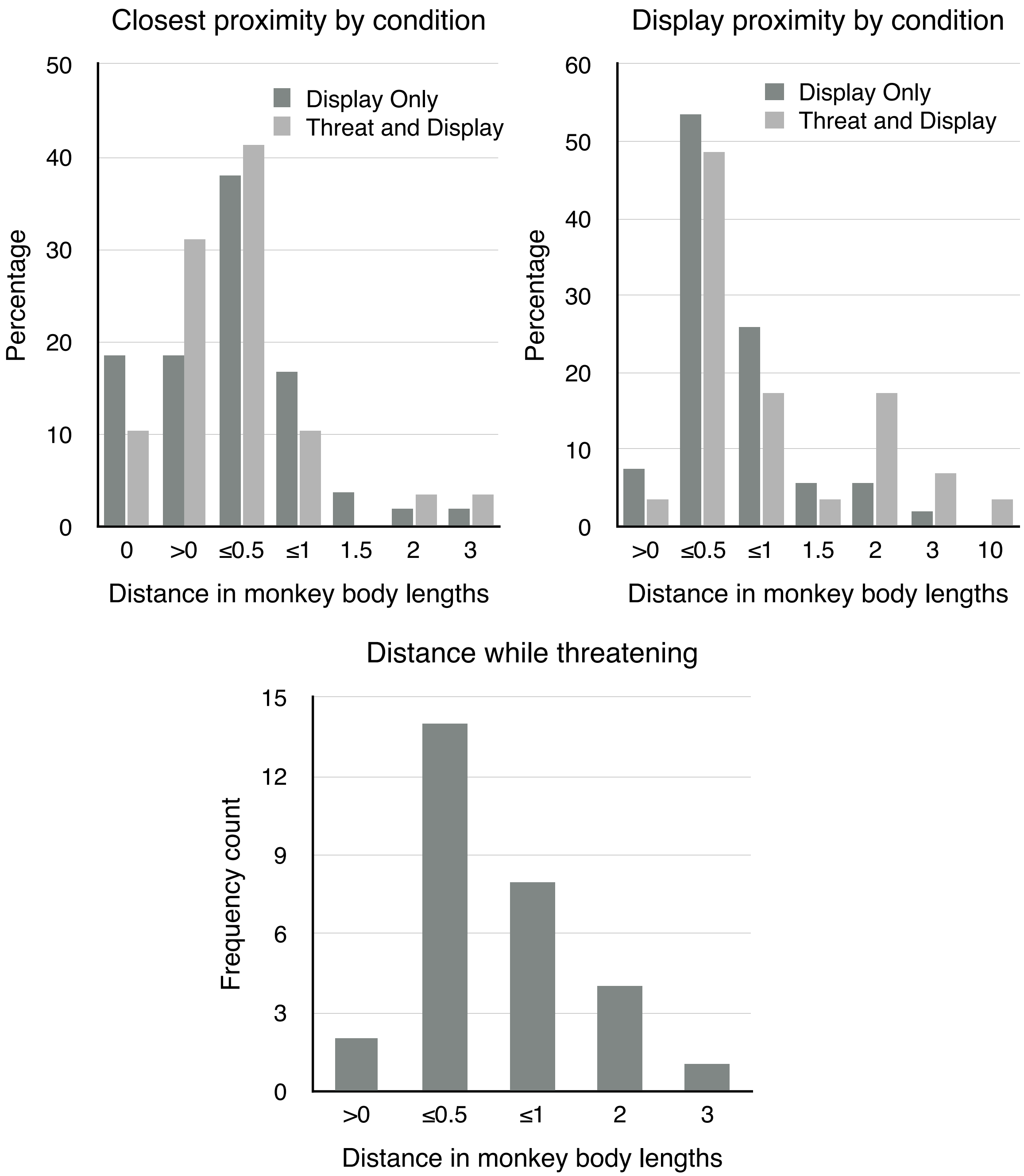


Figure 3.11. Proximity by condition, broken into closest proximity (top left), proximity during the display (top right) and proximity during a threat (bottom left).

not quite statistically significant (Fisher's exact test p = 0.07). Posture 2 for the display only condition primarily consisted of side on views (n = 28), and the same was true in the display and threat condition (n = 10). Posture 4 in the display only condition was primarily front on view (n = 23), however the other directions were also observed (side n = 7; behind n = 1; side/behind n = 3). In the display and threat condition, front (n = 7) and side (n = 8) orientations were nearly equally observed.

All measures of proximity are represented in Figure 3.11. The closest proximity that two animals would get during an interaction is shown in the top left graph. Here, regardless of condition, most interactions occurred equal to or less than one monkey length away (n = 67, 80.7% of total), well within striking distance. A surprising number of interactions that contained a display consisted of the animals making physical contact (n = 10, 18.5%), usually because the

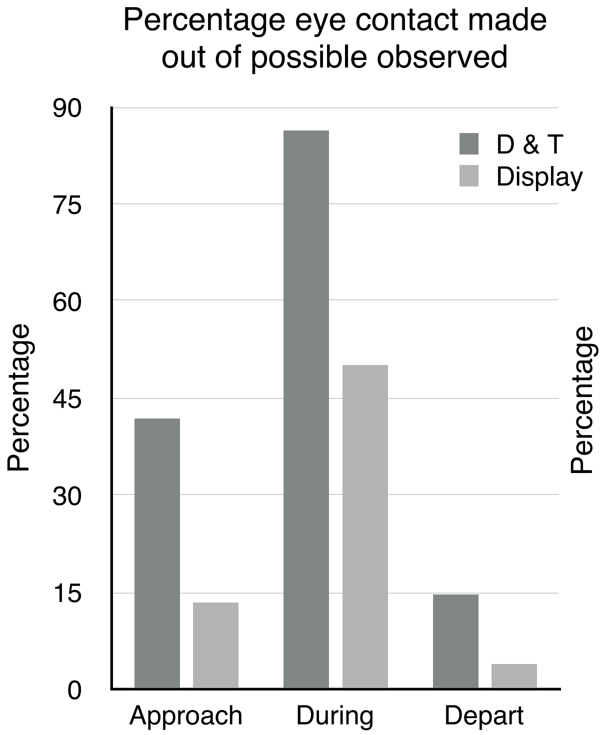


Figure 3.12. Percentage eye contact made during different segments of an interaction, split by condition.

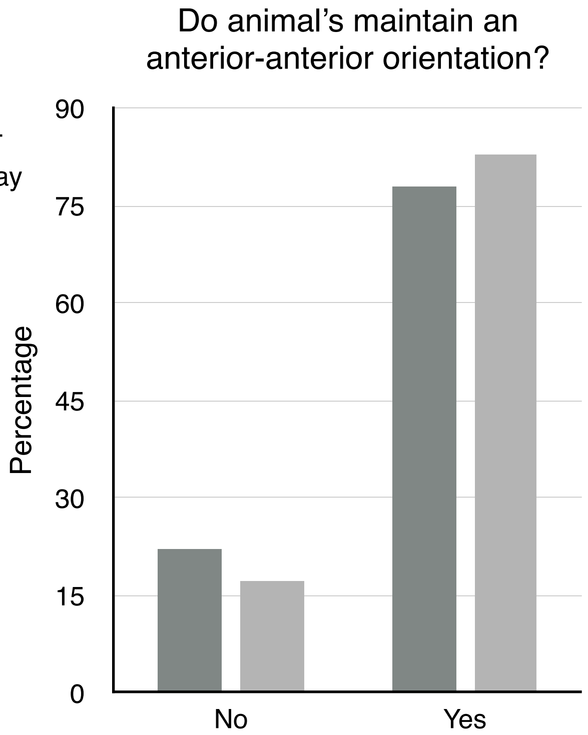


Figure 3.13. Proportion of interactions where animals strive to maintain an anterior-anterior orientation (yes) or do not, split by condition.

aggressor would place his hand on the recipient's head (n = 7, 13.0%). Occasionally the actor would grab (n = 2) or attempt to grab (n = 4) the recipient in a similar fashion that males grab females prior to mounting in order to copulate. The distance between monkeys during a display is similar (Figure 3.11, top right graph), where the majority were observed under 1 monkey body length (display only n = 47, 87.0%; display and threat n = 20, 69.0%), with some at a greater distance (display only n = 7, 13.0%; display and threat n = 9, 31.0%). Similarly, threats typically happened well within striking distance (≤ 0.5 n = 14, 48.3%; 1 n = 8, 27.6%).

Figure 3.12 illustrates the proportion of eye contact made out of all possible interactions in that condition. Overall, eye contact was least likely to be

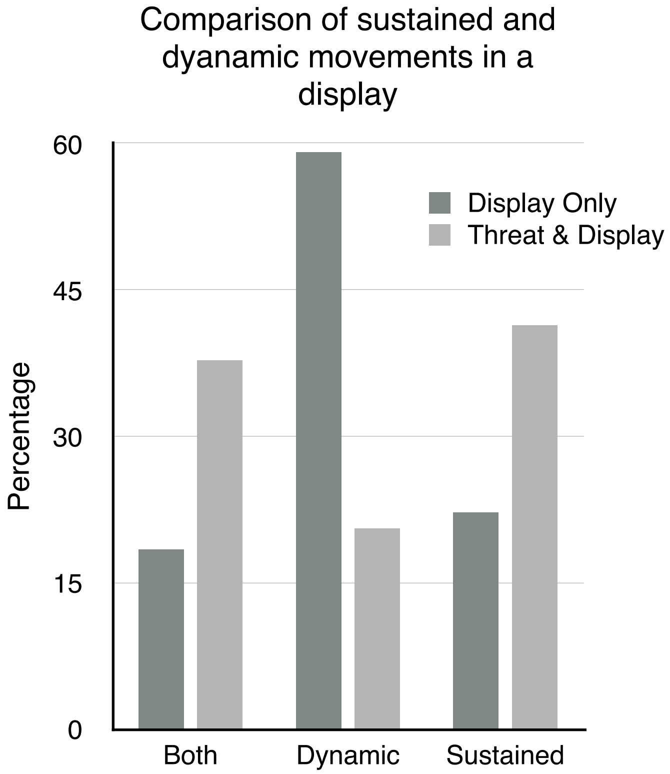


Figure 3.14. Frequency count of either sustained, dynamic or a combination

made while departing, however, it did occur (display and threat 14.8%; display only 4.0%). Eye contact was almost always observed in the display and threat condition (86.2%), which was less likely in the display-only condition (50%). For each point in the interaction, eye contact was more likely in the display and threat condition than the display only condition. Figure 3.13 shows that in general animals do strive to maintain an anterior-anterior orientation during a display, regardless of condition (display only: 77.8%; display and threat: 82.8%). Figure 3.14 shows that movements during a display were most likely to be dynamic during the display only condition (59.3%), and equally likely to be either sustained (41.4%), or both sustained and dynamic (37.9%).

3.7 Statistical analysis

From all of this descriptive work, two questions emerge: what is the difference between a condition that contains a display in isolation compared to a threat and a display, and what predicts a highly submissive response. I ran two multi-level mixed effect logistic regressions, the first predicting differences between the condition (video category membership) and the second predicting a highly submissive response based on the ‘homage’ display (Henzi, 1981).

Eye contact in particular was markedly different between the conditions, but one variable not as yet explored is the effect of rank. The calculation for rank is a sum of all prior encounters with other troop members, where higher ranking animals are assumed to display higher RHP because they frequently win contests. Henzi (1985) specifically states that during RWB displays, the displaying monkey is higher ranking. Perhaps this is the case for the display only category, where additional threats are a result of closer rank score. The ultimate question is what coincides with males who increase the aggressive nature of the interaction from a display to a more overt threat? The other side to this coin is what predicts when the other male will submit?

The submission response was a reliable and frequently observed response in the videos. In order to understand what predicts when males will back down, proximity may play an important role. Encounters that reach a closer maximal distance may be perceived as more intimidating, because the closer two animals are, the easier it is to quickly strike an opponent. I predict that males who strive to maintain an anterior-anterior orientation are more likely to also display the submission response. A male that shows clear signs of submission may be doing so because the threat of attack is more likely. Moreover, the presence of other monkeys may influence a willingness to back down, specifically if males are witnessing an interaction. Vervet males have been known to form coalitions, although rarely (Freeman, 2012). The possibility to recruit other males could lead to more severe aggression, where two big males are a more serious threat than just one. The opposite could also be true, where males may not show overt signs of submission in the presence of other males because of social facilitation, where one monkey could learn that the other is likely to submit in a contest situation.

3.7.1 Statistical analysis - method

For the first analysis, rank, eye contact and proximity were factors thought to influence condition membership (display only versus threat and display). Rank was based on the Normalized David Scores (NDS) described previously, but standardized in order to compare across groups. Standardized David Scores (SDS) take the rank of each animal and divide it by the animal with the highest rank, resulting in a score between 0 and 1 suitable to compare across troops. NDS, by contrast, are dependent on the size of the troop. A SDS difference score was calculated by subtracting the actor's SDS from the reactor's SDS. Eye contact, a binary variable, was indicative of whether monkeys made eye contact during the interaction. Finally, the closest proximity at any point during the interaction was used, recorded in monkey body lengths, as was previously described.

The submission response has three components: abducted testicles, hunched posture and lip-smacking submissively. A variable was generated to reflect whether this response was present when two or more behaviours were observed, or absent when one or none of this behaviours were observed. Since testicular state was not always visible, this seemed a fair way to reflect the possible completeness of such a response. Moreover, if more behaviours coincided, it may be that the response is perceived as more submissive. The closest point that two animals reach during the interaction was again used. Whether the reactor male strived to maintain a face-to-face orientation was recorded as a binary variable (0 no, 1 yes). The number of males present was recorded during the interaction. In both analyses, the identity of both the aggressor and victim were used as crossed-random factors.

Table 3.2. Results from multi-level mixed effects logistic regression predicting video condition

Predictor	β	Std Error	z	*p*	95% CIs
Eye contact	2.28	0.75	3.05	0.002	0.82 to 3.75
Rank Difference	0.64	2.46	0.26	0.79	-4.17 to 5.46
Maximum Proximity	0.062	0.08	0.77	0.43	-0.96 to 0.22
Constant	-2.71	0.87	-3.13	0.002	-4.42 to -1.01

Wald $X^2 = 10.09$, $p \leq 0.02$

3.7.2 Statistical analysis - results

The first logistic regression with video condition (display only versus threat and display) as the dependent variable was statistically significant in predicting the difference between conditions ($p \leq 0.02$, see Table 3.2 for results). The difference between rank (SDS difference) was not significantly related to condition ($z = 0.26$, $p = 0.79$), nor was proximity ($z = 0.77$, $p = 0.43$), however, eye contact during the interaction was statistically significant ($z = 3.05$, $p = 0.002$) where eye contact was more likely in the threat and display videos. The random

Table 3.3. Results from multi-level mixed effects logistic regression predicting a highly submissive response

Predictor	β	Std Error	z	*p*	95% CIs
Anterior-anterior	1.11	0.70	1.60	0.11	-0.25 to 2.48
Male(s) Present	-0.10	0.36	-0.28	0.78	-0.80 to 0.60
Maximum Proximity	0.007	0.09	0.09	0.93	-0.16 to 1.77
Constant	0.86	1.09	0.78	0.43	-1.28 to 2.00

Wald $X^2 = 2.96$, $p \leq 0.40$

factors did not significantly contribute to the model ($p = 0.53$).

The results from the second logistic regression looking at the homage response are reported in Table 3.3. The model was not statistically significant (Wald $X^2 = 2.96$, $p \leq 0.40$), and none of the factors contributed to the model (anterior-anterior: $z = 1.60$, $p = 0.11$; males present: $z = -0.28$, $p = 0.78$; maximum proximity: $z = 0.09$, $p = 0.93$) nor did the random factors significantly contribute to the model ($p = 0.78$)

3.8 Discusion

This chapter has explored an assortment of stable and variable elements of male vervet postural and threat displays. From the wounding data it is seems that males are more likely to turn and fight, incurring the most wounds on their forelimbs. This is likely a defensive tactic in an effort to guard some other target (or there may be no target). The location that is least likely to be wounded is the torso and tail, suggesting that males are attempting to, and perhaps successfully, guarding this area from high level aggressions. The type of aggression most likely to be observed are those with a medium level of intensity, where all behaviours in this category are specific to vervets. This supports the idea that aggression, and vervet specific behaviours, may function as communicative tools to negotiate social space.

Aggression did not function in a hierarchical manner according to my criteria, but rather threats frequently began and ended at the same intensity level. High intensity threats were rarely observed, but this was vanishingly so when looking specifically at the male-male sample. This is consistent with the idea that high intensity threats have the highest potential cost and are to be avoided whenever possible. This was especially the case when looking at males who aggressed towards other males, where the potential costs may be even higher given their overall larger physical size.

Components of the RWB and broadside displays were observed, but rarely with all elements concurrently. One factor that may have contributed this low overall frequency was that the tail and genitalia were not always visible. While this may be the case for the broadside, circling behaviour was alway possible to discern and it was not frequently observed. All elements described by Struhsaker (1967a) may be important elements generally, but the most commonly observed component was the side presented (85.2%). Furthermore, whenever there was a pause showcasing the actor's posterior (29.6%) the side was nearly always presented first (concurrence rate 93.3%). The most reliable of the three displays was the submission display, in spite of the fact that the reactor's scrotal state was not always visible. The reliability of the submissive display may have been in part a result of the video selection criteria, where a fearful or agitated reaction by the recipient was a part of the video inclusion criteria.

The directionality of the most frequently observed postures elucidated that within each posture, at particular stages of the interaction there is further variability within the display. This was true in most cases except during the interaction, where the side on view of the actor's torso was a relatively stable component during a display (n = 28, 80.0%). When a display also involved a threat, the direction of approach also became more stable, where the actor nearly always approached from the front (n = 12, 92.3%). This was perhaps because the actor is attempting to avoid inadvertently startling the recipient of the display. Vervets are easily startled and when approached from the front, an individual is most likely to be seen, thus reducing the likelihood that the recipient of the display will be caught unaware.

The data on eye contact supports this, where eye contact was more likely in general when a display also involved a threat compared to the videos that contained a display only. The logistic regression provided further evidence that eye contact played an important role in predicting when displays will escalate into additional threatening, while proximity and rank differential did not. Recognizing that another monkey is approaching by establishing eye contact means startling accidentally is highly unlikely. Furthermore, in order for a threat to be received, eye contact must be established, and this is also true in this case. In both conditions, monkeys strived to maintain an anterior-anterior orientation with their opponent, implying that they are possibly trying to maintain a stable perception of them and their weaponry, keep their own posterior away from their partner, or both.

All displays and threats in the videos occurred at a very close proximity (equal to or less than one monkey body length) and well within striking distance. Most postural displays tended to occur equal to or less than half a monkey body length, which looks in a way like a elaborate displacement, where the actor comes so close to the recipient that he is forced to move. Generally speaking it was clear that both postural and threat displays took place within a reasonable distance that they could be challenged should their authenticity be questionable.

Postures were most likely to be dynamic in the display only condition and equally likely to be either sustained or sustained and dynamic during the display and threat condition. Sustained postures during interactions that contained threats is slightly counterintuitive; why stay relatively more stationary when also threatening? One possible interpretation is that monkeys are again attempting to not startle one-another unnecessarily. Startles can quickly escalate into threats, By using sustained postures the animals have more opportunity to keep arousal low. It is also possible that by attempting to maintain relatively low overall arousal, monkeys are using threats as a means to negotiate within their social world and manage encounters where boundaries may have been crossed (e.g., access to food, mates, etc.). It also suggests that threat displays, which are specific to vervets, are communicative rather than combative. Displays, in contrast, were more likely to be variable and dynamic. They may be combative, however when displays were observed in conjunction with threats they manifest more as communicative tools. An alternative interpretation is that displays in isolation are socio-sexual in nature. In a few videos (n = 6, 7.2% of all videos) the actor grabbed or attempted to grab the recipient as though to mount him. This was in a very similar way that males grab females before copulating. Socio-sexual mounting is not uncommon among primates (Dixson, 2012) and was seen among juvenile vervets (personal observations). Perhaps in this way vervets are protecting their hindquarters from their opponents, to avoid successful mounts.

The extent that the RWB and broadside displays are continuations of the same display was not possible to determine in this case, due in large part to the low frequency of RWB displays. Of note is that both the broadside and RWB did occur in a separate population of wild vervet monkeys, although rarely in the archetypical way described by Struhsaker (1967a) and Henzi (1985). Although the elements of these postural displays did regularly occur in isolation. Given that cues are frequently the precursors of signals, another way to tackle this question might be instead to examine what elements of the display may have been cues initially. Might the side presented or ‘confident’ walk of a monkey serve to guide some future action about these interactions that were not represented here?

CHAPTER 4: TESTING THE PRESENCE OF DOMINANCE RELATED CUES

4.1 Introduction

In addition to overt signals or other communicative gestures there are subtle cues that relay additional information about an animal. Such cues have been shown to be reliable and hence useful in making correct judgements based on subtle or little information, such as recognizing the smell of nest mates among numerous vertebrates and invertebrates (Wyatt, 2010). A cue can be defined as information that is emitted unintentionally and/or as a necessary by-product of other processes or bodily structures, for instance, a quiver in a person's voice indicates that he or she is nervous, providing information on their internal state that they may wish to hide, or a man with large shoulders may tend to sway more when he walks relative to a more slightly built man. In both cases, neither individual may be aware of the cues they are giving off. As has been discussed in the introduction, the largest distinction between cues and signals is that cues are inadvertent, whereas a signal serves a direct purpose, such as communication. Thus, unlike signals, which serve a direct communicative function and are under the control of the sender, cues provide information to perceivers in ways that cannot be controlled by their senders. The purpose of this chapter is to explore if there are dominance related cues emitted by male vervet monkeys that could potentially function alongside more overt postural displays.

In the previous chapter, males were more likely to approach from the front alone if the interaction involved a threat and a display. The timing of the threat itself varied, they were equally to occur on approach or during the interaction, but the direction of the immediate approach was stable. The near complete convergence on this particular approach direction suggests that males may have a sense that an interaction is more ‘serious’ or the tension is heightened somehow before it begins, and only approach from the front so as to avoid startling the opponent unnecessarily. Many factors could contribute to this possibility, including rank differential, previous experience with known individuals, or as a result of some internal states such as being too hot, but I predict that males are also sensitive to dominance related cues that are produced inadvertently produced.

The selective pressures that shape how signals will ultimately manifest depend entirely on components that exist in the world already (Donath, 2011). In the words of a professor of mine, “There is no such thing as a free lunch.” Natural selection cannot operate on something that does not exist to some extent already. Instead, selection pressures shape the basic elements that are readily available, moulding traits or scaffolding behaviour to the extent that it may then become a reliable signal. A cue, an inadvertent by-product of some existing trait or behaviour, may sometimes (even frequently) be the basis for signals.

Considering the components of vervet displays that I have just shown to be reliable, there are a few that could readily function as cues in isolation. To recap briefly, displays reliably incorporated a display of the actor’s genitalia and showcasing a view of actor’s body (length wise, the long view). Other possible components might include a ‘confident’ walk, as described by Struhsaker (1967a) and elevated tail posture. It is possible that any one of these, when viewed in a non-social situation, may function as a cue of dominance rank. The length of the body may be a cue for physical size. The colour or amount of colouration visible at a given time may cue dominance, where more dominant animals showcase their genitalia more overall compared to less dominant animals. An elevated tail posture may facilitate the view of the genitalia and portray a more confident walk. Each of these might be components of vervet displays, but also cues when not presented in a social context.

The current study presented short video clips of vervet males engaged in a non-social activity to two different samples of observers. First to naive undergraduate students (i.e., individuals with no known previous experience with non-human primates, nor any training in collecting observational behavioural data) and second to a sample of experienced primatologists attending a conference. If a human observer, particularly one with no known training in this field, is able to detect cues related to dominance rank, it is likely that vervets themselves will be able to as well, since it would benefit them in particular to utilize such information. I predict that participants would be able to detect postural cues related to the animal's dominance rank. In particular, I predict that tail posture and the relative size of the animal will be a salient cue to the animal's rank.

4.2. Study 1 - Undergraduate observers

Method

Participants

Fifty-five undergraduates (17 male and 38 female, mean age = 20.9 ± 3.97 years) participated in the study. Participants received a 1% course credit.

Design

The experiment comprised two between-subject conditions: participants where asked to evaluate either how “high-ranking” or how “confident” the target animal was. For the rank condition, participants were directly asked to evaluate the dominance rank of target animal. Given that the participants had no consistent prior exposure to primates, nor had they received any training in behavioural observations, the confidence condition was also used as to assess how participants understood and used the term ‘dominance rank’. The word ‘confidence’ was chosen as one that is commonly used in everyday life, is associated with certain kinds of behaviours and postures (Briñol, Petty & Wagner, 2009), and is linked to aspects of dominance and assertiveness in the human world (Gay, Hollandsworth & Galassi, 1975).

Materials

Videos of male vervet monkeys were collected from two troops on the Samara Private Game Reserve, in South Africa from May to June 2013. In each case, the animals were filmed simply walking through the habitat with no other animals visible. No social interactions of any kind were included in the videos. During filming, the animal was tracked so that it remained in the centre of the camera's display screen and was viewed side-on. Each animal represented 1/6th of the total display screen during filming. This was accomplished using a video grid overlay on the Canon PowerShot SX50 HS display screen. All animals occupied the same amount of space on the screen.

A total of 28 4-second video clips were selected out of a possible 72 based on the following selection criteria: clear view of the animal, lack of distractions in the habitat (i.e., other conspecifics), and consistency of walking (i.e., not engaging in other behaviours, such as pausing to forage). In some instances, the videos were edited using the program Final Cut Pro X to remove unwanted behaviour, pauses, or the presence of other animals. Although these small cuts were noticeable, because there was a slight jump in the clip when a cut was made, however the majority of clips were exempt from any such disruption. The sound was removed from all clips. In this way, the only observable cues to the animal's rank (or confidence) were those produced by the animals' movements and body posture.

Two observers evaluated all 72 videos independently and, through subsequent discussion regarding the strengths and weaknesses of each clip with respect to the above criteria, came to an agreement regarding the clips to be used. Four seconds was set as the clip length as this maximized the number of clips that could be used, by ensuring there were at least two clips of this length available per subject animal.

Clips featured 14 individual males, with two unique videos for each male, giving a total of 28 video clips. Videos were divided into two blocks, with each animal viewed once in each block. Clips were randomized within blocks, and block presentation was also randomized. All participants watched a practice clip first to familiarize themselves with the experimental procedure. The example clip used was the same for all participants and was not included in subsequent analysis.

The video clips presented for each male were filmed while the male was resident in a particular troop, with the exception of two males that switched troops during filming (i.e., between May and June 2013). As a result, these two males have different rank scores depending on their troop of residence. These males were initially chosen because I wanted to investigate how much these elements were cues instead of signals, where a signal might manifest slightly differently for a different audience. After data collection was complete, however, this proved to be problematic for data analysis, as it created ties in the data where rank within a given male was not consistent. Consequently, these males were excluded from the analysis. The final analysis consisted of 12 individual males and 24 video presentations.

Procedure

Participants completed the study in groups of four, each working independently at their own computer. Each participant would enter the lab, be introduced to the study procedure by a research assistant (RO or LL), complete both a credit and a consent form, and sit at a computer for stimulus presentation. Participants were randomly assigned to one of the two conditions, and were asked either to assess, “How confident is this monkey?” or “How high-ranking is this monkey?”

The experiment was conducted on 21.5-inch iMac computers, using MetaCard software. Participants entered their age, sex, and first language into the computer before stimulus presentation began. Video presentations represented 65% of the total screen. Under each video clip, the text of the relevant question was presented (e.g., “How confident is this monkey?”), under this a sliding Likert scale was used to indicate and record participants’ responses. The scale was a computer graphic interface that allowed participants to slide the indicator bar to the left or right using the mouse. The sliding scale ranged from 1 to 12, where moving the slider to the left, towards 1, indicated the animal was either less confident or not very high-ranking. The slider was positioned at the centre of the slider (on the number 6) at the beginning of each trial and each participant was informed that the software would not allow them to leave the slider in the centre, and that they would be required to move it in order to record a response. Due to a technical error, however, discovered after the fact, some participants were able to leave the slider in the centre and did so occasionally (participants: n = 34, range = 1 - 8 times per participant, $\bar{x}$ = 2.79 times per participant). The extent that participants moved the slider away from the centre position reflected the confidence they had in their judgement of each video clip. Participants were permitted to view each video twice, if they so chose. After the 28 video presentations, participants were debriefed.

Measures

Dominance ranks for the male vervet monkeys used in this study are shown in Table 4.1, which lists both the ordinal rank and Normalized David Scores (NDS) (de Vries, Stevens & Vervaecke, 2006). NDS use the sum of all agonistic behaviours witnessed between males by multiple observers from April 2012 to June 2013. The NDS used here reflects the animals' rank at the time the video was taken. Four videos were taken in May 2013, the other 24 in June 2013. If the video was from May, the June data were not counted towards the overall NDS used in the analysis. This procedure was followed because male vervets can change ranks rather quickly during the mating season (Freeman,

Table 4.1. Ordinal rank within a troop and Normalized David Score (NDS)

Troop	Rank	NDS	Male ID
PT	1	5.28	Arb
	4	3.47	Uth
	5	3.43	Kei
	7	2.97	Lei
RBM	1	5.59	Oli
	3	5.24	Zoo
	4	5.23	Tyl
	5	5.11	Lar
	6	5	Pan
	8	4.82	Che
	10	4.53	Mor
	11	4.3	Fan

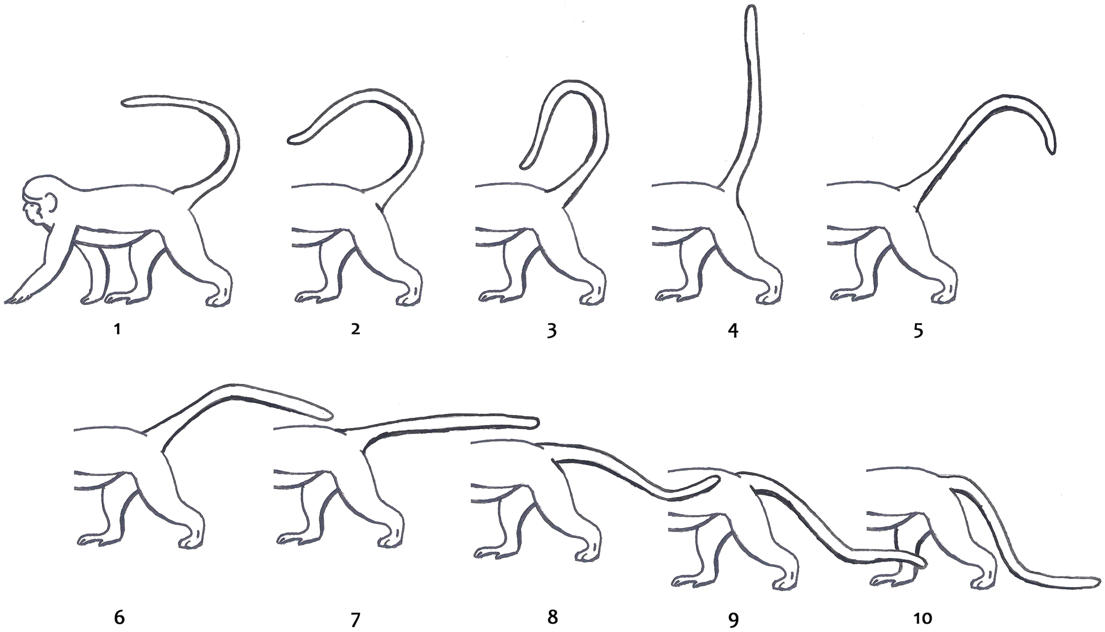


Figure 4.1. Drawings of tail positions of vervet monkeys based on Bernstein et al. (1978). These 10 tail position are shown in a continuous sequence from left to right. They have been redrawn from Bernstein et al., (1978)'s original depiction.

2012), which falls between April and June. NDS are typically used to assign ordinal rank alone, but for our purposes we used the NDS itself, to give a measure of the cardinal distance in dominance rank. For example, the difference in NDS between animals Oli and Zoo was very small, at only 0.35, yet this translates into ordinal ranks of 1 and 3 respectively. Using an ordinal ranking system can therefore inflate the apparent distance between ranks.

Other relevant information from the videos was coded after data collection with the participants was complete. As discussed in the previous chapters, vervet males have bright blue testicles, and the amount of blue visible to observers seems to be important to the interactions between male vervets themselves. To test whether our participants were sensitive to the amount of blue visible in the video clip, a categorical variable was generated. This score ranged from 0.5 to 2, where 0.5 was given when no blue was visible and/or it looked as though the male's testicles were abducted into his body. A score of 2 was given when the testicles were fully visible and prominent in the video. The distribution of scores was left skewed (0.5 n=3, 1 n=7, 2 n=14).

Tail posture and associated behaviours have been described previously (Bernstein, Smith, Krensky & Rosene, 1978), and these descriptions were used to code tail posture in the videos on a scale of 1 to 10. The drawings used are shown in Figure 4.1 (redrawn from Bernstein et al., 1978, p. 269) where the highest tail posture with the tail hanging above the head of the animal was coded as 1, and a tail that was half dragging on the ground as a 10. There was a tight range of tail postures (5 to 10) where the highest tail postures described in Bernstein et al. (1978) were not observed, and the majority of the tail postures were either 8 (n=10) or 9 (n=9). Other postures were observed, but not with high frequency (posture 5 n=1, posture 7 n=3, posture 10 n=1).

The relative size of the animal was also hypothesized to be important for human-related decisions associated with rank because size and height in particular is typically associated with dominance in humans (Judge & Cable, 2004), although this is not the case for vervets themselves (Gerald, 2001). To test if size was relevant in participants' decision making, all males (regardless of whether they were used in this study) were ranked according to their relative size. This size ranking was specifically how big a male was compared to his peers, and not some absolute measure of body weight, or shoulder height. This was first done within each troop by two independent field observers based on observations in the field, and these ratings had high concordance rates (Spearman's rank-order correlation: PT $p = 1.0$; RMB $p = 0.9$). For the purposes of analysis, rankings of relative size were collapsed across troops, where rankings went from 1 to 10 twice to 1 to 20 once. Finally, all individual males who were not in the videos were removed, and ranked size was collapsed to include only the males in the videos across both troops (range 1 to 12). Lastly, the presence or absence of a wound on the animal's body was noted using 0 (absent) or 1 (present).

Data Analysis

Using the principles of signal detection theory (SDT), the videos were categorized as containing either a top ranked animal, a bottom ranked animal, or a middle ranked animal. This categorization process was performed twice, first with the top and bottom 2 animals (2 vs. 2), and next with the top 5 and bottom 4 animals (5 vs. 4). The rational for the first split was that our animals live in 2 separate troops and this division of rank represented the top and bottom ranked animals within a given troop. The second breakdown represents a natural break in the distribution of NDS, displayed in Figure 4.2.

A general linear multilevel model (GLMM) was used to investigate how participants were making their judgments. A full model approach was employed to examine the effects of select independent factors on the participants responses. The analysis was conducted using STATA v13.1 Software (StataCorp, 2013). Subject and monkey ID were used as crossed-random factors so that the

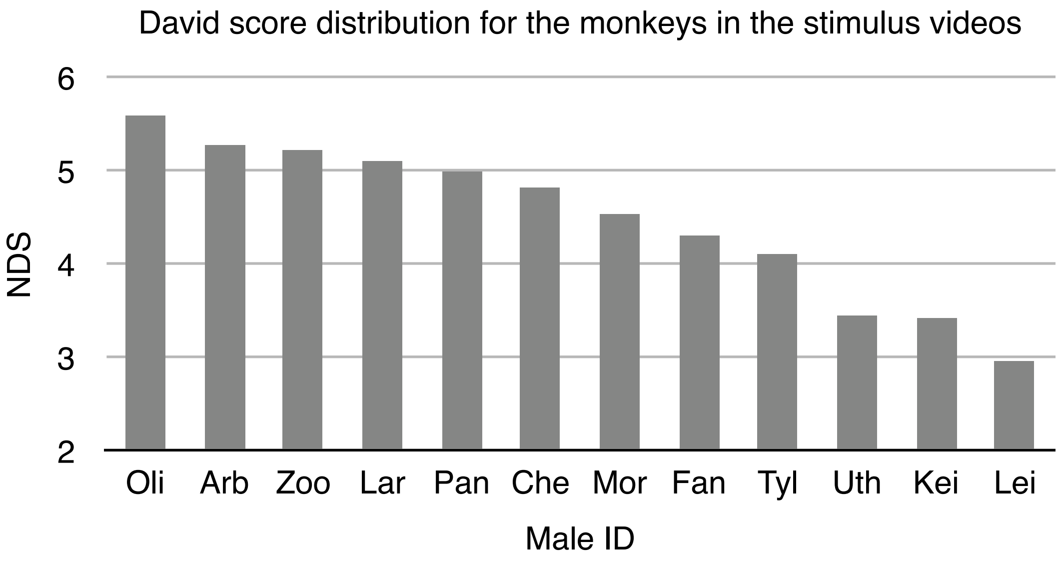


Figure 4.2. Distribution of Normalized David Scores (NDS) for monkeys in the stimulus videos

repetition of participant and monkey information would not inflate the sample size. The participant's response was the dependent variable and NDS, tail posture, degree of blue testicles visible, wound, stimulus presentation order and the animal's relative size were entered as independent factors.

Results

Signal Detection

Using the categorization of males as either high or low ranking, rates of hits and false alarms were calculated to generate a Receiver Operating Characteristic (ROC) curve based on participants responses (see Figure 4.3). ROCs were generated using the procedure from Hanely and McNeil (1982) and the web based software Enj. J. (n.d.).

The centre line that cuts the graph in two is equivalent to chance-level ability to detect a signal. Above average detection of a signal is when the curve rises above the centre line. The Area Under the Curve (AUC) indicates how masked the signal was, where larger area under the curve represents an increased ability to detect a signal. The plotted ROC curves comparing 2 vs. 2 (Confidence AUC = 0.649, Rank = 0.670), and 5 vs. 4 (Confidence AUC = 0.661, Rank AUC = 0.640) are very similar. These graphs show that participants in this sample could distinguish high from low ranking monkeys (all AUC ± confidence intervals > 0.50), but that they were not

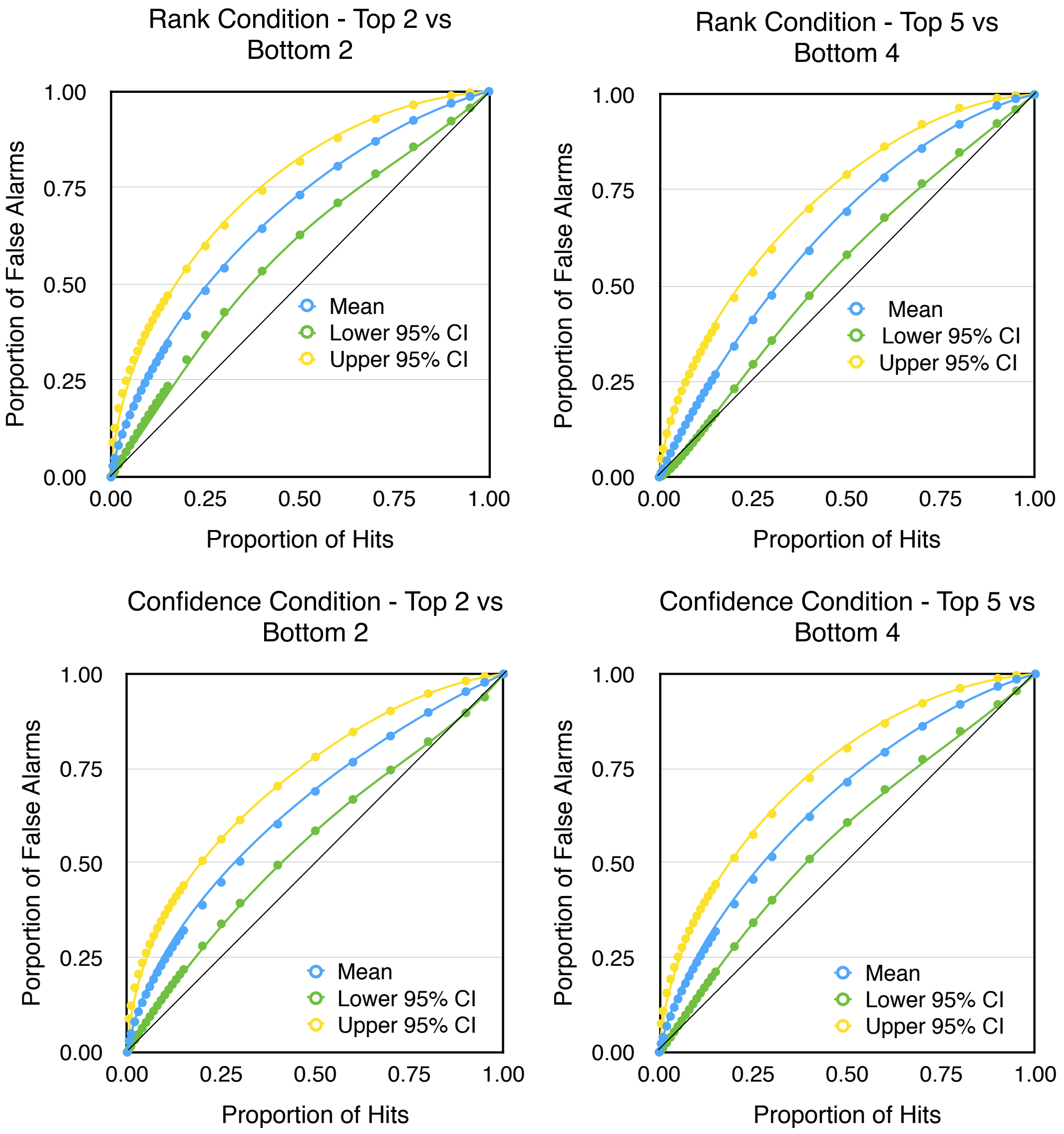


Figure 4.3. Receiver operating characteristic (ROC) curve for both confidence and rank conditions.

especially good at it. The similarity of the AUC between conditions suggests that participants treated the concepts of rank and confidence similarly when making their judgments.

Information Used to Form Judgements

Results from the GLMM are displayed in Table 4.2. The overall pattern is almost identical for both conditions. In support of my predictions, participants were able to identify the dominance rank of the subject animal (NDS $p \leq 0.0001$) and used tail posture (confidence $p \leq 0.001$, rank $p \leq 0.005$) and relative size to do so (confidence $p \leq 0.01$, rank $p \leq 0.02$). All statistically significant relationships were positive, meaning that higher ratings of both confidence and rank were

Table 4.2. Results from the general multi-level linear model (GLMM) by condition

	Z	**β**	***p***	**95% CIs**
a) Confidence condition				
David Score	5.98	0.652	0.0001	0.537 to 1.060
Tail Posture	3.43	0.279	0.001	0.142 to 0.520
Blue Visible	-0.3	0.29	0.762	-0.417 to 0.606
Wound	1.61	-0.119	0.107	-0.102 to 1.045
Order	0.91	0.018	0.361	-0.012 to 0.034
Relative Size	2.55	-0.088	0.011	0.0218 to 0.166
b) Rank condition				
David Score	4.7	0.798	0.0001	0.380 to 0.924
Tail Posture	2.79	0.331	0.005	0.083 to 0.476
Blue Visible	1.52	-0.056	0.129	-0.084 to 0664
Wound	-0.39	0.472	0.695	-0.714 to 0.476
Order	1.47	0.011	0.141	-0.006 to 0.041
Relative Size	-2.32	0.094	0.02	-0.163 to -0.014

associated with a higher NDS, higher tail posture, and larger relative body size in the rank condition. The relationship with relative size was negative in the confidence condition, however, thus participants judged relatively larger animals to be less confident than relatively smaller animals. The random factors of subject and monkey ID did not significantly contribute to the model.

Participants' responses were not influenced by the amount of blue genitalia visible (confidence $p \leq 0.0.762$, rank $p \leq 0.129$), the presence of wounds (confidence $p \leq 0.107$, rank $p \leq 0.695$), or the order of stimulus presentation (confidence $p \leq 0.361$, rank $p \leq 0.141$).

4.3 Study 2 - Expert observers

Method

Participants and Materials

Twenty-nine people (6 male and 23 female, mean age = 38 ± 13.5) attending the American Association of Physical Anthropologists conference participated in this study. Participants were recruited based on experience working with primates. They participated voluntarily and the study was conducted with the approval of the conference organizers. The design and materials were exactly the same as the previous study except we used two 13" MacBook Airs and LiveCode software to collect the data on site.

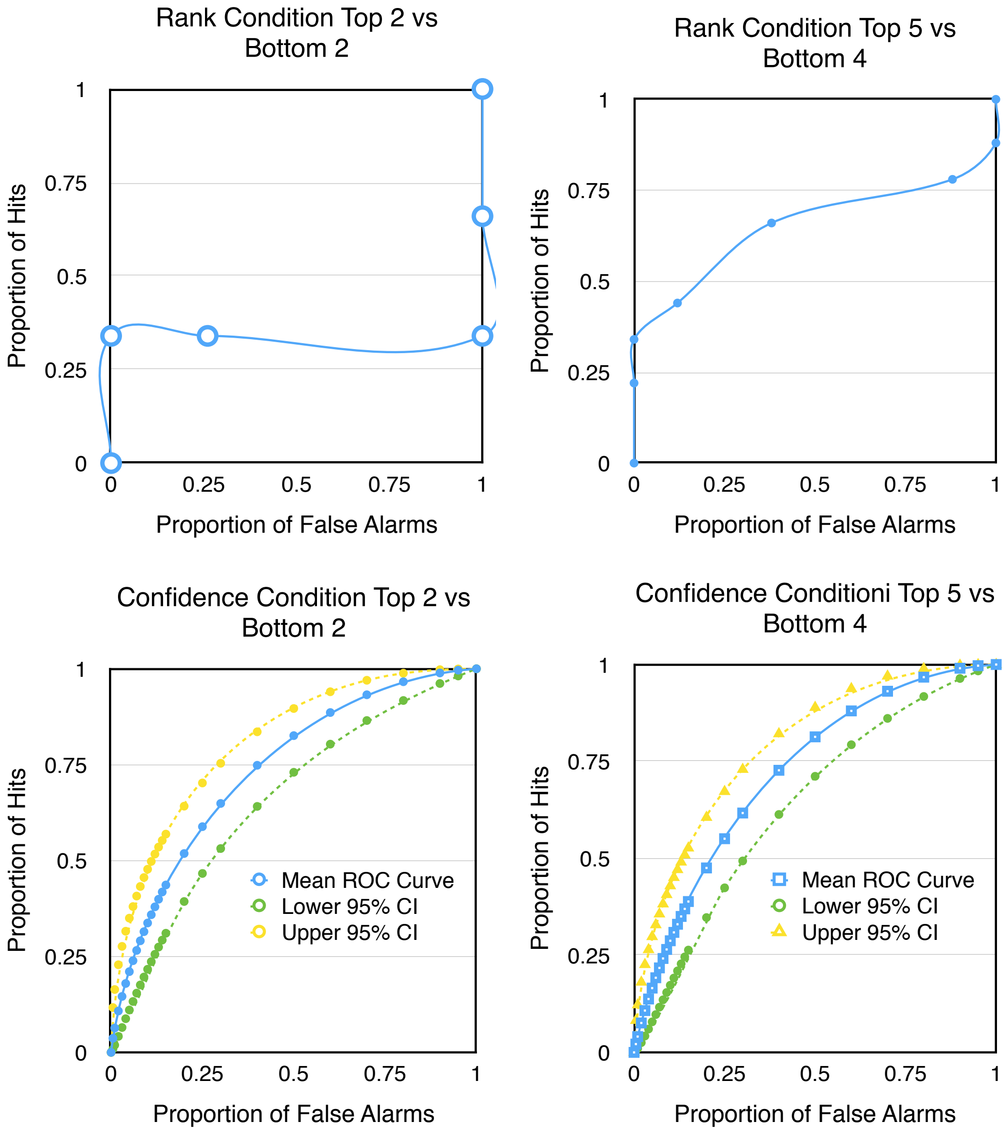
Procedure

The conference was three full days. On the first day the study was set-up in the main poster room and was subsequently relocated to outside one of the symposium rooms on the remaining two days. Participants were initially given a general overview of the task to encourage voluntary participation. Before the study began, participants would answer a few biographical questions using the computer, including: how many years they have worked the field, when was the last time they were there (the year), what species they studied primarily, their age, sex and first language. Participants were randomly assigned to the “rank” or “confidence” condition. They would then complete the task exactly as described in study 1.

Results

Signal Detection

Using the categorization of males as either high or low ranking, rates of hits and false alarms were calculated to generate a Receiver Operating Characteristic (ROC) curve using participants confidence scores (Hanely & McNeil, 1982; Eng, J., n.d.) (Figure 4.4). The area under the curve (AUC) was moderately high in the confidence condition (2 vs 2: 0.752, 5 vs 4: 0.717) and both weak and moderate in each of the rank comparisons (2 vs 2: 0.325, 5 vs 4: 0.656, confidence intervals were not possible to calculate). The sharp line in the ROC curve for the rank condition comparing only the top and bottom two animals reflects a clear decisiveness in judgements, where participants tended to respond using the extremes of the scale, indicating a higher level of confidence when making such judgements. By contrast, the confidence condition’s output shows a elegant curved line, where participants were more likely to use the full range of the scale available to them. Overall, participants were able to


Rank Condition Top 2 vs Bottom 2

Rank Condition Top 5 vs Bottom 4

Confidence Condition Top 2 vs Bottom 2

Confidence Conditioni Top 5 vs Bottom 4

Figure 4.4. Receiver Operating Characteristic (ROC) curves for the rank and confidence condition, split by the comparison of the top two ranked animals to the bottom two ranked, and the top five ranked animals to the bottom four ranked.

discriminate dominant targets from low ranking distractors, except in the rank condition when comparing the top and bottom two animals only.

Information Used to Form Judgements

Results from the GLMM are displayed in Table 4.3. In support of my predictions, participants were able to identify the dominance rank of the subject animal (NDS $p \leq 0.0001$) in both conditions. The random factors of subject and monkey ID did not significantly contribute to the model in either condition. In the confidence condition participants used tail posture ($p \leq 0.0001$) as an indication of a more confident animal. None of the other variables were significant in accounting for additional variance in responses, specifically experience in the

Table 4.3. Results from the general multi-level linear model (GLMM) by condition

	Z	β	*p*	95% CIs
a) Confidence condition				
David Score	6.48	1.079	0.0001	0.753 to 1.406
Tail Posture	4.57	0.527	0.0001	0.301 to 0.753
Blue Visible	0.88	0.196	0.38	-0.241 to 0.633
Wound	-0.02	-0.006	0.988	-0.796 to 0.784
Relative Size	-1.61	-0.075	0.107	-0.166 to 0.016
Years Experience	1.03	0.015	0.305	-0.014 to 0.044
b) Rank condition				
David Score	5.75	0.912	0.0001	0.601 to 1.223
Tail Posture	3.29	0.361	0.001	0.146 to 0.576
Blue Visible	2.02	0.428	0.044	0.012 to 0.844
Wound	-1.13	-0.437	0.257	-1.191 to 0.318
Relative Size	-3.55	-0.157	0.0001	-0.244 to -0.070
Years Experience	-2.32	-0.014	0.02	-0.027 to -0.002

field did not account for any variance in performance in the confidence condition. In the rank condition, in addition to being able to distinguish the dominance rank of the animal, the participants used tail posture ($p \leq 0.001$) and the amount of blue testes visible ($p \leq 0.044$) when making their judgements. These were positively related to the target animal's rank, where more blue and a higher tail posture were associated with higher ranking animals. The relative size of the animal ($p \leq 0.0001$) and the years of experience ($p \leq 0.020$) working with primates accounted for a significant portion of the variance, but negatively so, where smaller animals were perceived as more dominant, and more years of experience was associated with worse performance. Participants' responses were not influenced by the presence of wounds in either condition (confidence $p \leq 0.988$, rank $p \leq 0.257$).

Discussion

Human observers in the study with the undergraduate sample were able to discriminate cues of dominance rank among male vervet monkeys in non-social circumstances, and did so with no formal knowledge of primates or their social systems. Experts were likewise able to detect cues related to dominance rank, but appeared to rely on slightly different elements available to them in the videos. As the current investigation did not test the discriminatory ability of vervets themselves, this study can only provide evidence on how humans perceive cues of dominance in monkeys, rather than what monkeys themselves perceive as relevant. Nevertheless, it does suggest that males do give off perceptible cues that reflect their status or resource holding potential, even in the absence of social interactions, and that these are salient to even naive observers.

The most significant finding with the largest effect across both samples in the GLMMs was the dominance score (NDS), meaning that the measure of dominance was significantly correlated with participants' responses. Once the variance related to dominance was controlled for, the other factors that were significantly related to responses were tail posture and relative size. Both studies showed that participants relied on the dominance of the animal, the tail posture and to some degree relative size of the animal when making judgements of dominance. The variable of relative size yielded some contradicting results, and it is difficult to pinpoint what participants were actually tapping into here. Since it was not possible to compare any two animals directly, the variable 'relative size' may have been an indication of some other feature entirely, such as age. For instance, muscle mass is the last to grow between the juvenile and adult phase among vervets (Bolert & Zihlman, 2003). Since age was not available in this sample, it was not possible to test this.

Tail position was reliably an important factor in the judgements across both samples and conditions: tails held in a relatively high position were significantly associated with higher ratings of both dominance and confidence. It is important to note that there was low variability in tail posture measures and, as such, this finding should be interpreted with caution. According to previous research, lower tail postures, such as positions 8 and 9, correlate with locomotion, and are likely to be held in such a way so as to protect the tail from abrasion (Bernstein et al., 1978). As all the vervets in the videos were walking, it is not surprising that this was the most common tail posture. Previous work has also shown that higher tail postures appear specialized for display behaviour (Bernstein et al., 1978), which also coincides with reports of ‘confident’ walks while approaching other animals (Struhsaker, 1967a; Henzi, 195). It is therefore interesting to consider how our naive participants arrived at the concept that a higher tail position was indicative of a a more confident or dominant animal.

Despite their lack of experience with non-human primates, undergraduates were able to detect cues related to dominance rank. Although students may not have any formal training observing animals, they do interact with other humans, as well as household pets, like cats and dogs. The cues emitted by vervets may have been interpreted as a generalized expression of the cues picked up from other species with which participants are familiar. In dogs, for instance, an upright tail and perked ears are associated with a friendly and confident animal (Darwin, 1965). Regardless of what participants used as an exemplar, it’s curious that all samples converged on similar concepts to describe both dominant and confident animals.

Based on the patterns across both samples it appears that the words dominance and confidence are conceptually similar. Dominance, however, is a concept that, at its core, is relational, requiring social interactions in order to exist (Rowell, 1974; Drews, 1993). An individual cannot be dominant on their own; they are relatively more or less dominant than another individual. Using the word ‘confidence’ as an assessment of an internal property or state of an animal is probably a more accurate term to use. In this case, the undergraduate sample employed both words in much the same way, while the expert sample used them rather differently. Experts' responses were correlated with the amount of blue testes visible in the rank condition only, suggesting that this may be a relevant cue. Experience with primates may have made these observers more sensitive to such colourations, which undergraduates were relatively immune to. It was really only in the rank condition that experience was related to responses.

In addition to tapping into different cues across conditions, experts were also more likely to respond using the extremes of the scale, in a yes or no way for the rank condition. Although experts seemed confident with their judgments, this did not translate to improved performance. Moreover, more years of experience was related with worse performance. When speaking with the experts at the conference, they often reported that using the word 'confident' to describe a monkey was inherently strange and foreign. This likely contributed to the continuous range in scores found in the confidence condition, and inadvertently improved their ability to detect high ranking animals.

It is reasonable to assume that learning occurred over the course of trials as well: once participants had been exposed to a dominant or confident animal in a given block, and were confident in their own assessment of such an animal it may be that other animals were then scored in relation to prior exemplars. Since the present study randomized video presentation for each participant, it was not possible to pin-point an internal tipping point where ratings became more confident (by deviating further from the centre) after exposure to a particular animal, and this could be an interesting extension of the present work.

It is possible that the observers in this sample were using some other piece of information to make their judgements about dominance rank and confidence, such as the gait or head movements of the animal. An animal that moves quickly through its habitat while frequently looking around might appear apprehensive and fearful. Slow and deliberate movements that appear unhurried might be perceived as calm, confident or powerful. This is something that should be explored, but could not be included here due to time constraints. The fact that the stimuli used in the present study were dynamic images makes a wide range of information available to observers. Alternatively, it could be that no one feature constitutes the relevant cue, but rather that there is an overall gestalt that observers use, or perhaps a whole package of both movements and general body morphology (wounds, healed injuries, muscle tonus) is used.

It is worth considering where these particular cues sit in terms of their formalization and the in potential for signal evolution. Does the gait or movements of vervet males change depending on what other troop members are around? If so, perhaps aspects of the movement here are more of a signal than a cue. A cue would remain the same no matter the circumstance, whereas a signal might be an amplified version of a simple, basic movement, such as a swaying more while walking, or holding the tail in a higher position. Within the video clips used in the present study, the size and composition of the audience around the target animal varied, where occasionally some targets were walking on the group’s periphery with no other conspecifics visible. Perhaps walks and movements are influenced by the presence of other dominant, subordinate or similarly ranked animals. By testing how aspects of the target’s walk change or remain the same depending on other contextual factors, it might be possible to tease apart where on the spectrum of cue to signal some of these behaviours lie.

CHAPTER 5: DISCUSSION

One of the biggest questions I posed was whether male vervets use threat displays as a means of negotiating their social space with other troop members and not strictly as a negative social force. The descriptions of male vervet threat and postural displays have ranged widely from wound locations to the role of eye contact and non-social movement cues. Throughout all of this, I have demonstrated that there is a high degree of variability within male vervet postural displays and what may be more stable and relatively more important is maintaining a stable perception of your partner rather than stable behavioural routines.

Data collected on the location of wounds on vervet monkeys suggests that males and females exhibit high levels of aggression differently, where males turn into a fight exposing their head, neck and shoulders to possible wounds, while females typically flee from high intensity aggression incurring more wounds on their hind legs and tail. Because males are wounded somewhat less on their hind parts, it is also possible that this region is a target that is well guarded. Based on this, and looking to the video data, the question becomes, is protecting the hind-quarters a strategy commonly employed?

From what has been explored here, the answer is still not quite clear. Males do strive to maintain a face-to-face orientation during dyadic encounters. This strategy could be simply to keep the opponent in sight, to keep the posterior away from the opponent, or both. During displays that occurred in isolation, maintaining a face-to-face orientation but avoiding direct eye-contact was commonly seen when subsequent aggression was absent. Conversely, during encounters with both displays and threats, making eye contact was much more likely. Since aggression does not tend to progress hierarchically, it is not possible state conclusively that low intensity threats and displays function to mediate higher levels of aggression, however, given that aggression typically begins and ends at a particular intensity level, it is possible vervets are successfully avoiding threat escalation by utilizing only the threats that are necessary in the given context.

Male vervet postural displays were not frequently observed in the archetypical way that they have been described previously (e.g. Struhsaker, 1967a). Rather, components of the RWB, broadside and submission displays were represented as components of the display, but how they were employed varied widely. Three elements emerged as somewhat stable when looking at displays in isolation, which were that a) the aggressor drives the entire interaction, b) one submitting animal sits, while c) the other will stand in front of him with his side presented. Surrounding these three core elements are a high degree of variability and this was especially true when examining interactions with both displays and threats. I posit that the sitting and submitting animal actually affords the actor the opportunity to perform the display. When the submitting animal does not sit, there is no clear indication of what will happen next. In a handful of videos where one animal doesn’t sit, the pair seem to almost chase each other, changing direction quickly, which did not end until one animal eventually did sit and submit. Such interactions were longer and always involved additional threatening.

The role of postural displays in isolation were dynamic with some static elements, whereas displays that occurred in conjunction with threats tended to be more sustained. Overall this suggests that the function of both postural and threat displays are communicative rather than combative. Particularly when additional threats were involved, approaching from the front was a strategy possibly used to avoid startling the recipient of the display unintentionally. Given that both displays and threats both occurred at a very close proximity, the majority under one monkey body length apart, they were well within striking distance and could be readily challenged.

The amount of time animals spend on the ground will dictate the frequency that these displays are observed. Vervets who live in a more heavily forested areas will typically use more vocal rather than postural displays. This may have been one source of additional variation found in this population compared to Struhsaker’s (1967a) sample. This population of vervets spent most of the morning and early evening in trees, and midday foraging was typically on the ground. This is one of many possible future directions for this line of questioning.

Future directions

An important factor for aggressive encounters is the subjects history winning or losing previous interactions (Kasumovic, Elias, Sivalinghem, Mason & Andrade, 2010). Typically, an animal that has won previous contests is more likely to continue winning, compared to an animal who has recently lost. I posit that an animals readiness to sit may be predicted by the outcome of recent previous encounters. To some extent previous wins/loses are represented in the NDS, which is a sum (normalized based on group size) of previous wins and loses. A excellent starting point would be to look at the rank differential between pairs in the videos. Both Struhsaker (1967a) and Henzi (1985) state that there was a reliable rank difference between pairs, where the displayer was nearly always higher ranking.

In order to interpret these findings more fully, especially statistically, further research should examine when these postures are adopted and not perceived as aggressive. Specifically where the recipient does not react in an agitated manner in response to another animal presenting his side directly in front of him. Doing so would tease apart whether presenting the side in isolation is what is inherently threatening or causing agitation, or if it is some other aspect of the interaction, such as rank differential or prior social context that dictates why these postures carry a particular meaning. In this way, it may be possible to determine what components of the display are necessary or sufficient to the signal.

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Appendix A

Ethogram of behaviours

Behaviour	Definition
General	
Approach Success	A monkey approaches another monkey within at least 2m. Successful behaviour is not recorded during travelling and is not recorded if the actor does not stay in 2m for at least 5 seconds
Approach Fail	A monkey approaches another monkey within 2m and receives aggressive/opposing behaviour
Approach Displace	A monkey approaches another monkey within 2m and displaces other monkey
Depart	A monkey departs from another monkey's proximity (2m) involved in social activity. This behaviour is not recorded during travelling
Start Body Contact	Actor comes so close to another standing, sitting or laying Individual that parts of their bodies touch. No other social activity between the two individuals can be observed (hence not grooming, embracing, infant carrying etc. or physical contact during fighting). All individuals can simultaneously be involved in other activities (e.g. feeding, resting)
End Body Contact	Actor increases distance to recipient with whom it was in body contact, until no parts of their bodies touch anymore.
Start Groom	One monkey starts to groom another monkey, i.e. goes through the fur of another monkey with its fingers, removing dirt or parasites.
Role Reverse	swapping of roles between groomer and groomee
End Groom	One monkey stops grooming another monkey
Aggressive	
Aggression Unknown	Monkey known to be in aggressive interaction but behaviour not observed
Lunge	The monkey makes a sudden intense movement towards another monkey. It does not move over a large distance. Sometimes only the upper body is moved
Charge	A monkey chases another monkey for less than 5 metres.
Chase	The monkey chases another monkey partner at high speed.
Supplant	The monkey approaches another, who immediately moves, allowing the focal monkey to take his place
Vocal threat	The monkey vocalises at another individual with a tone and rhythm that is characteristic prior to aggressive encounters.

Ethogram of behaviours	
Behaviour	**Definition**
Submission only	The monkey makes room or gives ground by creating distance between itself and another monkey by moving away. The monkey may also present hind quarters for mount.
Physical contact	The monkey makes contact with another monkey in a way that is physically aggressive. This includes bites and scratches
Mount Dominance	A monkey mounts another as an indication of dominance.
Head bob	The monkey moves its head up and down in short, intense movements. This movement engages the forearms.
Eye threat:	Eyebrows are lifted exposing white of the eyelids. Often the mouth is also opened at the same time.
Solitary	
Start travel, move	When the general activity is traveling including short bouts of sitting and looking for the next steps to take or at the next individual in line. If in doubt about travel versus resting record what behaviour made up the majority of the preceding minute.
End travel:	When the above ends
Masturbate	The monkey touches its genital region over a prolonged time.
Scratching	The monkey scratches its own body, usually for no more than 2-3 seconds. Distinguish two different scratching events if they are separated by ≥ 10 seconds. Note nearest neighbour
Yawn	Monkey yawns. Note nearest neighbour
Start Feeding	Foraging, handling and consuming food (period commences if at least 3s feeding).
End Feeding	End Above (period ends of no feeding for at least 3s). Note nearest neighbour
Start Rest/Sleep	Starts rest in the absence of feeding or social activity.
End Rest/Sleep	End rest
Other	
Delete Last	Informs that there was a mistake and the previous record must be deleted.
Start Out of Sight	Monkey is missing or out of view of the observer. If this last over 2 minutes the focal is terminated.
End Out of Sight	Monkey is found after being missing or out of view of the observer.

Appendix B

All patterns observed during video analysis

Display Only		Display and Threat	
Pattern	**Count**	**Pattern**	**Count**
1A.1A.4A	1	1A.2A.4A	1
1A.2A.2A	1	1A.2A.TH.9A.4A	1
1A.2A.4A	20	1A.2A.TH.9V.4A	1
1A.2A.5V	1	1A.TH.1A.4A	1
1A.2A.NA	1	1A.TH.2A.4A	4
1A.3A.4V	2	1A.TH.2A.4V	1
1A.4A.4A	3	1A.TH.9A.4A	1
1A.7A.4A	2	1A.TH.9A.2A.9A.2A.4A	1
1A.7A.4V	1	3A.TH.1A.2A.1A.TH.4A	1
1V.7V.4A	1	3A.TH.1A.9A.4A	1
1V.9A.2A	1	3A.TH.2A.9A.4A	1
2A.2A.2A	1	8A.1A.4A	1
2A.2A.4A	2	8A.1A.TH.4A	1
3A.4A.NA	1	8A.4A.4A	1
3A.8A.11A	1	8A.TH.1A.7V	1
3M.2A.4A	1	8A.TH.3A.9A.2A	1
5A.2A.5A	1	8M.TH.2V.9A	1
6A.4A.4A	1	9A.TH.2A.4A	1
8A.2A.4A	1	Too Long	1
8A.2A.4V	1	ns.2A.TH.5V	1
8A.4A.4A	1	TH.1A.2A.2A	1
8A.7A.4V	1	TH.1A.TH.4A.4A	1
8A.7A.5A	1	TH.3A.2A.9A.4A	1
NA.2A.2A	1	TH.8A.1A.2A.4A.TH	1
NA.4A.2A	1		
NA.5A.4A	1		