Social foraging in captive baboons: implications for enrichment

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DECLARATION

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been previously submitted for any degree or examination in any other University.

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ABSTRACT

Positive affective states guide the proximate performance of the appetitive and consummatory components of behaviours, such as foraging, that ultimately increase an animal's fitness. Accordingly, promoting foraging in captive animals can enhance their welfare, defined as a predominance of positive (e.g. pleasure) over negative (e.g. stress) affective states. In three sets of experiments, I examined social foraging in two captive baboon troops housed at the Johannesburg Zoo, South Africa. I investigated (1) whether watching a demonstrator baboon forage cued conspecific observers to also forage; (2) how two factors known to influence the social transfer of foraging information and the motivation to forage (demonstrator status and hunger/satiation respectively) affected whether an animal was cued to forage upon watching a demonstrator forage; (3) the psychological mechanism through which this change in motivation to forage occurred; and (4) how socially-cued foraging behaviour could be incorporated into environmental enrichment protocols. I recorded the frequency of foraging for individual baboons and for each troop as a whole. I also scored the incidence of aggression in both troops. Upon watching a demonstrator forage from a monopolisable food source, observers increased their foraging efforts elsewhere in the enclosure. Demonstrator identity influenced the incidence of foraging by observers, with how well the demonstrator predicted food reward, rather than its status *per se*, determining observer foraging frequency. The psychological mechanism mediating the increase in foraging behaviour, as well as the effect of observer hunger/satiation on foraging, were unclear. The increased frequency of foraging by observers was accompanied by only a small rise in aggression. My data indicate that the use of social cues to motivate foraging behaviour could be employed to augment standard foraging enrichment protocols aimed at improving the welfare of captive animals.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Foraging

Foraging and feeding have played a pivotal role in the adaptation and evolution of all animals, with every organ system shaped by the demands of the organism to obtain sufficient energy and nutrients to survive and reproduce (Altmann, 1998). Complex brain systems have evolved to regulate feeding and feeding-related behaviours (e.g. Berridge, 1996; McLean, 2001; Toates, 2001), and the massive expansion of the primate cortex is thought to reflect either the cognitive demands imposed by sociality on foraging or, alternatively, the constraints on social relationships that food acquisition imposes (Altmann, 1998).

Foraging is an elaborate, multi-stage behaviour, comprising both appetitive (goal-seeking) and consummatory (goal-satisfying) components. Appetitive behaviours are flexibly-organised and exploratory, and serve to appropriately position the animal to perform consummatory behaviours (Panksepp, 1998; Berridge, 2004), the relatively stereotyped reactions to stimuli in the external environment (Toates, 2004). Locating, selecting, gathering or capturing, and processing food items are appetitive behaviours; food ingestion is consummatory behaviour (Lindburg, 1998).

1.2 What motivates behaviour in general, and specifically foraging?

The proximate mechanisms motivating appetitive and consummatory foraging behaviours are multiple and complex, involving external factors, such as the presence of food or the foraging behaviour of conspecifics, and internal factors, such as energy depletion and hormonal states (Toates, 2001; Figure 1.1). These factors act through a range of high-level processes (e.g. cognition and learning), intermediate-level processes (e.g. emotion), and low-level processes (e.g. reflexes, modal action patterns, the preceding behaviour performed by the animal, and circadian rhythms), together instigating, organising, directing, and terminating foraging bouts (Toates, 1986; 2001; 2004). Other internal and external stimuli may at the same time reduce the motivation to feed, and shift

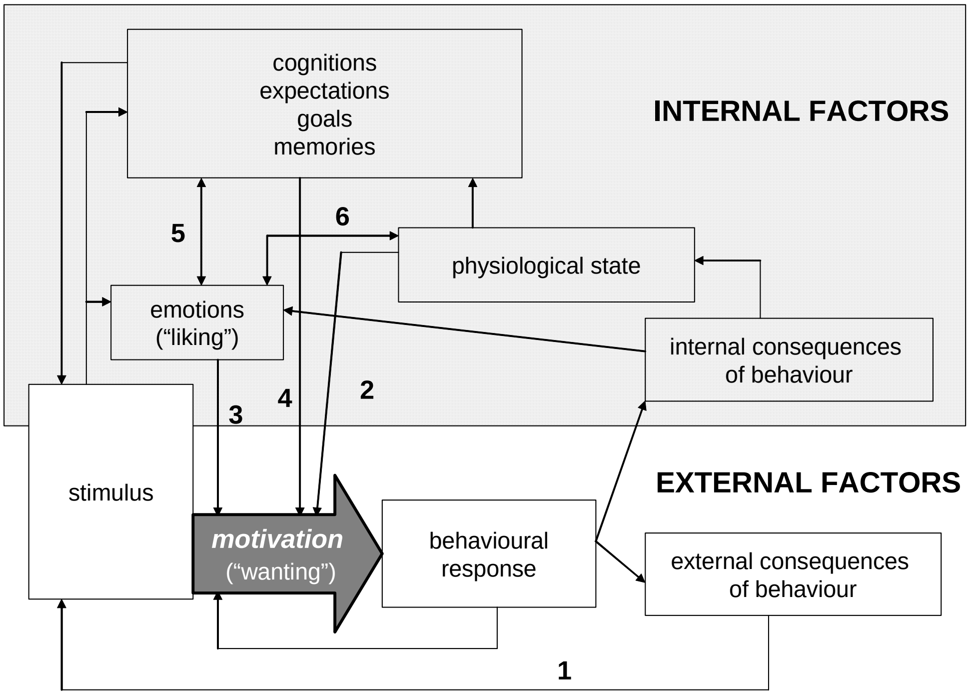

Figure 1.1: A model of the control of behaviour, adapted from Toates (1998; 2002; 2004). Motivational states influence if and how animals respond to stimuli. Stimuli may be physically present in the environment, or be cognitive representations of future states or goal objects. Internal factors (e.g. cognitions, expectations, goals, and memories; emotions; physiological states) act in concert with external factors (e.g. the preceding behaviour performed by the animal; environmental stimuli) to modulate the efficacy with which stimuli elicit behaviour (e.g. a hungry animal will attend to cues predictive of food more readily than a satiated animal). External consequences of behaviour change or remove the impinging stimulus (loop 1; e.g. appetitive foraging behaviours produced in response to cues predictive of food reward serve to bring an animal into contact with food, which it can then consume.) Internal consequences of behaviour alter physiological parameters (e.g. feeding increases blood glucose and causes satiety) and/or emotional states (e.g. appetitive foraging behaviour induces a positive affective state, as does consuming food), as well as cognition, expectation, and goals. Physiological and emotional states, and higher cognitive processes, in turn influence the motivation to continue responding to the stimulus (loops 2, 3, and 4 respectively). Emotions, or positive and negative affective states, provide the common currency through which the expected value of engaging in a particular behaviour, in light of the context and competing behavioural alternatives, can be evaluated. The behaviour that is recognised to maximise pleasure, the proxy of utility, determines behavioural expression. In addition, emotions influence and are influenced by (a) cognition, expectation, goals, and memories, by biasing information processing, attention, and storage and retrieval of memories (loop 5); and (b) physiological states (loop 6), so coordinating behavioural and physiological responses to internal and external stimuli.

behaviour towards competing demands, such as predator avoidance, or seeking mating opportunities (Toates, 1986; Morrell, 2004).

The motivation to forage sets up appetitive states during which animals actively engage the environment to seek out and make contact with the food reward, which may be either physically present, or a cognitive representation of a future state or goal-object (Figure 1.1; Panksepp, 1998; Ikemoto & Panksepp, 1999). Physiological variables indicating a deficiency, or expected deficiency, in tissue needs for energy or specific nutrients are important motivators of foraging, and are sufficient to trigger appetitive behaviours in the absence of food or external stimuli predictive of future food availability (Toates, 2001). This activation of behaviour is, in conjunction with descending input from higher cortical centres, accomplished by interoceptive neurons in the hypothalamus that detect homeostatic imbalances and arouse relevant brain systems (Panksepp, 1998; Toates, 2004).

The motivation to seek and consume food does have some autonomy from tissue needs, however: satiated animals may work to obtain food which they will not consume (e.g. Neuringer, 1969; Hughes & Duncan, 1988), or may resume eating when highly palatable or novel foods are presented to them (Toates, 1986); and cues predictive of food availability arouse feeding in animals for which food is available *ad libitum* (Weingarten, 1984). Irrespective of the underlying motivation, once foraging behaviour has been instigated, it appears that positive feedback occurs, promoting further feeding behaviour (Figure 1.1; Wiepkema, 1970). This confers stability on foraging behaviour by ensuring that the animal continues to feed for a significant amount of time, despite the presence of competing demands, thereby reducing the costs of unnecessarily switching behaviour (Toates, 1986).

Panksepp (1998) refers to the brain circuitry generating appetitive behaviour as the seeking system. The seeking system is positioned anatomically in the lateral hypothalamic corridor, which extends from the ventral tegmental area to the nucleus accumbens (part of the ventral striatum). Activity in this corridor is closely associated with dopamine release, although other neurotransmitters, such as norepinephrine and epinephrine (facilitatory role), and serotonin (inhibitory role), are also involved (Panksepp, 1998). Much research now shows that this dopamine release is triggered by the expectation of reward, but not the reward itself (e.g. de la Fuente-Fernandez et al, 2002).

The seeking system responds unconditionally to homeostatic imbalances and environmental incentives, aids learning about environmental contingencies, novel or unexpected stimuli, and predictors of reward (Panksepp, 1998), and facilitates movement towards incentives and away from threats (Berridge, 2004). When the seeking system is aroused by incentive stimuli, the resultant affective state resembles what we humans term “eager anticipation” or “engaged curiosity” (Panksepp, 1998).

The behavioural energisation elicited by the arousal of the seeking system was initially construed as evidence of its activation being rewarding (e.g. Old & Milner, 1954), but more recent research suggests that it is the termination of the activation of the seeking system, and not its activation *per se*, that is perceived as rewarding (Panksepp, 1998). However, the dopamine release may, by eliciting, modifying, and sustaining anticipatory behaviours, and by allowing an animal to ignore irrelevant signals, be a prerequisite for the functioning of other brain reward systems as it increases the probability that an animal will make contact with potentially rewarding events (Martin et al, 2004). In other words, the seeking system is involved in the incentive-salience or “wanting” aspect of goal-directed activity, and not the inherently rewarding “liking” aspect that arises from direct engagement with incentives (Berridge, 1996; Berridge & Robinson, 2003; Toates, 2004) (see below). Thus the role of dopamine is to link the hedonic evaluation of stimuli or potential future rewards with objects or actions (incentive salience attribution; Berridge & Robinson, 1998; Montague et al, 2004). It is beyond the scope of this study to deal with the role of dopamine in active avoidance, “a preparatory behaviour motivated by aversive reinforcement” (Tinsley et al, 2000, p24).

The discussion of motivation thus far has not addressed *how* individuals select appropriate foraging behaviours by attending to the complex and interrelated array of variables such as internal state, external stimuli, and previous experience (Spruijt et al, 2001). Moreover, it has not explained how conflicts among different motivational systems are resolved, how animals establish priority among demands, or how animals “know” which behaviours to perform in which contexts. To do so, it is necessary to examine the hedonic aspect of reward systems.

The ability to behave efficiently from an ultimate evolutionary perspective, and take actions that are most likely to maximise future rewards (Montague et al, 2004), is guided by proximate hedonic experiences through which animals gauge the expected utility or ultimate functionality of performing various behaviours (Panksepp, 1998; Spruijt et al, 2001). Ongoing behaviour is thereby selected and evaluated by the heuristic: what is proximally pleasurable is likely to have a high fitness value (Cabanac, 1971; 1991; 1992; Balasko & Cabanac, 1998). The experience of pleasure thus rewards and reinforces proximate behaviours that have proved ultimately adaptive during the evolutionary history of the species (Toates, 2001) and ensures that events associated with pleasure are in future attributed incentive salience and thus "wanted" (Berridge, 2004). In addition, the conditioned induction of a positive affective state prior to collecting reward assists in counteracting the potential stress and pain that an organism must endure to reach its goal (Spruijt et al, 2001).

Assigning an affective weighting to various stimuli and/or courses of action, in the form of a generic reward or punishment value, provides a proxy by which animals can compare behavioural options directly using the "common currency" of affect (Cabanac, 1971; 1991; McFarland & Sibly, 1975; Rolls, 2002; Berridge & Robinson, 2003) to gauge the expected utility of their outcome (Spruijt et al, 2001). Actions maximising the reduction of the discrepancy between a current state and a desired state are perceived as the most rewarding behavioural options, and so determine behavioural expression (Toates, 2001; 2004).

That which an organism finds innately rewarding or punishing, and thus either approaches or avoids respectively, is influenced by the animal's evolutionary history and predisposes it to behave in ways that are likely to increase its fitness (Rolls, 2002). However, the emotional response to stimuli is not genetically fixed, but is modulated by prior experience as well as immediate internal signals such as physiological needs for energy, and external stimuli such as the availability and palatability of food, or the presence of danger (LeDoux, 1994). The rewarding value of a stimulus is thus not inherent in the stimulus, but is modulated according to the predicted benefits or costs of engaging with the stimulus in a particular context, at a particular time, and in the presence of other competing stimuli. For example, food may be perceived as very rewarding when an animal is hungry and in a safe area, while water may be perceived as more rewarding than food when an animal is satiated for food but in need of fluid. The perception of a stimulus as either pleasant or unpleasant depending on the physiological state of the organism, is termed alliesthesia (Cabanac, 1971).

The concept of positive affect/pleasure and negative affect/pain is closely linked to emotion (Damasio, 2000). The integration of signals from the body, stimuli from the environment, cognitions from higher cortical levels, and affective weightings assigned to stimuli or behaviours, produces emotional states which, in turn, recursively influence these parameters (Toates, 2002). Emotions, which need not be conscious (LeDoux, 1998; Damasio, 2000; Rolls, 2002; Berridge & Robinson, 2003), hence provide the neural interface between sensory systems, motivation, action selection, and motor execution (Rolls, 2002). Although it is possible for behaviour to be regulated by taxes and tropisms, fixed stimulus-response sequences, or modal action patterns (Dawkins, 1998; Toates, 2001), the evolutionary advantage of emotions is that they direct behaviour towards goals, rather than specifying fixed action sequences. Emotional states thus permit behavioural flexibility in changing environments (McGuire & Troisi, 1998). Other functions of emotions include the coordination of behaviour and physiology (endocrine and autonomic responses), the facilitation of the storage and recall of memories, and the production of motivation and direction for behaviour that persists beyond the duration of contact with the stimulus object (Damasio, 2000; Rolls, 2002).

Whereas dopamine is considered the primary neurotransmitter of the appetitive seeking system, opioids are the principal neurotransmitters responsible for mediating the positive affective states associated with both the performance of situationally appropriate consummatory behaviours (Panksepp, 1998) and with the resultant reduced discrepancy between the animal's actual and desired state (Spruijt et al, 2001). Opioids, acting in various subcortical brain areas such as the basal ganglia and amygdala, in addition to the GABA (gamma-amino-butyric-acid)/benzodiazepine systems and their associated neuroanatomical structures such as the ventral pallidum (Berridge, 1996; Berridge & Robinson, 2003), are involved in the evaluation of stimuli as “liked” or “disliked”. By influencing the incentive value of stimuli, opioidergic activity indirectly affects “wanting”, which in turn causes the seeking system to form and maintain specific behavioural strategies (Spruijt et al, 2001). The appetitive (“wanting”) and consummatory (“liking”) components of motivational systems thus have separable functions and neurobiological substrates (Robinson & Berridge, 1993; Berridge & Robinson, 1998; 2003; Berridge, 1996), but nevertheless function reciprocally to motivate ongoing contextually-appropriate behaviour.

1.3 Motivation, emotion, behaviour, and welfare

Because much of an animal’s behaviour is evaluated and guided by positive and negative affective states, an animal that is able to perform the behaviours for which it is motivated by internal and/or external factors, and which reduce the discrepancy between actual and expected states, is likely to experience ultimate fitness as well as proximate pleasure. Whilst affect is necessarily ephemeral, depending on the ongoing evaluation by the organism of its ever-changing internal milieu and external environment, an animal in which positive affective states predominate over negative affective states can be considered to have better welfare than an animal in which negative affective states predominate (Spruijt et al, 2001). Thus welfare, when seen from a combined psychological, physiological, neurobiological, and behavioural perspective, may be defined as the relative balance between positive and negative affective states (Spruijt et al, 2001).

In an animal’s natural environment, that is its environment of evolutionary adaptation (EEA; McGuire & Troisi, 1998), the animal is cued to perform behaviours for which it is pre-adapted and predisposed. Not only do these behaviours contribute to its fitness, their performance also provides the animal the means with which it can regulate its affective state. In contrast, in captive environments, environmental deficiencies such as limited space, restricted foraging opportunities, exposure to inescapable stressors, or simply inadequate stimulation, may have several adverse consequences: (1) Animals may not be afforded the opportunities to exhibit or experience the functional consequences of behaviours which in their EEA would either counteract threats to fitness (i.e. reduce an aversive state), or directly enhance fitness (i.e. engender a positive affective state). (2) They may fail in their behavioural attempts to regulate physiological and psychological states (Dawkins, 1988; 1998). (3) They may not be motivated to perform behaviours which, in the usual course of events, would be pleasurable through their display (Hughes & Duncan, 1988). The over-arousal of the seeking system in response to unfulfilled and often unfulfillable expectations may engender frustration, negative affect, and activation of the stress-related hypothalamic-pituitary-adrenocortical axis (Toates, 2004). This, in turn, may encourage the animal to perform alternative consummatory acts, such as compulsive or stereotypic behaviours, in an attempt to reduce its experience of excessive appetitive arousal (Panksepp, 1998).

Avoiding injury, disease, malnutrition, and death are obvious means through which to safeguard welfare (Dawkins, 1998; 2004). However, welfare is more than simply the absence of states of suffering since, in the final analysis, welfare depends on the animal's subjective experience of itself within its environment (Dawkins, 1988; 2004; Duncan, 1995; Broom & Zanella, 2004). A largely unresolved issue, fraught with both methodological and conceptual problems (Rushen, 2003), is determining which aspects of an animal's EEA should be incorporated into the captive environment to provide sufficient behavioural opportunities to ensure good welfare. This issue is further complicated by the fact that naturalness of behaviour is not necessarily synonymous with good welfare – clearly captive animals do not suffer if they have no predators from which to flee (Dawkins, 1998).

In captivity, situations arise in which animals may experience aversive mental states, although the captive environment may meet all of their physiological needs. Animals may be motivated to escape or hide from perceived threats, even when their survival is not threatened (Dawkins, 1998). Alternatively, animals may attempt to perform behaviours which are physiologically unnecessary in the captive environment (Shepherdson, 1998), yet which may have internal motivating factors and hence be inherently pleasurable (Hughes & Duncan, 1988).

The term behavioural need describes the motivation to perform specific behaviour patterns, even if the physiological needs which the behaviour ultimately serves have been fulfilled (Dawkins, 1983; Hughes & Duncan, 1988, Jensen & Toates, 1993). This term is comparable to Lorenz's (1950) description of behaviour patterns which, in his terminology, represent the discharge of an accumulation of internal motivation. Some behaviours, especially those that are critical for survival but which lack immediate physiological consequences, or for which the ultimate benefit is derived only in the distant future, appear to be inherently pleasurable (Duncan, 1995). These behaviours are therefore rewarding as a result of their display rather than purely their consequences (Rolls, 2002; Spruijt et al, 2001), and it is the performance of the behaviour that decreases the motivation to perform that behaviour more than its ultimate functional consequences (Rushen & de Passille, 1995). Examples of such behaviours include searching for food when none is available, grooming, play, and reproductive activities (Duncan, 1995).

The adaptive value of behaviours being internally rewarded is that, if the animal persists with the behaviour for a sufficient time, its efforts should lead to the discovery of the primary incentive object (Rolls, 2002). The converse of this, though, is that even if an animal's physiological needs are met in captivity, thwarting certain behaviours may result in suffering akin to that experienced were the animal to be physiologically deprived (Hughes & Duncan, 1988).

Ensuring good welfare, or a predominance of positive affective states, therefore involves not only good health and the prospects of future good health, but also the perception of this by the animal, as well as the animal's active participation in achieving these states (Dawkins, 1998). During the course of evolution, selection for emotions as mediators between stimuli and behavioural expression, rather than for specific stimulus-response sequences (McGuire & Troisi, 1998), has conferred flexibility on animal behaviour. As already mentioned, this behavioural flexibility likewise bestows the associated cost that animals may find certain situations negatively reinforcing, or lacking in positive reinforcement, even when their fitness is not threatened (Dawkins, 1998). The likelihood of such mis-assessment of the situation is greatly increased in captivity because the proximate "rules" which guide behaviour were shaped by natural selection in the context of the animal's EEA. Although we may know that there is no physiological need for certain behaviours, animals are not privy to this insight (Spruijt et al, 2001), and thus blindly follow a set of emotional response rules malsuited to the artificial context in which we place them.

Environmental enrichment addresses, *inter alia*, the aforementioned concerns about the welfare of captive animals, and provides a system in which interventions designed to improve the physiological and psychological well-being of animals can be objectively designed, implemented, and assessed (Newberry, 1995; Shepherdson, 1998; Mellen & MacPhee, 2001; Young, 2003). Accordingly, one of the primary aims of environmental enrichment is to promote species-typical behaviours and, thus indirectly, to engender positive affective states. Among the most successful interventions are protocols that encourage and prolong foraging (Reinhardt & Roberts, 1997; Lindburg, 1998), a behaviour which, as explained above, is not only critical for survival, but appears to be rewarding by its performance alone, even if food is not consumed.

1.4 Ecology of foraging in social groups: competition, dominance, and aggression

For group-living animals, foraging occurs in a social context. Giraldeau and Caraco (2000) define social foraging as the concurrent foraging of two or more animals, each of which influences the other's energetic gains and losses. Social foragers may coincidently or deliberately provide conspecifics with information about food resources, indicating when and where to eat, what foraging techniques to use, and which foods are available and suitable for consumption (Altmann, 1998; Galef & Giraldeau, 2001). Such information may reduce search and processing time, and so increase overall foraging rate and efficiency. Although it appears that the main factor driving the evolution of social groups is the reduction of predator risk (Dunbar, 1988; Rowell, 1999), the fact that group members can share information about foraging opportunities and processes provides another indisputable advantage to group life for many species (Altmann, 1998), and may also compensate for some of the disadvantages of group living (see below). For example, sharing foraging information in baboons may underlie their adaptability to, and success in, diverse and highly variable habitats (Altmann, 1998).

In contrast to the possible foraging and anti-predator benefits accrued from group living, within-group feeding competition over limited food resources is a potential cost of sociality (Dunbar, 1988; Giraldeau & Caraco, 2000; Pruetz & Isbell, 2000; Gillespie & Chapman, 2001). As groups grow in size, the density of individuals at feeding sites increases (Giraldeau & Caraco, 2000). This results in heightened competition for access to resources, as indicated by more frequent interference, displacement, and aggressive behaviours. Consequently, members of large groups must expend more energy and time on foraging than animals in small groups, all other factors, such as predation risk, being equal.

Group members differ in their food-finding capacities, as well as in their abilities to compete for or retain access to discovered food items or patches (Ranta et al, 1996). Two foraging strategies have emerged: some animals preferentially invest in searching for food (producers), some animals in exploiting the food found by others (scroungers; Ranta et al, 1996; Liker & Barta, 2002). In practice, an animal's foraging strategy is not fixed, but varies spatio-temporally according to the extent to which resources can be shared, the dominance ranks of the competing individuals, the level of tolerance of conspecifics, and the quality of the resource.

Competition for access to resources can assume one of two forms, depending on the amount, quality and, most importantly, the distribution of food resources (Wrangham, 1980; Gore, 1993). Scramble competition typically occurs when food is dispersed, of low quality, and possibly meagre. Animals are unable to monopolise such a resource, and each individual obtains roughly the same amount of food (Gore, 1993). Scramble competition may be reflected by an increased rate of feeding compared to that at which animals would feed if alone (Clark & Mangel, 1986). Contest competition, in which dominants usurp resources from subordinates through displacement or aggression (Pruetz & Isbell, 2000), is especially prevalent when a high-quality resource is clumped in discrete patches (Gore, 1993), or when the food source is slowly renewed and/or depleted during foraging (Pruetz & Isbell, 2000). The outcome of contest competition is that producers are often displaced from resource sites by more dominant scroungers. Dominants thus obtain more food, or food of higher quality, at a faster rate than do subordinates (Clark & Mangel, 1986). There is, though, some evidence in primates that low ranking animals may deliberately search for less nutritionally valuable foods than do higher ranking animals (Dunbar, 1988). This tactic may improve net energy gain by minimising the adverse effects of interference whilst feeding.

Aggression is one of the possible outcomes of competition for access to resources, and is used to influence the behaviour of conspecifics so that the aggressor can obtain the desired object (e.g. food) or, possibly, end (e.g. high rank; de Waal, 1986). As is the case for competition in general, agonistic interactions are most frequent when animals compete for access to clumped, limited, and high quality foods, as well as when competitors are in close proximity (Dunbar, 1988; Barton, 1993; Bercovitch & Strum, 1993; Barton et al, 1996; Pruetz & Isbell, 2000). In contrast, dispersed and abundant resources of low-quality foods do not appear to promote aggression possibly because, as optimisation models of foraging predict, these foods do not yield sufficient energy gain per unit time to justify competitive interference (Shopland, 1987).

The benefits of resource attainment by the aggressor are frequently offset by costs to all individuals involved in the aggressive interactions. These costs include disturbed social relationships (de Waal, 1986), physical injuries (Bercovitch & Strum, 1993; Palombit, 1993; Wittig & Boesch, 2003), and time and energy expenditure (Wittig & Boesch, 2003). A number of mechanisms have evolved to regulate within-group feeding competition by means other than aggression. Examples of these are the establishment of dominance hierarchies, and the associated displays of behaviours such as submissive posturing, the movement of subordinates away from the areas occupied by dominants, and reconciliatory grooming (de Waal, 1986). Indeed, the formalisation of dominance relationships and the unequivocal communication of relative status may, even in competitive situations, frequently permit peaceful determination of order of access to resources.

As a result of the above regulatory mechanisms, free-ranging primates show relatively low levels of aggression, even in competitive feeding situations (de Waal, 1986), although higher levels of agonistic interactions have been observed for the same species in captive environments (Box, 1986; Dunbar, 1988). This aggression is probably the result of animals in captivity being housed at high densities, their food being presented in a clumped rather than a dispersed form, and/or a lack of space for animals to distance themselves from competitors.

1.5 Background to current research

In the following chapters, I report on a set of three experiments that examined social foraging and aggressive behaviour in two captive baboon troops when they were provisioned with a monopolisable food source. The features of baboon social structure described below, in combination with their foraging behaviour and ecology, make this an ideal taxon for studies of foraging in social contexts (King, 1999).

Baboons (*Papio*) are among the most widespread, abundant, and adaptive of cercopithecine monkeys, inhabiting a wide variety of habitats throughout the African continent as well as the coastal areas of Saudi Arabia and Yemen (Kummer, 1995; Altmann, 1998). Most subspecies of *Papio* (e.g. chacma baboons, *P. hamadryas ursinus*; yellow baboons, *P. h. cynocephalus*; anubis/olive baboons, *P. h. anubis*; common/guinea baboon, *P. h. papio*) live in multi-male, multi-female troops. The size of these troops ranges from less than five to over 100 individuals, depending primarily on resource availability and predation risk (Estes, 1991; King, 1999). Dominance hierarchies form among the females (i.e. matrilines). The social structure of the hamadryas baboon (*P. h. hamadryas)* is unique among old world primates, since it comprises a four-tier, female-transfer social system (Kummer, 1995). The smallest social group is the one-male unit, consisting of a dominant adult male and several, usually unrelated, females and their offspring (Kummer, 1995). During the day, one-male units may join to form clans, which then may form even larger bands. At night, three to four bands combine to form a troop and share a sleeping cliff. The hamadryas fission-fusion social system is thought to have evolved in response to ecological demands for smaller foraging groups, and yet larger groups to share the limited sleeping rocks and help defend against predators (Kummer, 1995).

Baboons have been described as eclectic, opportunistic omnivores (Altmann, 1998): they have a very broad, flexible diet in terms of types of plants and animals eaten, but are selective about which parts are consumed and which parts discarded (King, 1999).

Foraging in environments that are frequently energy-scarce is a time-consuming activity, with baboons often spending about half their waking hours foraging (Altmann, 1998). Most foods are manipulated and processed in various ways, manually and/or orally, to render selected food items ingestible (King, 1999), or to extract concentrated, nutrient-dense parts of the food item (Altmann, 1998). For example, individuals may have to dig out roots from the ground, or may need to remove the outer casing of seeds or fruits before they can be consumed (Gore, 1993).

During previous research on foraging behaviour in captive hamadryas baboons (Jones & Pillay, 2004), troop members that were excluded from a monopolisable food by the alpha-male increased their foraging efforts in other areas of the enclosure, despite no additional food having been provided in these areas. This increased foraging effort was predominantly appetitive, although fallen vegetation from outside the enclosure and remnants of the previous day's meal were occasionally consumed. There was no concomitant rise in aggression accompanying this increased foraging unlike that which occurred when individuals fed at a non-monopolisable food source that all could simultaneously access.

Because foraging behaviour is considered to engender positive affective states, even if no food is consumed, we regarded the monopolisable food device as a source of environmental enrichment for all members of the group, although only accessed by the alpha-male (Jones & Pillay, 2004). Our research accordingly suggested that foraging in social animals could be indirectly encouraged by manipulating the behaviour of only one member of the group (hereafter demonstrator). The demonstrator's feeding behaviour would then provide the motivation for other group members (hereafter observers) to perform presumably inherently rewarding foraging behaviour. However, this previous study did not investigate the mechanisms mediating the observers' increased foraging upon watching a demonstrator forage; nor did it address whether the observers' reactions to the demonstrator were innate or learned, or how this process might be used to augment conventional foraging enrichment protocols.

Using two groups of captive baboons as my subjects, I firstly investigated how two factors known to influence social information transfer (demonstrator status;

hunger/satiation) affected whether animals begun to forage upon watching a demonstrator forage. Secondly, I established whether the response of observers to a foraging demonstrator was innate or learned. Finally, I evaluated whether socially-mediated foraging behaviour could be incorporated into environmental enrichment protocols aimed at improving the welfare of captive animals. I also recorded levels of aggression, which is a natural consequence of feeding competition, since high frequencies of aggression represent a welfare concern (Dawkins, 1998).

1.6 Layout of dissertation

This thesis comprises six chapters. The present chapter, Chapter 1, provides a broad introduction to the research topic; Chapter 2 outlines the general materials and methods; Chapters 3, 4, & 5 are experimental chapters, each containing an introduction, materials and methods, results, and discussion section; and Chapter 6 contains a general discussion as well as concluding statements for the dissertation as a whole. To prevent unnecessary overlap, the discussion of points pertaining to more than one experiment is restricted to Chapter 6 only. Lists of figures and tables appearing in Chapters 1 to 6 are presented on pages ix-xi. All cited literature is contained in one reference section at the end of the dissertation.

CHAPTER 2: GENERAL MATERIALS and METHODS

I start this section by describing the study subjects (two baboon troops) and their housing and husbandry. Thereafter I report the methods and findings from the baseline study, during which time no experimental manipulation occurred, and then describe the general procedure for Experiments I, II, and III, in which I introduced an apparatus (box) into each troop's enclosure as well as various food items. Finally, I explain my methods of data collection and statistical analysis. Detailed procedures for each experiment are given in Chapters 3-5.

2.1 Subjects

The chacma and hamadryas baboon troops used in this study were housed in separate enclosures within the baboon complex at the Johannesburg Zoo, South Africa. The baseline study, which was conducted to measure the frequencies of foraging and aggressive behaviours prior to experimental manipulation, took place in April and May 2003. Experimental treatments were implemented in three phases between September 2003 and February 2004, as outlined in Table 2.1. For the hamadryas troop, Experiment III was not completed because of safety concerns for two infants that were born after the completion of Experiment II.

Table 2.1: Dates and sequences of the baseline study and experiments for the chacma and hamadryas baboon troops.

	chacma troop	hamadryas troop
Baseline study	27 April – 5 May 2003	27 April – 5 May 2003
Experiment I	4 September – 24 October 2003	4 September – 24 October 2003
Experiment II	9 November – 3 December 2003	10 November – 4 December 2003
Experiment III	2 February – 26 February 2004	

2.1.1 *Chacma baboons* (*Papio hamadryas ursinus*)

The composition and history of the chacma troop are given in Table 2.2. The group comprised seven animals: one vasectomised adult male, one castrated adult male, and five adult females. All animals were reared by their mothers. Grist, the dominant male, interacted predominantly with the adult females Tina or Nina and only occasionally with the other females during the periods when they when they showed perineal swellings and were thus sexually receptive. There was little interaction between Grist and the younger castrated male, Knuckle, who usually distanced himself from Grist, or otherwise presented to Grist if they came into close contact. The females not associated with Grist interacted freely with each other and with Knuckle.

Table 2.2: Composition and history of the chacma (*Papio hamadryas ursinus*) troop housed at the Johannesburg Zoo. Troop composition remained the same throughout my study.

Name	Sex and reproductive status	Birth year	Age at end 2003	Birth environment
Grist	Adult male (vasectomy 1996)	1986	17	Wild
Tina[a]	Adult female	1987	16	Wild
Natasha	Adult female	1990	13	Captive
Nancy	Adult female	1990	13	Wild
Nina	Adult female	1992	11	Captive
Knuckle	Adult male (castrated 1999)	1995	8	Captive
Stompie	Adult female	1995	8	Captive

a – dam of Nina and Knuckle

2.1.2 *Hamadryas baboons (Papio hamadryas hamadryas)*

The composition and history of the hamadryas troop are given in Table 2.3. The group comprised six baboons: one adult male, one castrated adult male, three adult females, and one juvenile female. All animals were reared by their mothers. Romeo, the adult male, was the highest ranking troop member, and Jane the highest ranking female. Romeo and Jane interacted frequently and amicably. For the first few months of the study, Celina, the juvenile female, occasionally suckled from her mother, Jane, but otherwise associated predominantly with Rocky, the castrated male, and Noxolo, a young adult female. As Noxolo matured (she had her first oestrus in May 2003), she spent increasingly more time with Romeo, and less time with Celina and Rocky. Rolex, the old female, interacted very little with other troop members, except for rare grooming by Romeo or Rocky. Noxolo and

Jane were pregnant for the duration of the study: Noxolo gave birth to her first offspring, a male, on 15 December 2003. Jane gave birth to her fourth offspring, a female, on 4 January 2004. Both offspring were sired by Romeo.

Table 2.3: Composition and history of the hamadryas (*Papio hamadryas hamadryas*) troop housed at the Johannesburg Zoo for the duration of the study period up until 15 December 2003.

Name	Sex and reproductive status	Birth year	Age at end 2003	Birth environment
Romeo[a]	Adult male	1988	15	Captive
Rolex	Old female (hysterectomy 1996)	1989	14	Captive
Jane[b]	Adult female	1993	10	Captive
Rocky	Male (castrated)	1994	9	Captive
Noxolo	Adult female	1999	4	Captive
Celina	Juvenile female	2000	3	Captive

a – sire of Jane, Rocky, Noxolo, and Celina; b – dam of Noxolo and Celina

2.2 Housing and husbandry at the Johannesburg Zoo

The chacma and the hamadryas troops were housed in octagonally-shaped, open-roofed concrete enclosures with a perimeter of roughly 54 m (Figure 2.1). Each enclosure contained a central, 6 m high fibreglass rock formation, the base of which began to rise about 2 m in from the 3.7 m high perimeter walling. Each enclosure contained a mulch patch, one of which was approximately 2 m x 2 m (hamadryas), and the other 2 m x 4 m (chacma), with 30 cm high containing walls. About 30 logs/branches were placed in either fixed or movable positions within the enclosure. The mulch patches were empty during the baseline and first experimental treatment. When the patches were filled with straw between the end of the first and start of the second experimental treatment, the troops explored the substrate initially, but only very rarely after a few days (< 1% of time observed), except when food was scattered in it by zoo staff or by myself during experimental treatments.

The nightrooms of both troops were roughly 2.2 m wide, 3.2 m long, and 2.2 m high, and opened directly into their outdoor enclosures. The baboons had free access to their enclosures and nightrooms, except when either of these areas was being cleaned. Nightrooms were cleaned daily and enclosures usually thrice weekly.

Baboons were fed once a day in their nightrooms. Their diet comprised fruit (e.g. apples, bananas, oranges) and vegetables (e.g. carrots, sweet potatoes, broccoli). Various other foods, such as sunflower seeds, horse cubes, peanuts, and marrow bones, were provided as part of standard enrichment protocols. The baboons were not deprived of food during the study. Water was available *ad libitum*.

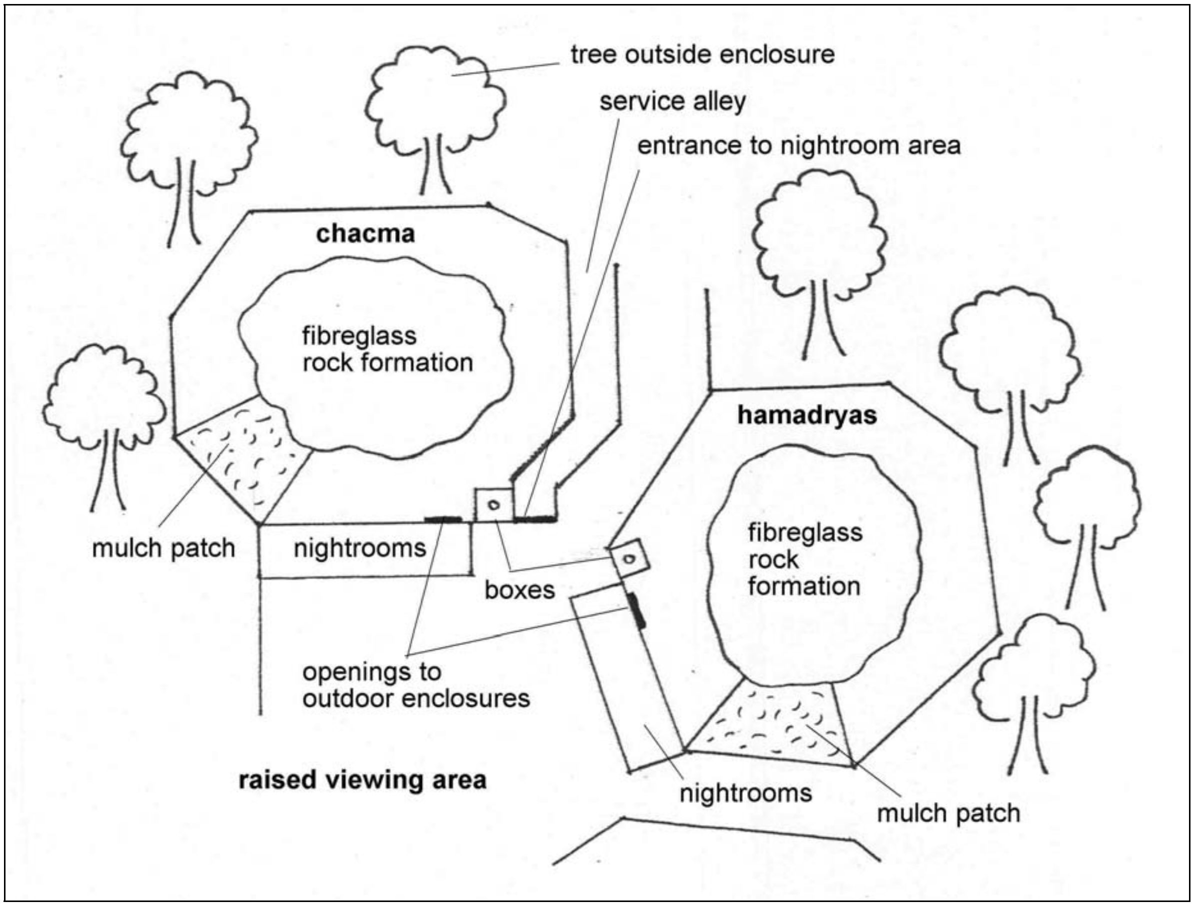

Figure 2.1: Schematic plan (not to scale) of the chacma and hamadryas enclosures at the Johannesburg Zoo.

2.3 Baseline study

Baseline observations were conducted before experimental manipulation took place to establish foraging frequency and levels of aggressive interactions for individual troop members and collectively for both troops. During these observations, no apparatus was introduced into the enclosures. Each troop was observed for a total of seven, non-consecutive, days.

As expected, levels of foraging in both the chacma and hamadryas baboons troops were very low (Figure 2.2). Individual animals varied in the amount of time they spent foraging. Although these differences were not analysed statistically, it appeared that the younger and also lower ranking baboons displayed more foraging behaviour than did the older and higher ranking individuals. In experiments, therefore, it was likely that treatment and individual characteristics would affect the frequency of foraging behaviour, thus confirming the appropriateness of focal rather than group sampling methods. No aggressive interactions were observed during the baseline study in either the chacma or hamadryas troop.

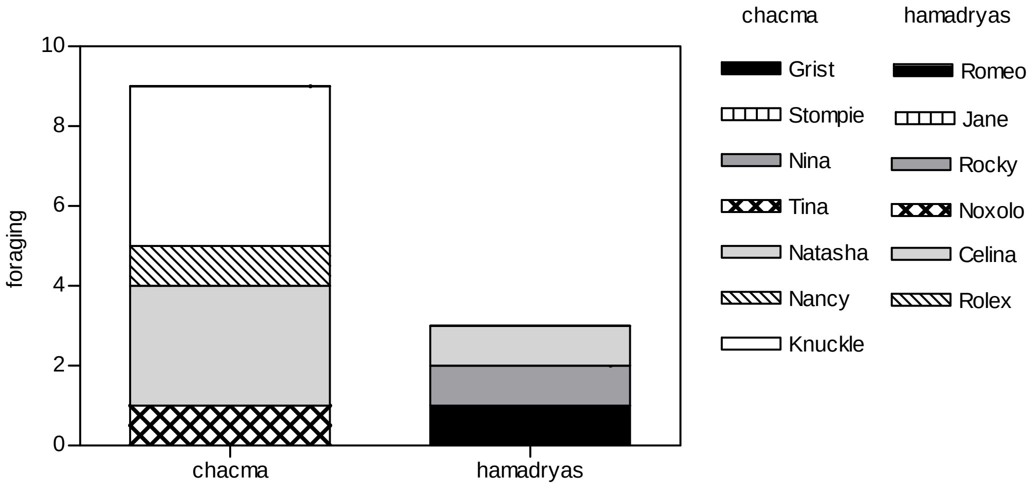

Figure 2.2: Median frequency of foraging during the baseline study for the chacma and hamadryas troops.

2.4 Experiments

Experiments were conducted to determine how various presentations of a monopolisable food source (treatments) affected the frequency of foraging elsewhere and levels of aggression in individual troop members, as well as in the group as a whole. Each treatment was presented on either eight (Experiment I – 5 treatments; Experiment III – 2 treatments) or seven (Experiment II – 3 treatments) occasions.

2.4.1 *Apparatus*

A wooden box, measuring 30 cm x 30 cm x 30 cm, was introduced into each enclosure. Each box was secured with two rawl bolts to the floor of the concrete enclosure, adjacent to the external wall of the nightrooms, and below the viewing area (Figure 2.1). The upper surface of each box had a round 10 cm diameter opening, through which only one baboon at a time could access the interior. An additional wooden base was fitted onto the inside lower surface, into which 25 equally-spaced, cylindrical depressions, 3 cm diameter and 1.5 cm deep, had been drilled (Figures 2.3 and 2.4).

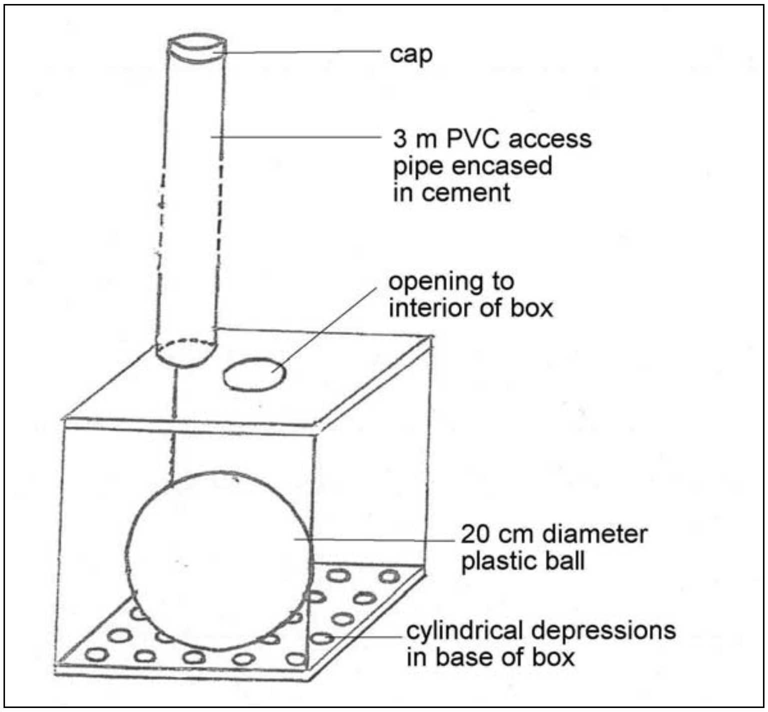

Figure 2.3: Experimental apparatus used for the hamadryas troop.

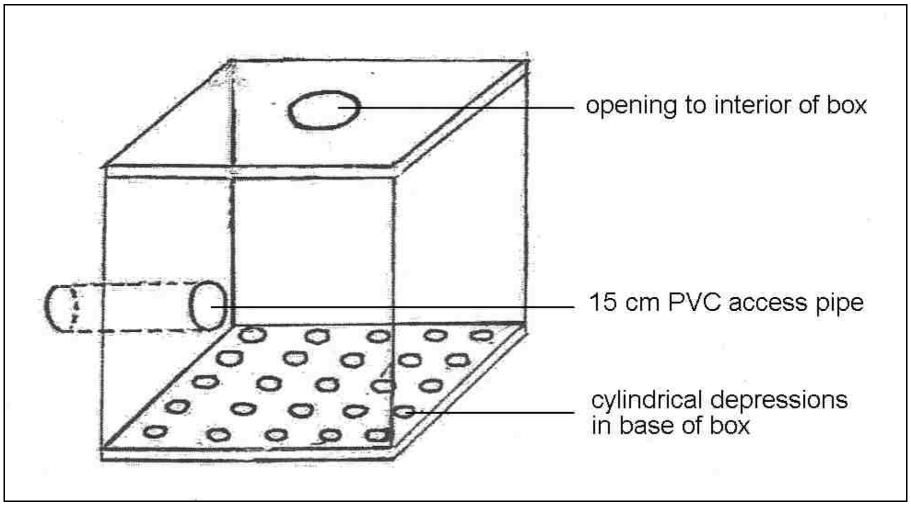

Figure 2.4: Experimental apparatus used for the chacma troop.

For the hamadryas troop, a 20 cm diameter plastic ball was placed into the box to increase the time needed to extract food from the box. A 3 m long, 8 cm diameter PVC pipe exited from the top surface of the box, and ran perpendicularly up the wall of the enclosure, terminating just beneath the public viewing area (Figure 2.3). The pipe was encased in cement to prevent the baboons from either destroying it or from climbing up it and attempting to escape from the enclosure. Food was introduced into the box through the upper opening of the pipe, which was otherwise kept capped to prevent the insertion of any other objects or foodstuffs into the box by zoo visitors.

For the chacma baboons, a 15 cm long, 8 cm diameter PVC pipe exited from one side of the box, and ran through the wall of the enclosure, just above ground level, into the adjacent service lane used by the keepers to access the nightrooms (Figure 2.4). Food was introduced into the box through the pipe which opened into the service alley. Initially, a ball was placed in the wooden box. However, when the box was provisioned with food, instead of simply manipulating the ball to access the food, as did the hamadryas baboons, the chacma baboons ripped off parts of the box lid to access the interior of the box, and punctured and removed the ball. The lid of the box was repaired, but it was not possible to replace the ball. To protect the box, a metal cover was affixed to the exposed surfaces of the box.

2.4.2 *Food items*

In pilot trials conducted after the baseline and before experiments began, I established that peanuts were a prized food item for both hamadryas and chacma baboons, and thus would be monopolised by the hamadryas alpha-male, Romeo, for most of the observation period, and likewise by the dominant chacma male, Grist. Currants were identified as a less-preferred food for which Romeo would seldom forage, and for which Grist spent less time foraging than he did for peanuts. The peanuts were presented in a nibbed form to the chacma baboons to slow down the rate at which they were gathered (the box no longer contained a ball to increase foraging difficulty and time). Whole peanuts were given to the hamadryas (whose box still contained a ball) because, in pilot observations, Romeo had spilt the nibbed peanuts outside the box which allowed other troop members to feed on the peanuts, thereby violating the precondition of a monopolisable food source from which only one animal could feed at a time. In contrast, only one chacma baboon ever fed at or around the box at any given time, even if some nibbed peanuts had been spilt outside the box.

2.5 Data collection

During the baseline study and experiments, observations were conducted from the raised public viewing area. The baboons were observed between 10h00 and 11h30, after normal feeding times for the hamadryas, but usually before the chacma baboons were fed. Chacma feeding time varied as the animals would not reliably retreat into their nightroom at a particular time for food.

For each troop, data were collected during 30-minute observation periods using scan sampling of individuals (Martin & Bateson, 1993), with a 30-second interscan interval, yielding 60 data points per observation period. Three behaviours were recorded using this sampling method: foraging elsewhere, foraging at the box (experiments only), and other. In addition, I noted when an individual was out-of-sight. Scores for the chacma and hamadryas troops as a whole were calculated by summing the scores for the individual animals. Because aggression levels in the hamadryas and chacma troops were very low, the frequency of aggression was scored using continuous recording (Martin & Bateson, 1993).

During pilot trials conducted between the baseline studies and the experiments, three of the hamadryas females would occasionally show displacement activities when watching Romeo, the alpha-male, feed from the box. These behaviours were considered displacement activities as they appeared to be irrelevant to the context, and tended to occur in situations of psychological stress (i.e. heightened levels of group tension resulting from competition for access to food; ambivalence between approaching and withdrawing from the animal foraging at the box; after Maestripieri et al, 1992). Because of the apparent relationship between treatment and displacement activity, I recorded the frequency of displacement activities during experiments, again using focal scan sampling. No displacement activities were observed in the chacma troop. The definitions of all the behaviours scored are given in Table 2.4.

2.6 Data analysis and reporting

All statistical analyses were conducted using GraphPad Instat 3.06 for Windows (GraphPad Software, 2003). Differences were considered significant if $p < 0.05$; a trend was considered when $0.05 < p < 0.10$. All statistical tests were two-tailed.

Preliminary analysis showed high variability in the frequency of all behaviours, both among and within individuals. Data were therefore not normally distributed (Kolmogorov-Smirnov normality test; $p < 0.10$), and could not be transformed for parametric analysis because of the large number of zeros in the data sets. Non-parametric statistics were accordingly used throughout.

To account for the times when animals were not in view, adjusted frequencies for foraging elsewhere and displacement behaviour were calculated by multiplying the percentage of observations individuals spent foraging or performing displacement activities by 60, the total number of possible observations per session. For example, if an individual was recorded as foraging 8 out of a total of 54 times (i.e. it was not seen during 6 of the 60 scans), the adjusted frequency of 9 (8.8889) was calculated by multiplying 8/54 by 60.

Table 2.4: Descriptions of behaviours scored.

Behaviour	Description
Foraging elsewhere	Actively searching for, harvesting, processing (peeling, stripping outer covering, and so forth), and/or consuming food. During experimental treatments, this excluded food within the box.
Foraging at the box (experiments only)	Searching for, or consuming food within the box, or food that had been spilt from the box.
Other	The baboon could be seen, but was not foraging elsewhere, foraging at the box, or performing displacement activities.
Overt aggression	A physical interaction in which one animal bites, grapples with, or chases another. This unidirectional chasing is an action of supplantation or assertion of authority by a dominant individual over a subordinate, and is thus distinguishable from the bi-directional chasing that occurs in play. Each interaction, rather than separate behavioural components thereof, was scored as one aggressive episode.
Displacement activity	Displacement activities had two similar forms: (1) A baboon partially flattened its body, stomach-down, on the ground and directed its gaze towards another animal, and made repeated to-and-fro movements of the hand and lower arm, either with the palm on the ground, or the hand raised about 10 cm above the ground. (2) A baboon partially flattened its body on the ground, gazed directly towards the ground and made a repetitive, scraping movement with its index finger from the ground towards its face.

These corrected frequencies are reported in the text, tables, and figures, and permit a direct comparison of behavioural frequencies among individuals.

Studies of zoo animals are notorious for small sample sizes and pseudo-replication (Young, 2003). My study is no different since I sampled each troop repeatedly and regarded each observation as an independent replicate, which unavoidably created pseudo-replication. For comparisons between treatments, I used appropriate repeated measures tests where possible to compare the performances of individuals and the troop among treatments and to minimise the problems associated with pseudo-replication within treatments.

CHAPTER 3: EXPERIMENT I

Social foraging: internal and external factors influencing motivation

3.1 Introduction

3.1.1 *Social cues and behaviour*

A rapidly accumulating body of evidence indicates that an animal's behaviour is strongly affected by information acquired in the context of interactions with other animals (Box, 1999; Danchin et al, 2004). Making use of cues produced by conspecifics, rather than relying solely on personal learning, enhances an animal's fitness by decreasing the costs of acquiring information (King, 1999; Danchin et al, 2004), information which in turn enables individuals to adjust flexibly and rapidly to the demands of their environments (Box, 1999). For the most part, these cues are not specialised or co-evolved signals, but are coincidentally produced while animals perform their routine daily activities (Galef & Giraldeau, 2001).

Coussi-Korbel and Fragaszy (1995) define behavioural coordination as "the coordination of behaviour patterns between two or more conspecific individuals when one individual's activity channels the attention of its conspecific(s) to an activity or element of the environment, such that behavioural similarity between the two individuals increases" (p1443). Behavioural coordination, which may occur in either time and/or space, supports social learning by placing animals in situations from which they can potentially learn (Coussi-Korbel & Fragaszy, 1995). In addition, it is thought to promote group cohesion which may in turn contribute to the detection and avoidance of predators and the efficient exploitation of resources.

In social animals, such as baboons, the behaviour of group members influences individuals' foraging behaviours and diet selections (Altmann, 1998; King, 1999). By either actively seeking information, or receiving it as an unintended consequence of other foraging activities (King, 1999), animals gain general information about when to eat, where to find food, and when to leave a food patch (Templeton & Giraldeau, 1996), and more specific information about what foods to eat (and possibly not eat) as well as which methods to use to process and consume foods (Galef, 1996; Terkel, 1996; Zentall, 1996; Galef & Giraldeau, 2001).

Information acquired from interactions with conspecifics can enhance foraging efficiency (Galef & White, 1997). Such social learning is predicted to be most advantageous at intermediate levels of environmental variation, where environments are variable but relatively predictable within and between generations (Sibly, 1999; Wilkinson & Boughman, 1999; Laland & Kendal, 2003) and, whilst this prediction is seldom tested, recent experimental studies in rats (*Rattus norvegicus*) have provided some empirical support for it (Galef & Whiskin, 2004). Use of public information may underlie the adaptability of baboons to diverse habits, as well as to the large within-habitat seasonal and spatial fluctuations in resource availability and quality (Altmann, 1998). In other words, the principal advantage of social learning is to track and predict environmental variation that is too rapid to be followed using genetic transmission of information (Lefebvre, 1996).

Conspecifics influence each other's behaviour in a number of ways. Demonstrators may affect the actions of observers by directly altering their motivational state, without any learning occurring, as in social facilitation and behavioural contagion (Fragaszy & Visalberghi, 1996). Alternatively, learning may mediate behavioural changes in the observer. Different mechanisms of social transfer of information are addressed in Chapter 4.

3.1.2 *Factors affecting the transfer of social information*

The identity, appearance, and age of a demonstrator, pre-existing social and kin relationships between a demonstrator and observer, the internal state and temperament of the observer, and the social context in which the demonstrator is observed, all affect opportunities for social learning as well as the propensity of the observer to learn from the demonstrator (Nicol & Pope, 1994; 1999; Coussi-Korbel & Fragaszy, 1995; Hatch & Lefebvre, 1997; Box, 1999). Some animals are more influential demonstrators than others, possibly because observers have learned that these animals, which may be older or of higher social rank (Galef & Whiskin, 2004), are better predictors of the availability of food (Nicol & Pope, 1999). In hens (*Gallus gallus domesticus*), Nicol and Pope (1999) hypothesise that dominant individuals are more effective demonstrators than subordinates because (1) they attract the continuous attention of subordinates; (2) their appearance is more striking or noticeable; and/or (3) dominance is a correlate of some other indicator of quality such as foraging ability. Learning that occurs differentially as a function of the identity of the demonstrator is termed directed social learning (Coussi-Korbel & Fragaszy, 1995). This contrasts with non-specific social learning, in which the identity of the demonstrator does not influence the learning process.

An animal's internal state may also affect the social learning process. In general, learning is less likely if animals are food deprived (Nicol & Pope, 1994), presumably because the animal's attention is focused on finding food and not on acquiring non-food-related information from a demonstrator. However, social learning about food or foraging may actually be enhanced by moderate hunger (or specific nutrient deprivation; Galef, 1996). This is because the animal perceives the food as more rewarding when hungry, and consequently preferentially attends to food-related stimuli (Spruijt et al, 2001; Toates, 2001). The salience of cues to forage is also modified by the observer's prior exposure to the food item and the general taste properties of the food (Toates, 1986). Therefore, an observer will pay more attention to a demonstrator engaging with a preferred than a lesser-preferred food item, and so be more likely to learn from that demonstrator. Thus, the perceived value of the food and the motivation to forage may differ among food items and over time. Temperament (e.g. fearfulness or curiosity) is also thought to determine how well individuals attend to conspecifics' behaviour and thus whether they can take advantage of the public information available to them (reviewed by Box, 1999).

Another factor that influences opportunities for social learning is an animal's social context, with high levels of social tolerance facilitating social learning (Coussi-Korbel & Fragaszy, 1995). This is because sociability (1) facilitates temporal and spatial coordination of behaviour, thus bringing animals into close proximity during foraging, and making close-range observations (as well as co-feeding or tolerated scrounging; Fragaszy & Visalberghi, 1996) possible, and/or (2) reduces anxiety levels, allowing animals to attend to foraging cues, rather than monitoring their environment for, perhaps, potential aggressors or predators (van Schaik et al, 1999). Baboon societies, in particular the hamadryas subspecies, are characteristically tolerant, especially of infants. This tolerance promotes the acquisition of troop-specific foraging skills, and allows young to co-feed with or scrounge from older, more experienced individuals. Juveniles can thus sample foods and experiment with food processing techniques, opportunities they would not otherwise have been afforded on their own (Fragaszy & Visalberghi, 1996). Lastly, social learning is more likely to occur if the number of observers relative to demonstrators remains small (Nicol, 1995).

3.1.3 *Objectives and predictions*

This experiment investigated potential internal and external factors cueing observer baboons to forage upon watching a demonstrator animal feed from a monopolisable food source. The frequency of aggressive behaviours was also examined. I presented the chacma and hamadryas baboons with the apparatus (described in Chapter 2) under five different conditions in order to (1) confirm the findings of a previous study (Jones & Pillay, 2004) that watching a demonstrator animal accessing food motivates observer animals to increase their frequency of foraging behaviour in non-provisioned areas of the enclosure; and (2) identify the internal signals (hunger/satiation) and external conditions (demonstrator identity) that influence an individual's motivation to forage.

I made three predictions: (1) If watching a demonstrator forage, and not just the mere presence of an inaccessible food, motivates observer animals to also forage, baboons will only show an increase in foraging behaviour when a demonstrator forages for food placed in the box (temporal coordination of foraging behaviour), and not during treatments when no animal is demonstrating foraging behaviour. (2) If the identity of the demonstrator influences whether observer animals are motivated to forage in other areas of the enclosure, the frequency of foraging elsewhere will be greater during the treatment in which a dominant animal forages at the box than during the treatment when a subordinate forages at the box. (3) If the level of observer satiation affects whether observers are motivated to forage upon watching a demonstrator forage, it would be expected that the frequency of foraging elsewhere will be lower when the baboons are fed prior to the observation period. Previous research (Jones & Pillay, 2004) suggested that the frequency of aggression would not be substantially increased by the experimental treatments.

3.2 Materials and methods

3.2.1 *General materials and methods*

Subjects, housing and husbandry, apparatus, and data collection are described in Chapter 2, General Materials and Methods.

3.2.2 *Procedure*

The boxes were presented to the two troops in five different treatments, as outlined below. During the 40, not necessarily consecutive, days of observations, one of five treatments was presented each day in a randomly determined order, resulting in eight observation sessions for each treatment.

3.2.2.1 Treatment 1: control

Boxes were empty, and apparatuses were not manipulated in any way.

3.2.2.2 Treatment 2: peanuts

250 g peanuts (whole for the hamadryas; nibbed for the chacma) were placed in the boxes immediately before the start of observations. The alpha-male was expected to monopolise the peanuts, a prized food item, and so act as the demonstrator for other troop members.

3.2.2.3 Treatment 3: currants

250 g currants were placed in the boxes immediately before the start of observations. The dominant male was not expected to monopolise the currants, as they were not a preferred food, so allowing other group members to demonstrate foraging behaviour to the rest of the troop.

3.2.2.4 Treatment 4: hidden peanuts

Immediately before the start of observations, a small (6 cm diameter, 10 cm long) metal canister containing peanuts was inserted into the boxes through the access pipe and anchored with a metal chain to the external entrance of the pipe. The base of the metal canister was made of wire mesh, permitting the baboons to smell and see the peanuts, but not access them. This treatment was included to control for whether the mere presence of an inaccessible food, as opposed to watching a demonstrator animal accessing food, was sufficient to motivate observer animals to increase their foraging behaviour in other areas of the enclosure.

3.2.2.5 Treatment 5: peanuts & peanuts

250 g peanuts were placed in the boxes immediately before the start of observations. Thirty minutes before the start of the observations, each troop was provided with whole peanuts (the seven-member chacma troop received 700 g whole peanuts and the six-member hamadryas group 600 g). As the hamadryas would reliably return to their nightrooms each day for feeding, the peanuts could be placed in a number of piles on the floor of the outdoor enclosure before the troop was let out. For the chacmas, which would not reliably re-enter their nightrooms each morning for feeding, the peanuts had to be spread into the outdoor enclosure from the viewing area above. The chacma and hamadryas baboons alike picked up or ate all the peanuts within two to three minutes of accessing them, although it took them up to 20 minutes to finish eating those peanuts they had stored in food pouches in their mouths. Ideally, the peanuts should have been fed to both troops in their nightrooms to prevent the possibility of any peanuts being left on the floor of the outdoor enclosures, and subsequently searched for and consumed during observation periods. However, this was not practical because of the high levels of aggression shown when a prized food was fed in the very restricted nightroom areas.

3.2.3 *Data analysis*

The total number of observations for each animal was calculated by subtracting the number of out-of-sight observations from 60, the total possible number of observations per day.

Foraging elsewhere data for each day of observation, for each individual as well as each troop as a whole, was converted to a ratio of

$$\frac{\text{frequency of foraging elsewhere}}{\text{(total number of observations – frequency of foraging at the box)}}$$

Displacement activity data for each day of observation, for each individual as well as the hamadryas troop as a whole, was similarly converted to a ratio of

$$\frac{\text{frequency of displacement activity}}{\text{total number of observations}}$$

The non-parametric, repeat-measures, Friedman Analysis of Variance (ANOVA) was used to test for differences in the frequency of foraging elsewhere, foraging at the box, displacement activity, and aggressive behaviour among the five treatments. A repeated measures test was chosen because the same group of subjects was tested under each of the five treatments (Siegel & Castellan, 1988). The data were initially analysed using a Friedman ANOVA because treatments were administered in a random design, and were thus related to each other. Thereafter, if the Friedman statistic was significant, Mann-Whitney U-tests were used for pair-wise comparisons to detect differences between specific treatments. Mann-Whitney U-tests were used in preference to Wilcoxon paired rank tests because, although the same subjects were used in both treatments, the treatments were randomly implemented and logical pairs could not be formed.

For the chacma baboons, Friedman ANOVA was used to test for differences in the proportion of time animals in the group foraged elsewhere as a function of the identity of the individual foraging at the box. This test was not conducted for the hamadryas because Romeo, the dominant male, very rarely permitted other animals to feed from the box.

The relationship between the frequency of aggression and the frequency of displacement activity was assessed using Spearman's Rank Correlation Coefficient analysis.

3.3 Results

3.3.1 *Chacma baboons*

3.3.1.1 Foraging elsewhere

The foraging elsewhere behaviour of the chacma baboon troop differed significantly among treatments (Fr = 23.900, $p < 0.0001$; Figure 3.1). The frequency of foraging elsewhere was approximately twice as high during the peanuts, peanuts & peanuts, and currants treatments, when a demonstrator was foraging for food from the box, than during the control treatment when no food was available, or during the hidden peanuts treatment, when the food was inaccessible. In contrast to my predictions, a pre-feeding of peanuts did not reduce the frequency of foraging elsewhere during the peanuts & peanuts observation sessions; moreover, the frequency of foraging elsewhere was not higher during the peanuts treatment, when the alpha-male was the main demonstrator, than during the currants treatment, when subordinate animals were demonstrators for most of the observation period. Summary results for individual animals are presented in Table 3.1: although the baboons differed in their levels of foraging elsewhere within and among treatments, the general direction of effect of treatment on foraging elsewhere was relatively consistent among individuals.

3.3.1.2 Foraging at the box

The frequency of foraging at the box, as well as the identity of the baboon foraging at the box, was significantly affected by treatment (Fr = 25.686, $p < 0.0001$; Figure 3.2). The troop only very occasionally attempted to find food in the box during the control and hidden peanuts treatments. During treatments when there was food in the box, however, a baboon almost always foraged at the box (peanuts: 56.5 (47-60), median frequency (range of frequencies); peanuts & peanuts: 55.5 (49-59); currants: 51 (49-59)). When peanuts were presented in the box, Grist, the alpha-male, initially monopolised the

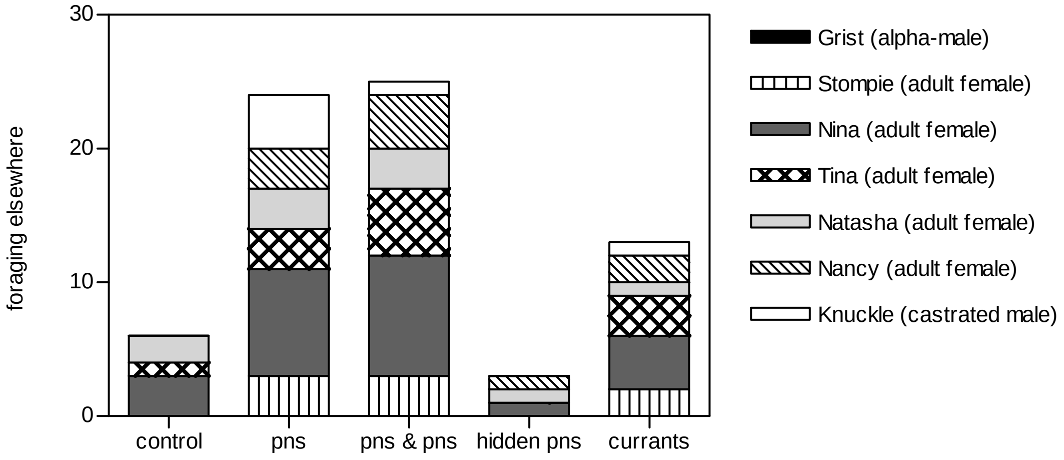

Figure 3.1: Median frequency of foraging elsewhere per observation session (n = 8) for the chacma baboons. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

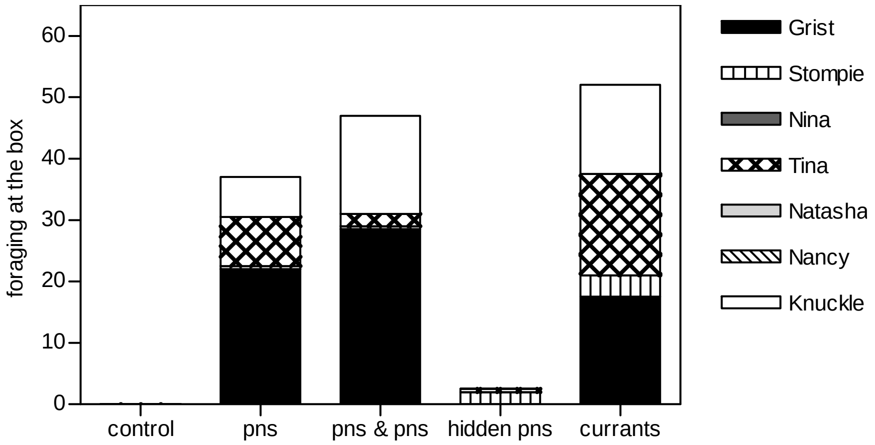

Figure 3.2: Median frequency of foraging at the box per observation session (n = 8) for the chacma baboons. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

food, often for over half the observation period (peanuts: 22 (6-59); peanuts & peanuts: 28.5 (0-55)). Thereafter, Tina (peanuts: 8 (0-43); peanuts & peanuts: 16 (0-26)) or Knuckle (peanuts: 6.5 (0-26); peanuts & peanuts: 16 (0-26)) tended to extract the peanuts. When the box was provisioned with currants, Grist monopolised the food source for a significantly shorter period (17.5 (5-39)) than when peanuts were available, and hence Tina, Knuckle, and, rarely, other troop members were able to access the box for significantly longer periods than during the peanuts, or peanuts & peanuts, treatments.

3.3.1.3 Effect of demonstrator identity

When data for the peanuts, peanuts & peanuts, and currants treatments were combined, the identity of the demonstrator significantly influenced the frequency of foraging elsewhere by observer animals (Fr = 10.135, p = 0.0382; Figure 3.3). Mann-Whitney U-tests indicated that levels of foraging elsewhere were significantly higher when Knuckle was feeding at the box, than when either Grist, Tina, or another animal were feeding, or when no baboon was present at the box. Within treatment effects of demonstrator identity on foraging activity elsewhere were not significant however, possibly because of the small sample sizes (n = 8) and large variation in the data sets.

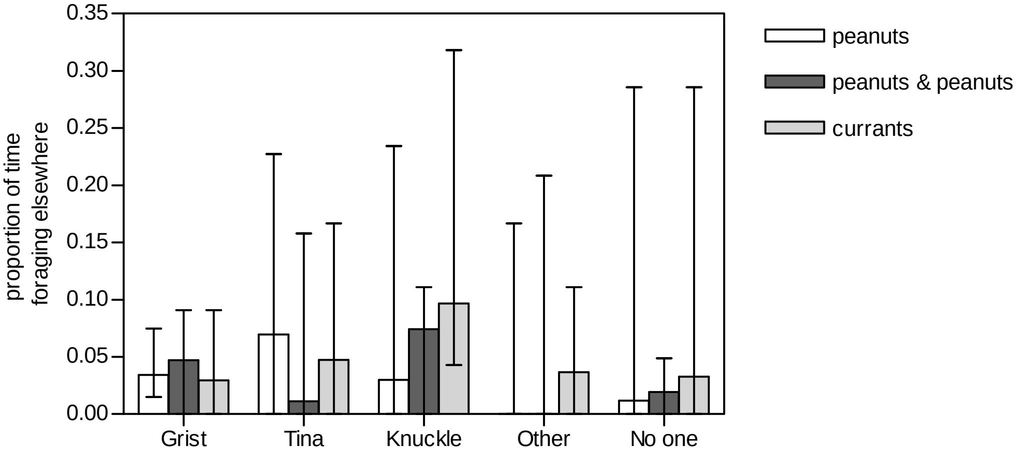

Figure 3.3: Median proportion of time troop members spent foraging elsewhere per observation session (n = 8) as a function of the baboon foraging at the box. Bars represent range.

Table 3.1: Frequency of foraging elsewhere across treatments for the chacma baboons.

Individual	Frequency of foraging elsewhere per observation session [median (range)] n = 8					Friedman statistic (Fr)	Pair-wise comparisons (if Friedman ANOVA significant) (Mann-Whitney U-statistic)	
	control	pns	pns & pns	hidden pns	currants			
Grist	0 (0-0)	0 (0-5)	0 (0-5)	0 (0-4)	0 (0-0)	28.526***	control < pns	0***
							control ≈ currants	32
							pns > currants	0***
							pns < pns & pns	7**
							pns > hidden pns	8*
Stompie	0 (0-3)	3 (0-10)	3 (0-6)	0 (0-2)	2 (1-7)	12.100*	control < pns	8*
							control < currants	7**
							pns ≈ currants	32
							pns ≈ pns & pns	31
							pns > hidden pns	10*
Nina	3 (0-11)	8 (3-19)	9 (4-15)	1 (0-5)	4 (0-19)	15.900**	control < pns	14#
							control < currants	11*
							pns ≈ currants	29
							pns ≈ pns & pns	17
							pns > hidden pns	3**
Tina	1 (0-9)	3 (0-8)	5 (0-7)	0 (0-4)	3 (0-11)	10.700*	control ≈ pns	16
							control < currants	14#
							pns ≈ currants	28
							pns ≈ pns & pns	30
							pns > hidden pns	7**
Natasha	2 (0-12)	3 (0-11)	3 (0-10)	1 (0-10)	1 (0-16)	4.100		
Nancy	0 (0-7)	3 (0-12)	4 (1-11)	1 (0-5)	2 (0-13)	15.700**	control < pns	9*
							control < currants	5**
							pns ≈ currants	22
							pns ≈ pns & pns	29
							pns > hidden pns	14#
Knuckle	0 (0-4)	4 (0-11)	1 (0-7)	0 (0-1)	1 (0-6)	20.800***	control < pns	9*
							control < currants	14#
							pns ≈ currants	16
							pns > pns & pns	14#
							pns > hidden pns	4**
Group Total	13 (1-20)	20 (12-67)	24 (19-41)	8 (1-14)	21 (6-36)	23.900***	control < pns	6**
							control < currants	1***
							pns ≈ currants	23
							pns ≈ pns & pns	28
							pns > hidden pns	1***

# p < 0.10 * p < 0.05 ** p < 0.01 *** p < 0.001; pns = peanuts, pns & pns = peanuts & peanuts, hidden pns = hidden peanuts

3.3.1.4 Aggression

The frequency of aggressive interactions was low across all treatments, but nonetheless differed significantly among treatments (Fr = 15.276, p = 0.0042; Figure 3.4). Aggression was more frequent when accessible food was provided (peanuts: 2 (0-4); peanuts & peanuts: 0 (0-2); currants: 1 (0-4)), than during the control (0 (0-1)) or hidden peanuts (0 (0-1)) treatments.

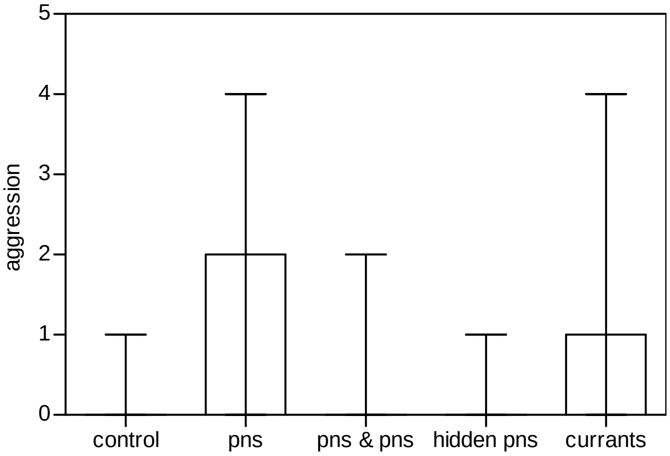

Figure 3.4: Median frequency of aggressive behaviour per observation session (n = 8) for the chacma baboons. Bars represent range. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

3.3.2 *Hamadryas baboons*

3.3.2.1 Foraging elsewhere

Foraging elsewhere data and analyses of the hamadryas baboon troop are summarised in Table 3.2. Overall, frequency of foraging elsewhere differed significantly among treatments (Fr = 12.500, p = 0.0140; Figure 3.5). The levels of foraging elsewhere were approximately twice as great during the peanuts treatment, when Romeo, the alpha-male, foraged for peanuts from the box, than during both the control (U = 11, p = 0.0281) and currants (U = 11, p = 0.0281) treatments, and approached significance for the hidden peanuts and peanuts & peanuts treatments (U = 14; p = 0.0650 for both). This trend for foraging elsewhere levels to be higher during the peanuts rather than the peanuts & peanuts treatment suggests that, as predicted, a pre-feeding of peanuts reduces the frequency of foraging elsewhere during the peanuts & peanuts observation sessions

(Table 3.2). Foraging elsewhere levels were also significantly higher during the peanuts & peanuts treatment than during the hidden peanuts treatment (U = 13, p = 0.0499).

When foraging elsewhere data for individual baboons were compared, similar trends to those of the group emerged: although the individuals in the troop differed among themselves in levels of foraging behaviour within and among treatments, the general direction of the effect of treatment on individual foraging behaviour was relatively consistent among animals. Both Rocky and Noxolo foraged significantly more during the peanuts than the control treatments (U = 12, p = 0.0379 for both animals), with a similar but non-significant trend appearing for Jane and Rolex. There were very few individual differences among other treatments, during which foraging elsewhere levels were uniformly low for the most part.

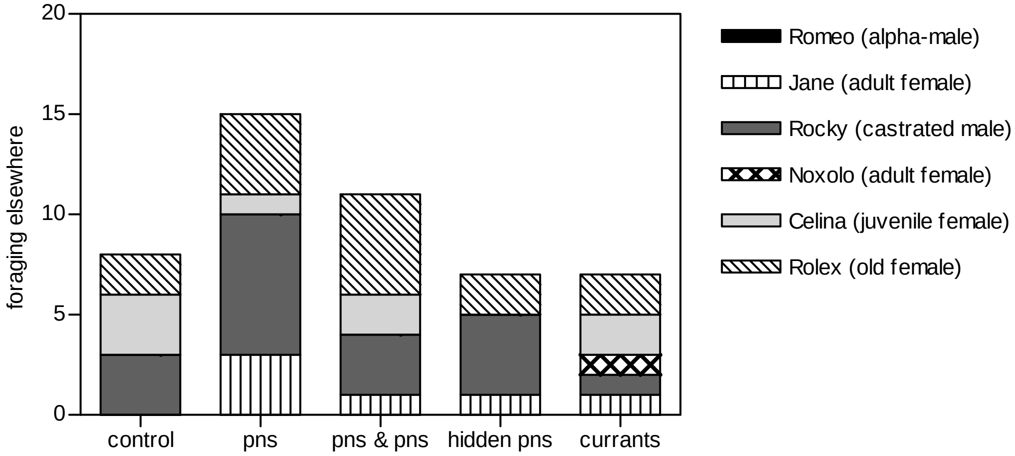

Figure 3.5: Median frequency of foraging elsewhere per observation session (n = 8) for the hamadryas baboons. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

Table 3.2: Frequency of foraging elsewhere across treatments for the hamadryas baboons.

Individual	Frequency of foraging elsewhere per observation session [median (range)] n = 8					Friedman statistic (Fr)	Pair-wise comparisons (Mann-Whitney U-statistic)	
	control	pns	pns & pns	hidden pns	currants			
Romeo	0 (0-2)	0 (0-0)	0 (0-30)	0 (0-1)	0 (0-4)	21.800***	control > pns	0***
							control < currants	14#
							pns < currants	0***
							pns < pns & pns	0***
							pns < hidden pns	0***
Jane	0 (0-7)	3 (0-10)	1 (0-6)	1 (0-3)	1 (0-16)	8.000		
Rocky	3 (0-9)	7 (3-17)	3 (0-11)	4 (0-9)	1 (0-28)	9.700*	control < pns	12*
							control ≈ currants	28
							pns > currants	15#
							pns > pns & pns	8*
							pns > hidden pns	14#
Noxolo	0 (0-5)	0 (0-2)	0 (0-2)	0 (0-3)	1 (0-4)	10.900*	control > pns	12*
							control < currants	12*
							pns < currants	12*
							pns pns > pns	10*
							pns < hidden pns	14#
Celina	3 (0-8)	1 (0-6)	1 (0-1)	2 (0-9)	0 (0-5)	12.500*	control ≈ pns	26
							control > currants	5**
							pns > currants	8*
							pns ≈ pns & pns	17
							pns ≈ hidden pns	20
Rolex	2 (0-6)	4 (1-12)	2 (0-7)	5 (0-10)	2 (0-8)	4.000		
Group Total	12 (0-21)	21 (7-29)	8 (1-46)	13 (8-21)	9 (2-59)	12.500*	Control < pns	11*
							control ≈ currants	32
							pns > currants	11*
							pns > pns & pns	14#
							pns > hidden pns	14#

# $p < 0.1$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$; pns = peanuts, pns & pns = peanuts & peanuts, hidden pns = hidden peanuts

3.3.2.2 Foraging at the box

Foraging behaviour at the box differed significantly among treatments (Fr = 24.629, $p < 0.0001$), as did the identity of the animal feeding at the box (Figure 3.6). When no food was available (control), or when the available food was inaccessible (hidden peanuts), Celina (3 (0-10); 6.5 (0-24)) and Noxolo (2.5 (0-16); 5 (0-22)), and very occasionally Rocky (0 (0-1); 1 (0-3)), attempted to extract food from the box by manipulating the ball within the box or pulling at the canister containing the inaccessible peanuts. In contrast, Romeo, after having cursorily investigated the box the first time the hidden peanuts treatment was implemented, did not thereafter forage at the box during the control or hidden peanuts treatments, even though the treatments were implemented in a random order.

When the box was provisioned with food, one or sometimes two animals almost always foraged at the box (peanuts: 58 (50-60); peanuts & peanuts: 58.5 (53-60); currants: 50.5 (32-69)). During the treatments when peanuts were available, Romeo monopolised the food for almost the entire observation period (peanuts: 56.5 (41-60); peanuts & peanuts: 58 (45-60)), during which time Jane, Noxolo, and Celina would often sit in very close proximity to Romeo and the box, usually grooming Romeo or each other. Occasionally, Noxolo (peanuts: 0 (0-13); peanuts & peanuts: 0 (0-2)) or Celina (peanuts: 0.5 (0-4); peanuts & peanuts: 0.5 (0-8)) would access the box, either whilst Romeo was feeding, or on the brief occasions when he was chasing other animals from the box. Rolex, Rocky, and Jane never fed from the box during either the peanuts or the peanuts & peanuts treatments.

During the currants treatment, Romeo fed from the box significantly less frequently than when peanuts were available (8.5 (0-17); U = 0, $p = 0.0002$). Thereafter, in no particular order, Jane (8.5 (0-17)), Rocky (3.5 (0-20)), Noxolo (12 (4-33)), or Celina (15.5 (8-21)) accessed the currants. Again, Rolex never fed from the box.

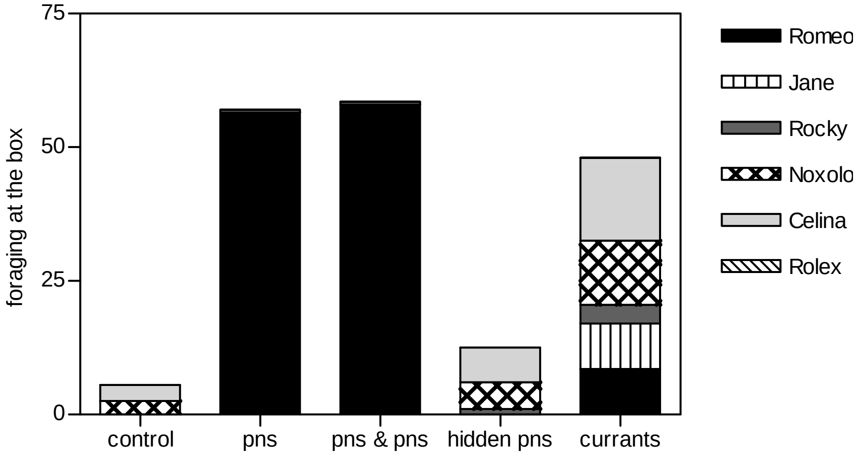

Figure 3.6: Median frequency of foraging at the box per observation session (n = 8) for the hamadryas baboons. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

3.3.2.3 Aggression

The frequency of aggression was relatively low across treatments. Notwithstanding these low aggression levels, the various treatments significantly affected the frequency of aggressive behaviour (Fr = 13.560, p = 0.0088; Figure 3.7). Aggression was highest during the currants (3 (0-8)) and peanuts (3 (0-5)) treatments, lower during the peanuts & peanuts treatment (1.5 (0-5)), and virtually absent during the control (0 (0-1)) and hidden peanuts (0 (0-1)) treatments.

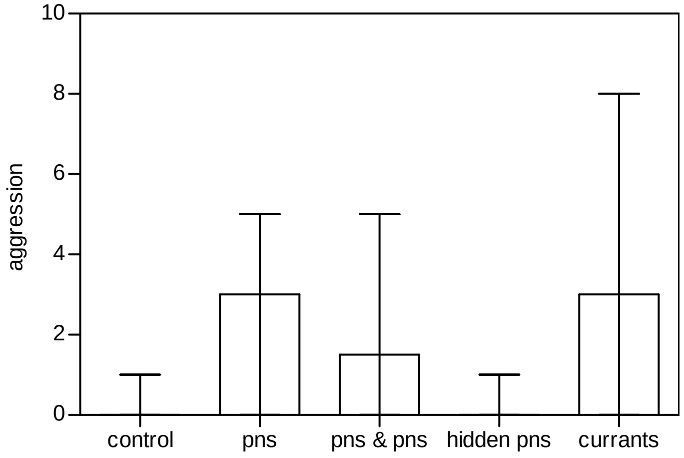

Figure 3.7: Median frequency of aggressive behaviour per observation session (n = 8) for the hamadryas baboons. Bars represent range. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

3.3.2.4 Displacement activity

Only Jane, Rocky, Noxolo, and Celina showed displacement activity. The performance of this behaviour was significantly affected by treatment (Fr = 11.600, p = 0.0206; Figure 3.8). Overall, levels were highest during the currants treatment (6 (0-14)), lower during both the peanuts (4 (0-8)) and the peanuts & peanuts (4 (0-8)) treatments, and virtually absent during the control (0 (0-4) and hidden peanuts (0 (0-6)) treatments. However, these differences were only significant between the control and all treatments except the hidden peanuts treatment ($U \leq 10$, $p < 0.05$); the peanuts and hidden peanuts treatments ($U = 13$, $p = 0.0499$); and the hidden peanuts and the peanuts & peanuts treatment ($U = 10$, $p = 0.0207$). The results for individual animals generally paralleled those of the group.

Positive and significant relationships existed for the frequency of aggression and the frequency of displacement activity for Jane ($r_s = 0.5113$, $p = 0.0007$), Noxolo ($r_s = 0.5683$, $p = 0.0001$), as well as the group as a whole ($r_s = 0.4349$, $p = 0.0050$; Figure 3.9).

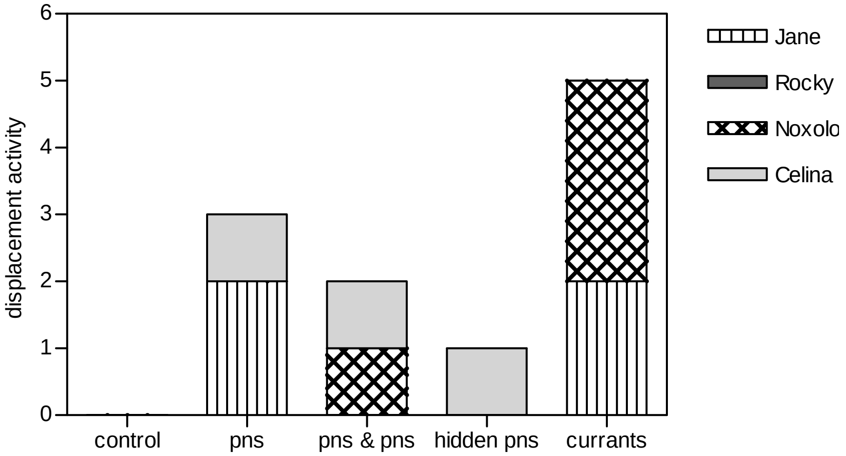

Figure 3.8: Median frequency of displacement activity per observation session (n = 8) for the hamadryas baboons. pns & pns = peanuts & peanuts; hidden pns = hidden peanuts.

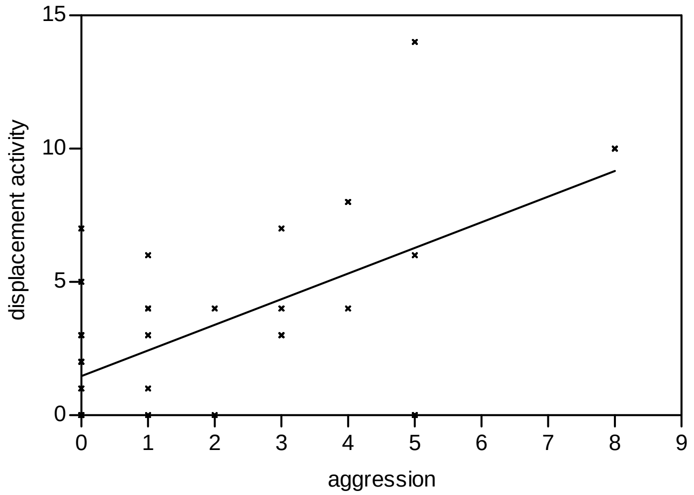

Figure 3.9: Relationship between the frequency of aggression and the frequency of group displacement activity. Each point represents data from one observation session (n = 40).

3.4 Discussion

In comparison to treatments in which no food was available (Treatment 1: control) or when food was present but inaccessible (Treatment 4: hidden peanuts), the incidence of foraging in non-provisioned areas of the enclosure was significantly higher for both the chacma and hamadryas troops when one member was feeding on peanuts (Treatment 2: peanuts) and, for the chacma baboons only, when an individual fed on currants (Treatment 3: currants). These results indicate that the frequency of foraging elsewhere increased in response to the availability of food, as shown by an animal foraging, and/or the behaviour of the foraging animal *per se*, and was not simply related to the food or the foraging device. These findings are in agreement with results from a similar study conducted on the hamadryas troop (Jones & Pillay, 2004), and the qualitative observations by Shepherdson et al (1989) that when a group of meerkats (*Suricata suricatta*) was provided with a mealworm dispenser, digging behaviour increased throughout the enclosure.

Table 3.3: Summary of questions, predictions, and observed trends for foraging elsewhere during Experiment I. F = foraging frequency; yes = prediction was met at $p < 0.05$; yes? = prediction was met at $p < 0.10$; no = prediction was not met.

Critical comparisons between treatments	Question	Prediction	Observed	
			chacma	hamadryas
1a. control vs peanuts 1b. control vs currants	Does watching a demonstrator animal forage motivate observer animals to forage?	$F_{peanuts} > F_{control}$ $F_{currants} > F_{control}$	yes yes	yes no
2. peanuts vs currants	Does the identity of the demonstrator influence whether observer animals are motivated to forage when they watch a particular demonstrator foraging?	$F_{peanuts} > F_{currants}$	no (but see text)	yes
3. peanuts vs peanuts & peanuts	Do levels of observer hunger influence whether a foraging demonstrator motivates observers to forage?	$F_{peanuts} > F_{peanuts\ \&\ peanuts}$	no	yes?
4. peanuts vs hidden peanuts	Is the presence of an inaccessible food, without a demonstrator accessing the food, a sufficient stimulus to motivate observer foraging?	$F_{peanuts} > F_{hidden\ peanuts}$	yes	yes?

A number of studies in a variety of species have reported that demonstrator identity affects whether an observer changes its behaviour as a result of watching a particular demonstrator (e.g. hens; Nicol & Pope, 1994; 1999, chacma baboons; Cambefort, 1981, but see Galef & Whiskin, 2004). In this experiment, I attempted to manipulate the identity of the individual demonstrating feeding behaviour by placing either high-value (peanuts) or low-value (currants) food items in the box. This method of manipulating the demonstrator was successful for the hamadryas group, but less so for the chacma baboons.

For the hamadryas, the frequency of foraging elsewhere was higher during the peanuts treatment (Table 3.3), when Romeo monopolised the food, than during the currants treatment, when one of the females or the castrated male fed from the box. This suggests that Romeo was a more influential demonstrator than other individuals because troop members had learned that his foraging predicted the availability of high quality food (discriminative learning; Dickinson et al, 2000) or, less likely, because group members monitored his behaviour closely as a result of his high status or distinctive appearance (Nicol & Pope, 1999; but see below for an alternative explanation).

In contrast to the hamadryas, the chacmas showed no difference in the frequency of foraging elsewhere between the peanuts and currants treatments (Table 3.3). This was unsurprising as I did not succeed in manipulating the identity of the demonstrator by providing food items of different value. During the peanuts treatment, Grist, the alpha-male, monopolised the box for only a little over half the observation period and not the entire period, as had Romeo. As a result, other individuals fed from the box for a substantial proportion of the observation period, when I had intended only the alpha-male to feed. During the currants treatment, even though currants were a less-preferred food than peanuts, Grist nonetheless foraged at the box for about a third of the observation period, only after which could other individuals feed from the device. Unlike Grist, Romeo virtually never consumed the currants.

For the chacma group, comparing the frequency of foraging elsewhere between the peanuts and currants treatment was not a particularly valid or useful way to infer effects of demonstrator identity. Instead, to assess the effects of demonstrator identity on observer foraging behaviour, I calculated and compared the proportion of time individuals spent foraging elsewhere during each observation session according to which individual was demonstrating foraging behaviour. When Knuckle, the castrated male, demonstrated foraging behaviour, the incidence of foraging elsewhere was higher than when Grist, the alpha-male, or a female was at the box. This finding contradicted my hypothesis that a dominant or older animal is a more influential demonstrator than a lesser-ranking or younger animal, as had been found for the hamadryas group.

A potential explanation for the above is the difference in social dynamics between the hamadryas and chacma groups. Whilst the foraging behaviour of both Romeo and Grist indicated the presence of a high quality food, when Romeo foraged, he was relatively tolerant of the other hamadryas troop members that approached the feeding site, and who could thus feed on nearby food items. In the chacma baboons, when Grist was feeding, troop members did not approach him or the resource. However, when Knuckle fed, other chacma individuals would approach and either scrounge food or supplant him. Thus, whilst

Grist's foraging activity signalled the presence of food, this food was not necessarily accessible by other group members, as it was when Romeo (hamadryas) or Knuckle (chacma) foraged. This is in agreement with the predictions of Coussi-Korbel and Fragaszy (1995) that more extensive and frequent behavioural coordination in time and space will occur in groups with more tolerant styles of group dynamics.

A disadvantage of manipulating demonstrator status by changing the type of food available was that I could not control for the effect of food type on the motivation of observers to forage elsewhere. Accordingly, the lower foraging frequency observed in the hamadryas during the currants treatment may have resulted from currants being less "liked" and "wanted" than peanuts, rather than being a consequence of demonstrator status. Unfortunately, it was logistically impossible to manipulate demonstrator status in any other way.

Hunger is one of the most potent variables motivating foraging behaviour (Toates, 1986; 2001). I thus predicted that hungry animals would forage elsewhere at a higher frequency in response to seeing a demonstrator foraging than would satiated animals, as the internal signal of hunger would enhance the incentive value of food to motivate feeding behaviour (alliesthesia; Cabanac, 1971). Because it was not possible to manipulate whether the chacma and hamadryas were fed their daily meal before or after the observation sessions, I instead attempted to manipulate their level of hunger/satiation by pre-feeding them with peanuts before the start of the observation periods (Treatment 5: peanuts & peanuts). The disadvantage of this was that I had less control over general hunger/satiety. However, the pre-feeding of peanuts did control for sensory-specific satiety, defined as the absence of hunger for a specific taste or nutrient recently ingested (Toates, 2001). Even if the animal is satiated, presenting it with a novel, highly palatable food, such as peanuts, could lead to renewed feeding (Toates, 1986). The pre-feeding with peanuts reduced the likelihood that satiated animals would nonetheless increase the frequency of foraging elsewhere because of the availability of a highly palatable food (peanuts).

For the hamadryas, foraging elsewhere tended to be lower when animals had received a pre-feeding of peanuts than when they had not been given peanuts prior to the commencement of observations (Table 3.3). For the chacma baboons, however, there was no difference in the levels of foraging elsewhere between the peanuts and peanuts & peanuts treatments (Table 3.3). The results are thus equivocal and difficult to interpret. Because the pre-feed of peanuts had been given to the animals in their outdoor enclosures, in which they were later observed, it is possible that fragments of peanuts remained, for which the animals may have foraged during the observation sessions. This might explain why the pre-feeding of peanuts did not decrease the frequency of foraging elsewhere for the chacma baboons, and why the trend did not reach significance for the hamadryas; the effects of satiation may have been counteracted by the availability of a prized food for which they could forage. Alternatively, it is possible that the amount of peanuts (approximately 100 g) provided to each individual was not sufficient to cause satiation. The hamadryas troop was usually fed before observations, whereas the chacma troop was often only fed later in the day. Because of their later feeding time, the chacma were presumably hungrier than the hamadryas before they consumed the pre-feed of peanuts, and thus less likely to be satiated after the pre-feeding.

Levels of overt aggression across all treatments remained relatively low in both the hamadryas and chacma groups, although the frequency of aggressive interactions did increase when peanuts or currants were provided. Whereas previous studies of provisioned primates have shown that the frequency of aggression increases dramatically when food resources are highly clumped (Dunbar, 1988), my results suggest that this is not necessarily the case, provided an individual is able to monopolise a food source using indirect aggressive behaviour, and subordinates are able to withdraw to other areas of the enclosure: crowding of animals, rather than the a clumped food source *per se*, promotes aggression (Jones & Pillay, 2004). Aggression and its relationship to hierarchy are further addressed in Chapter 6, the general discussion.

The frequency of displacement activity, which occurred only in the hamadryas group, was highest during the currants treatment, lower during the peanuts and peanuts & peanuts treatments, and negligible during the control and hidden peanuts treatments. The cause of these behaviours appeared to be social tension (and hence increased aggression) in consequence of competition for food, as well as ambivalence among troop members about how to behave in the frustrating situation of being aware that food was available, but being prevented by conspecifics from accessing it (Maestripieri et al, 1992). In Chapter 6, I discuss this topic in more detail, with particular reference to how it relates to instability in the dominance hierarchy.

CHAPTER 4: EXPERIMENT II

The social transfer of foraging information: psychological mechanism(s)

4.1 Introduction

4.1.1 *Information transfer in groups*

Dynamic social processes shape all aspects of life for group-living animals (Coussi-Korbel & Fragaszy, 1995). Conspecific presence and/or activity can affect the behaviour of other group members through a number of psychological processes such as social facilitation, behavioural contagion, and social learning (Fragaszy & Visalberghi, 1996). Because of these mechanisms, foraging animals need not rely on only themselves to discover food, but may also secure information about the spatial and temporal location of food sources from conspecifics (e.g. in baboons, Cambefort, 1981; King, 1999).

4.1.2 *Social facilitation and behavioural contagion*

Behavioural coordination of behaviour may occur without any learning taking place, as happens during social facilitation and behavioural contagion (Zentall, 1996). Social facilitation (or social enhancement; Galef, 1988) occurs when the motivational state of the observer is transiently altered by the mere presence of a conspecific (Laland & Plotkin, 1990; Zentall, 1996). For example, the physical presence of an adult hen at a feeding site encourages pecking behaviour in young chicks (Tolman, 1968). Behavioural contagion, on the other hand (sometimes confusingly also referred to as social facilitation; Fragaszy & Visalberghi, 1990; Forkman, 1991), refers to instances when a demonstrator's behaviour serves as a releaser for the same behaviour in other individuals (Galef, 1988; Zentall, 1996). Predator evasion and coordinated feeding behaviour in flocking animals (Zentall, 1996), and yawning and laughter in humans (Provine, 1996), are examples of contagious behaviours. Behavioural coordination, arising from social facilitation and behavioural contagion, may facilitate social learning by positioning and orientating the observer suitably to learn from the demonstrator or the demonstrator's context (Coussi-Korbel & Fragaszy, 1995).

4.1.3 *Social learning*

An observer's behaviour may also change as a result of social learning (Laland & Plotkin, 1990). Galef (1988) defines social learning as that which is influenced by the observation of, or interaction with, at least one other conspecific or its products. More generally, learning refers to the reversible process/procedure by which an animal changes its behaviour or acquires the potential to change its behaviour (Toates, 2001). Associative learning is mediated through reward and punishment processes, during which certain responses are linked to stimuli predictive of reward (classical/Pavlovian conditioning), or reinforced by their rewarding outcomes (instrumental conditioning; Rolls, 2002). Extinction, which in some ways may be considered the reversal of learning (but see LeDoux (1998) and Morgan et al (2003) for evidence that the process of extinction merely inhibits the performance of learned responses), refers to the alteration of behavioural responses when the environmental contingencies no longer apply (classical conditioning), or when reinforcement is no longer provided (instrumental conditioning; Toates, 2001).

Instances of social learning have been recorded in a large variety of species, with a substantial proportion of the examples involving a foraging task (Zentall & Galef, 1988). For example, the complex pine-cone-opening technique of black rats (*Rattus rattus*) in Israeli pine forests is socially transmitted from dams to their pups, enabling these animals to exploit an environmental niche which they would otherwise not be able to inhabit (Aisner & Terkel, 1992; Terkel, 1996).

In cases of social learning, learning "how" (as in imitation) is far less common than the more pervasive learning "about" (as in non-imitative learning; Heyes, 1996; Moore, 1996; Zentall, 1996; Giraldeau & Caraco, 2000). Indeed, recent reviews suggest that unlike apes, monkeys as well as most other mammals are incapable of imitation (Lefebvre, 1996; Zentall, 1996). Learning "about" may result from simple social mediation of observer trial-and-error learning (King, 1999) through either (1) exposing the animal to generic situations from which it can learn, or (2) drawing its attention to specific learning opportunities (Tomasello et al, 1993). Stimulus and local enhancement refer respectively to the facilitation of learning that results from a demonstrator animal focusing the attention of an observer on a particular object or location, and thereby providing trial-and-error learning opportunities in close temporal and spatial proximity to a reinforcer (Tomasello et al, 1993; Zentall, 1996).

However, the behaviour of a demonstrator may not only bias the attention of the observer but can, in addition to enhancement processes, become associated with particular environmental states, and so serve as a cue for motivating future contextually-appropriate behaviours (Zentall, 1996; Sibly, 1999). This form of associative conditioning is termed matched-dependent behaviour. An example of this behaviour is when animals learn that a foraging conspecific signals food reward, or the location of a foraging site (Sibly, 1999). In this manner, the demonstrating forager becomes a conditioned stimulus (CS) and, when it displays foraging behaviour, elicits anticipatory behavioural patterns in the observer (Toates, 1986; Spruijt et al, 2001). Although the observable outcome of this process is similar to that of behavioural contagion, matched-dependent behaviour differs from contagious behaviour in that it is mediated through associative learning rather than being the result of a simple, innate shift in motivational state. Such learning confers flexibility to behaviour and would, for example, allow an animal to learn that certain animals are better predictors of food reward than are others (see Chapter 3).

4.1.4 *Objectives and predictions*

The aim of this experiment was to establish the psychological mechanism (behavioural contagion or matched-dependent behaviour) through which observer animals were cued to forage in response to seeing a demonstrator forage. During an initial period, I paired the cue of a demonstrator foraging from a monopolisable food device with the availability of food throughout the enclosure so that the baboons could learn this association. I then assessed the change in foraging behaviour over time when a demonstrator was foraging from this device, but no food was available elsewhere (i.e. during extinction).

If observers had learned to forage in response to seeing a demonstrator forage, the frequency of foraging behaviour should have progressively declined during the extinction phase, as the observers learned that the foraging animal was no longer a predictor of food reward. This would indicate that social learning had mediated the process whereby observer animals were cued to forage in response to seeing a demonstrator forage (i.e. matched-dependent behaviour). Alternatively, if there was no decline in the frequency of foraging during the extinction phase, this would indicate that the increase in observer foraging upon seeing a demonstrator forage was an innate motivational process (i.e. behavioural contagion), and that it was not affected by prior learning. Finally, even if the incidence of foraging elsewhere declined during the extinction phase, but such activity in non-provisioned areas of the enclosure nonetheless remained higher than baseline levels, this would support results from Experiment I which showed that watching a demonstrator forage motivates observers to also forage.

4.2 Materials and methods

4.2.1 *General materials and methods*

Details of the troops, housing and husbandry, experimental apparatus, and data collection are described in Chapter 2, General Materials and Methods.

4.2.2 *Procedure*

Boxes were presented during three treatments. Observations were made on 21 consecutive days, in sequential blocks of seven days per treatment, so that I could examine within-treatment change in behaviour over time, as well as differences in behaviour among treatments. However, because the treatments were necessarily implemented sequentially, rather than in random order as in Experiment I, when I compared differences in behaviour among treatments there was no appropriate control for a possible change in behaviour over time.

4.2.2.1 Treatment 6: control

On days 1-7, no food was placed in the boxes or in the outdoor enclosure. For the chacma baboons, a few handfuls of coarse river sand were cast from the viewing area into the enclosure to control for the similarly scattered peanuts on days 8-14 (Treatment

7: box & scattered peanuts). This control was necessary because, unlike the hamadryas, the chacma baboons did not reliably enter their nightrooms for feeding, so preventing my accessing their outdoor enclosure to scatter the peanuts as I did for the hamadryas. Treatment 6 established baseline foraging levels.

4.2.2.2 Treatment 7: box & scattered peanuts

On days 8-14, 250 g peanuts (whole for the hamadryas; nibbed for the chacma) were placed in the boxes and a further 600 g (for the six hamadryas) or 700 g (for the seven chacma) nibbed peanuts were scattered over the floor of the outdoor enclosure and in the mulch patche before the troop was released from the nightrooms (hamadryas), or cast from the viewing area whilst the individuals were in the outdoor enclosure (chacmas). During this treatment, I expected the troop members would form a conditioned association between a demonstrator foraging (CS) at the box and the availability of food elsewhere in the enclosure (US). I scattered nibbed rather than whole peanuts in order to increase search and handling time.

4.2.2.3 Treatment 8: peanuts

On days 15-21, 250 g peanuts (whole for the hamadryas; nibbed for the chacma) were placed in the boxes. No nibbed peanuts were scattered elsewhere in the outdoor enclosure. As in Treatment 6, a few handfuls of coarse river sand were cast from the viewing area into the enclosure of the chacma baboons to control for the similarly scattered peanuts on days 8-14 (Treatment 7: box & scattered peanuts). By looking at the change in incidence of foraging elsewhere, this treatment was designed to test which psychological mechanism (behavioural contagion or matched-dependent behaviour) motivated observers to forage upon watching a demonstrator forage.

4.2.3 *Data analysis*

Foraging elsewhere data for each day of observation, for each individual as well as the group as a whole, was converted to a ratio of

$$\frac{\text{frequency of foraging elsewhere}}{(\text{total number of observations} - \text{frequency of foraging at the box})}$$

Displacement activity data for each day of observation, for each individual as well as the hamadryas group as a whole, was similarly converted to a ratio of

$$\frac{\text{frequency of displacement activity}}{\text{total number of observations}}$$

Non-parametric Friedman Analysis of Variance (ANOVA) was used to test for differences in the frequency of foraging elsewhere, foraging at box, displacement, and aggressive behaviours among the three treatments. Pair-wise Mann-Whitney U-tests were used to detect between treatment differences. The reasons for using Friedman ANOVA and Mann-Whitney U-tests are given in Chapter 3.

The relationship between the frequency of aggression and the frequency of displacement activity shown by the hamadryas baboons was assessed using Spearman's Rank Correlation Coefficient analysis. Spearman's Rank Correlation was also used to detect changes in foraging elsewhere frequency over time during Treatment 8: peanuts.

4.3 Results

4.3.1 *Chacma baboons*

4.3.1.1 Foraging elsewhere

At the group level, the frequency of foraging elsewhere differed significantly among treatments ($Fr = 12.286$, $p = 0.0003$; Figure 4.1; Table 4.1). During the box & scattered peanuts treatment, animals not foraging at the box spent most of the session eating the scattered peanuts. Consequently, foraging levels were significantly higher than

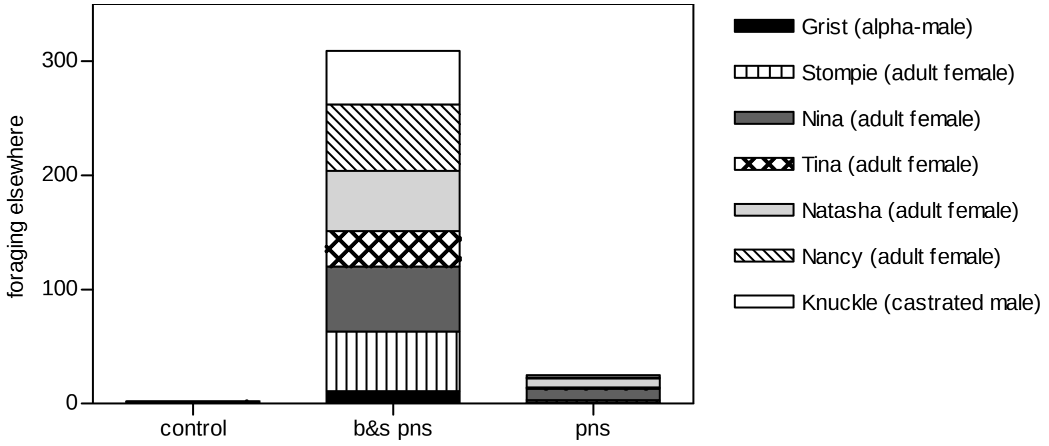

Figure 4.1: Median frequency of foraging elsewhere per observation session (n = 7) for the chacma baboons. b&s pns = box & scattered peanuts; pns = peanuts.

during the control or peanuts treatments (U = 0, p = 0.0006). The incidence of foraging elsewhere was also significantly higher during the peanuts treatment, when a demonstrator was feeding from the peanuts provided in the box, than during the control treatment when no animal demonstrated foraging behaviour (U = 5, p = 0.0111).

When data from individual baboons were analysed, similar trends for foraging elsewhere were found (Table 4.1). Although the baboons differed among themselves in levels of foraging elsewhere within and among treatments, the effect of the treatment on individual foraging elsewhere was relatively consistent among animals in direction, if not magnitude. For all animals, there was a significant effect of treatment on the frequency of foraging elsewhere (Fr > 8.857, p < 0.001), with the frequency of foraging elsewhere during the box & scattered peanuts treatment being significantly higher for all animals (except Grist, for whom the trend just failed to reach significance; U = 9, p = 0.0530) when compared with the peanuts or control treatments (U ≤ 5, p < 0.05). During the peanuts treatment, the frequency of foraging elsewhere was significantly higher than during the control treatment for Grist, Tina, and Nancy (U ≤ 8, p < 0.05).

In contrast to my prediction, the frequency of foraging elsewhere during the peanuts treatment, when analysed for the group or for individuals using Spearman's Rank Correlation, did not change significantly over time (Table 4.1).

Table 4.1: Frequency of foraging elsewhere across treatments for the chacma baboons.

Individual	Frequency of foraging elsewhere per observation session [median (range)] n = 7			Trend over time for pns treatment	Friedman statistic (Fr)	Pair-wise comparisons (Mann-Whitney U-statistic)	
	control	b&s pns	pns	Spearman Rank Correlation (r_s) n=7			
Grist	0 (0-0)	11 (0-45)	1 (0-15)	-0.3424	12.286***	control < b&s pns	0***
						control < pns	0***
						b&s pns > pns	9#
Stompie	1 (0-5)	52 (44-56)	2 (0-7)	0.5045	10.571**	control < b&s pns	0***
						control ≈ pns	17
						b&s pns > pns	0***
Nina	1 (0-5)	57 (51-60)	10 (0-58)	0.5045	10.571**	control < b&s pns	0***
						control ≈ pns	17
						b&s pns > pns	0***
Tina	0 (0-12)	31 (21-51)	1 (0-11)	0.2143	8.857**	control < b&s pns	0***
						control < pns	7*
						b&s pns > pns	5*
Natasha	0 (0-6)	53 (50-59)	8 (1-16)	-0.2182	10.571**	control < b&s pns	0***
						control ≈ pns	23
						b&s pns > pns	0***
Nancy	0 (0-8)	58 (54-60)	1 (0-13)	0.3929	10.571**	control < b&s pns	0***
						control < pns	8*
						b&s pns > pns	0***
Knuckle	0 (0-4)	47 (13-54)	2 (0-10)	-0.4505	10.571**	control < b&s pns	0***
						control ≈ pns	13
						b&s pns > pns	0***
Group Total	1 (0-4)	43 (42-48)	5 (1-10)	-0.2143	12.286***	control < b&s pns	0***
						control < pns	5*
						b&s pns > pns	0***

# $p < 0.10$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$; b&s pns: box & scattered peanuts, pns: peanuts

4.3.1.2 Foraging at the box

Foraging behaviour at the box was significantly affected by treatment (Fr = 10.571, p = 0.0027; Figure 4.2). During the control treatment, no individual was present at the box. When peanuts were placed in the box during the box & scattered peanuts and peanuts treatments, one individual fed from the box for nearly all of the observation period (51 (41-59), median frequency (range of frequencies); 56 (52-60) respectively). During both these treatments, Grist, the alpha-male, monopolised the peanuts for at least the first third of the observation period (22 (13-43); 17 (8-36) respectively), and only thereafter were Knuckle (23 (8-30); 27 (13-41) respectively), Tina (0 (0-13); 3 (0-19) respectively), or Stompie (4 (0-15); 0 (0-7) respectively) able to feed from the box. Other group members very rarely foraged at the box.

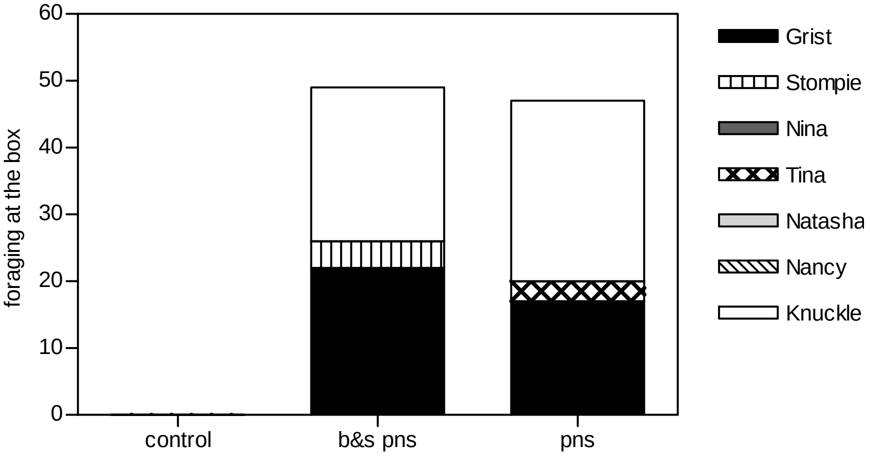

Figure 4.2: Median frequency of foraging at the box per observation session (n = 7) for the chacma baboons. b&s pns = box & scattered peanuts; pns = peanuts.

4.3.1.3 Aggression

Levels of aggression were low throughout Experiment II, but nonetheless differed significantly among the three treatments (Fr = 9.5, p = 0.0087; Figure 4.3): aggression was highest during the box & scattered peanuts treatment (1 (0-8)), lower during the peanuts treatment (0 (0-1)), and absent during the control treatment.

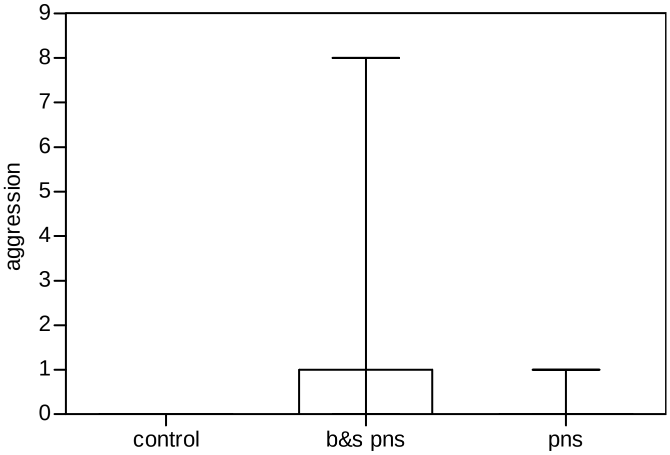

Figure 4.3: Median frequency of aggressive behaviour per observation session (n = 7) for the chacma baboons. Bars represent range. b&s pns = box & scattered peanuts; pns = peanuts.

4.3.2 *Hamadryas baboons*

4.3.2.1 Foraging elsewhere

For the hamadryas group as a whole, the frequency of foraging elsewhere was significantly affected by treatment (Fr = 11.143, p = 0.0012; Table 4.2, Figure 4.4). When peanuts had been scattered on the floor of the outdoor enclosure during the box & scattered peanuts treatment, individuals spent most of the observation period foraging for these peanuts, except for Romeo who foraged for peanuts from the box. Accordingly, foraging elsewhere levels were significantly higher during the box & scattered peanuts treatment than during either the control or peanuts treatments (U = 0, p = 0.0006 for both). In contrast to my prediction, group foraging elsewhere levels did not differ significantly between the peanuts and the control treatments.

Individual baboons responded similarly to treatments as did the group as a whole, although individuals did differ among themselves in the magnitude of change in the incidence of foraging elsewhere (Table 4.2). For all baboons, foraging elsewhere levels were significantly higher during the box & scattered peanuts treatment than during either the control or peanuts treatment (U = 0, $p < 0.001$). There were no significant differences in foraging elsewhere levels between the peanuts and control treatments for any individuals, but these levels tended to be higher in the peanuts treatment for Jane and Rocky ($U \leq 10$; $p < 0.10$).

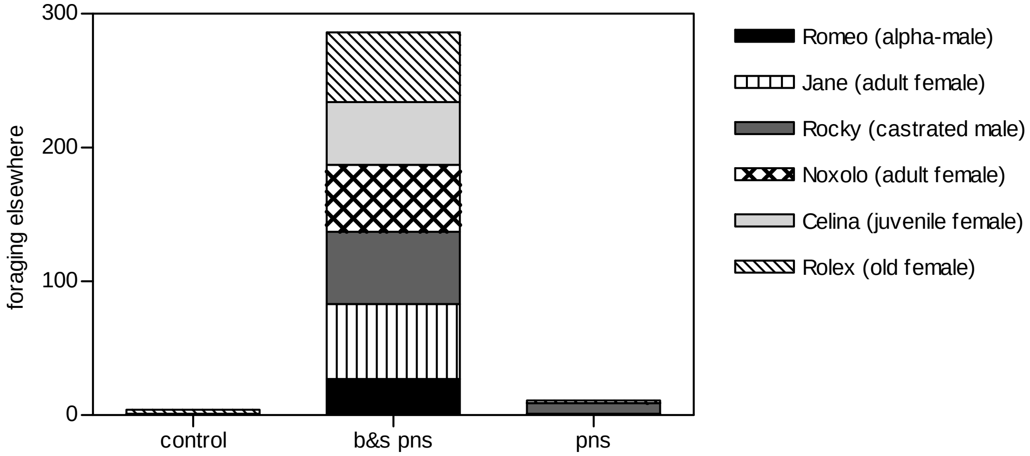

Figure 4.4: Median frequency of foraging elsewhere per observation session (n = 7) for the hamadryas baboons. b&s pns = box & scattered peanuts; pns = peanuts.

The frequency of foraging elsewhere during the peanuts treatment for the group and individuals did not change significantly over time (Spearman's Rank Correlation Coefficient; Table 4.2).

Table 4.2: Frequency of foraging elsewhere across treatments for the hamadryas baboons.

Individual	Frequency of foraging elsewhere per observation session [median (range)] n = 7			Trend over time for pns treatment	Friedman statistic (Fr)	Pair-wise comparisons (Mann-Whitney U-statistic)	
	control	b&s pns	pns	Spearman's Rank Correlation (r_s) n=7			
Romeo	0 (0-0)	27 (15-47)	0 (0-0)	0	13.455**	control < b&s pns	0***
						control ≈ pns	24
						b&s pns > pns	0***
Jane	0 (0-1)	56 (50-59)	1 (0-3)	-0.1112	12.286***	control < b&s pns	0***
						control < pns	9#
						b&s pns > pns	0***
Rocky	0 (0-28)	54 (48-57)	8 (1-35)	-0.2857	14.000***	control < b&s pns	0***
						control < pns	10#
						b&s pns > pns	0***
Noxolo	0 (0-0)	50 (38-54)	0 (0-1)	0.6124	14.000***	control < b&s pns	0***
						control < pns	0***
						b&s pns > pns	0***
Celina	1 (0-5)	47 (39-53)	0 (0-1)	-0.4082	14.000***	control < b&s pns	0***
						control > pns	3**
						b&s pns > pns	0***
Rolex	3 (0-5)	52 (46-57)	2 (0-45)	-0.3214	14.000***	control < b&s pns	0***
						control > pns	3**
						b&s pns > pns	0***
Group Total	7 (0-38)	287 (258-319)	13 (5-82)	-0.2857	11.143**	control < b&s pns	0***
						control ≈ pns	15
						b&s pns > pns	0***

# $p < 0.1$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$; b&s pns: box & scattered peanuts, pns: peanuts

4.3.2.2 Foraging at the box

Foraging at the box was significantly affected by treatment (Fr = 12.074, p = 0.0024; Figure 4.5). When peanuts were available, one, or occasionally even two, animals were almost always present at the box (box & scattered peanuts: 57 (52-62); peanuts: 59 (57-62)). Romeo monopolised the peanuts in the box during both Treatments 7 and 8 (box & scattered peanuts: 50 (38-57); peanuts: 43 (33-52)), during which time three of the females, Jane, Noxolo, and Celina, often sat in very close proximity to Romeo, with Noxolo (box & scattered peanuts: 6 (0-9); peanuts: 9 (2-23)) or Celina (box & scattered peanuts: 2 (0-5); peanuts: 6 (0-7)) occasionally accessing the peanuts either simultaneously with Romeo or, more usually, when Romeo was chasing other animals from the box. Jane, Rocky, and Rolex never accessed the peanuts within the box.

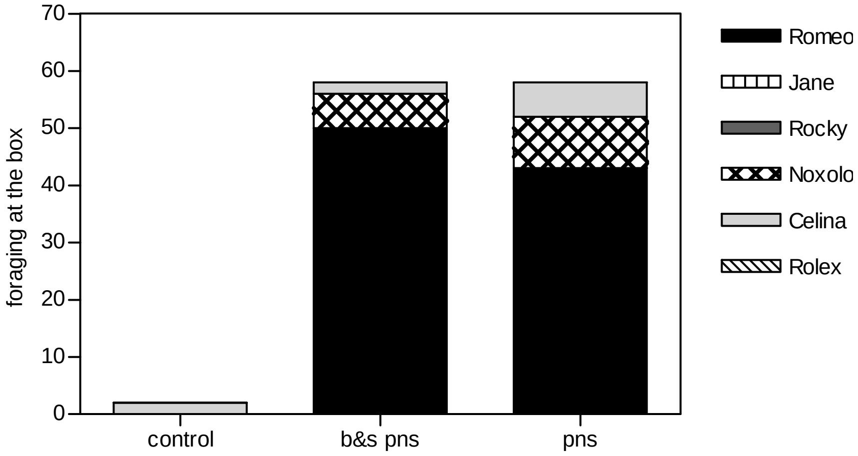

Figure 4.5: Median frequency of foraging at the box per observation session (n = 7) for the hamadryas baboons. b&s pns = box & scattered peanuts; pns = peanuts.

4.3.2.3 Aggression

The frequency of aggression was relatively low the whole of Experiment II, but its levels were nonetheless still significantly influenced by treatment (Fr = 8.240, p = 0.0162; Figure 4.6). Aggressive interactions were most frequent during the peanuts treatment (4 (0-6)), less frequent during the box & scattered peanuts treatment (0 (0-4)), and virtually absent during the control treatment (0 (0-1)).

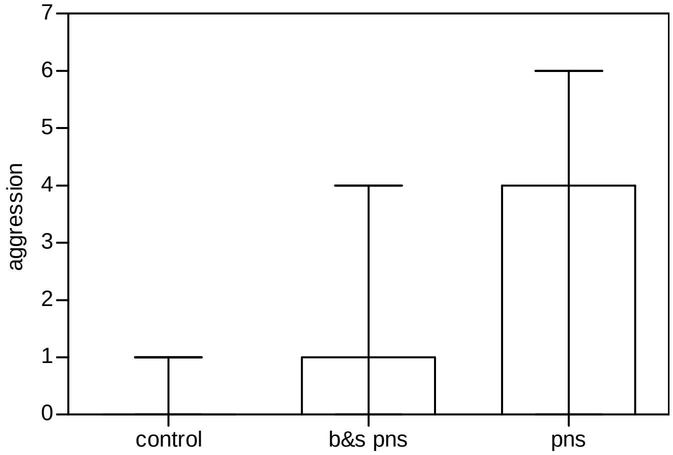

Figure 4.6: Median frequency of aggressive behaviour per observation session (n = 7) for the hamadryas baboons. Bars represent range. b&s pns = box & scattered peanuts; pns = peanuts.

4.3.2.4 Displacement activity

Only Jane (1 (0-3)), Noxolo (0 (0-2)), and Celina (0 (0-3)) exhibited displacement activities, and then only at low levels and only during the peanuts treatment. The frequency of displacement activity, for individuals and the group as a whole, correlated strongly with the level of aggression ($r_s > 0.6138$, $p < 0.001$; Figure 4.7).

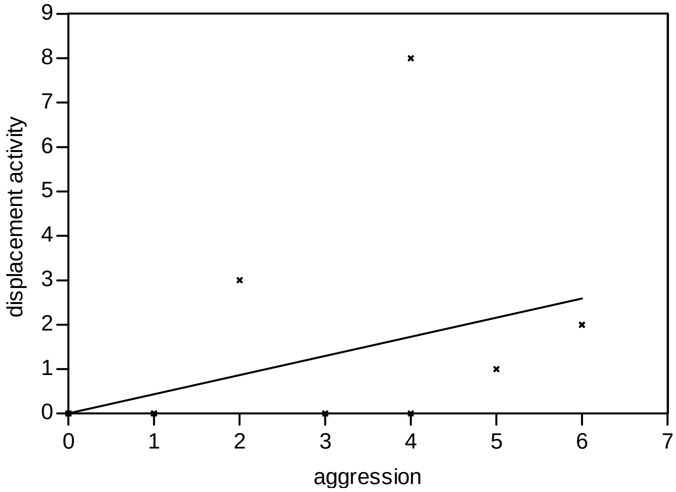

Figure 4.7: Relationship between the frequency of aggression and the frequency of group displacement activity for the hamadryas baboons. Each point represents data from one observation session (n = 21).

4.4 Discussion

Temporal and/or spatial coordination of behaviour can be mediated by innate and/or learned psychological mechanisms (Coussi-Korbel & Fragaszy, 1995). The present results do not suggest that the increase in observer foraging upon watching a demonstrator forage was mediated by learning as, for both troops, no change in behaviour over time was evident during the extinction phase (Treatment 8: peanuts; Table 4.3). However, results for the chacma group do show that the frequency of observer foraging was significantly increased upon watching a demonstrator forage, in agreement with the findings from Experiment I. A possible reason why this was not observed in hamadryas group is discussed in Chapter 6.

Table 4.3: Summary of questions, predictions, and observed trends for foraging elsewhere during Experiment II. F = foraging frequency; r_s = Spearman's Rank Correlation Coefficient; yes = prediction was met at $p < 0.05$; no = prediction was not met.

Critical comparisons between and within treatments	Question	Prediction	Observed	
			chacma	hamadryas
1. control vs peanuts	Does watching a demonstrator animal forage motivate observer animals to also forage?	$F_{peanuts} > F_{control}$	yes	no
2. trend through time in foraging frequency during the peanuts treatment	Does the frequency of foraging behaviour decrease through time as observer animals learn that a foraging demonstrator no longer predicts the availability of food?	$r_s < 0$ (i.e. foraging elsewhere frequency decreases over the course of the peanuts treatment)	no	no

Considering behaviour over time in Treatment 8 (peanuts), a positive finding (i.e. a decrease in foraging elsewhere frequency over the treatment) would have indicated that learning had occurred, in which an animal had either learned the association between the cue of a demonstrator foraging and the availability of food elsewhere (Pavlovian conditioning), and/or because its response to the cue of a demonstrator foraging had been rewarded by its finding food to eat (instrumental conditioning). However, the negative results obtained do not necessarily imply that the temporal coordination of behaviour is mediated solely by behavioural contagion, a non-learned mechanism, and not match-dependent behaviour, a learned mechanism (Zentall, 1996). Instead, it is possible that the experimental design was an invalid method to test for the occurrence of social learning, for at least four reasons: (1) During Treatment 7 (box & scattered peanuts), animals may have been too busy foraging for the scattered peanuts to form an association between the cue of the demonstrator foraging at the box and the availability of food elsewhere in the enclosure. For match-dependent learning to occur, the observer would have had concurrently to attend to both stimuli (Coussi-Korbel & Fragaszy, 1995). It follows that if a response had not been first learned, it could not be extinguished, hence explaining why the incidence of foraging elsewhere did not decline over the course of the extinction phase (Treatment 8: peanuts). (2) Even if individuals had learned the association between a demonstrator foraging at the box and the availability of food elsewhere in the enclosure, it is possible that any such learned behaviour extinguished within the first few minutes of each observation period, as the animals quickly determined when no food had been provisioned. In contrast to previous models suggesting that individual modification of social learning does not occur, or takes place over extended time scales (e.g. Boyd & Richerson, 1988), a series of experiments by Galef and Whiskin (1995) indicate that the effects of social influence on food choice are transitory, and that animals may rapidly learn to modify socially-acquired behaviour, and so track short-term changes in their immediate environment. (3) The stable membership of both troops, and therefore the long-term nature of the social relationships within these groups, indicates that animals may have already learned which troop members were better predictors of food reward than others. The brief conditioning phase (Treatment 7: box & scattered peanuts) might have reinforced this association, but the learned association was nonetheless already sufficiently strong to not be extinguished during Treatment 8 (peanuts). The fact that, in Experiment I, demonstrator status was shown to influence the frequency of foraging elsewhere by observers would support the third explanation for the negative result, as it would have been necessary for individuals to learn to discriminate between demonstrators (Coussi-Korbel & Fragaszy, 1995) because the foraging behaviour of only some individuals predicted the availability of food elsewhere. (4) Another possibility is that baboons do not have the cognitive abilities to learn that a conspecific foraging predicts the availability of food elsewhere. However, this is unlikely as the results of Experiment I (Chapter 3) showed that the identity of the demonstrator influenced the incidence of foraging elsewhere: learning presumably underlies this discrimination.

Further research is thus required to determine the psychological mechanisms underlying the increase in foraging behaviour on watching a demonstrator forage. In all likelihood, however, both processes operate with behavioural contagion facilitating matched-dependent learning through inducing a motivational state in the observer that expedites the learning process. Indeed, once the seeking system has been activated, as it would have been through behavioural contagion, the individual is predisposed to attribute causal explanations to contingencies between events in its environment (Panksepp, 1998), and so acquire matched-dependent behaviours more readily.

For both the chacma and the hamadryas troops, levels of aggression were virtually absent in Treatment 6 (control), but higher in both Treatment 7 (box & scattered peanuts) in which food was available at a monopolisable food source as well as dispersed throughout the enclosure, and Treatment 8 (peanuts), when the only food available was that at the monopolisable box. For the chacma troop, aggression was significantly higher during Treatment 7 (box & scattered peanuts) than either Treatment 6 (control) or Treatment 8 (peanuts). In contrast, aggressive behaviour was significantly higher in the hamadryas troop during Treatment 8 (peanuts) than in either of the other treatments. This difference between the groups was possibly the result of differences in social dynamics. Because of the very tolerant social nature of hamadryas baboons (Kummer, 1971; 1995), when a relatively dispersed food was available (box & scattered peanuts), animals foraged relatively equitably for it. During the peanuts treatment, however, members of the hamadryas troop frequently approached and assembled around the box from which Romeo, the alpha-male, was feeding. This crowding of animals around a limited resource, as has previously been observed in this group (Jones & Pillay, 2004), presumably triggered the observed aggression. In contrast to the hamadryas, the less socially-tolerant chacmas might have viewed Treatment 7 (box & scattered peanuts) as a competitive situation, and so behaved aggressively, but when a monopolisable food was presented they exhibited little aggression because their distinct and enforced dominance hierarchy usually prevented subordinates from approaching the box, or attempting to supplant the animal foraging at the box.

This heightened conflict in the hamadryas troop during Treatment 8 (peanuts) might also explain why displacement activities were shown by three of the females during this treatment only, as these activities are known to emerge in emotional states of uncertainty and anxiety (Maestripieri et al, 1992). The frequency of displacement behaviour and aggression for each day of observation in this experiment were positively correlated, further supporting the association between these two behaviours. This relationship is discussed in more detail in Chapter 6.

CHAPTER 5: EXPERIMENT III

Foraging enrichment: the effect of social cues

5.1 Introduction

5.1.1 *What is environmental enrichment?*

Environmental enrichment is an animal husbandry principle that seeks to enhance the welfare of captive animals by providing the environmental stimuli necessary for psychological and physiological well-being (Shepherdson, 1998). Enhanced welfare is reflected by a reduction in abnormal behaviours (e.g. stereotypy) and negative affective states (e.g. fear and frustration), increased species-typical behaviour, and improved health and reproductive success (Chamove, 1989; Newberry, 1995; Young, 2003). Enriched environments are also associated with structural and biochemical brain changes, such as an increase in dendritic arborisation as well as in the number and density of neurons and synapses (van Praag et al, 2000; Wurbel, 2001). The functional consequences of these changes (as well as their potential causes) include enhanced memory, learning, and, perhaps most importantly, the ability to cope with environmental challenges.

In practice, there are many varied ways to enrich the physical and social environments of captive animals. These include introducing biologically relevant items/features, designing more suitable exhibits, increasing the number and diversity of behavioural opportunities, providing shelters so that animals can escape from perceived threats, stimulating animals cognitively through training, and housing social animals in groups rather than individually (Newberry, 1995; Shepherdson, 1998; Mellen & MacPhee, 2001; Young, 2003).

Some of the most successful and popular enrichment protocols to date have been those promoting foraging activity (Newberry, 1995; Crockett, 1998). Foraging behaviour may be encouraged by increasing the variety of foods offered, by altering the form in which the food is presented, by increasing the difficulty of accessing and consuming the food, and/or by changing the frequency or predictability of provisioning (Lindburg, 1998). Conventional methods used to achieve these goals include, *inter alia*, scattering or hiding the animals' daily ration around the exhibit or in a substrate such as straw, presenting food in puzzle feeders, and providing whole natural food items (e.g. carcasses to carnivores; natural vegetation for omnivores and herbivores; Reinhardt & Roberts, 1997).

5.1.2 *Why is foraging enrichment so successful?*

Considering the greatly reduced time and energy invested in foraging in captivity compared with the wild, as well as the important survival value of the actual feeding, it is not surprising that promoting foraging activity offers such excellent opportunities for enriching captive animals (Newberry, 1995; Reinhardt & Roberts, 1997; Lindburg, 1998). Moreover, the food items in their natural form are inherently interesting to animals and elicit a range of manipulative and exploratory behaviours (even when consumption is not the objective). Another benefit of foraging enrichment is that as animals are less likely to habituate to food than non-food items, food items maintain an animal's attention for a longer duration than non-food items (Lindburg, 1988).

The fields of psychology and neurobiology provide further explanation as to why foraging opportunities are so important for captive animals. There is now much evidence indicating that even when an animal's physiological needs for food are met, the animal may still be internally motivated to perform the appetitive components of feeding behaviour (Hughes & Duncan, 1988). For example, callictrichid monkeys prefer peanuts that they have to remove from their shells prior to consuming over peanuts which are already shelled (Chamove, 1989), and lion-tailed macaques (*Macaca silenus)* will peel foods orally (as they do with many foods found in their natural environment) even though the foods provided in captivity do not require such processing (Smith et al, 1989). Captive animals may thus have a behavioural need to display natural foraging behaviours (Hughes & Duncan, 1988), the survival value of which, and hence internal motivation and reward, has been ingrained by natural selection (Spruijt et al, 2001). Depriving animals of the opportunities to perform such behaviours can thus cause frustration or stress (Shepherdson, 1998), comparable to that arising when physiological needs are not met (Hughes & Duncan, 1988), and/or may remove the animal's natural capacity to regulate its affective state through its behaviours and their consequences (Spruijt et al, 2001). This suggests that captive animals, especially omnivores like baboons which use complex feeding methods and spend a long time feeding (Altmann, 1998; Lindburg, 1998), should be provided with as many foraging opportunities as practicable.

A frequently encountered but undesirable side-effect of enrichment through foraging is an increase in aggression among group members competing for a resource (Mench, 1998). As a result, certain enrichment protocols in the past have had to be withdrawn or modified, as their effects could not be restricted to only promoting foraging. In order to minimise accompanying aggression, it is usually recommended that more than one foraging device per group is always made available, or that the provided forage material is widely distributed throughout the enclosure (Shepherdson, 1998).

5.1.3 *Objectives and predictions*

This experiment investigated whether watching a demonstrator feeding motivates observer baboons to forage for food which they would otherwise not have foraged. In addition, I examined how this intervention affected the frequency of aggression. I presented the chacma baboons with the apparatus (described in Chapter 2) under two different treatments: one in which a non-preferred food item was scattered in the outdoor enclosure, and the second in which, in addition to the non-preferred food present in the enclosure, a demonstrator was foraging at the device. The results are of possible application to enrichment protocols in that this method of promoting foraging activity could be used to rekindle interest in enrichment food items after their initial novelty has worn off, apart from simply promoting foraging for non-preferred food items.

I predicted that if watching a demonstrator animal forage motivated observer animals to forage, the frequency of foraging for a non-desired food item (bran) for which the baboons would not usually forage, would be higher when a demonstrator was eating peanuts from the box, than when no individual demonstrated foraging behaviour. Based on the findings of previous research (Jones & Pillay, 2004), I did not predict a concomitant increase in aggression.

5.2 Materials and methods

5.2.1 *General materials and methods*

Only the chacma baboons were tested in this experiment. Housing and husbandry, apparatus, and data collection are described in Chapter 2, General Materials and Methods. The hamadryas were not used because, after four days of data collection, it became clear that Noxolo's newly-born infant (15 December 2003) might be accidentally injured by Romeo during his aggressive encounters with Noxolo in response to her frequent attempts to supplant him at the box.

5.2.2 *Procedure*

The chacma troop was studied under two treatments, as outlined below. During the 16, not necessarily consecutive, days of observations, one treatment was presented each day in a randomly determined order, resulting in eight observation sessions for each of the two treatments.

5.2.2.1 Treatment 9: bran

The box was empty, and 125 g digestive bran was scattered from the viewing area over the floor of the outdoor enclosure. This treatment established the frequency of foraging behaviour for a non-desired food.

5.2.2.2 Treatment 10: bran & peanuts

250 g nibbed peanuts were placed in the box, and 125 g digestive bran was scattered from the viewing area over the enclosure floor. This treatment aimed to test whether observers were motivated to forage for a non-desired food upon watching a demonstrator forage.

5.2.3 *Data analysis*

Foraging elsewhere data for each day of observation, for each individual as well as the group as a whole, was converted to a ratio of

$$\frac{\text{frequency of foraging elsewhere}}{\text{(total number of observations} - \text{frequency of foraging at the box)}}$$

Mann-Whitney U-tests were used to test for differences in the frequency of foraging elsewhere, foraging at box, and aggressive behaviours between the bran and bran & peanuts treatments. The reasons for using Mann-Whitney U-tests are given in Chapter 3.

5.3 Results

5.3.1 *Foraging elsewhere*

As predicted, the frequency of foraging elsewhere was significantly affected by the treatment (Figure 5.1; Table 5.1). Foraging elsewhere levels were approximately double during the bran & peanuts treatment than during the bran only treatment ($U = 5$, $p = 0.0030$). The foraging elsewhere behaviour of all group members, with the exception of Tina, followed this trend, although differences between treatments were only significant for Grist, Stompie, Natasha, and Nancy. A summary of the data and the analyses is presented in Table 5.1.

Table 5.1: Frequency of foraging elsewhere across treatments for the chacma baboons.

Individual	Frequency of foraging elsewhere per observation session [median (range)] n = 8		Mann-Whitney U-statistic	
	bran	bran & peanuts		
Grist	1 (0-2)	3 (0-5)	bran < bran & pns	11*
Stompie	3 (1-8)	18 (5-33)	bran < bran & pns	2***
Nina	5 (1-25)	13 (6-40)	bran < bran & pns	15#
Tina	14 (1-24)	6 (2-13)	bran ≈ bran & pns	18
Natasha	3 (0-8)	8 (2-16)	bran < bran & pns	12*
Nancy	3 (0-9)	18 (5-29)	bran < bran & pns	3**
Knuckle	3 (1-10)	6 (1-19)	bran ≈ bran & pns	19
Group Total	36 (11-66)	73 (49-109)	bran < bran & pns	5**

# $p < 0.10$ * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$; bran & pns: bran & peanuts

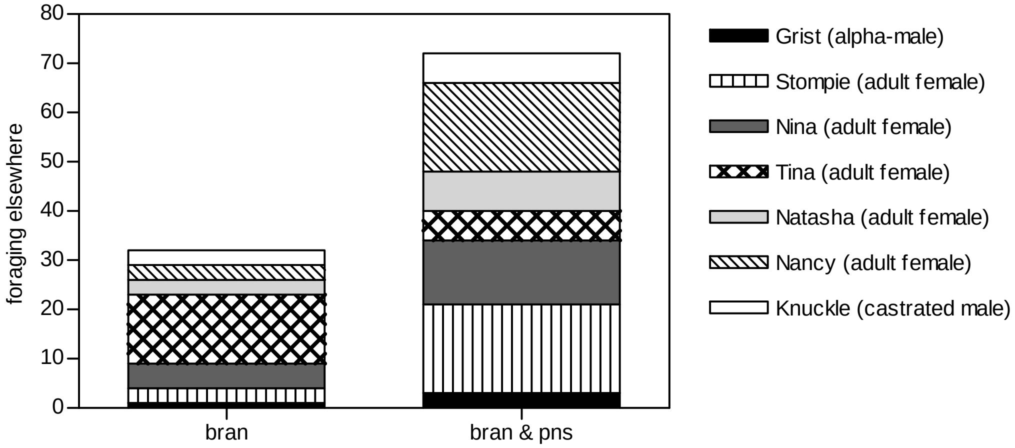

Figure 5.1: Median frequency of foraging elsewhere per observation session (n = 8) for the chacma baboons. bran & pns = bran & peanuts.

5.3.2 *Foraging at the box*

Foraging behaviour at the box was significantly higher when the box contained peanuts than when no food was available (U = 5, p = 0.0054; Figure 5.2), with one animal present at the box for nearly the entire duration of the bran & peanuts treatment (57.5 (49-60)), and never present during the bran treatment. The peanuts within the box were monopolised by Grist for the first half of the bran & peanuts sessions (28 (18-40), median frequency (range of frequencies)), after which Tina (21 (0-28)), Knuckle (6 (1-28)), or very occasionally another baboon, accessed the peanuts.

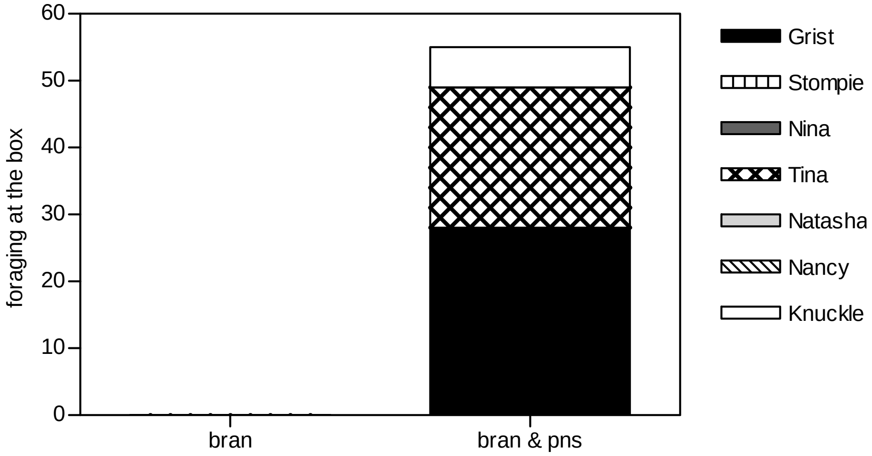

Figure 5.2: Median frequency of foraging at the box per observation session (n = 8) for the chacma baboons. bran & pns = bran & peanuts.

5.3.3 *Aggression*

Aggression levels were relatively low during both the bran and bran & peanuts treatments, but were nonetheless significantly higher (U = 9.5, p = 0.0200; Figure 5.3) when peanuts were available (3.5 (0-5)) than during the bran treatment (0 (0-1)).

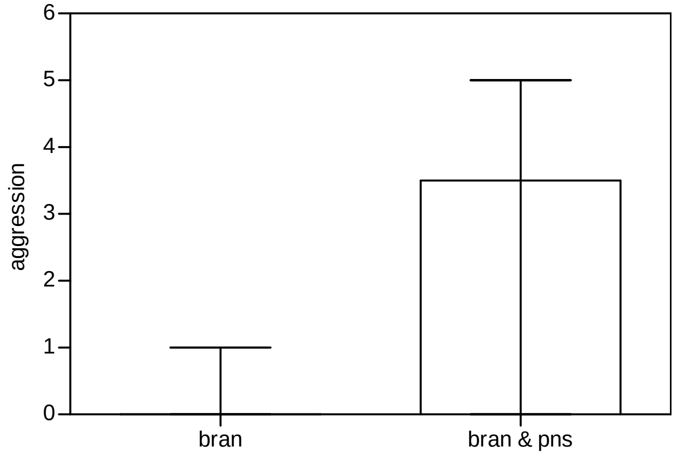

Figure 5.3: Median frequency of aggressive behaviour per observation session (n = 8) for the chacma baboons. Bars represent range. bran & pns = bran & peanuts.

5.4 Discussion

Demonstrator foraging behaviour clearly influenced the frequency of observer foraging for a non-desired food: a significant group-level increase in foraging elsewhere occurred when a demonstrator fed at the box (Treatment 10: bran & peanuts) compared with Treatment 9 (bran) in which there was no demonstrator (Table 5.2). The results from Experiment I (Chapter 3) indicate that it was the demonstrator foraging for peanuts, and not the peanuts *per se*, that cued this foraging elsewhere.

The foraging elsewhere behaviour of all individuals, with the exception of Tina, followed the same trend as did the group as a whole. Tina possibly did not increase her foraging effort in response to watching a demonstrator forage because, being able to access the peanuts in the box once Grist finished feeding, she attended to cues predictive of his leaving instead of adopting a producing foraging tactic as did the other troop members.

However, should this be the case, the question remains why both Grist and Knuckle, who also fed from the box, nonetheless increased their foraging elsewhere when they were not eating from the apparatus.

Table 5.2: Summary of questions, predictions, and outcome for foraging elsewhere during Experiment III. F = foraging frequency; yes = prediction was met at $p < 0.05$; no = prediction was not met.

Critical comparison between treatments	Question	Prediction	Outcome
1. bran vs bran & peanuts	Does watching a demonstrator forage motivate observers to forage for food for which they would otherwise not be motivated to forage?	$F_{\text{bran \& peanuts}} > F_{\text{bran}}$	yes

Cues predictive of food are known to initiate feeding in animals that are either fed *ad libitum* or are satiated, indicating that an individual's motivation to feed may be relatively independent of the availability of food or of its energy status (Weingarten, 1984; Toates, 1986). For example, animals may use social information to decide when to feed (Galef & Whiskin, 2000), and the results of this experiment show that, in baboons, the social cue of a demonstrator foraging is sufficient to initiate seeking behaviours in observers. The performance of appetitive foraging behaviours by the baboons in Treatment 10 (bran & peanuts) in turn resulted in the bran being found and consumed, possibly because the bran was attributed greater incentive salience during the bran & peanuts treatment than the bran treatment, and hence was more "wanted". Another possible treatment to have included in this experiment would have been a bran & bran treatment, in which bran was scattered in the enclosure and presented in the box. However, in pilot trials, the baboons would not forage at the box when only bran was provided.

The increase in aggression during Treatment 10 (bran & peanuts) compared with Treatment 9 (bran) was, although statistically significant, relatively small. That aggression increased, however, does indicate that there was competition for access to the resource, but its low levels suggest that much of this competition was mediated through indirect means, such as increased inter-individual spacing.

The results from this experiment, in combination with the literature, suggest three points. (1) Animals may be encouraged to forage for a non-preferred food, or food left over from, for example, a previous day's scatter feed, by observing the foraging behaviour of another group member. (2) Even if only one animal monopolises a feeding device, other group members may nonetheless derive indirect benefits from the enrichment item, despite such benefits not previously having been considered to occur (Kreger et al, 1998). Moreover, when only one device is provided, if animals search elsewhere for food rather than competing for access to the device, there is unlikely to be a large rise in frequency of aggression, which otherwise would represent a welfare concern. (3) The success of social housing as a means of improving welfare (Visalberghi & Anderson, 1993) may not result solely from its providing animals with opportunities for direct positive interactions with conspecifics (e.g. grooming). Observing the behaviour of group members may additionally motivate individuals to actively engage their environment, make contact with incentives and, in so doing, reap the benefits of displaying and consummating inherently rewarding species-typical behaviours, such as foraging.

CHAPTER 6: USING SOCIAL CUES TO MOTIVATE FORAGING

Mechanisms, implications, and directions for future research

6.1 General

The three experiments showed that, in two troops of captive baboons, watching a demonstrator forage from a monopolisable food source cued observer baboons to forage in other areas of the enclosure. These redirected foraging efforts were primarily appetitive, but occasionally resulted in individuals finding and consuming either fallen vegetation from the trees outside their enclosures, remnants from a previous day's scatter feed (Experiments I and II), or a non-preferred food (bran) for which they would otherwise not have foraged (Experiment III). The identity of the demonstrator influenced the incidence of observer foraging elsewhere, with the factor of how well the demonstrator predicted food reward, rather than the demonstrator's status *per se*, determining observer behaviour. Although the food provisioned during the experiments was highly clumped and therefore not simultaneously available to all individuals, and often highly valued (peanuts) - conditions which are known to increase competition for access to resources (Barton et al, 1996) - levels of aggression did not rise substantially when food was provided compared with treatments when no food was provisioned, or when the food provided was not accessible. Moreover, aggressive interactions involved primarily chasing and threats, little if any physical contact, and did not cause injury. Accordingly, the significant rise in aggression was not considered a welfare concern. Unfortunately, neither the psychological mechanism(s) mediating the presumed shift in foraging motivation, nor the effect of observer hunger/satiation on foraging behaviour, was clear. In the hamadryas troop only, displacement activities were shown by some individuals during treatments when a monopolisable food was provided, but when these individuals were excluded from the food source by another individual. The frequency of these displacement activities was positively correlated with the frequency of aggression, indicating a possible common cause or, alternatively, a causal relationship between the two behaviours.

In the following discussion, I have introduced additional qualitative data when appropriate to explain the quantitative findings reported in Chapters 3, 4, and 5.

6.2 Foraging

The primary objective of this study was to assess whether watching a demonstrator baboon feeding from a monopolisable food source motivated other troop members to forage elsewhere in the enclosure. Incentive motivation is a cognitive and affective state triggered by (1) stimuli associated with the perception of an unconditioned stimulus (US; e.g. food) or a conditioned stimulus (CS; e.g. a conspecific foraging) that predicts the proximity or availability of an US (Ikemoto & Panksepp, 1999), or (2), in the case of conditioned reinforcement, a CS (e.g. a location predictive of food reward; Everitt et al, 2001). Upon watching a demonstrator baboon forage, it appeared that the observer chacma and hamadryas baboons were motivated to similarly forage. However, because a dominant individual prevented subordinates from accessing the box, subordinates increased their foraging efforts elsewhere in the enclosure. This redirected foraging occurred despite no additional food, or only a non-preferred food (i.e. bran), having been provided in these other areas.

Free-ranging baboons are known to watch each other, and even sniff each others' muzzles and breath, to determine when and on what conspecifics are feeding (Altmann, 1998). For example, in yellow baboons, when one troop member begins to feed rapidly and continuously on the berries of the needle bush, *Azima tetracantha*, other animals that were previously widely scattered converged on the feeding site (Altmann, 1998). For animals in the wild that are subject to time and energy constraints, responding to the naturally occurring feeding signals of conspecifics may improve rates of nutrient gain whilst minimising investment time (Toates, 1986). However, this argument only applies if patches are sufficiently large for all or most group members to feed without undue competitive interference (Wrangham, 1980). In many cases, though, social transfer of information might only partially compensate for the costs that group living imposes on foraging behaviours (e.g. sharing of resources; Dunbar, 1988).

The control of foraging behaviour is not mediated by a single, dedicated brain centre, but is instead hierarchically organised at different levels of the nervous system (Berridge, 2004; Toates, 2004). Whilst simple motivated consummatory acts, like chewing and swallowing, are generated in the brain stem, more complex foraging behaviours, such as searching for and processing food items, or responding appropriately to cues predictive of food reward, are governed by intermediate and high level processes such as the subcortical and cortical dopaminergic and opioidergic systems (Toates, 2001; 2004). Dopaminergic systems mediate (1) appetitive "wanting" behaviours, (2) learning and cognitive "wanting", as well as (3) appetitive motor movements (mesoaccumbens dopamine, mesocortical dopamine, and nigrostriatal dopamine respectively; Horvitz, 2000). In contrast, the opioidergic systems determine whether rewards are "liked" or "disliked" (Berridge & Robinson, 1998). "Liking" of rewards is in turn an important determinant of future incentive salience "wanting" (Berridge, 2004). Acting in concert, these systems facilitate the acquisition and updating of skills and information that enable individuals to adjust to the demands of a changing environment (Berridge, 2004). The utility of the affective "liking" component of reward resides in its ability to guide behaviour by opening "an infinite register of new responses", and benefits the organism because "it is far more simple to maximise pleasure than to accumulate within the central nervous system an infinite number of instinctual responses" (Cabanac, 1992, p196). The functionality and evolutionary importance of emotions is further supported by the fact that affective neurocircuitry is very strongly built into brain organisation (Berridge, 2004).

The results of Experiment II were unfortunately inconclusive, and I was unable to determine the psychological mechanism(s) through which the coordination of foraging behaviour occurred (i.e. behavioural contagion and/or match-dependent behaviour; Zentall, 1996; Sibly, 1999). However, it appears that both processes are closely linked behaviourally and, potentially neurophysiologically, differing only in whether the shift in motivation and hence behaviour occurs following the presentation of a US or a CS; see Tinsley et al (2001) who discuss how dopamine facilitates both conditioned (CR) and unconditioned (UR) behavioural responses. I suggest that the neurobiological mechanisms effecting the shift in motivation brought about by an US in behavioural contagion and a CS in match-dependent behaviour (mechanisms described in the literature on social learning; e.g. Galef, 1988; Zentall, 1996), are analogous to the process which in the neuroscience literature is termed Pavlovian-to-Instrumental Transfer (PIT; e.g. Cardinal et al, 2002; van den Bos et al, 2004).

Pavlovian processes can influence goal-directed behaviour through (1) PIT; (2) discriminated approach; and/or (3) conditioned reinforcement (Everitt et al, 2001). Pavlovian conditioning refers to the learning mechanism whereby repeated pairing of an initially neutral stimulus with a biologically relevant US (Cardinal et al, 2002) results in the neutral stimulus becoming a CS that is capable of motivating a response (Dickinson et al, 2000; Everitt et al, 2001). Pavlovian CSs that are relevant to the animal's current motivational state are able to potentiate related instrumental behaviours through the process of PIT. In this manner, for example, a CS for a sucrose solution will enhance instrumental responding, a CR, for sucrose (response-specific PIT), or even for a different outcome such as dry food pellets (conditioned motivation; Cardinal et al, 2002). Research by Tinsley et al (2001) suggests that CSs might elicit unconditioned behaviours (URs) as well as activities that are explicitly conditioned.

It seems likely that the baboons in this study had learned the instrumental response-outcome contingency between searching for food and consuming food, and that "the incentive properties of [the food] reward are…mediated by an association between the response [appetitive foraging behaviours] and reward [consuming the food item; post-ingestive consequences]" (instrumental incentive learning; Dickinson et al, 2000, p480). In addition, the baboons are likely to have formed a direct Pavlovian associative link between the discriminative stimulus (CS; e.g. a particular demonstrator foraging) and the reward (US; e.g. food; Pavlovian incentive learning; Dickinson et al, 2000). Through the process of PIT, the motivation to forage was strengthened via the activation of a CS-US (conspecific foraging-availability of food) link. Interestingly, on its own, the US of food in Experiment I was insufficient to motivate foraging behaviour, with the frequency of foraging elsewhere only increasing above baseline levels when a demonstrator was consuming the food. Moreover (although results are admittedly somewhat inconclusive because the method used to manipulate demonstrator identity required changing the type of food presented), it appeared that the identity of the demonstrator might have influenced the decision by animals excluded from the food source to forage elsewhere in the enclosure. The above two points taken together suggest that it was a CS rather than a US that enhanced instrumental responding for possible food rewards, and hence that matched-dependent behaviour, rather than simply behavioural contagion, occurred. However, the inconclusive nature of negative results obtained in Experiment II warrants further assessment of the psychological mechanisms mediating the temporal coordination of foraging behaviour, as well as their underlying neurobiology. Nonetheless, irrespective of the precise proximate mechanism through which foraging behaviour was encouraged, the inferred activation of the seeking system, with the concomitant release in subcortical dopamine, heightened general arousal and activity and increased the probability that a baboon would encounter potentially rewarding stimuli (e.g. food particles, the searching for and consumption of which is associated with opioid release in the brain; Timberlake, 1999; Martin et al, 2004).

The neural basis for PIT (which is similar to, but dissociable from, that for the closely related Pavlovian discriminated approach behaviour and conditioned reinforcement) involves the mesolimbic dopamine system and areas such as the central nucleus of the amygdala and the nucleus accumbens core (Everitt et al, 2001). That Pavlovian CSs can potentiate instrumental foraging behaviour through brain circuitry and neurotransmitter systems implicated in the seeking system, highlights the interconnectedness of learning and motivation which, together with emotion/affect, comprise the three psychological components of reward (Berridge & Robinson, 2003). If PIT is indeed analogous to behavioural contagion and matched-dependent behaviour, research from the neuroscience field might be used to identify the neurobiology underlying flexible and adaptive social behaviour. This would provide a way for various aspects of reward and welfare to be scientifically linked and investigated. In particular, the above suggested synthesis could facilitate an understanding of how and what animals learn about foods and foraging techniques, the mechanisms responsible for the generation of positive affective states when displaying appetitive and consummatory foraging behaviours and, finally, why captive animals are motivated to perform certain behaviours, for which there may be no physiological need in captivity.

6.3 Individual differences in foraging behaviour

Motivational concepts (Figure 1.1; Chapter 1) help us understand how psychological processes guide behaviour, why different individuals react in different ways to the same environments and stimuli, and why the behaviour of any one individual changes over time (Berridge, 2004). Whereas group responses indicate the general effect of treatment on foraging behaviour, individual differences point to possible within-animal variation that affects motivation, learning, and emotion, and hence behaviour.

In general, in the current experiments, individuals in the chacma and hamadryas baboon troops responded similarly to treatments as did their respective troops. However, the magnitude of the shift in foraging behaviour appeared to be consistently greater for some individuals than for others (although this was not compared statistically). For example, regardless of which treatment was implemented, three individuals in the chacma group (Stompie, Nina, and Tina) often performed more foraging elsewhere than did other individuals in their troop (see Tables 3.1, 4.1, 5.1). Similarly, two hamadryas individuals (Rocky and Rolex) consistently displayed a higher frequency of foraging elsewhere than other members of their troop (see Tables 3.2, 4.2).

Inter-individual differences in response to the cue of watching a demonstrator forage are to be expected as, notwithstanding the identity of the demonstrator, the characteristics of the observer and the relationship between the demonstrator and the observer are known to influence social learning opportunities, as well as the ability and/or propensity of the observer to attend to and/or act on social and environmental stimuli (Coussi-Korbel & Fragaszy, 1995). Whilst the experiments in this study did not aim to assess the complexity of differences in individual reactions, the following three factors seem likely to explain at least some of the observed inter-individual differences in foraging behaviour: (1) the age of the observer; (2) the temperament of the observer; and (3) the status of the observer. These individual characteristics are discussed below.

6.3.1 *Age of the observer*

Juvenile foraging behaviour differs from that of adults in a number of well-documented ways (e.g. Altmann, 1998). For example, juveniles are slower, less efficient, and less successful foragers than adults, and consequently ingest food at lower rates (Janson & van Schaik, 1993). Reasons for this include their not having yet learned the requisite foraging skills, insufficient practice at locating and handling particular foods, and smaller body size (which is particularly applicable to juveniles of species that prepare and consume large, tough food items; Janson & van Schaik, 1993). Consequently, juveniles may have to invest much time and considerable energy in foraging in order to meet growth and metabolic demands (Chapais & Gauthier, 1993).

Another characteristic of juvenile foraging behaviour is that they explore and play-feed on a variety of food items not usually consumed by adults (Janson & van Schaik, 1993; Milton, 1993). In brown capuchin monkeys (*Cebus apella*), for example, juveniles will practice breaking open any dead twigs they encounter. In contrast, adult capuchins are highly selective of which twigs they process in order to eat (Janson & van Schaik, 1993). Juveniles thus appear to sacrifice foraging efficiency for opportunities to develop foraging skills (Watts & Pusey, 1993) or, alternatively, have simply not yet learned how best to select foods in order to maximise energy and nutrient gain and minimise time and energy expenditure (Janson & van Schaik, 1993). Furthermore, playful feeding behaviour may be more common than in older animals because (1) juveniles are generally more active, inquisitive, and playful than adults (Chapais & Gauthier, 1993; Fagen, 1993); (2) they occupy a permissive social environment; and (3) they are not yet constrained by the demands on attention of monitoring the behaviour and location of dominant animals (Pereira & Fairbanks, 1993). I suggest that sensitisation of opioid and dopamine brain systems might underlie some of the abovementioned behavioural differences between juveniles and adults, and be the proximate cause of the presumed increased "liking" and "wanting" of these food items.

Whilst the above reasoning suggests that the younger baboons, in particular the hamadryas female, Celina (regrettably the only juvenile in the study), should have shown more foraging behaviour than older individuals (irrespective of treatment), this was not observed in this series of experiments. Reasons for this are discussed in the next section. However, in a previous study conducted on the hamadryas group (Jones & Pillay, 2004), it was qualitatively clear that most of the redirected foraging behaviour was shown by Celina and Noxolo, an infant and juvenile respectively at the time of data collection. Unfortunately, quantitative individual data were not recorded in that study.

6.3.2 *Temperament of the observer*

Little is currently known about how mammalian temperament mediates social learning and behaviour (Box, 1999). Box (1999) describes temperament as an individual's characteristic and enduring style of emotional and behavioural responsivity towards a variety of situations. Differences in temperament likely reflect subtle inter-individual differences in brain microstructure and neurochemistry (e.g. hypothalamic-pituitary-adrenocortical axis reactivity; central concentrations of the neurotransmitter serotonin; Box, 1999).

However, temperament is known to mediate the acquisition of ecologically relevant information and whether the animal acts on this information (Box, 1999). For example, more fearful and inhibited animals show lower levels of exploratory and play behaviour than more confident individuals; they also interact less with conspecifics or objects in their social and physical environment respectively and, as a result, experience fewer opportunities to feed, especially on novel foods, or acquire new foraging skills.

In the context of this research, the argument for temperament mediating foraging behaviour necessarily begs the question: individuals showing a higher than expected frequency of foraging behaviour compared with other group members are assumed to be more confident and active, and less fearful and inhibited, and this is then used to explain their behaviour. However, it would be possible to escape the circularity of this argument by using the concept of temperament to make new predictions rather than merely restating what has already been observed (Berridge, 2004). Further research into the area of temperament and foraging behaviour is clearly needed.

6.3.3 S*tatus of the observer*

Demands for frequent visual monitoring of dominant individuals may limit the amount of attention that can be paid to other stimuli (Coussi-Korbel & Fragaszy, 1995), such as cues predictive of food reward. Social status might also affect (1) how close an observer can get to a demonstrator, and thus how well the observer can monitor and learn from the activities of the demonstrator (Coussi-Korbel & Fragaszy, 1995), as well as (2) the foraging strategy adopted (Dunbar, 1988). For example, subordinates are known to search for and consume different foods to dominant animals, in part because dominants prevent subordinates from accessing choice resources, but also because this strategy minimises competitive interference (Dunbar, 1988). Individuals in both the chacma and hamadryas baboon troops that foraged elsewhere more frequently than other group members, appeared to have adopted the strategy of searching for lower-quality food in other areas of the enclosure.

Future research into the field of individual differences is warranted to facilitate a greater understanding of social learning and factors that influence foraging behaviour, to generate hypotheses for empirical research, and to understand the adaptive value of population-level variability in temperament (Box, 1999). In addition, such research is necessary in order to predict the effects of environmental enrichment on individuals within a group of animals, and so be able to tailor environmental enrichment protocols to suit the requirements of individuals. Moreover, understanding inter-individual differences should provide a formal framework for assessing the susceptibility of captive animals to developing abnormal behaviours such as stereotypies, and allow specific preventative measures to be taken (van Lierop et al, in preparation).

6.4 Foraging strategies: scrounging versus producing

Scrounging usually inhibits the performance of food-finding behaviours and retards social learning (Lefebvre & Giraldeau, 1994), possibly because attention is drawn to the end object, rather than the behaviour which the demonstrator employs to obtain the goal (Lefebvre & Helder, 1997). In the hamadryas troop, the two adult females (Jane and Noxolo) and the one juvenile female (Celina) showed relatively little foraging elsewhere in response to the cue of Romeo, the alpha-male, foraging at the box. Instead, these females typically clustered around Romeo at the device, and so appeared to adopt a scrounging strategy (Ranta et al, 1996; Liker & Barta, 2002). In contrast, the old female (Rolex) and the castrated male (Rocky) adopted a producing strategy, possibly in order to avoid conflicts with Romeo (Barton, 1993), who would not tolerate their close proximity as he would with the adult and juvenile females.

Failure to perform an appetitive producing behaviour, however, does not necessarily imply that scroungers were not motivated to forage, but may instead reflect a different strategy through which to consummate the feeding goal. However, during the course of these experiments, scrounging was largely unsuccessful as, even on the rare occasion when Romeo spilt food from the box, he would immediately pick up and eat the spilt food items. Only exceptionally rarely were the scrounging females able to access spilt food or the food within the box itself.

In a previous study (Jones & Pillay, 2004), no animals had clustered around Romeo, but instead directed their foraging efforts to other areas in the enclosure. Whilst it is not possible to exclude carry-over effects from the previous study, how learning would have caused this change in response is unclear. Instead, I feel it more likely that the shift in response strategy occurred because, as Celina matured from an infant to a juvenile, the troop's social dynamics changed.

6.5 Aggression

A second objective of the present study was to determine the effects of food provisioning on overt aggression. Previous research conducted on the hamadryas troop used in this study (Jones & Pillay, 2004; Jones & Saacks, unpublished) showed that when the food source was either (1) monopolisable by the dominant (only the dominant animal accessed the resource, and other troop members did not crowd around the food source), or (2) dispersed (all individuals could access the food, without undue crowding), the frequency of overt aggression remained low. Under these conditions, competition for access to the resource appeared to be regulated primarily through indirect aggressive behaviours, such as threats (e.g. brow-raising), or was virtually absent. This was either because subordinates avoided dominant individuals, or because subordinates behaved submissively when in close proximity to high status baboons. However, when the hamadryas had been presented with a clumped but non-monopolisable resource, there was a significant increase in the incidence of aggression (Jones & Pillay, 2004).

In my experiments, it was thus expected that during treatments when limited quantities of food were available from a monopolisable food source, the frequency of aggression would remain relatively low. Quantifying aggression was important since high levels of aggression might have offset the potential benefits of foraging enrichment: if increases in aggression were substantial, particularly if individuals were injured during aggressive encounters, the net effect of the foraging enrichment would have reduced rather than improved the welfare of the baboons.

In all experiments, for both the chacma and hamadryas baboons, the frequency of aggression was significantly higher during treatments when food was available, but nonetheless remained relatively low, and was not considered a welfare concern. For the chacma baboons, in the few instances when aggression occurred, it was usually initiated by Tina and directed towards Knuckle, and typically involved chasing Knuckle away from the box. Grist very rarely initiated an attack, but did join Tina occasionally in chasing subordinates from the box. None of the chacma baboons incurred visible injury as a result of the aggression and the animals only rarely made physical contact with one another. In the hamadryas troop, aggressive interactions usually began among the females congregating around the box. These terminated when Romeo intervened, by either chasing an individual (usually the female to whom the aggression was directed) from the box, or superficially biting this animal on the back of the neck. As for the chacmas, no individuals were obviously injured during any aggressive episodes.

A comparison of aggression frequency among treatments, in particular between Treatment 2 (peanuts) and Treatment 3 (currants), pointed to possible proximate mechanisms regulating the expression of aggressive behaviour. In the hamadryas troop, the frequency of aggression was highest during the currants treatment and lower, although not significantly so, during the peanuts treatment. However, the intensity of the aggression, as well as its duration, appeared far greater during the currants treatments. Unfortunately, duration and intensity data were not recorded.

During the peanuts treatment, Romeo, the alpha-male, monopolised the food source for almost the entire observation session. The other individuals (Rolex and Rocky) would either distance themselves from him or, in the case of the two adult females, Jane and

Noxolo, and the juvenile female, Celina, sometimes sit in very close proximity to Romeo and either vigorously groom his mantle or groom one another. In primates, grooming is known to be important in the regulation of aggression by influencing the internal state of the animal performing or receiving the grooming (e.g. by providing reassurance, decreasing arousal, serving as an appeasement gesture; Spruijt et al, 1992), and by restoring affiliative social relationships (e.g. a dominant will groom a subordinate after conflict has occurred; de Waal, 1986). By either maintaining distance from Romeo, or submissively approaching him and not attempting to access the peanuts, troop members unambiguously acknowledged Romeo's rank and thus, for the most part, forestalled potential aggression (de Waal, 1986). In addition, it is likely that by performing grooming behaviours, or being groomed, females reduced the anxiety experienced as a result of their close proximity to Romeo whilst he was feeding. The above notwithstanding, when the females fought among themselves, or occasionally attempted to access the peanuts, Romeo would respond aggressively by either chasing the offending individual from the box, or biting the animal on the neck.

In contrast to Treatment 2 (peanuts), when currants were presented in Treatment 3, Romeo would eat from the box for only the first few minutes of the observation session, after which he would withdraw to a distance of about 5 m, and watch as Jane, Noxolo, and Celina, and occasionally the castrated male, Rocky, competed for the currants. Despite Romeo no longer monopolising the food source, he still maintained priority of access to it: for example, he would occasionally, usually after aggressive episodes, return to the box and immediately displace whichever individual was feeding at the time. Indeed, in many primate species, dominant individuals will not always enforce priority of access to resources, depending on various factors such as an individual's position in the hierarchy, social relationships between dominant and subordinate animals, degree of tolerance shown by dominants towards subordinates, and resource value (de Waal, 1986). Currants, unlike peanuts, were not a preferred food and were thus, for Romeo, a resource of low value and not worth defending.

During the peanuts treatment, Romeo's clear dominance over the other troop members negated the need for aggression. However, during the currants treatment, when

Romeo was not a competitor, other individuals of approximately equal rank to one another clustered around the box and simultaneously attempted to access the currants. This resulted in an increased frequency of aggression. This agrees with two findings from previous studies. Firstly, it has been shown that conflict partners with small rank differences (as among the hamadryas females and castrated male) tend to behave more aggressively towards one another than individuals with large rank differences (as among Romeo and the rest of the group), which may be due to their more equally matched competitive abilities, and thus each individual's increased likelihood of benefiting from instigating aggression (Wittig & Boesch, 2003). Secondly, in pigtail macaques (*Macaca nemestrina*), the alpha-male appears to regulate aggression among females, with increased aggressiveness shown by females in areas distant to him (Anderson et al, 1977). Thus, whilst peanuts had higher absolute resource value than the currants, there was more competition among the hamadryas females and castrated male for the currants than for the peanuts because of their similar competitive status and, possibly, the lack of regulation by Romeo.

In the chacma baboons, there was no difference in aggression between the currants and peanuts treatments. However, it appeared that levels of aggression differed according to whether Grist, the alpha-male, or another individual, was feeding at the box. When Grist was foraging from the box for either currants or peanuts, other troop members never attempted to displace him. In contrast, when Tina or Knuckle were foraging, other animals would approach to within a metre of them. In response, the feeding animal would threaten the potential opponent, aggressively chase it away from the box, or leave the box so that the approaching animal could feed.

For both the hamadryas and the chacma baboons, it therefore appeared that large rank differences, as between Grist and Romeo and their respective troop members, and the clear-cut acknowledgement of the alpha-male's rank, facilitated non-aggressive determination of order of access to resources. In contrast, when differences in rank among competitors were smaller, or were poorly defined, and especially if baboons were in close proximity to each other and the resource, individuals would use aggression to attain access to the resource.

6.6 Displacement activities

Although this study was not specifically designed to assess displacement activities, their frequency was recorded because of their apparent close connection to treatment and aggression. Displacement activities occurred in the hamadryas troop only.

Displacement activities represent incomplete sequences of behaviour which terminate suddenly without fulfilling the normal function for the activity (Tinbergen, 1952; Zeigler, 1964; McFarland, 1966), and appear to be irrelevant to the situation in which they occur, or to the animal's ongoing behaviour (Maestripieri et al, 1992). For example, in an aggressive context, domestic cocks may peck the ground, as though to pick up food (Tinbergen & van Iersel, 1947) and gulls may perform preening behaviours (Tinbergen, 1952).

Displacement activities are characteristic of two general circumstances: (1) situations of internal conflict, in which an animal is simultaneously motivated to perform two incompatible motor behaviours, such as approach and withdrawal; and/or (2) frustrating situations, in which the animal is prevented from performing or completing a motivated behaviour, or from obtaining reward (Zeigler, 1964; Schino et al, 1988; 1990). Although motivational conflict is a necessary proximate causal factor for displacement activities, the type of displacement activity displayed is influenced by the same external causal factors that regulate the display of similar behaviour patterns in their usual context: the frequency of displacement grooming in terns (*Sterna paradisaea*) is influenced by the state of the plumage (van Iersel & Bol, 1958), and the degree of prior food deprivation affects the incidence of displacement feeding in Barbary doves (*Streptopelia risoria*; McFarland, 1965).

In the hamadryas baboons, displacement activities emerged either (1) in situations where individuals were motivated to both approach the box to obtain food (or possibly to reconcile with the dominant after aggressive interactions), but also to withdraw from the apparatus to avoid the individual feeding (conflict situation), or (2) when an individual was prevented from feeding because of the presence of a dominant at the box (frustrating situation). The data collected did not allow these two possibilities to be distinguished as the conditions generating conflict between approach and withdrawal also frustrated feeding behaviour.

The fact that the two adult females and the young female showed more displacement behaviour than the castrated male, Rocky (for whom the occurrence of displacement activity was rare) and the old female, Rolex (who never showed displacement activities), suggests that these individuals either found the feeding situation more frustrating than did others, or experienced greater internal conflict. Because of their lower status, Rolex and Rocky generally did not approach the feeding area, and thus appeared to accept that they could not access the food. In contrast, during the peanuts treatment, the other females tried to access the resource when Romeo was feeding, although their attempts to feed were almost always prevented, either by Romeo's aggressive chasing of them from the box or his only tolerating their proximity if they groomed him. Diezinger and Anderson (1986), who examined the displacement activity of scratching in rhesus macaques (*Macaca mulatta*) at a feeding site, similarly concluded that intermediate ranking animals seemed to experience greater arousal and frustration than dominants (who were able to monopolise the food) and subordinates (who showed no attempts to access the feeding area). During the currants treatment, the females would compete amongst themselves for access to the box after Romeo had finished feeding. Thus, whilst there was an increased probability of their obtaining food, the probability of aggressive interactions also increased because of the close proximity of similarly ranked individuals.

The displacement activities shown by the hamadryas baboons were similar in form to grooming behaviours, the most common form of displacement activity observed in primates (Schino et al, 1988; Masestripieri et al, 1992). However, the displacement activities recorded here occurred in situations in which individuals were unable to consummate the grooming behaviour on the appropriate substrate – the repeated to-and-fro movements of the hand and lower arm resembled vigorous searching through Romeo's mantle, but took place either with the palm on the ground, or the hand raised about 10 cm from the ground. Similarly, the other displacement activity observed, a repetitive scraping movement of the ground by the index finger, was very similar in form to an abbreviated grooming behaviour performed by young hamadryas males at the Zurich Zoo that wished to approach the alpha-male to groom him, but were fearful to do so (Kummer, 1995).

6.7 Displacement activities and aggression

In this and other primate studies, a positive association has been found between the frequency of displacement activities and aggressive encounters (Maestripieri et al, 1992). Unfortunately, in my experiments, the sequence of aggressive events and displacement activities were not recorded, so preventing a causal analysis. Three mechanisms, however, could potentially explain the observed correlation: (1) a common causal factor increased the frequency of both displacement activities and aggression, independently of one another; (2) aggression increased the display of displacement activities; and (3) the performance of displacement activities increased the incidence of aggression. Available evidence from this and other studies supports the first two hypotheses. Increased proximity among individuals at feeding sites, as occurred during the currants treatment, is known to increase aggression, and is presumably also associated with anxiety, itself a predictor of displacement activities (Maestripieri et al, 1992). This supports the first hypothesised mechanism whereby a common causal factor, social tension, increases the occurrence of both aggression and displacement behaviours independently of one another. However, it also seems likely that aggression might directly increase the occurrence of displacement activities by increasing the ambivalence an animal experiences between withdrawing, to avoid future aggression, and approaching, to achieve reconciliation with the aggressor or to access the resource (Maestripieri et al, 1992). In addition, aggression may further increase anxiety, which in turn promotes the performance of displacement activity.

6.8 Reward systems and welfare

Over the last five years, a group of Dutch scientists has been examining anticipatory behaviour in a Pavlovian conditioning paradigm as a means to study the sensitivity of the mesolimbic dopamine reward neurocircuitry and thus, non-invasively, to assess an animal's welfare (e.g. van den Berg et al, 1999; von Frijtag et al, 2000; 2001; 2002; Spruijt et al, 2001; van der Harst et al, 2003a; 2003b; van den Bos et al, 2002; 2004; Vinke et al, 2004).

Through the repeated pairing of a previously neutral stimulus with an incentive such as food, sucrose, or social contact, the neutral stimulus becomes a CS, the presentation of which produces an anticipatory response (van den Berg et al, 1999) due to the combined activation of the mesolimbic opioidergic and dopaminergic reward centres in the brain (Spruijt et al, 2001). The opioidergic system's appraisal of the stimuli as liked/disliked contributes to how motivated an animal is to obtain the reward, or the degree to which the animal "wants" it (Berridge, 1996). "Liking" and "wanting" thus act together to determine the intensity and duration of the anticipatory behaviour.

Sensitivity to reward, that is the extent to which an incentive is liked and wanted, is influenced by previous experience, such as the exposure to chronic or acute stressors (van der Harst et al, 2003a), or pharmacological agents (Cabib & Puglisi-Allegra, 1996), which alter the sensitivity of the opioidergic and dopaminergic systems. For example, when rewards are abundantly present, an animal develops a certain degree of tolerance for them, but when deprived of essential stimuli, and hence stressed, it eagerly responds to cues predictive of rare and valued rewards. This often long-term change in sensitivity for reward explains why rats housed in enriched (and presumably less aversive) environments show lower levels of anticipatory behaviour than standard housed and relatively deprived controls which are sensitised to rewards and thus "like" and "want" them more (van der Harst et al, 2003a). On the other hand, severe or chronic stress, such as social defeat followed by individual housing, is associated with a decrease in, or even a complete lack of, reward-related anticipatory behaviour, comparable to the anhedonia symptomatic of human depression (von Frijtag et al, 2000; 2001; van der Harst et al, 2003a).

The Dutch researchers accordingly suggest that measuring anticipatory activity in expectation of a reward is a useful parameter for assessing the welfare of an animal and the status of its underlying reward-related neurocircuitry (Spruijt et al, 2001; van den Bos et al, 2002; van der Harst et al, 2003a; 2003b; Vinke et al, 2004). Animals showing heightened motivation for reward or, alternatively, lacking reward-related anticipatory behaviour, are likely to be experiencing (or have experienced) more stress and poorer welfare than animals exhibiting moderate or "normal" anticipatory responses.

The findings of the Dutch researchers have implications for the usefulness of providing social cues to motivate foraging behaviour. If animals have been severely or chronically stressed they are unlikely to display anticipatory behaviour. Consequently, foraging behaviours would not be elicited in response to the cue of seeing a demonstrator foraging, and animals would be generally unresponsive to environmental stimuli. Conversely, relatively deprived animals may display a heightened response to cues predictive of reward. If sufficient opportunities are provided for animals to perform behaviours for which they are motivated, providing social cues for foraging behaviours might improve the welfare of captive animals by encouraging natural and pleasurable interactions with the environment. This may in turn help offset the negative effects of other stressors. For example, providing social cues predictive of food reward might be used to encourage use of enrichment devices to which animals have habituated or, as I observed in the baboons in this study, to promote manipulation and consumption of browse that was, after the first day, ignored by the animals (personal observations).

However, manipulating motivation as a form of enrichment carries an important caveat: if an animal's motivation to perform a behaviour is increased, but suitable opportunities to perform the motivated behaviour are lacking, such over-arousal of the seeking system (whilst thwarting of the performance of the behaviour) might result in frustration (Panksepp, 1998), and the elicited appetitive behaviours may then develop into abnormal behaviours such as stereotypies (Mason, 1991).

6.9 Conclusions

In this study, I have proposed that to understand the psychological and behavioural needs of captive animals, particularly those needs related to food acquisition, as well as to ensure adequate all-round welfare, we need to be cognisant of the physiological, psychological, and neurobiological systems that motivate, organise, evaluate, and reinforce foraging behaviour.

Appetitive and consummatory foraging behaviours have the ultimate function of ensuring that organisms obtain the energy and nutrients necessary for survival and reproduction. Much time is devoted to these critical activities, the many subcomponents of which are regulated by complex, hierarchically-organised brain structures and physiological systems (Toates, 1986; 2001; 2004). In their environment of evolutionary adaptation (EEA), animals typically meet their nutritional needs in flexible and efficient ways (McGuire & Troisi, 1998), with behaviour directed by hedonic/aversive experiences, a proxy of ultimate utility (Cabanac, 1971; 1992). The performance of behaviours which the animal experiences as proximately pleasurable thus promotes its ultimate fitness, in addition to providing the animal the means with which it can regulate the relative balance between positive and negative affective states (welfare; Spruijt et al, 2001).

By confining animals in unnatural conditions, we place them in situations in which the evolutionarily entrenched rule, what is proximally pleasurable/stressful is ultimately beneficial/harmful (Cabanac, 1971), may no longer be a valid guide to adaptive behaviour. If we do not appreciate the mechanisms that have evolved to regulate an animal's behaviour in its natural environment, we may fail to see the purpose of providing captive animals with opportunities to perform activities for which they have no ultimate physiological need, but which are nonetheless vital for their proximate well-being (Hughes & Duncan, 1988; Dawkins, 1998; Spruijt et al, 2001). However, equipped with such knowledge, we are better able to tackle the difficult-to-answer question of which aspects of an animal's EEA ought to be incorporated into the captive environment to provide sufficient behavioural opportunities for animals to attain a predominance of positive over negative affective states.

Whilst basing the definition of welfare upon subjective states or emotions has in the past been criticised as anthropomorphic (reviewed in Dawkins, 1998), failing to acknowledge and address affective states is tantamount to ignoring their indisputable role as the interface between sensory systems and behaviour (McGuire & Troisi, 1998; Rolls, 2002). Moreover, scientific methods are now available to assess welfare in terms of the underlying state of the neural circuits involved in affective processing (e.g. van den Berg et al, 1999; von Frijtag et al, 2000; 2001; 2002; Spruijt et al, 2001; van der Harst et al, 2003a; 2003b; van den Bos et al, 2002; 2004; Vinke et al, 2004), without resorting to the contentious use of human terms such as “boredom” or “unhappiness”.

In the natural environment, it is the functional outcome of behaviour that is of primary importance, with the attainment of positive affective states only of secondary importance to survival and reproduction. In captivity, however, where an animal is not faced with threats to survival, attaining a positive affective state may be of primary importance in order to ensure adequate welfare. Providing suitable cues and contexts can encourage animals to perform behaviours, the functional outcome of which may be irrelevant to their ultimate fitness, but which are nonetheless proximately pleasurable and thus welfare enhancing. Promoting appetitive and/or consummatory foraging is a suitable way of achieving this because, as previously explained, foraging appears to be rewarding by its own performance, even if food is not always ingested.

The study reported here investigated an alternative means to increase foraging in two troops of captive baboons. In these experiments, social cues signalling the availability of food, rather than food items *per se*, were successfully used to motivate foraging behaviour. Because of the positive hedonic experiences known to accompany foraging behaviours, using social cues to motivate foraging, as well as providing appropriate substrates on which to perform these behaviours, would enhance the welfare of captive animals. Such motivated foraging could thus be used to augment standard foraging environmental enrichment protocols that currently rely chiefly on altering the way in which food is presented (Reinhardt & Roberts, 1997). In this study, the duration of each observation session was 30 minutes. Whilst results from Treatment 8 (peanuts) in Experiment II indicated that the baboons did not habituate to the treatment from one day to the next, it is unknown whether they would habituate to treatments if the duration was increased beyond half an hour.

Much work is still necessary to gain a more complete knowledge of what motivates and regulates the behaviour of captive animals, especially those behaviours for which there is no physiological need in captivity. It will also be important to determine what constitutes adequate or good welfare in terms of the extent to which positive affective states must outweigh their negative counterparts. In particular, other means of minimising the increased aggression in reaction to the introduction of a monopolisable food source should be considered: whilst levels of aggression remained relatively low they were, nonetheless, significantly higher during treatments when food was provided than during control treatments.

In the realm of foraging, further research is required to (1) determine the psychological and neurobiological mechanisms through which animals learn, both socially and individually, about foods and foraging techniques; (2) identify and provide in captivity the many cues motivating foraging behaviours; and (3) provide the appropriate substrates on which to perform these activities. In addition, one will need to investigate the neural mechanisms that generate positive affective states during the performance of appetitive and consummatory feeding activities, including how these systems can be activated through environmental enrichment. Finally, examining inter-individual differences in behaviour, and the factors such as temperament, status, and age that underlie this variability, would permit the tailoring of environmental enrichment protocols to individual animals, as well as extend our knowledge of how internal factors mediate the animals' responses to stimuli in their environment.

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