An investigation of biases in social learning and social attention in wild vervet monkeys (*Chlorocebus aethiops pygerythrus*) and captive tufted capuchins (*Sapajus apella*).

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University of St Andrews

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Abstract

Researchers in the field of social learning have suggested that certain biases may exist in whom animals learn from, creating a non-random flow of social information. A number of potential biases have been proposed based upon theoretical models, including biases to copy more dominant individuals or individuals who receive the best payoff from their behaviour, but empirical evidence for these biases is lacking. This thesis presents the first examination of dominance-based bias in a wild population of primates and of a payoff-based bias in captive capuchins.

In two field experiments, dominant and low-ranking females from each of three wild groups of vervet monkeys (*Chlorocebus aethiops pygerythrus*) in KwaZulu-Natal, South Africa were trained to demonstrate contrasting behaviours to their group before observers were provided with a choice between the two modelled preferences. No evidence was found for a consistent bias to copy the behaviour of the dominant female in either experiment. Instead, in both experiments, a preference for one behaviour emerged, regardless of model rank. In the latter experiment, higher-ranking females were significantly more likely to match the dominant model's action than were low-ranking females. The low-ranking models were more likely than their high-ranking counterparts to switch behaviours, despite their trained behaviour continuing to be productive. An analyses of the observations revealed that observers were biased towards attending to kin, and observer age appeared to influence access to the dominant models, but no overall preference to attend to the dominant female was found. Together these findings indicate that kinship, sex, age and preferences for specific behaviours are more important factors than model rank in vervet monkey social learning.

Finally, I examined whether captive tufted capuchins (*Sapajus apella*) utilized a payoff-based social learning bias in their foraging decisions. Subjects did not utilize public information when choosing between demonstrated resource-rich and resource-poor sites, suggesting that the social learning abilities of capuchins may not extend to determining the profitability of feeding sites, although limitations of the study are discussed.

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Chapter 1: Introduction

In an attempt to further understand how social learning operates in non-human animals, this thesis examines social learning biases in wild and captive monkeys. This chapter provides an overview of the field of cultural transmission research focussing on the past and current literature on social learning biases, with particular regard to the study species and questions addressed within this thesis.

1.1: Culture

Once thought to be the preserve of humans, the question of culture in non-humans has long been debated by researchers, a debate partly fuelled by different uses of the term ‘culture’. It has been argued that in choosing which definition of culture to use, this inherently biases to which species we may ascribe culture (Laland & Hoppitt, 2003; Dean et al., 2013). Hoppitt & Laland (2013) define culture as “group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information” (p. 4). This definition is broad enough to allow a useful assessment of non-human culture whilst not limiting the mechanisms of social transmission that may be used and as such will be the definition used throughout this thesis. Social learning, in turn, can be defined as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (Heyes, 1994, p. 207). With these definitions to hand, we can thus explore the plethora of evidence that exists for non-human culture.

1.1.1: Culture in primates

Following earlier reports of potential cultural behaviours in wild chimpanzees (McGrew & Tutin, 1978; Goodall, 1986; McGrew, 1992), in 1999, Whiten and colleagues compiled information from across seven long-term chimpanzee field sites and identified 39 behavioural variants that appeared to be culturally transmitted. This was achieved by eliminating all behaviours that appeared explicable through genetic or ecological reasons, such as the presence or absence of a particular food at each site (Whiten et al., 1999; 2001). This repertoire has since been extended to include other traditions, such as the recently described patterns of stone-throwing in wild chimpanzee populations in West Africa (Kühl et al., 2016) and it seems likely that, with continued observation of more populations, more cultural variants may emerge.

Following Whiten and colleagues (1999), cultural repertoires were also identified for the other great apes; orangutans were found to exhibit a number of cultural behaviours (van

Schaik et al., 2003, although the exact number is still under debate; see van Schaik et al., 2009), bonobos were found to exhibit 14 cultural traits (Hohmann & Fruth, 2003) and more recently, Robbins et al. (2016) have identified 23 traits that appear to vary across gorilla field sites and meet the above criteria for cultural behaviours. Later reports have also conducted further in-depth analyses to confirm cultural transmission as the most likely candidate for the spread and maintenance of group-typical behaviours in apes (van Leeuwen, Cronin, Haun, Mundry, & Bodamer, 2012; Krützen, Willems, & van Schaik, 2011).

Whilst the great apes seem to exhibit the greatest repertoire of cultural behaviours of the primate family, culture is not absent from monkey species. Both white-faced and tufted capuchins appear to exhibit culturally transmitted behaviours. White-faced capuchins have been observed participating in dyadic ‘games’ which involve such behaviours as poking fingers in one another’s eyes (Perry et al., 2003); both their pattern of presence/absence and their seemingly arbitrary nature suggest they are cultural behaviours. Tufted capuchins, upon which Chapter 6 of this thesis focuses, have also displayed cultural acquisition in nut-cracking behaviours (Ottoni & Mannu, 2001; Ottoni & Izar, 2008). In addition to capuchins, Japanese macaques also exhibit cultural behaviours in their stone handling patterns (Huffman, 1996).

Santorelli et al. (2011), whilst reporting 22 behavioural traditions found in different spider monkey populations, point out that, of these 22 behaviours, more than half are in the social domain (as opposed to e.g. extractive foraging). Thus a focus upon traditions based on extractive foraging and tool-use may eclipse other cultural activities in species without the manual dexterity or ecological necessity to display these behaviours.

1.1.2: Culture beyond the primates

This possible bias towards looking for cultural behaviours in the extractive foraging domain has perhaps led researchers to somewhat overlook other candidate species for cultural behaviour that do not show particular prowess at extractive foraging, such as vocal culture in birds (Slater & Ince, 1979; Bluff, Kacelnik & Rutz, 2010) and cetaceans (Payne, 2000; Whitehead & Rendell, 2015). Additionally, a somewhat anthropocentric focus on primate culture has been criticised, with some researchers claiming a primate-centred bias leads us to overlook other animals and the evidence for culture which comes from fish, birds and whales, rather than primates (Laland & Hoppitt, 2003).

Certainly, cetaceans exhibit a wide variety of behaviours that can be considered cultural, including feeding patterns, migratory routes and arbitrary ‘fad’ behaviours (Rendell & Whitehead, 2001; Whitehead & Rendell, 2015) and provide some of the best examples of culture outside of the primate family. The most well-known of these examples is the cultural evolution of the song of the humpback whale whose song changes over time sometimes dramatically, and for which the change in song can be tracked across geographic regions over time, thereby implying social learning (Payne, 2000; Garland et al., 2011). Several other cetacean species provide convincing evidence of traditions in their vocalisations, such as killer whales (Ford, 1991; McDonald, Mesnick, & Hildebrand, 2006) and sperm whales (Rendell, Mesnick, Dalebout, Burtenshaw & Whitehead, 2012), as well as in apparently arbitrary ‘fad’ behaviours, such as killer whales balancing dead salmon on their heads (Whitehead, Rendell, Osborne, & Würsig, 2004) and in foraging behaviours, such as ‘sponging’ in bottlenose dolphins (Krutzen et al., 2005) and lobtail feeding in humpback whales (Allen, Weinrich, Hoppitt & Rendell, 2013).

Given that there is currently evidence for culture, or at least traditions, not only in cetaceans, but also other mammals such as meerkats (Thornton, Samson & Clutton-Brock, 2010), and some birds (Madden, 2008; Hunt & Gray, 2003, although see Holzhaider, Hunt & Gray, 2010), it seems that culture must be an adaptive trait and one that is certainly not restricted to humans. Of course, it would be misguided to argue that culture in non-human animals is comparable to human culture. Humans have developed material, linguistic and social cultures far beyond anything found in non-human animals (henceforth simply ‘animals’). Researchers have suggested that this is due to a cumulative type of learning in humans, in which individuals build upon the knowledge of others to create tools and behaviours that could not be invented by one individual alone (Tennie, Call & Tomasello, 2009). This is known as cumulative culture, or the ‘ratchet effect’ (Tomasello, Kruger & Ratner, 1993; Dean, Vale, Laland, Flynn & Kendal, 2013). There have been some arguments for cumulative culture in non-humans, such as the modification of tools in New Caledonian crows (Hunt & Gray, 2003), but as of yet, none that yield highly convincing evidence for cumulative culture in exhibiting a behaviour that could not be innovated by one individual alone (Dean et al., 2013). Thus, as it stands, there is convincing evidence for culture, but not for significant cumulative culture in animals. As we have seen, there is a large and growing body of evidence for cultural behaviours in wild animal populations, yet there are also limitations on what these observations can provide.

Whilst testing for cultural behaviours in wild populations is an extremely useful and informative research strategy, it does not inform us particularly well of how behaviours actually spread. Indeed there is contention among researchers as to whether the 'exclusion method', which seeks to rule out ecological and genetic explanations when deciding if a behaviour is socially learned, is strict enough to attribute culture without risking false positives (Laland & Janik, 2006; Krutzen, van Schaik & Whiten, 2007) or indeed false negatives, for at least some behaviours can be culturally transmitted, but also dependent upon or adapted to ecology (e.g. lobtail feeding in humpback whales, Allen et al., 2013). As per our definition, culture is dependent upon the behaviours being socially learned, yet when researchers find a behaviour already present in a group, it is difficult to provide direct evidence that it was socially transmitted.

However, researchers were recently able to witness the innovation of a behaviour in wild chimpanzees, 'moss-sponging', and track its spread throughout the group (Hobaiter, Poisot, Zuberbuhler, Hoppitt & Gruber, 2014). By using a statistical technique known as Network Based Diffusion Analysis (NBDA, Franz & Nunn, 2009), the authors were able to reveal that the pattern of spread was best explained by a model which included social learning, based on the authors' records of which individuals observed the behaviour. This technique has also been used to trace the social transmission of a lobtail feeding technique in humpback whales (Allen et al., 2013) and appears to be a highly useful tool in allowing researchers to attribute naturally-occurring behaviours to social learning. Yet, whilst extremely fruitful when it can be used, NBDA requires extensive and intense observation of a community, the ability to identify all study animals and also a high degree of luck in first catching an innovator 'in the act', or at least recognising the earliest stages of an innovation's diffusion. Accordingly, controlled experimentation is able to tell us something more about the nature of social learning in non-human animals.

1.1.3: Experiments in Social learning

Often aimed at primates but applied also to other aniamls, laboratory-based experiments have historically focused on the *mechanisms* of social learning (Heyes, 1994); *how* information is transmitted between individuals. Much research has attempted to reveal whether non-human primates are capable of teaching and imitation, the mechanisms initially suggested to be necessary for cumulative culture (Galef, 1992), although this is still a debated issue (Caldwell & Millen, 2009; Tennie, Call & Tomasello, 2012). Researchers have attempted to assess the extent to which human and non-human primates utilise the mechanisms of imitation (copying bodily actions, Whiten & Ham, 1992) and emulation (copying the end-state of the behaviour, Tomasello, 1996) by using a range of innovative experiments with captive animals (Horner & Whiten, 2005; Tennie, Call & Tomasello, 2006; Hopper, Lambeth, Schapiro & Whiten, 2008; Buttelmann, Carpenter, Call & Tomasello, 2013). Currently this issue also remains under debate and whilst some experiments have found chimpanzees seemingly capable of imitation (Horner & Whiten, 2005), other recent findings suggest that imitation is extremely rare in non-enculturated apes (Tennie et al., 2012). Similarly, the issue of teaching in non-human animals remains contested, with studies of cooperative-breeding animals thus far providing the best evidence for teaching in non-humans (Thornton & McAuliffe, 2006; Franks & Richardson, 2006) whereas studies of primates show minimal evidence for teaching (Boesch, 2003, although see Musgrave et al., 2016 for recent evidence of tool transfer as teaching in wild chimpanzees).

Whilst these debates surrounding social learning mechanisms are extremely interesting and important for understanding the role of these processes in the evolution of human culture, this thesis instead focuses on a somewhat lesser-studied, yet equally intriguing aspect of social learning - *when* and *from whom* individuals use social learning. This next section will provide an overview of both the theoretical implications and empirical evidence for biases in social learning use in human and non-human animals.

1.2: Social Learning Biases

Whilst social learning would seem to provide many benefits and avoid the costs related to asocial learning (Clark & Mangel, 1984; Rendell et al., 2010, but see Heyes, 2016), not all social learning need be adaptive (Giraldeau, Valone & Templeton, 2002). There is evidence that maladaptive behaviours may also be socially learned, such as taking the longer of two routes (Laland & Williams, 1998; Pongracz, Miklósi, Kubinyi, Topál & Csányi,, 2003). Laland (2004) suggested therefore that individuals would benefit from being selective in when and from whom they choose to socially learn and proposed that individuals rely on certain ‘strategies’ in order to enhance the profitability of their social learning. Laland (2004) categorised these as ‘when’ and ‘whom’ strategies, examples of which are, *copy when uncertain* and *copy older individuals*.

The idea of such strategies (or ‘biases’ as I shall refer to them throughout this thesis, to emphasize that animals need not necessarily be aware that they are engaging in them, or understand how they function, as per Laland, 2004) in how individuals socially learn had been put forth by Coussi-Korbel and Fragaszy (1995), who first coined the term ‘Directed Social Learning’. This proposes that “particular individuals are more influential models for certain individuals than are others” (p. 1444) and as a result, information flow throughout a group may not be uniform as it might be with random copying, but may be influenced by biases in who learns from whom. For instance, Laland (2004) suggested such biases as *copy older individuals*, or *copy successful individuals*, amongst others, which may provide more useful information to the learner. Laland (2004) also suggests biases based upon the payoff received by the model, which will be discussed in greater detail in a later section.

Whilst several studies have looked at theoretical models concerning predictions made from these biases in various different environments (Boyd & Richerson, 1985; Kendal, Giraldeau & Laland, 2009), there is less empirical evidence available to either support the predictions of these models or show the presence of these biases in learners. Whilst researchers have begun examining these biases in humans (Rendell et al., 2010; Mesoudi, 2011; Wood, Kendal & Flynn, 2013), few studies have yet examined them in non-human animals and even fewer have examined such biases in wild populations; these are discussed below.

It should be noted here that, thus far, the predominant arguments for these social learning biases are based around their adaptiveness in increasing information whilst minimising cost to the individual (Laland, 2004). However, as we know from classic studies of human behaviour (Asch, 1956), humans at least will copy the behaviour of others, not only for informational reasons, but also for social reasons, for instance to adhere to group norms (Claidiere & Whiten, 2012). I do not think it too controversial to suggest that social learning biases in animals may have evolved to also serve social, rather than purely informational functions, potentially leading to increased affiliation with others which may serve to increase fitness. Laland (2004) argues that to study them, the reasons that these ‘strategies’ are adopted should not be important and biases that serve informational and social functions would likely lead to the same outcomes. However, it may prove useful in interpretation to consider the motivations for these biases.

It should also be noted that the extent to which these social learning strategies are domain-specific evolved mechanisms (Henrich & McElreath, 2003) is currently the subject of much contention, with some researchers arguing that the empirical evidence can be explained by the same learning processes as for asocial learning (Heyes, 2016), thereby suggesting a more domain-general process. However, whilst acknowledging this discussion, the aim of this thesis is not to investigate the underlying cognitive mechanisms, but rather to focus on the behavioural outcomes of these potential biases; do specific biases play a role in the social learning of monkeys, and if so, what effect do they have upon how behaviours spread throughout a group?

Here I provide an overview of the social learning biases most studied and most relevant to this thesis. I begin with dominance-based bias.

1.2.1: Dominance and prestige

An adaptive bias should serve to enhance the fitness of the individual. It has been suggested that a *copy successful individuals* strategy, proposed by Henrich & Gil-White (2001), may relate to dominance rank in non-human animals (Laland, 2004); it may be argued that copying the dominant individual could be a useful strategy, if dominance were used as a proxy for success (Hoppitt & Laland, 2013). Particularly in primates, dominance is often a central aspect of the social lives of individuals (Cheney & Seyfarth, 1990), with more dominant individuals often receiving more grooming (Seyfarth, 1977) and having priority access to food and mates (Cheney & Seyfarth, 1990; Cowlishaw & Dunbar, 1991; Pusey, Williams & Goodall, 1997). However, there is evidence that dominance may only effect reproductive success under certain environmental conditions, such as when resources are scarce or monopolizable (Whitten, 1983; van Noordwijk & van Schaik, 1999). Therefore, high rankers may be regarded as successful models. In humans, there is some evidence that demonstrator social rank may influence copying; McGuigan (2013) found that young children were more likely to over-imitate the higher-ranked of two adult models. Additionally, Flynn & Whiten (2012) found children more likely to attend to the actions of more dominant and prestigious children, although these two characteristics were highly correlated (see below for further discussion on this topic).

However, few studies have investigated dominance-based bias in non-human animals. Nicol & Pope (1999) found domestic hens were more likely to copy the pecking behaviour of more dominant hens. Interestingly, in a second experiment the authors of this study also manipulated the previous foraging success of the dominant hens over a two week period and found this did not affect the results. This would either suggest that the dominance-based bias operates without reference to success, or perhaps that two weeks was not long enough to override previously ingrained knowledge of which individuals were more successful.

An experimental study with captive tufted capuchins failed to find evidence for a dominance-based bias (Dindo, Leimgruber, Ahmed, Whiten, & de Waal, 2011). Capuchins are among a very limited number of monkeys to have had traditions documented in the wild (Perry et al., 2003; Santorelli et al., 2011), particularly tool-use traditions (Ottoni & Izar, 2008) and thus their social learning processes are of considerable interest to primatologists. When able to choose between watching two models participating in an extractive foraging task, the capuchins studied by Dindo et al. (2011) showed no preference to attend to a more dominant individual and no preference to copy their method at the task (although a subset of participants did show a kinship bias, as discussed below). This lack of a bias in capuchins could be considered somewhat surprising, given that they have previously been shown to preferentially attend towards the more dominant and most-skilled individuals in semi free-ranging groups in one of the few studies to assess social attention in primates (Ottoni et al., 2005; Coelho et al., 2015). However, it should be noted that in their captive study, Dindo and colleagues (2011) used female models as they found adult males far harder to train. Thus, it is possible that a dominance bias only presents with a specific sex, based on the social structure and/or ecology of the species. A further experiment with male capuchin models would be useful to test this.

In contrast to these negative findings with monkeys, two recent studies with captive chimpanzees have revealed dominance-based biases in social learning. Horner, Proctor, Bonnie, Whiten & de Waal (2010), using a two-model paradigm, found what they labelled a 'prestige'-based bias in captive chimpanzees. Prestige can be viewed as similar to dominance, but rather than obtaining status through force, it is 'freely-conferred deference' (Henrich & Gil-White, 2001), such as may be seen as akin to celebrities or elected leaders in modern human culture. These authors argue that high status is achieved through deference shown by observers to skilled individuals in an attempt to gain more access to that individual and therefore should be viewed as distinct from dominance (Henrich & Gil-White, 2001). Horner and colleagues (2010) trained two chimpanzees per group at a token-deposit task, where the two models used different receptacles for the tokens to obtain a food reward. One model per group was older, more dominant and more experienced at experimental tasks than the other and was termed the more prestigious of the two. The authors found a bias towards individuals copying the more prestigious model. Whilst this may show evidence of a dominance-based bias, hierarchy was confounded with the variables of age and previous experience (to create this 'prestige' label) which may have led to the observed findings. Indeed, children have been shown to copy more reliable models (Harris & Corriveau, 2011), thus showing a bias towards past success rates, although as discussed above, manipulating hens' foraging success did not alter the dominance-bias shown in this species (Nicol & Pope, 1999). Nevertheless, caution must be exercised in interpreting these findings.

However, another recent study with captive chimpanzees also found a bias for individuals to copy more dominant individuals (Kendal et al., 2015) and was able to disentangle this from prestige. This paradigm used just one mid-ranking model trained at an extractive foraging task and then used statistical techniques to assess which separate biases existed, finding evidence for copying both high-ranking and trained individuals. Kendal and colleagues (2015) proposed that this dominance bias (perhaps in concert with conformist transmission) may help maintain the between-group differences observed in chimpanzee populations (Whiten et al., 1999). As low-ranking chimpanzees are the more frequent innovators (Reader & Laland, 2001), a bias towards copying high-rankers may hinder the spread of innovations from these individuals (who are often likely to be immigrated females) and thus sustain behavioural homogeneity in the group (Kendal et al., 2015). However, a more recent study using just one high *or* low-ranking model within each group, again with captive chimpanzees, found that the method used on an extractive foraging task was learned socially when the demonstrator was of low rank (and in this case, not when they were of high rank) (Watson et al., submitted).

Thus the evidence for dominance-based biases in primate social learning is mixed. Whilst some studies suggest that dominance bias does occur in animals, this has yet to be investigated in a wild population of primates. It is possible that the artificial group structures of a captive group, as opposed to naturally formed groups, may cause these socially-based biases in learning to differ in captivity when compared to wild individuals. Additionally, the spatial distribution of primates in captivity can be vastly different to that of those in the wild, leading to forced proximity compared to, for example, a more natural, fission-fusion social structure such as that seen in wild chimpanzees (Goodall et al., 1986). Indeed, low-ranking chimpanzees appear to avoid proximity with high-rankers in the wild (Murray, Mane & Pusey, 2007) and thus the forced proximity of captive living may then alter social dynamics, including social learning. Therefore, with these potential confounds in mind, it is necessary to test this bias in wild populations.

1.2.2: Kinship & affiliation

Despite being perhaps the most intuitive path of social learning, relatively little empirical evidence is at hand to demonstrate a selective copying of kin by individuals.

Researchers often speak of infant primates being attentive to their mother (e.g. Boesch, 2003), but little empirical evidence is available to show whether this attentiveness translates to learning. Rather, it can be inferred from circumstance; in primates and many other species, individuals spend almost all of their infancy in close proximity with their mother. Hence the mother becomes the primary model for the infant and much of its learned behaviour is likely to be acquired under the influence of the mother, showing vertical transmission. In a recent paper and one of the few studies examining this, Wrangham and colleagues (2016) found that chimpanzee offspring exhibited a bias to use the grooming technique preferred by their mother. Lonsdorf, Eberly, & Pusey (2004) found a correlation between mother and daughter chimpanzees in terms of length of preferred stem tools when termite fishing. Interestingly, these data also revealed sex biases in social attention; female juveniles appeared to attend more to their mothers during fishing bouts and learn faster than their male counterparts. In orangutans, infants appear to learn their diet from their mothers, with infants selectively paying greater attention to their mothers during the more difficult extractive foraging techniques (Jaeggi et al., 2010; Schuppli et al., 2016). Furthermore, recent findings show that the greatest periods of increased social attention (‘peering’) towards the mother coincide with increased exploratory behaviours and improving skills in immature orangutans (Schuppli et al., 2016), thereby providing more evidence for a link between social attention and social learning. There is also evidence of this kind in non-primates, for example southern right whale calves appear to learn migratory routes and the location of feeding grounds while travelling close to their mothers, with whom, like primates, they spend an extended infancy (Valenzuela et al., 2009).

Few experiments have compared learning from kin to learning from non-kin. In a field experiment mimicking the famous sweet potato-washing macaques (Kawai, 1965), wild vervet monkeys were offered grapes covered in sand (van de Waal, Bshary & Whiten, 2014). The monkeys displayed differences in cleaning techniques to remove the sand, which were recorded by the authors. It was found that infants matched their mothers’ food cleaning techniques preferentially over other adult females in the group, who they also had visual access to during the tests (van de Waal et al., 2014), thereby exhibiting a kinship-based bias. Schwab, Bugnyar, Schloegl & Kotrschal (2008) used a stimulus enhancement task to compare information use between sibling and non-sibling pairs of ravens. The authors found that within sibling pairs, the observer showed a preference for the object handled by their sibling, whereas, within non-sibling pairs, the observers showed no preference (Schwab et al., 2008). This is particularly interesting as it shows a kinship bias outside of the mother-infant dyad and represents enhanced interest horizontally, as well as vertically. Hoppitt & Laland (2013) suggest that a *copy kin* bias may be adaptive as individuals are likely to inhabit the same space and have similar behaviours and reactions to kin over non-kin. They also suggest that, following Hamilton's (1964) rule, social learning between kin may be proportional to their relatedness.

Similar to kinship, Hoppitt & Laland (2013) also suggest that a *copy friends* bias may operate in animals. This may depend on the definition of 'friendship', although there is evidence that guppies learn foraging routes faster from familiar over unfamiliar demonstrators (Swaney, Kendal, Capon, Brown & Laland, 2001) and that the social network can lead to directed social learning in captive squirrel monkeys, with centrality in the social network predicting speed of acquisition and adoption of the behavioural variant seeded in the group (Claidiere, Messer, Hoppitt & Whiten, 2013).

1.2.3: Age

In addition to dominance, age has also been proposed as an adaptive proxy for success (Laland, 2004). This is again a seemingly intuitive bias as older individuals are likely to possess more knowledge about their environment than younger individuals. However, once again, relatively little empirical evidence exists to support this. Duffy, Pike & Laland (2009) found that nine-spined sticklebacks copied the foraging patches of older, larger fish over younger fish, thus displaying a *copy older individuals* (and therefore, larger) bias. Additionally, Choleris, Guo, Liu, Mainardi & Valsecchi (1997) revealed a slightly more subtle effect of age on social learning of mice, wherein socially learned food preferences were longer lasting when the demonstrator was an adult compared to when it was a pup. Perhaps most relevant here is the finding of Biro and colleagues (2003) who used a 'field laboratory' to study the nut-cracking behaviour of the wild chimpanzees of Bossou, Guinea. Analyses of attention around nut-cracking bouts found that individuals selectively observed individuals of the same age or older, but not younger during these bouts (Biro et al., 2003). Whilst there is no direct evidence that that these individuals learned socially from these observations, as discussed above, correlations between selective attention and copying behaviour have been shown in wild chimpanzees and orangutans (Lonsdorf et al., 2004; Schuppli et al., 2016).

1.2.4: Payoff-based biases

Up until now I have discussed social learning biases which are based upon the characteristics of the model, such as age and rank. However, Laland (2004) also suggested that an adaptive strategy may be for individuals to copy others based upon the payoff of the model's behaviour, i.e. copy if better than your own behaviour. This differs from the previously discussed model-based biases in that it requires the animal to make a judgement about the productiveness of another's behaviour. In order to selectively copy another's behaviour based upon their payoff, it follows that an animal needs to be able to distinguish a productive patch/behaviour from an unproductive one, an ability that is often assumed, but rarely tested (Hoppitt & Laland, 2013). In the context of foraging behaviour, the use of social behaviour to assess the productiveness of a particular foraging patch/behaviour is also termed 'public information use' (Valone, 1989).

A payoff-based bias has been shown in humans playing a computer-based game, but was not utilised to the extent expected (Mesoudi, 2011). Similar to other social learning biases, there is limited empirical evidence for payoff-based biases in non-human animals, although some studies have been conducted with birds and fish. A study of starlings found they were able to assess patch quality better after witnessing conspecifics foraging (Templeton and Giraldeau, 1996). Doligez, Danchin & Clobert (2002) manipulated the perceived reproductive success of flycatchers at certain breeding sites (by transfer of nestlings) and found fewer immigrants at sites with lower reproductive success (based on quantity, but not quality of young). Additionally, nine-spined sticklebacks were able to distinguish between high and low quality feeders after observing the behaviour of conspecifics (Coolens, Bergen, Day & Laland, 2003). Perhaps surprisingly, given this ability in fish and birds, captive marmosets did not have a higher foraging success when paired with a knowledgeable conspecific compared to when foraging alone (Voelkl & Huber, 2007); the authors argued this may have been due to social factors hindering social learning.

Vale, Flynn, Lambeth, Schapiro & Kendal (2014), using a similar paradigm to Coolens et al. (2003), presented captive chimpanzees with videos of a conspecific feeding at different rates from differently coloured feeding boxes and then gave them the choice between each box. The chimpanzees displayed a significant preference for the more productive box, thus showing an ability not only to discriminate between the two boxes based on resource quality, but to use this to inform their own foraging decisions. The authors then suggested that this ability to discern and copy a better behaviour is an important factor in cumulative culture, by allowing a change to more and more beneficial behaviours (Vale et al., 2014), although they also noted that there are a range of individual and social factors which may affect whether this ability is utilised in wild chimpanzees.

1.3: Social Learning in Vervet Monkeys: An Overview

The majority of experimental chapters (3-5) in this thesis focus on vervet monkeys (*Chlorocebus pygerythrus aethiops*) as the test species. Accordingly what follows is a background overview of the literature specifically regarding social learning in this species.

There is, as of yet, little evidence for behavioural traditions in wild vervet monkeys; only one published study has attempted to provide evidence for between-group variation, based upon diet. Tournier et al. (2014) examined the diet of six neighbouring groups of wild vervet monkeys from a population in South Africa and compared their consumption of items from 14 tree species to the abundance of each tree species in of the corresponding group's home range. The authors found that, although consumption was positively correlated to abundance for each species, there were also differences between the groups in the relative importance some species played in each group's diet. Whilst these differences may signal between-group traditions in the composition of diet in these vervet monkeys, variables such as group size and composition were not controlled for, and as such, may instead indicate individual preferences rather than group-level homogeneity (Tournier et al., 2014). Further data are required to clarify this point before these differences can be confidently labelled as traditional.

Whilst Tournier and colleagues (2014) provide tentative evidence for differential diets between groups, relatively little is known about how and from whom vervet monkeys learn about diet, although similar to other primates, the close mother-infant dyad would suggest that the mother likely has a central role. Unlike in some species of New World monkeys, there is no evidence for food transfer or sharing in vervet monkeys (Rappaport & Brown, 2008) and no reports of teaching. Hauser (1993) found that infant survival positively correlated with the amount of time an infant spent co-feeding with its mother, but it is not clear from this study whether the infants learned about the diet from their mothers, or simply obtained more food when co-feeding (Rappaport & Brown, 2008).

There have been some studies which have experimentally examined social learning in wild vervet monkeys, primarily by van de Waal and colleagues who have used field experiments to examine this issue. As described above, a food cleaning experiment revealed preferential copying of the mother's food cleaning technique over that of other group females (van de Waal et al., 2014) revealing a kinship-based bias. Sex-based social learning biases have also been revealed in vervet monkeys; a simple artificial fruit task using a box which could be opened via one of two doors was presented to wild vervets and models were trained in opening using one of the two doors (van de Waal, Renevey, Favre & Bshary, 2010). The authors found that social learning of the opening technique followed only in groups where the model was female. The authors found no greater levels of aggression from male models than female models and so ruled out the effects of lowered tolerance from the males. Instead, while analysing attention around the demonstrations, they found a selective attention bias towards the female models. As females are philopatric in vervet monkey social groups, this may represent an adaptive strategy; to learn from the sex that will have the most relevant knowledge of the local environment (van de Waal et al., 2010), when compared to males who migrate through several home ranges throughout their lives (Cheney & Seyfarth, 1983). This result is also consistent with evidence from observations of natural foraging which show enhanced social attention towards female vervet monkeys from conspecifics (Renevey et al., 2013). Sex-based biases have also been found in other species, whereby individuals, sometimes of a certain sex, prefer to copy individuals of a specific sex (Katz & Lachlan, 2003; Benskin, Mann, Lachlan & Slater, 2003; Nicol & Pope, 1999).

It should be highlighted here that the models of both sexes in the van de Waal et al. (2010) study were dominant individuals (owing to a monopolisation of the task during training). This study shows that vervet monkeys are capable of copying the dominant female in a social learning task. However, given that the only available models in this task were dominant individuals, it remains to be seen whether, when given a choice, a vervet would choose to copy the dominant female over another model of differing rank. This is a question pursued in Chapters 3 and 4.

Field research has also revealed that both infants and migrating males copy the food type preference (in this case differentiated by colour) of their social group; a new group in the case of migrating males (van de Waal, Borgeaud & Whiten, 2013). The authors trained four groups of vervet monkeys in a wild population to prefer either blue or pink corn using distasteful mountain aloe juice soaked alongside one of the two options to render it unpalatable. When the males migrated from a blue-eating group to a pink-eating group (or vice versa), 9 out of 10 males (in the absence of a more dominant monkey) chose the group's preferred colour – the same colour which they had previously learned to be distasteful through individual learning. This change is quite remarkable and the authors interpreted these findings as evidence of a potent conformity bias from these males (van de Waal et al., 2013). A similar finding of conformity was soon after revealed in great tits (Aplin et al., 2015a), although there has been some debate as to whether the majority of individuals or majority of actions copied constitutes conformity (van Leeuwen & Haun, 2014; van Leeuwen, Kendal, Tennie & Haun, 2015). Further analyses by authors of both studies found that the frequency of action was actually correlated with frequency of individuals performing that action, so selective learning in relation to either would have similar effects (Aplin et al., 2015b; Whiten & van de Waal, 2016). The operational use of the term conformity remains contested (van Leeuwen, Acerbi, Kendal, Tennie & Haun, 2016).

Definitions of conformity aside, it has been suggested that a possible alternative for the results found in the study of van de Waal et al. (2013) could be that the individuals were copying not the majority of individuals, but instead a single, high-ranking individual within the group (Tennie, Fischer, Haun & Galef, 2013). Such biases towards dominance have been found in captive chimpanzees (Kendal et al., 2015, as above), and would generate a similar pattern of behaviour as conformity, making them indistinguishable within both this experiment and a follow-up experiment which showed low-ranking females continued their preference for the group colour after a group fission, despite not having ingested both colours themselves (van de Waal et al., under review). Thus, until it is known whether vervet monkeys display a bias towards the dominant female in their social learning, we are unable to rule out this alternative explanation for these findings.

1.4: Aims of this thesis

The research programme reported in this thesis had several aims consistent with the current state of knowledge in the field at present. A first aim has been to investigate social learning biases, specifically dominance-based bias, in social learning in wild vervet monkeys. No previous work (to my knowledge) has assessed dominance-based biases in wild primates and thus it remains unclear whether this preference exists in wild primate groups, and specifically within wild vervet monkeys. Additional to this was the aim to assess how dominance rank affects social attention in vervet monkeys under an experimental setting. Whilst social attention has been previously investigated in natural observations (Renevey et al., 2013), it is important to understand what effects the experimental manipulations of field experiments may have upon the ecological validity of social attention and learning.

Finally, this research also aimed to investigate public information use in captive tufted capuchins. Capuchins were used as opposed to vervet monkeys due to their accessibility in captivity and their relatively impressive cultural repertoire in the wild (Ottoni & Izar, 2008), as well as the cultural transmission identified in these monkeys in captive experiments (Dindo, Thierry & Whiten, 2008; Dindo, Whiten & de Waal, 2009). Whilst another monkey species that has not been reported to exhibit traditions in the wild has failed to show public information use in experimental tests (marmosets, Voelkl & Huber, 2007), other species have proven adept at it (Coolens et al., 2013; Vale et al., 2014). Therefore, the question was asked whether or not tufted capuchin monkeys were able to utilise public information in a captive setting. More generally, the aim of this research was to add greater understanding to our knowledge of whether and how social learning biases operate within primates, what any such biases look like in terms of behaviour, and the experimental, individual and environmental pressures which affect them and their expression.

1.5: Thesis Outline

Chapter 2 describes aspects of methodology relevant for Chapters 3-5, which were all undertaken at the same field site. It gives details of the study species, field site, general experimental methods and methods used for calculating measures of kinship, social network and dominance hierarchy in the vervet monkey groups. Chapter 3 presents a food colour experiment which utilised a novel paradigm in wild primates to investigate whether dominant models are preferentially copied over lower-ranking models. Chapter 4 asks this same question but utilised a different paradigm, an artificial fruit method, to test whether results were consistent across different domains in vervet monkeys. Chapter 5 presents the analyses of social attention data collected during the demonstration phases of the previous two experiments to investigate whether there were biases in whom the vervet monkeys attended to in experimental contexts. Chapter 6 examines public information use in tufted capuchins and tested whether they utilise public information to inform their own foraging decisions in an experimental, captive setting. Chapter 7 provides a general discussion on the results obtained from these four experiments and considers their implications for the field as well as limitations of the studies and proposed avenues for further research.

Chapter 2: General Methods for Chapters 3-5

The data for chapters 3-5 were collected at the Inkawu Vervet Project, KwaZulu-Natal, South Africa with wild vervet monkeys *(Chlorocebus pygerythrus aethiops).* This chapter provides details of the field site, an overview of the study species and details of the general methodology used, including use of individualised covers to train demonstrator females and a detailed methodology for the calculation of hierarchy, social network and kinship measures.

2.1: Study Species

Vervet monkeys *(Chlorocebus pygerythrus aethiops)* are a species of Old World monkey found throughout sub-Saharan Africa. They are one of the most prolific monkey species in Africa, having adapted to a diverse range of habitats. They are semi-arboreal, spending a significant portion of their day on the ground (Cheney & Seyfarth, 1990). Groups are multi-male, multi-female, with males dispersing at sexual maturity whilst females remain in their natal groups throughout their lives (Cheney & Seyfarth, 1983). Females first reproduce at around 4-5 years of age and exhibit yearly reproduction cycles, with the birth season lasting roughly from September to December. Vervet monkeys are omnivores, eating a variety of plant species and parts, as well as invertebrates and some vertebrate preys (Struhsaker, 1967; Whitten, 1988; Cheney & Seyfarth, 1990).

Figure 2.1: A matriline of vervet monkeys at the Inkawu Vervet Project, South Africa. The photograph shows an infant (front, Toul), a juvenile male (back left, Tal) and adult female (back right, Troi) from the NH group.

Vervets exhibit a linear dominance hierarchy whereby if A is above B and B is above C, then A will be above C (Cheney & Seyfarth, 1990; Isbell & Pruetz, 1998). Rank in females is linked to kinship, with the youngest female offspring of the mother inheriting the rank directly below hers and the older female offspring following in rank. Whilst the male hierarchy changes depending on migrations, strength and acceptance by females, the female hierarchy is relatively stable (Walters & Seyfarth, 1983). Males and females have separate hierarchies, although conflicts are often context dependent (Cheney & Seyfarth, 1990); whilst a male may displace a female, a coalition of females may displace a male. Whilst adult females show knowledge of the female hierarchy (Borgeaud, van de Waal & Bshary, 2013), adult males and juveniles exhibit less detailed understanding of the female hierarchy (Borgeaud, Alvino, van Leeuwen, Townsend & Bshary, 2015).

Vervet age classes are generally defined as infants (<12 months), juveniles and adults; males after their first dispersal and adult females after their first birth (Seyfarth et al., 1980; Isbell et al., 1991). Individuals between three years and adulthood are sometimes referred to as sub-adults (Isbell et al., 1991), however this extra category was not used in the current experiments. Chapter 3 categorises infants as juveniles (due to the very small number of individuals <12 months of age participating in the experiment), whereas in Chapter 4, no juveniles under the age of 12 months participated in the test phase. In Chapter 5, attention was not recorded for infants as they could not be reliably identified in all three groups at the time of the experiment.

The strict (and for females, stable) linear hierarchy, semi-terrestrial nature, non-endangered status and previous success on social learning tasks (e.g. van de Waal et al., 2015) make vervet monkeys an excellent species with which to conduct dominance-based social learning studies.

2.2: Field Site

Data for Chapters 3-5 were collected at the Inkawu Vervet Project (IVP), Mawana Game Reserve, KwaZulu-Natal, South Africa (S 28° 00.327; E 031° 12.348). The project is a collaboration between researchers from the University of Neuchâtel and the University of Zürich (Switzerland) and the University of St Andrews (Scotland). Researchers began habituating the current groups in 2010, therefore the main three groups with which experiments were conducted have been habituated for at least five years: “Ankhase” (AK), “Baie Dankie” (BD) and “Noha” (NH). Habituation for the other three groups has been ongoing since 2012

(“Kubu” (KB)), 2014 (“Crossing” (CR)) and 2010, but non-consistently and made more difficult due to the group’s experience with humans as hunters (“Lemon Tree” (LT). Researchers generally follow each group six days per week. Past experimental research conducted with this population has included playback studies (Borgeaud et al., 2013), food–based (van de Waal et al., 2013) and object manipulation-based social learning studies (van de Waal et al., 2015), studies into reciprocity (Borgeaud et al. 2015) and investigation of between-group conflicts (Arseneau, Taucher, van Schaik & Willems, 2014). An individual from each group is fitted with a VHF collar to allow for tracking of the groups using radio telemetry.

The majority of past research on vervet monkey behaviour and demographics comes from a population at the Amboseli National Park, Kenya, conducted by Dorothy Cheney, Robert Seyfarth and colleagues (Cheney & Seyfarth, 1990). Whilst this research is extremely valuable and much is relevant to the vervet monkeys in the current study population, it should be noted that the monkeys at Amboseli occupy a different habitat to the population at IVP, with the Mawana Game Reserve having relatively little open savannah and relatively high levels of invasive acacia species (*Acacia tortillis, Acacia nilotica)*. Additionally, levels of predation and infant mortality appear lower at Mawana than Amboseli over the study period (Isbell, 1990 & unpublished data).

2.2.1: Role of MSc student and field assistants

From January to August 2015, I acted as the primary field supervisor for Mathilde Grampp, an MSc student of Strasbourg University, France. Her thesis, “Social attention in natural and experimental foraging situations in wild vervet monkeys” (Grampp, 2015) incorporated data from both natural foraging observations and the attention data from the demonstrations in Chapter Four. Mathilde led the training of one of the demonstrator females (Riss, BD), following training from myself, and assisted in the collection of the attention data in Chapter 5. The publication of the natural foraging data collected for this MSc thesis is currently in preparation (Grampp, Botting, van de Waal & Sueur, in prep).

Field assistants consisting of students and volunteers at IVP assisted with some aspects of each experiment in this thesis. In the test phases of Chapters 3 and 4, either two or three field assistants assisted with the set-up of apparatus and identification of monkeys. This involved setting up the apparatus, rebaiting the boxes and calling out for the video record the monkey identities and the manipulative methods they used, which were later checked using the video footage by myself. Assistants occasionally also assisted in the demonstrations phases of each experiment.

2.2.2: Identification of monkeys and inter-observer reliability

Monkeys at the project are individually identified using facial and body features. Detailed description files are kept and updated by students and volunteers of IVP, listing names, ages, kinship and descriptive features for each monkey. A life history file is kept for each individual, detailing the above information in addition to dates of dispersal or disappearance/death. All students and field assistants are required to undertake both tests of identity recognition and inter-observer reliability tests before being permitted to collect data for the project. The identity test is conducted by a senior student/field assistant who has previously passed this test and requires the individual to identify each monkey three times in a row in less than 30 seconds. The inter-observer reliability test is conducted by the senior student/field manager and requires the individual to match the tester's answers on a series of measurements used in the scan data collection; activity, height, distance from refuge and location in group, across 60 test scans.

2.2.3: Demonstrator training & individual covers

The training of the monkey models for social learning experiments was done by utilising previous training methods developed by another PhD student, C. Borgeaud, with the same study population (as in Borgeaud & Bshary, 2015). As part of this previous training, individualised covers were used to attract specific females to baited boxes. Each cover was painted with a specific, coloured pattern and each female was trained to approach her assigned cover using positive reinforcement (only the box topped with her specific cover would be opened via remote control and release a small piece of apple when she approached). Matching covers were made to fit the apparatus used in Chapters 3 and 4 (Fig 2.2) and placed over or beside the boxes during training and demonstration, thus increasing the likelihood of the target female approaching the boxes and reducing the likelihood of other monkeys attempting to interact with the boxes.

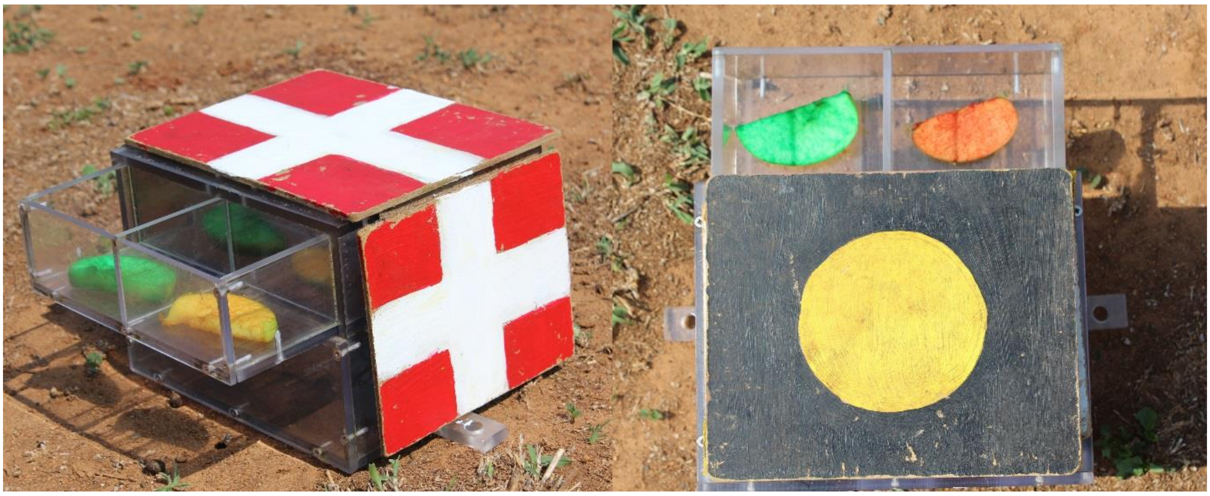

Figure 2.2: Remote-controlled boxes used in Chapter 3, with individualised, patterned covers used to attract the target model to the box during the training and demonstration sessions.

2.3: Hierarchy analyses

2.3.1: Demonstrator selection

Chapters 3-5 required the training of females of high and low ranks in each group as demonstrators (models). For the selection of the female models, the results from direct conflicts between dyads recorded by IVP researchers and field assistants were used (see below for details on conflict data collection and selection). In this way, the female who was ranked #1 of the females in her group (from observations of dyadic conflict and food competition) was used as the dominant female model. Given the difference in group sizes, the low-ranking demonstrator was not of the same ordinal rank for all groups, but was a female chosen from the lower half of the hierarchy. Females who had previously participated in experiments with boxes (non-social learning experiments) were preferentially chosen due to their willingness to approach the apparatus and their recognition of the individualised covers. Four of the six models remained the same for both experiments whereas Riss replaced Mooi (BD) in Chapter 4 after the disappearance of Mooi and Nkos replaced Isil (AK) in Chapter 4 after aggression from the ‘I’ matriline was increasingly recorded towards previously more dominant matrilines. Nkos was chosen as her agonistic encounters placed her in a stable, low-ranking position in the female hierarchy.

2.3.2: Individual ranking

In order to obtain an ordinal rank for each individual in the group, a hierarchy analysis was run using the R package 'EloRating' (Neumann et al., 2011) with conflict data collected ad libitum from the groups. The EloRating system is a dynamic method of assessing the hierarchy, taking into account presence and absence of individuals and allowing a hierarchy to be extracted for any date within the observation period. The benefits of Elo ratings over non-dynamic ranking systems such as David's Scores are still being debated, with some suggesting that it is not known if the temporal relation of the conflicts is important from a biological perspective (McDonald & Dillon, 2015). However, given the relatively high levels of migration in our study population, it was decided that this dynamic method of hierarchical analysis was more useful to this study than non-dynamic alternatives.

The Elo rating system becomes more precise when more data is added, therefore data were used from 2011 up until, and including, 2015, despite several former group members being absent on the date used for analyses ("extraction date"). In addition to a winner-loser matrix organised by date, a presence matrix was calculated, showing each date within the timeframe used and whether each individual was present or absent from the group on that date.

All data came from ad libitum conflict data collected by students and researchers at the Inkawu Research Project, South Africa. The form used to collect the data recorded the initiator ("aggressor") and the recipient ("victim"). The date and time of the conflict were collected as well as all behaviours by the two individuals, from the IVP ethogram (see appendices, Table A.1). To ensure the winner and loser in each dyad was clear, only interactions that ended in an unambiguous submissive behaviour (retreat, flee, crawl, avoid or jump aside) were considered. Additionally, those interactions that ended with an unambiguous submissive behaviour followed by a non-aggressive/neutral behaviour were considered (e.g. flee followed by vocalisation, or grooming).

For these hierarchies, the date of extraction was the date of the first test experiment run in each group. Interactions involving infants were not included in the analyses as there were so few interactions that this may have biased the data. Once the EloRating had been calculated, the corresponding ordinal rank was given to each member of the hierarchy. In order to account for the differing group sizes, these ordinal ranks were then standardised using the following formula;

$$\text{Standardised Rank} = (N-R)/(N-1)$$

as per Robbins et al. (2005), where N= number of individuals in the group and R= the ordinal rank from the EloRating.

Whilst male and female hierarchies are generally considered separate in vervet monkeys (Cheney & Seyfarth, 1990), the open nature of the current studies meant that all individuals were competing with each other for access to the food/demonstrations. Therefore, I decided to input all sex and age classes into the same hierarchy as this was the most relevant to the paradigms used. For this reason the results of the Elo rating may differ slightly from the female linear hierarchy used to select female models.

2.4: Social Network Analyses

Social Network Analysis (hereafter SNA, Whitehead, 2009) was conducted with the main experimental three groups; NH, BD, AK.

Scan sampling data (Altman, 1974) collected by students and volunteers at the Inkawu Vervet Project (as detailed above) were used to create the association matrices. Scans are conducted once per week in each group, every 30 minutes from sunrise until sunset. The measure used for the current networks was ‘Individuals within one metre’, which records all individuals within one metre of the focal individual at the time of the scan. This measure was used as it indicates tolerance between members of a dyad, and as such, a certain level of affinity, incorporating dyads who are grooming, sitting or sleeping in contact and foraging in close proximity to one another.

Data from the seven months preceding the test phases for Chapters 3 and 4 were used for the social network analyses. For Chapters 3 and 5, data collected between February and August 2014 were used. For Chapters 4 and 5, data collected between January and July 2015 were used. Analyses were run using the software SOCPROG version 2.6 (Whitehead, 2009).

In order to calculate a measure of friendship, which was used to determine if friendship with the models had an impact on the observations of her demonstrations (Chapter 5) and which behaviour individuals adopted in Chapters 3 and 4, preferred dyads were extracted using Monte Carlo permutation tests in SOCPROG (Whitehead, 2009; 1000 permutations, 5000 trials per permutation, significance level=0.05). Preferred dyads had a real association index greater than 97.5% (Whitehead, 2009). Full lists of preferred dyads for each model and each time period can be found in the appendices (Table A.2). The preferred partners of each model were coded as her ‘friends’, whilst all others were ‘non-friends’.

2.5: Kinship data

Kinship was coded as direct offspring of i) the dominant model, ii) the low-ranking model or iii) neither model. The studied groups have been followed with individual identification for 6 years, thus allowing for identification of direct offspring since this point. As sibling relationships of the adult female models could not be confirmed, these were not included in the kinship data. Whilst genetic data from faecal and tissue samples are currently being analysed by members of the Inkawu Vervet Project, too few individuals used in this study have as of yet been classified and therefore only direct kin known through observation were included.

2.6: Ethical permissions

Ethical permission was granted from the relevant bodies for the three experiments in this thesis. Permission to conduct field experiments with the wild vervet monkeys was gained from the local wildlife board in South Africa, Ezemvelo Wildlife Board and from the landowner of the Mawana Game Reserve, Mr Kerneels van der Walt. Permission to conduct the experimental research in Chapter 6 at the Living Links Research Centre was provided by Edinburgh Zoo. All studies were reviewed and given ethical permission by the University of St Andrews Ethics committee. All letters of permission can be found in the appendices.

2.7: Health and safety

All research was conducted in line with the health and safety guidelines of the University of St Andrews, the Inkawu Vervet Project and Edinburgh Zoo. Strict health and safety protocols were followed when working with the monkeys to ensure no disease transmission would occur. All apparatus were thoroughly cleaned between uses and experimenters wore gloves or cleaned their hands thoroughly before touching any food intended for the monkeys. Strictly no physical contact with the monkeys is permitted at IVP and provision of food for experiments was carefully controlled by IVP and Edinburgh Zoo.

Chapter 3: Do wild vervet monkeys exhibit a model dominance-based bias in socially learned food preferences?

Animals may use a number of social learning biases to acquire the most useful information about their environment. Among suggested biases is a *copy the dominant individual* bias which has recently been demonstrated in captive chimpanzees. However, this has yet to be studied in a wild primate population. Using a novel methodology, a dominant and a low-ranking female from each of three wild groups of vervet monkeys in KwaZulu-Natal, South Africa were trained to prefer and avoid contrasting colours of dyed apple, presented to them in remote-controlled boxes. They were then allowed to demonstrate this preference to the rest of the group over the course of 50 demonstrations each. In the test phase, each group was provided with large amounts of each colour of dyed apple and the first choice of each individual was recorded. No consistent preference was found for either models' colour based upon her rank. Instead, a pre-existing preference for the yellow-dyed apple seemed to govern most individuals' foraging decisions, as supported by results from control and one-model groups. These findings are discussed in reference to the current literature and directions for future research are suggested.

3.1: Introduction

Whilst initial research into social learning in non-human animals placed emphasis upon the mechanisms behind social learning (Heyes, 1994; Whiten et al., 2004; Tomasello, 1996), more recently researchers have begun investigating the importance of individual characteristics and social relationships in the spread of behaviours, in relation to transmission biases (Boyd & Richerson, 1985). 'Directed social learning' (Coussi-Korbel and Fragaszy, 1995) suggests that an individual may obtain more social information from certain individuals than from others, depending upon, for example, each individual's sex, age and the social relationship between the two. Following this, Laland (2004) described a number of 'strategies' that an animal may adopt to maximise the benefit from social learning, including a number of model-based strategies (hereafter, 'biases'), such as *copy older individuals*, or *copy related individuals* (Laland, 2004).

Observations from the field suggest that certain individuals, such as kin and older individuals are looked to as 'models' in social learning (Matzusawa, 2001; Biro et al., 2003), although this is largely based on attention data as opposed to documenting the spread of behaviours. Alongside this theoretical and observational work, empirical research with a variety of non-human animals has yielded a range of model-based characteristics which appear to bias social learning including age (fish, Duffy et al., 2009; mice, Choleris et al., 1997), social network (squirrel monkeys, Claidiere et al., 2013; humpback whales, Allen et al., 2013), sex (zebra finches, Katz & Lachlan, 2003; vervet monkeys, van de Waal et al., 2010) and kinship (vervet monkeys, van de Waal et al., 2014). The finding of multiple social learning biases in the same species (e.g. van de Waal et al., 2010; van de Waal et al., 2014; Kendal et al., 2015) suggests that biases may also work in concert to allow an individual to obtain the best available information.

One potential bias that has received recent attention is that of copying successful individuals (Henrich & Gil-White, 2001; Laland, 2004). Whilst this has been put forth as an adaptive strategy by theoreticians (Boyd & Richerson, 1985), there is less empirical evidence to show that this bias is actually utilised. It is intuitive that copying individuals who are successful should in turn make one successful, although the question remains of how success should be judged in others (Laland, 2004). Henrich & Gil-White (2001) suggest that in humans ‘prestige’ has emerged due to individuals copying, and showing deference to, highly skilled individuals and it has been suggested that dominance rank in animals may relate to prestige in humans (Laland, 2004).

Horner and colleagues (2010) found that when two alternative behaviours were modelled by two females within a captive chimpanzee group, individuals showed a preference for the behaviour of the older, more dominant female, who also had previous success with experimental tasks. This may reveal a bias towards dominant individuals, but is also entangled with age and past success. More recently, Kendal et al. (2015), by using just one mid-ranking model per group, found a bias for captive chimpanzees to copy more dominant individuals. Thus it may be that chimpanzees use dominance as a proxy to success. Indeed, human children have also shown this bias towards attending to more dominant and more prestigious children (Flynn and Whiten, 2012). In the only test thus far conducted with monkeys, no evidence for this bias was found in captive tufted capuchins (Dindo et al., 2011). However, it should be noted that all of these tests were conducted in captivity, which could have influences on the animals’ social learning due to unnatural group composition or spatial distribution; no direct test of dominance-based biases in social learning has yet been conducted in wild non-human primates. The dominance hierarchy plays an important role in vervet monkey society, with strict linear female and male hierarchies and access to resources dependent upon rank (Walters & Seyfarth, 1987; Cheney et al., 1981; Cheney & Seyfarth, 1990), thereby making vervets an ideal species with which to test dominance-based bias in the wild.

3.1.1: Social learning in vervet monkeys

Previous work in vervet monkeys has revealed biases of infants to match their mother's food processing techniques (van de Waal et al., 2014) and for individuals to attend to and copy females rather than males (van de Waal et al., 2010). Potent social learning was also revealed in wild vervet monkeys when migrating males forwent previously learned information about the palatability of coloured corn in order to match the colour preferred by members of their new group (van de Waal et al., 2013). Whilst the authors suggested that the behaviour of the males reflected conformity to the behaviour of the majority of individuals (van de Waal et al., 2013), it is also possible that the males were copying the behaviour of particular individuals within the group, for example the most dominant individuals (Tennie et al., 2013). This study therefore aimed to assess whether model rank affects social learning in wild vervet monkeys.

The role of social learning in diet selection in vervets is unclear. There is evidence that different groups within the same population vary in the composition of their diet, which may be a result of social learning (Tournier et al., 2014, although possible alternative explanations remain, such as differences between individuals within the group). Past research suggests that the time infants spend feeding synchronously with their mother on the same foods has a positive relationship with their life expectancy (Hauser, 1993). However, research with other primate species suggests that co-feeding does not necessarily lead to same food selection and serves instead to coordinate group feeding activity (Tarnaud, 2008). Indeed a series of experiments with captive capuchins have revealed that the presence of conspecifics feeding on a familiar food is sufficient to increase intake of a novel food (Visalberghi & Addessi, 2000), thereby suggesting that the social learning of diet in monkeys may not always be item specific, but rather social facilitation to general feeding (Visalberghi & Addessi, 2004). Nonetheless, the infant and adult male vervet monkeys in the above mentioned coloured corn study (van de Waal et al., 2013) showed specificity in their choice of corn colour, seemingly by using social information from conspecifics. Thus it appears that vervets can show social learning of specific coloured foods from a young age, at least in some contexts.

3.1.2: Chapter aims

The aim of the current study was to investigate dominance-based biased social learning in food choice in wild vervet monkeys. To investigate this, a paradigm similar to Horner et al. (2010) was utilised, wherein two female models of differing rank were trained to prefer and avoid contrasting colours of food. This methodology allowed for near synchronous demonstrations of contrasting social information from a dominant female and a low-ranking female. Past research has shown that vervet monkeys selectively copy the foraging actions of female and not male conspecifics (van de Waal et al., 2010), so the models selected for the demonstrations were three dominant and three low-ranking adult females from three groups of wild vervet monkeys.

3.2: Methods

3.2.1: Participants

The experiment was conducted at the Inkawu Vervet Project, in Mawana game reserve, KwaZulu Natal, South Africa. Participants were 174 wild vervet monkeys *(Chlorocebus aethiops pygerythrus)* in the test phase of the experiment (including 7 trained models). 123 lived in four experimental groups: Noha ('NH'), Ankhase ('AK'), Baie Dankie ('BD') and Kubu ('KB'), with a further 24 and 27 monkeys participating in control conditions in the Lemon Tree ('LT') and Crossing ('CR') groups. Whereas NH, AK and BD had two trained models of differing rank, KB had only one high-ranking model. Eight individuals were able to taste the experimental food during the demonstration phase, due to the model dropping a small piece; this invalidated the experimental manipulation for these individuals and they were excluded from the analyses, leaving 108 individuals tested (without models, Table 3.1).

Group	Adults	Juveniles	Total
BD	14	18	32
AK	9	15	24
NH	13	19	32
KB	7	13	20

Table 3.1: Numbers of adults and juveniles from each group participating in the test phase of the experiment.

Model ranks were determined from the results of one-on-one conflicts recorded by researchers at the field site. Dominance rank in vervet monkeys is relatively stable amongst females and changes are rare (Cheney & Seyfarth, 1990). The high-ranking females in the two-model groups were all rank #1 and the low-ranking females were between the middle and lowest ranks. Due to differences in group size, the low-ranking individuals were of differing ordinal ranks, but all were taken from the lower half of the hierarchy. Due to the KB group being less well habituated, only one model could be trained; the model in KB was rank #2 due to the shyness of the dominant female and no low-ranking female was trained in this group.

3.2.2: Apparatus & training

A custom-built, remote controlled box was made for this experiment (see Figure 3.1). This plastic 19cm x 14cm x 15cm box was fixed to the ground using pegs. It contained a drawer divided into two compartments, which could be opened and closed by means of a remote control unit held by the experimenter, when the correct female approached. The monkeys habituated quickly to the sound and movement of the box and were able to take food from the drawer within a small number of training trials. Individualised covers, as detailed in Chapter 2 and illustrated in Figure 3.1, were used to attract the correct female model to the box.

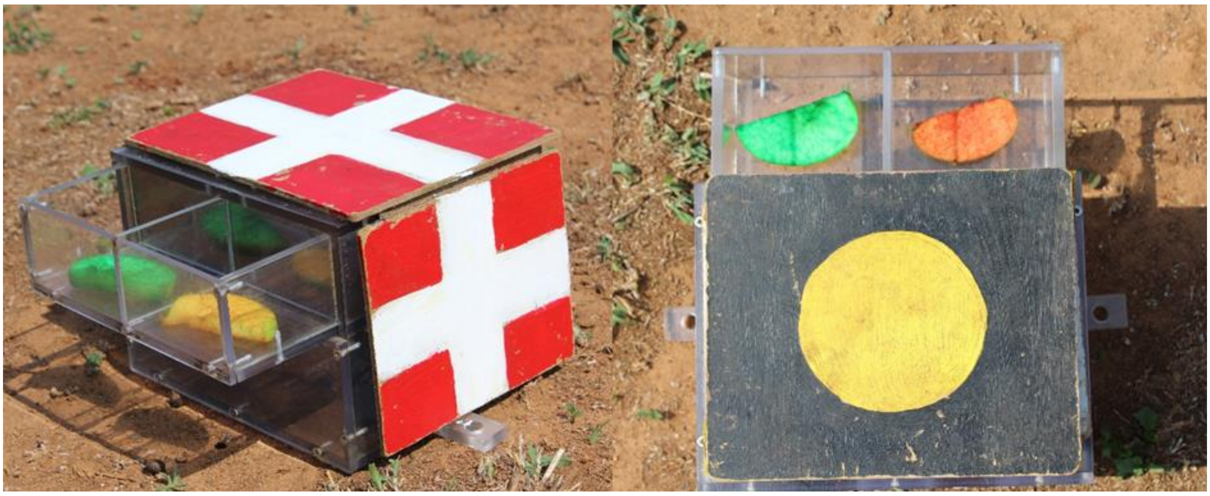

Figure 3.1: Remote-controlled box with two compartments, each containing a slice of dyed apple (left, green and yellow and right, green and orange). Individualised covers for Gene (left, NH) and Gaga (right, AK) are pictured.

Slices of peeled apple approximately 5mm thick were used in both demonstration and test phases. To create a preference for a certain colour, three colours were used; green, orange and yellow. These were chosen as they were closer to ‘natural food colours’ and the study population had not received food dyed of these colours in previous experiments. Colours were counter-balanced across groups, as shown in Table 3.2. To dye the apple, slices were placed in a container and covered with water. Food dye was then added (yellow: 6 drops yellow 'Robertsons yellow food dye'; green: 5 drops green 'Moir's green food dye'; orange: 10 drops red 'Robertsons red food dye' & 5 drops yellow 'Robertsons yellow food dye'. This was left for 5 minutes and then drained.

To create a bitter taste, a method was used that has previously been found to be effective in this study population (van de Waal et al., 2013), which involved soaking the apple overnight alongside aloe leaves (mountain aloe, '*Aloe marlothii'*). Slices of apple were placed in a plastic container and covered with water; the cut aloe leaf was then placed vertically in the water to allow the bitter taste to permeate the apple. Vervet monkeys find food soaked alongside aloe leaves highly distasteful and will reject it after either sniffing or tasting a small amount (van de Waal et al., 2013). The bitter apple was always presented alongside a normal tasting apple slice, to ensure the monkeys always had the choice of which to take.

Group	**Dominant colour (DC)**	**Low-ranker colour (LC)**
NH	Yellow	Green
AK	Green	Orange
BD	Orange	Yellow
KB	Yellow	None*

Table 3.2: Counter-balancing of demonstrator food colours across groups. Columns indicate the trained preferred colours of dyed apple for both the dominant model (DC) and the low-ranking model (LC) from each group. * In KB no low-ranker was trained, but the high-ranking model ate yellow and avoided green in the demonstrations. Yellow and green apple was offered to the group at the test phase.

3.2.3: Protocol

Opportunities for monkeys to watch a model perform her trained action ('demonstrations') were created on an opportunistic basis. A model was located within the group and when she had one or more individuals within 10 metres of her, a demonstration was engineered (depending on terrain/movement of the group etc.). To do this, the box was placed within 20 metres of the female and the experimenter moved back. The remote-controlled drawer was then opened when the female was within 5 metres of the box and closed again after she had taken one piece of apple. Initially, only the palatable colour was presented until the model reliably approached the box and took the food. From then on, the aloe-soaked apple was presented alongside the palatable apple. All individuals within a 10 metre radius of the female when she was at the box or whilst she ate the apple slice were identified and coded in the field by myself and field assistants. Demonstrations were recorded with a Panasonic HD (HC-X920M) hand-held camera.

After each model had demonstrated her preference for the palatable colour of apple 50 times, the test phase was conducted. The group was located at sunrise at their sleeping site. The experimenters approached, making food calls which the monkeys have been taught heralds the presence of available food from humans. Two plastic containers measuring 35cm x 15cm x 12cm, each containing the two colours of apple that the group had previously encountered in the demonstration phase, were place at two locations near the sleeping site, roughly 10 metres apart (see Figure 3.2 for an illustration of experimental set-up). This two-station configuration was used to minimise conflict and to allow individuals to obtain their first choice of colour. Four handheld Panasonic HD (HC-X920M) video cameras recorded the two feeding stations. Myself and either two or three field assistants identified the monkeys that approached the apple. Monkey identities were spoken aloud so they were recorded in the video records in the field and again checked from the video, with identities confirmed by another long-term field student. The colour of the first piece of apple eaten by each individual was recorded, as well as the identities of the other individuals at the feeding station. The test was ended when either one colour of apple had been depleted or the group had moved away from the site of the experiment. Three test sessions were conducted; however due to difficulty in recording which individuals were eating which colour (due to visual occlusion), only the data from the first experimental session were used, with the exception of NH group. On the first test with NH, the group was split and only half of the individuals were present at the sleeping site. Therefore, the first choice of NH individuals who were not present at the first test session were taken from the second test session. The one-model group, KB, was tested in the same way as the two-model groups.

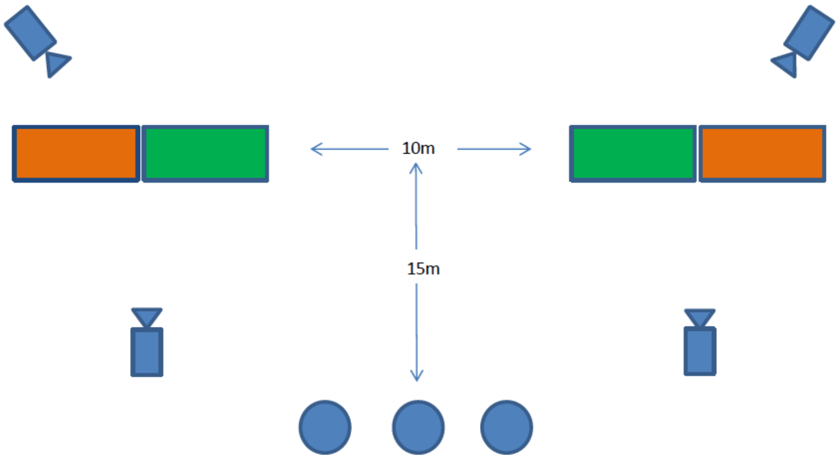

Figure 3.2: Experimental set-up showing positions of four containers of coloured apple, four video cameras and experimenters, represented by circles.

3.2.4: Control Tests

Control tests for colour preference were run at a local sanctuary, by providing containers of yellow and green-dyed apple and comparing the number of monkeys at each container every minute until a colour was depleted (as individual IDs were not known). Additionally, further control tests were run with two wild groups (CR and LT) who were provided with the choice of yellow versus green apple or yellow versus orange apple. The first choice of each monkey was recorded.

3.3: Results

3.3.1: Control and one-model tests

In the one-model group, KB, binomial tests found no significant preference for either the modelled or non-modelled colour at the test phase (n=20, p>0.05). Prior to the field experiments, colour preference tests run at a local sanctuary found no preference for yellow over green, or vice versa (paired samples t-test, t=1.44, df=20, p >0.05). Following the experimental tests, preference tests conducted with a wild group (Lemon Tree, ‘LT’) found a non-significant trend towards yellow-dyed apple over green when each individual’s first choice was considered (binomial test, n=24, p=0.064). A preference test conducted with a second wild group (Crossing, ‘CR’) found no preference when tested with orange- and yellow-dyed apple pieces (binomial test, n=26, p>0.05). No naïve wild group was available to test orange- with green-dyed apple.

3.3.2: Is food eaten by dominants preferred over that eaten by low rankers?

The first choice of colour of each individual was recorded (DC = colour modelled by dominant; LC = colour modelled by low-ranker). Binomial tests found a significant preference for the LC (yellow) in BD (n=32, p=0.007, 95% CI [0.57, 0.89]), a near-significant preference for the DC (yellow) in NH (n=32, p=0.05, 95% CI [0.5, 0.84]) and no significant preferences in AK (n=24, p>0.05, 95% CI [0.26, 0.67]). Individuals in NH and BD groups showed a preference for the yellow-dyed apple, irrespective of the rank of model that ate it (see Fig 3.3). Accordingly there was no consistent preference for DC or LC across the groups, but there was a preference for the yellow-dyed apple in the two groups to whom it was presented.

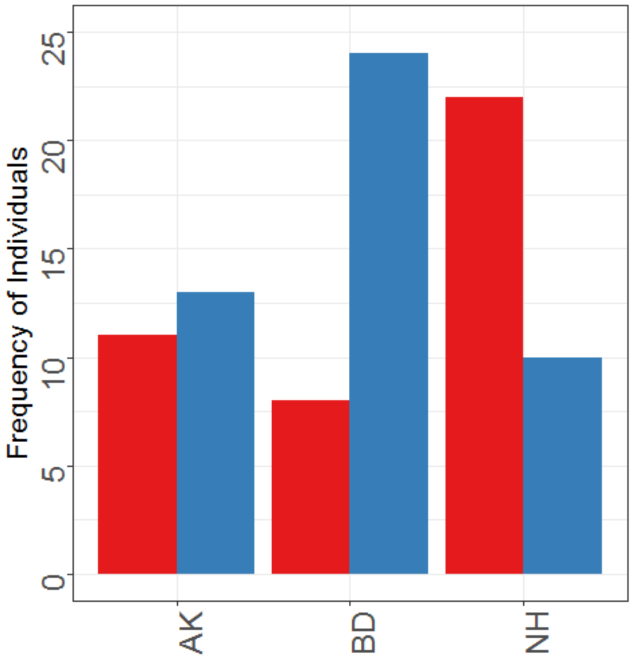

Figure 3.3: Frequency of individuals from the two-model groups (AK, BD & NH) who chose either the dominant's trained colour (DC, red bar) or the low-ranker's trained colour (LC, blue bar) as their first choice of apple in the test phase.

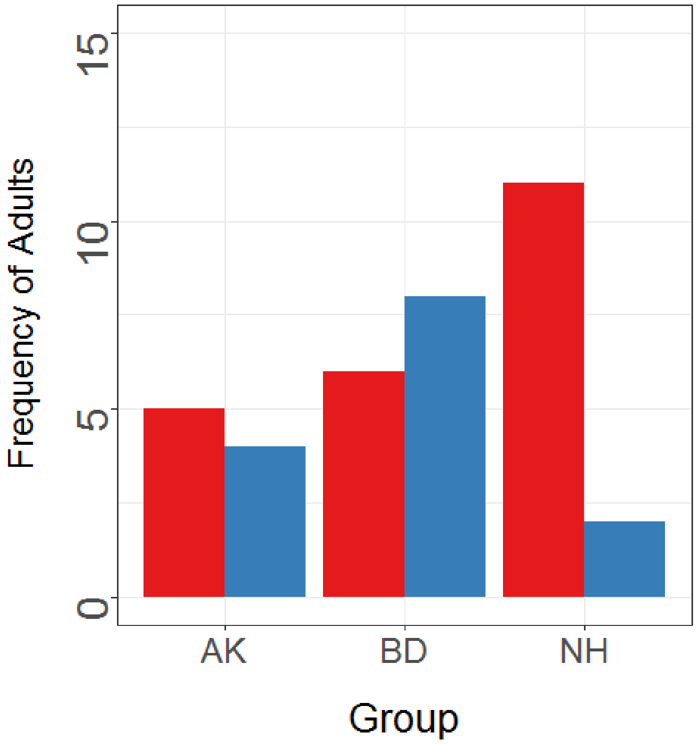

Figure 3.4: Frequency of adults only from the two-model groups (AK, BD & NH) who chose either the dominant's trained colour (DC, red bar) or the low-ranker's trained colour (LC, blue bar) as their first choice of apple in the test phase.

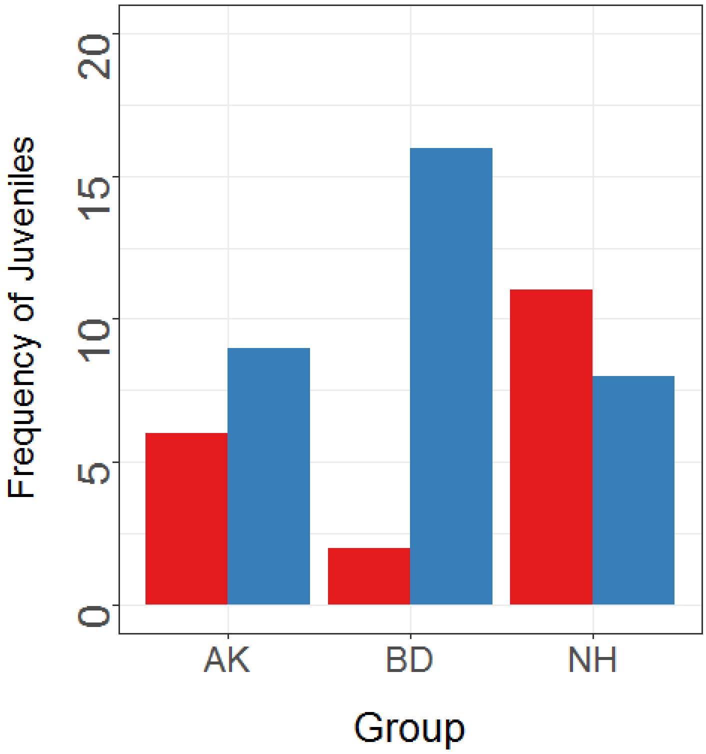

Figure 3.5: Frequency of juveniles from the two-model groups (AK, BD & NH) who chose either the dominant's trained colour (DC, red bar) or the low-ranker's trained colour (LC, blue bar) as their first choice of apple in the test phase.

3.3.3: Effects of demonstrations observed, observer rank, sex, age, kinship and friendship to the models

A Generalised Linear Mixed Model (GLMM) with binomial error structure and logit link was run with individuals' first choice (DC/LC) as the outcome variable. Group, number of demonstrations observed and observer age and sex were added as fixed effects. Rank, friendship and kinship were all found to be collinear, so could not be entered into the model together. The best predictor was found by entering each in turn into the full model and selecting the variable which resulted in the best-fitting model, as judged by the Akaike Information Criterion (AIC, Akaike, 1974). The addition of rank rather than kinship or friendship led to the better fitting model, therefore rank was also included as a fixed effect. A random intercept of ID was used. The full model is reported and interactions were only included in the model if they were significant predictors.

No significant predictors were found in the full model. However, the predictor 'group' was near significant (p=0.05), suggesting that the colour the dominant female demonstrated had an effect upon whether or not individuals matched that colour in the test phase. A Tukey's post-hoc test found that individuals in NH (DC=yellow, LC=green) were more likely to match the dominant model, than individuals in BD (DC=orange, LC=yellow). Similarly, age was a near-significant predictor (p=0.06), with juveniles less likely to match the dominant females' colour than adults.

Fixed effects	β	SE	z	P
Intercept	2.29	1.36	-	-
Group	3.77	1.64	2.30	0.05
Dominant demos observed	-0.12	0.08	-1.54	0.12
Low-ranker demos observed	0.17	0.10	1.73	0.08
Observer variables				
Rank	-2.45	1.53	-1.6	0.11
Sex	-0.08	0.74	-0.12	0.91
Age	-2.10	1.12	-1.88	0.06

Table 3.3: Factors predicting the first choice of individuals (DC/LC) in the test phase.

To further test the effect of age, adults and juveniles' first choices were analysed separately; when only adults were analysed, there was a significant preference for DC in NH (binomial tests, n=13, p=0.02, 95% CI [0.55, 0.98], but no significant preferences in BD (n=14, p>0.05, 95% CI [0.29, 0.82] or AK (n=9, p>0.05, 95% CI [0.14, 0.79], see Figure 3.4. Similarly, when only juveniles were analysed, there were no significant preferences in AK (n=15, p>0.05, 95% CI [0.16, 0.68] and NH (n=19, p>0.05, 95% CI [0.33, 0.80], but there was a significant preference for yellow, the LC in BD (p=0.004, 95% CI [0.02, 0.38], see Figure 3.5.

To test for biases in immigrated males, the first choices of adult males were analysed separately; there was no significant preference for either DC or LC (binomial test, n=14, p>0.05, 95% CI [0.35, 0.87]). To test for biases in kinship, whether or not individuals matched their mother in the first choice of apple was analysed; individuals did not show a significant preference for matching the first choice of apple by their mother (binomial test, n=39, p>0.05, 95% CI [0.23, 0.55]), although the mother did not always choose before the infant

3.3.4: Model behaviour during test phase

The first piece chosen by each model was recorded at the test phase. The low-ranking model (Bogo) from NH did not eat the apple at the test phase. Of the 6 remaining models, 4 chose their trained colour as their first colour. The exceptions were Ouli, the dominant model from BD, who chose yellow instead of her trained orange, and Yeni, the sole model from KB who chose yellow instead of her trained green (although this coincided with monopolisation of the green by the dominant male of the group, Nil).

3.4: Discussion

This study aimed to test whether wild vervet monkeys displayed a dominance-based bias in the social learning of novel foods when presented with models of differing ranks. The vervet monkeys in this study did not show a significant preference to copy the foraging behaviour of the dominant female over that of a low-ranking female. Instead, the results showed a preference for the dominant females' colour of apple in one group, but for the low-rankers' colour in another group. In both cases the preference was for the yellow-dyed apple over the alternative of either orange or green. This is therefore highly suggestive of a preference for this colour of apple, regardless of model rank.

3.4.1: Colour preference

The explanation of colour preference in the experimental groups is somewhat supported by the trend towards this colour seen in the LT control group, although the preferences seen in BD and NH were more extreme and were not seen when orange was provided alongside yellow in the CR control group. Additionally, in the one-model group, KB, there was no preference for the colour modelled (green); more individuals did choose the alternative (yellow), but this did not reach significance. This preference for the yellow-dyed apple may stem from preferences for naturally-occurring yellow food items, such as fruits and flowers, although in general yellow tends to signal an unripe fruit, whereas a green colour signals a ripe fruit. Additionally, a large part of this study population's diet is made up of green seedpods from acacia species (*Acacia tortillis; Acacia nilotica),* as has been found for vervet populations in other areas (Lee, 1984). However, it is possible that the green dye used in this study was too artificial to be in keeping with vervets' natural food preferences for green items and that the yellow dye was closer in colour to the natural colour of the apple, with which all groups were familiar. Additionally, this preference for yellow-dyed apple could also be linked to a learned preference for yellow corn with which the monkeys at the field site are generally provisioned with on a once-monthly basis in order to assess hierarchy and assist with identification. With regards to the apparently inflated preference in the experimental groups compared to the control, it is possible that the preference seen in the experimental groups compared to the control may have been enhanced by seeing a model (regardless of rank) ingesting the yellow-dyed apple prior to the test. These monkeys have been shown to learn from a non-dominant model in conditions with only one model (van de Waal et al., 2015), therefore this may have enhanced existing preferences for this colour of food.

Whilst it could be argued that the colour preference seen here may have masked any potential effects of model-based bias, the results of a previous study on social learning with this population contrast with this argument. The male vervets tested in van de Waal et al. (2013) showed a remarkably potent bias towards copying the behaviour of their new group, despite having individually-learned information about the food colour palatability to the contrary. Whilst the authors proposed that this effect was a frequency-biased conformity effect, it was suggested that the males may have been copying a certain individual, such as a highly ranked female, when making their choice rather than the majority (Tennie et al., 2013). However, if a bias towards copying a high-ranking individual was so potent in the van de Waal et al. (2013) study, as to cause the vervets to forego their previous individually-learned information, then we would expect to see this bias overcome a food colour preference in the current study. This effect was not found and therefore it seems reasonable to conclude that the vervets in the current study show no bias towards copying a dominant female over a low-ranking female. It may also provide indirect support for the proposal that the behaviour switching seen in the van de Waal et al. (2013) study was indeed an effect of conformity to the majority, rather than copying a dominant individual in their new group (although see van Leuuwen et al., 2016 for alternative arguments).

3.4.2: Is copying the dominant an adaptive strategy?

It can be argued that copying the behaviour of the dominant may be beneficial, if the dominant's status is a proxy for success (Laland, 2004; Kendal et al., 2015); dominant primates have been shown to have priority access to monopolizable food resources, which in turn may improve reproductive success (Pusey et al. 1997; van Noordwijk & van Schaik, 1999). Indeed biases towards copying both prestigious and successful individuals have been found in chimpanzees (Horner et al., 2010; Kendal et al., 2015) as well as in humans (Mesoudi & O'Brien, 2008; Atkinson, O'Brien & Mesoudi, 2012). However, evidence for rank-related differences in reproductive success in vervet monkeys remains mixed (Wrangham, 1981; Cheney & Seyfarth, 1987). Previous research with vervet monkeys in Kenya has shown that, although there were differences in causes of mortality (more death from predators for high-rankers and from lack of food and water for low-rankers), there was no overall rank-based difference in reproductive success (Cheney et al. 1981), although this may change during periods of resource scarcity (Cheney & Seyfarth, 1987). Therefore, if reproductive success were used as a measure of success (Laland, 2004), dominant female vervets might not become obvious models (although it could be argued that the differences in mortality could create a perceived difference in fitness).

Additionally, this bias towards copying the dominant may also be a very limiting strategy. Individuals in this study saw two models, ingesting contrasting colours, therefore both providing information to the rest of the group that each colour was palatable. It could potentially be maladaptive for an observing individual to ignore the social information from one of these models based on rank particularly if, due to the hierarchy, they were more readily able to access the lower-ranking model's food source.

The lack of a dominance-based bias found in this study is somewhat in contrast with previous findings with captive chimpanzees (Horner et al., 2010; Kendal et al., 2015), although consistent with findings from captive capuchins (Dindo et al., 2011). Two experimental studies with captive chimpanzees found a bias towards preferentially copying more dominant (but also older and more successful) individuals both in the type of token used (Horner et al., 2010) and in the opening of an artificial fruit (Kendal et al., 2015, although see Watson et al., submitted for evidence that social learning from low-ranking models does occur). It has been proposed that this bias may, perhaps in conjunction with conformity, lead to the between-group differences observed in chimpanzees (Kendal et al., 2015). There may be a number of reasons why the vervets in the current study did not exhibit the same bias, related to both study species and environment. Vervet monkeys exhibit differences to chimpanzees and other primates when it comes to learning about diet. Unlike apes and some New World monkeys, food sharing does not regularly occur in vervet monkeys (Cheney & Seyfarth, 1990; Rappaport & Brown, 2008) and, unlike in apes, there are no reports of vervet mothers preventing the ingestion of harmful substances by their infants (Rappaport & Brown, 2008). Between-species differences in the opportunities for social learning in primates have previously been found, with some species affording more opportunities to learn about diet, but others to learn more about social behaviours (Bebko & Russon, 2015). Additionally, neither of the chimpanzee tasks discussed above involved food choice. It could be the case that foraging technique is more easily affected by the behaviour of others than actual diet choice, the importance of which would make copying the wrong individual disastrous. Thus, it may be that diet preferences are learned early in life and may take a more powerful stimulus than the observation of a single dominant individual to influence. Overall, given the differences in magnitude of cultural repertoire that we see between apes and other monkeys (Whiten et al., 1999; Perry et al., 2003; Whiten and van Schaik 2007), it is perhaps unsurprising that we may find differences in their social learning biases.

Vervet monkeys in particular have already been found to utilise both sex and kinship biases in their social learning of foraging techniques (van de Waal et al., 2013; van de Waal et al., 2014). Therefore it is possible that these biases may override any other potential model-based biases in social learning. However, in contrast to previous work (van de Waal et al., 2014), no effect of kinship was found in the current study; individuals did not show a significant preference to eat the same colour as their mother. This may have been because the pre-existing preference for yellow led individuals to disregard any social information with regards to colour choice, or perhaps because individuals were able to witness large numbers of individuals eating both colours of food and thereby signalling it to be safe. If the monkeys are influenced by frequency of models (which they appear to be, van de Waal et al., 2013; Whiten & van de Waal, 2016), then this may act as a more powerful stimulus than what their mother is eating. Further research comparing kinship to majority bias may help clarify this point.

3.4.3: Comparing captive and field experiments

Aside from species differences, there are also vast environmental and life history differences between the chimpanzees tested in captivity and the free-ranging vervet monkeys in this study. The chimpanzees in the above studies have spent the majority, if not all, of their lives in captivity and the testing was also conducted in captivity (Horner et al., 2010; Kendal et al., 2014). It has been shown that animals in captivity may exhibit different behaviours to those in the wild (Nash, Fritz, Alford & Brent, 1999; van Schaik et al. 2016), so it is possible that a lifetime in captivity may change the species-typical mechanisms of social functioning; social learning included. Additionally, the spatial confines of captivity differ greatly to the fission-fusion group dynamics seen in the wild (Kummer, 1971; Goodall, 1986). Given that much social learning can be related to proximity through opportunities for observation (van Schaik, 2003; Rappaport & Brown, 2008), it is highly plausible that this change in group dynamics may lead to changes in directed social learning. Whether chimpanzees in the wild show this same preference to copy dominant individuals remains to be seen, and will no doubt shed greater light on the process of social learning biases in the maintenance of between-group differences. It is also interesting to note that the vervet monkeys tested in the sanctuary prior to the field experiments showed no preference for the yellow-coloured food. This is likely because sanctuary-housed monkeys are provisioned with a great variety of food and tend to be less neophobic towards food than wild monkeys (personal observations). This highlights some of the crucial pressures acting upon wild animal behaviour that may be missed in captive settings.

3.4.4: Group differences in social learning?

Aside from a pre-existing preference for yellow, it could be argued that the individuals in the NH group were biased towards copying the dominant female, whereas individuals in the other two groups were not, thus displaying group-level differences in social learning. Given that humans have been found to show individual differences in how they utilise social learning strategies (Mesoudi, 2011; Molleman, van den Berg & Weissing, 2014), this could be a possibility. Previous research with the same groups of vervet monkeys has found significant differences in how hierarchy relates to the social networks between the groups (Borgeaud, Sosa, Sueur & Bshary, 2015). However, the social network analyses for these groups for the time period of the experiment (see appendices, Table A.4) show that, whereas the eigenvector centralities of the dominant models in BD and AK are roughly twice that of the low-ranking models', the same pattern does not hold in NH; the dominant model (Gene) is no more central to the network than the low-ranking model (Bogo). Given past research with primates has shown eigenvector centrality to be important in the spread of information (Claidière et al., 2013), it would then be surprising for the least central dominant female to be copied the most. On these grounds, the colour-preference explanation seems the more likely, although group-level differences in social learning cannot be ruled out.

Finally, previous research found that low-ranking macaques inhibit problem solving skills in a foraging paradigm when in a group with high-ranking individuals (Drea & Wallen, 1999). It has thus been suggested that low-rankers may not be as effective models as high-ranking individuals due to this inhibition (Laland, 2004) and this may lead to increased copying of high-ranking individuals relative to low rankers. However, the Drea & Wallen (1999) study was conducted in captivity and does not take account of the subgroups which may form during foraging in wild primates; for instance low-ranking chimpanzees have been shown to avoid high-rankers in the wild (Murray et al., 2007). The demonstrations for this experiment were conducted on an opportunistic basis and models performed their demonstrations in front of the subgroup they are naturally surrounded by, thus mimicking a natural encounter with a foraging problem. Since no bias towards copying the dominant was found here, it follows that this inhibition may not be as relevant to free-ranging primates as it may be to captive individuals.

3.4.5: Age effects

Whilst no bias to copy the dominant female was found in the populations studied, there was a non-significant trend for adults to match the DC more often than juveniles. However, when tested alone there was a significant preference for adults for DC in only one group (NH) and a significant preference from juveniles for LC in only one group (BD). It is possible that this age effect reflects different biases in information use at different life stages, as has been found in humans (Henrich & Broesch, 2011; Lucas et al, in press), or possibly reflects a poorer understanding of the hierarchy in juveniles, as has been previously demonstrated in vervets (Borgeaud et al., 2015). However, if these vervets exhibited an age-based difference in social information use, we would expect to see this across the groups. Since the preferred colour in each of these cases was yellow, it seems likely that this, again, is an artefact of a preference for the yellow colour.

3.4.6: Conclusions

In conclusion, no evidence for a strong dominance-based bias in food choice was found in wild vervet monkeys in this experiment. Instead choices seemed primarily governed by natural food preferences, which may have been intensified by the observation of the food’s ingestion by a group mate, regardless of rank. Whilst it is possible that a dominance-based bias may exist in social learning in this species, it was not uncovered using this paradigm and indeed, such a bias would have to be relatively weak to be masked by a food colour preference. These findings contrast with findings from captive chimpanzees and highlight differences in social learning biases that may exist between species and between test environments. The field would benefit from future studies which examine the role of dominance in social learning in more species of wild animals. These results also highlight the importance of pre-existing preferences in studies of social learning which might govern which behaviours are adopted, irrespective of the experimental manipulations; future studies should thus investigate these preferences and their role in the spread of behaviours via social learning.

Chapter 4: Do vervet monkeys exhibit a model dominance-based bias in the social learning of how to open an artificial fruit task?

Following from the results of the previous chapter, this experiment used an artificial fruit paradigm to further test for dominance-based bias in wild vervet monkeys. A box was constructed, the door of which could be opened in one of two ways; via a ‘push’ or a ‘pivot’, to reveal a food reward within. One dominant and one low-ranking female from each of three wild groups of vervet monkeys were trained at alternative methods of opening the box. They were then allowed to demonstrate their preferred method to the rest of the group 100 times. During the test phase, unlocked boxes were presented to each of the three groups and all openings recorded. Whilst no preference to match the dominant models’ method (DMM) or low-rankers’ method (LRMM) was found in the first opening of each individual, they were significantly more likely to match the DMM on the first method used successfully. However, this bias soon disappeared and no overall preference was recorded over the course of 10 test sessions. Instead, an overall preference emerged for the pivot method, but only in groups where this was modelled (not in control groups). Effects of participant rank, sex and age were found on likelihood to match the DMM and on the likelihood of models to display their trained preference, with higher-ranked individuals more likely to match the DMM and dominant models more likely to stick to their trained method than low-ranking models. These findings and their implications for the field are discussed with reference to the current literature.

4.1: Introduction

It has been suggested that, rather than random copying, biases may exist in whom animals socially learn from (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). It has been proposed that copying successful individuals may be an adaptive strategy (Boyd & Richerson, 1985) and that hierarchy may be used as a proxy to success in non-human animals (Laland, 2004). Previous studies with captive chimpanzees have investigated model biases and found preferences for chimpanzees to copy the dominant individual using tasks requiring both object manipulation (Kendal et al., 2015) and token exchange (Horner et al., 2010, although dominance here was entangled with age and past success on tasks). On the basis of these findings, it has been suggested that this bias towards copying dominant individuals could, in a similar way to conformist transmission (Boyd & Richerson, 1985), lead to the between-group variation found in wild chimpanzees (Kendal et al., 2015). However, this bias has not yet been assessed in wild chimpanzees and recent findings suggest that chimpanzees can also learn from low-ranking models (Watson et al., submitted). Contrastingly, Dindo and colleagues (2011) found no evidence of dominance-based biases in social learning or social attention in captive tufted capuchin monkeys. These capuchins were given visual access to a high-ranking and low-ranking model demonstrating alternative methods of opening an artificial fruit. The capuchins showed no preferences to either attend to, or copy from, the more dominant model, although a subset of the participants did show a bias towards observing their kin (Dindo et al., 2011).

The previous chapter (Chapter 3) used a food choice paradigm to investigate dominance-based biases in social learning and found no evidence that vervet monkeys are biased towards matching the food choice of a dominant female model, rather than a lower-ranking female model. However, food choice is just one domain in which social learning may occur in the wild; it is possible that model-based biases may operate only in certain domains and as such should be tested with more than one experimental procedure. Past studies with vervet monkeys have used extractive foraging devices (van de Waal et al., 2010; van de Waal et al., 2015), with the former study finding a bias for individuals to attend to and copy females more than males. This was hypothesized to be an adaptation to females being the philopatric sex and thus having a better knowledge of the local environment than males who migrate throughout their lives. Both models in this study were the dominant individual of their sex, chosen as models due to their monopolisation of the task, as is common in captive testing (Whiten, Horner & de Waal, 2005). However, in a separate study, vervets learned to open a different artificial fruit from a non-dominant female model in their group (van de Waal et al., 2015). Therefore whilst dominance does not seem to be a necessary factor for social learning, the effects of two models of differing rank using an extractive foraging paradigm have yet to be investigated in this species.

4.1.1: Chapter aims

The current study employed an artificial fruit in a paradigm similar to that used in Horner et al. (2010) and also in Chapter 3 to investigate this very question. For two decades, and with a variety of primate species, ‘artificial fruits’ have been used in social learning research (Custance, Whiten, Sambrook & Galdikas, 2001; Whiten et al., 2005; Kendal et al., 2010).

These artificial fruits are designed to mimic extractive foraging in the wild (Whiten, Custance, Gomez, Teixidor & Bard, 1996), whereby the edible part of a food item needs to be accessed by extraction from the non-palatable, outer layer. The traditional use for these artificial fruits, which can be opened to reveal a food reward using multiple different methods, is to train one model per group to use different methods and then record whether the seeded method becomes each group's preferred method (e.g. Whiten et al., 2005). The current study used a variation on this paradigm and instead trained two models of differing rank within the same group at alternative methods of opening the artificial fruit and gave both the opportunity to demonstrate their method to their groupmates. By presenting these alternative models almost side-by-side, I investigated whether a certain rank of model, and thus one method, was preferred over the other in an extractive foraging task.

4.2: Methods

4.2.1: Study site and participants

The research was conducted at the Inkawu Vervet Project, located on the Mawana Game Reserve in KwaZulu Natal, South Africa. This site has been used to conduct social learning experiments on groups of wild vervet monkeys for over three years (van de Waal et al., 2013; 2015). The monkeys are currently followed six days a week for habituation, scans and experiments from other researchers and one member of each group is fitted with a VHF collar to allow researchers to follow them with radio telemetry. No physical contact with the monkeys is permitted and the amount of food occasionally provisioned to the monkeys to facilitate experimental testing is carefully controlled by the Inkawu Vervet Project. All individuals were known by either myself (n=4 groups: AK, BD, NH, KB) or by field assistants who assisted with the tests (in groups LT & BD).

Experiments were conducted between May and December 2015 on five of the vervet groups at the field site; four experimental (Ankhase (AK), Baie Dankie (BD), Noha (NH) and Kubu (KB)) and a control group (Lemon Tree (LT)). A total of 100 monkeys were exposed to the demonstration phase, whilst 42 monkeys participated in the test phase of the experiment.

4.2.2: Procedure

Two models of differing rank were selected for each of the three 'two-model' groups (AK, NH and BD, see Table 4.1) and trained to demonstrate alternative methods for opening a baited artificial fruit. In the fourth experimental group, KB, one mid to low-ranking female only was trained to demonstrate one method of opening this artificial fruit, with no high ranking model demonstrating an alternative action. This was in order to explore the effects of witnessing a low-ranking model in the absence of a high ranker demonstrating an alternative action. In the control group (LT), no models were trained, so as to investigate how the monkeys opened the artificial fruit in the absence of a demonstrator.

Group	**Condition**	**Description of Condition**
AK	DV	Dominant models pivot, Low-ranker models push
NH	DV	Dominant models pivot, Low-ranker models push
BD	DS	Dominant models push, Low-ranker models pivot
KB	LS	Low-ranker models push
LT	Control	No models

Table 4.1: Allocation of monkey groups to condition and description of each condition

4.2.3: Apparatus

To create two alternative behaviours in the two models, an artificial fruit (hereafter simply ‘box’) was used. The box was made from polycarbonate, used in previous research with this population, with all pieces securely attached and no sharp edges. The sides and top were painted black and only the door left transparent to direct the monkeys’ attention to this part of the box. A small wooden triangle was fitted to the base, allowing the box to be tilted back at a roughly 30 degree angle, making opening easier for the monkeys. Two metal hooks allowed the box to be secured by hammering pegs into the ground.

This box could be opened using one of two different methods to operate the same door. The door was attached via a bolt in its top centre, allowing it to pivot around this bolt. The door also contained a smaller section which was attached with hinges at the top, so this could be pushed inwards and upwards as an alternative means of opening. Therefore the two methods were ‘Pivot’ whereby the entire door was pivoted to the left or right to reveal the opening, or ‘Push’ whereby the smaller section of door was pushed in to reveal the opening, as shown in Figure 4.1. Magnets held both door elements in place, such that they could not be accidentally opened.

These two options were used as they were judged to be the most natural movements for vervet monkeys, differing from the ‘pull’ option used in some other primate studies (Tennie, Call & Tomasello, 2006; Dindo et al., 2008; Claidière et al., 2013). A previous study with this population used a slide vs. pull artificial fruit (van de Waal et al., 2015) and therefore alternative actions were used in this experiment.

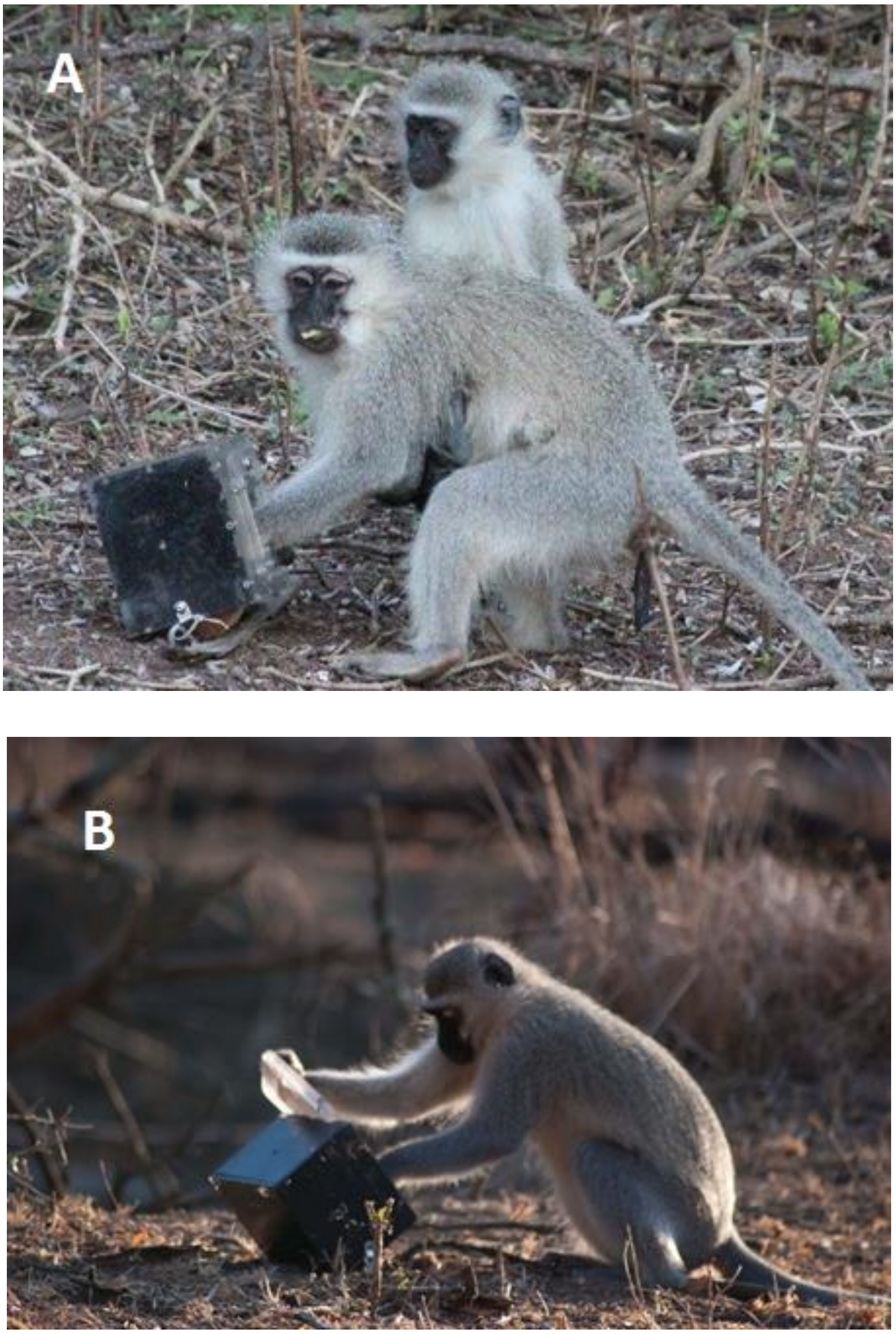

Figure 4.1: Examples of the box being opened via the (A) ‘push’ method and the (B) ‘pivot’ method.

The boxes also contained two types of locking mechanism. A manual lock allowed one method of opening to be disabled by inserting a bolt, such that the door could either not be pushed, or not be pivoted. When training a model with the push method, the pivot method was therefore disabled and vice versa. In addition, to ensure that only the trained models opened the box during the training and demonstration phases, a remote control locking system was used. When the 'lock' function was selected on the remote control, a servo motor rotated so that a lever would block the opening. Two training boxes were used with a remote control lock that either locked the pivot or the push, depending on the model being trained. The box was thus locked remotely until the target female had approached and experimenters moved back from the box only for the target female, thus ensuring only she was able to interact with it prior to the test phase.

4.2.4: Training Phase

As with the previous study (Chapter 3), the dominant female and a mid to low-ranking female (hereafter low-ranking) were selected from each of AK, NH and BD and one low-ranking female only from KB and were trained as demonstrators. Some females had previously been trained to approach boxes with patterned covers for a food reward during a PhD study at the site (Borgeaud & Bshary, 2015). In the present study these covers were placed on top of the boxes during the training and demonstration phase to encourage the target females to approach the boxes (see Chapter 2 for further details); however not all models had previously been trained on a cover, so covers were not used with Riss (low-ranker, BD) and Ness (low-ranker, KB).

Training was conducted over a period of 7-9 days on an opportunistic basis. In general, both models were trained on each day of training, in no particular order. The food reward used for each opening was one 20th of an apple, consistent with previous rewards provided to these groups during experiments (van de Waal et al., 2015). On a training day, the model was located within the group, and when she was as isolated as possible, the training began. The training was completed in several stages, beginning with the box being baited fully open and then the door being closed by steps until it was fully shut and held closed by the magnet. Once a model had successfully opened the box 10 times without error on two consecutive sessions, she reached criterion for demonstration. All individuals within 10 metres of a model and the box during training were identified and their ID codes recorded in writing. Training was conducted by myself (six models) and a Masters student, Mathilde Grampp (MG, one model).

4.2.5: Demonstration phase

Once the models reached criterion, the demonstration phase began. All demonstrations in NH, BD and AK were conducted by myself and MG. In KB, demonstrations were conducted only by myself due to the shyer nature of the group. All demonstrations were recorded using two Panasonic HD (HC-X920M) handheld video cameras held by myself or MG (one camera was used in KB).

In total, 100 demonstrations were conducted with each model on an opportunistic basis over 6-8 days with no more than 20 demonstrations conducted per model, per day. Demonstrations were conducted with both models each day in no particular order. A model was located within the group and when she had at least one other monkey within 10 metres of her the demonstration began. The procedure consisted of the experimenter placing the box within 20 metres of the model, holding up the food reward (one 20th of an apple), opening the box (using the model's assigned method as the other method was locked), placing the apple inside, closing the box and walking backwards to allow the model to approach. A successful demonstration consisted of the model successfully opening the box and obtaining the food, with at least one other individual within 10 metres and with a clear line of sight. All individuals judged by the two experimenters as either within 5 metres or 10 metres and as either looking or not looking at the time of opening, based on head orientation, were called aloud for the camera and later coded from the video. The identities of potential observer monkeys, and whether they were attending or not, were called aloud for the video record at the time of test and also verified by video afterwards. At each demonstration, when the model first touched the box, one experimenter (either myself or MG) would say "touch" and when the model removed the apple from the box the same experimenter would say "take". Any monkey whose head was oriented towards the model and box between these two time points was coded as 'attending'. For the analyses, only individuals within five metres of the box and attending were considered as 'observers'.

4.2.6: Test phase

Once 100 demonstrations had been conducted with each model, the test phase began. Tests were conducted by myself and at least two field assistants. The first test was run the day following the last demonstrations in each group. The group was located shortly after sunrise at their sleeping site and food calls were used to attract the monkeys. In the first test phase, five unlocked boxes were presented to the group (for tests 2-10, six boxes were used). Boxes were secured to the ground in two rows perpendicular to an imagined line between the experimenters and at least five metres apart. The boxes were placed with the doors facing outwards and less than 5 metres between the boxes in the rows. The boxes were assigned numbers from one to five (or six in tests 2-10).

The test phases were recorded using either two or three video cameras mounted on tripods. At each interaction with the box by any monkey, the monkey was identified and all individuals within 10 metres were identified by commentary recorded by the cameras. At each opening, the method of opening was coded in this way at the test, as well as the success of the opening. Once all the boxes were emptied, they were rebaited. If the door had fallen closed, it was opened using the method most recently used to open it for consistency, although monkeys were more than 5 metres away during rebaiting and the rebaiting was mostly occluded by the experimenter's body. An upper limit of 30 pieces of apple per day was used for each monkey. The boxes were continuously rebaited until the group moved away or an individual attained 30 pieces. If the latter occurred, no further rebaits occurred until that individual had moved out of sight. The test session was ended when all monkeys had moved away from the boxes and out of sight. Ten tests phases were conducted in each group, with the exception of the control group LT, where five tests sessions were conducted.

4.2.7: Data analysis

Data were analysed using the statistical software 'R' (R Core Team, 2013). Generalized Linear Mixed Models (GLMMs, Bolker et al., 2009) were used with binomial error structures and logit links for models with binomial outcome variables and Gaussian error structures for models with continuous data (latency analyses). Individual rank, age and friendship were collinear and thus could not be entered into the same model, therefore the best predictor of the three was found using the lowest AIC value (Akaike Information Criterion, Akaike, 1974) of the full model and entered without the remaining two effects in relevant models. Full models containing all fixed effects are reported and interactions are only included in the reported model where they are biologically relevant and are significant at $\alpha=0.05$. In the cases where models failed to converge, the optimiser 'bobyqa' was added to the model (Bates et al., 2016).

4.3: Results

4.3.1: Model Behaviour

The six trained models were given access to the *unlocked* boxes for the first time in the test sessions. Binomial tests were run to compare the number of openings that matched their trained method. All three dominant females maintained a significant preference for their trained method (Gaga, n=97, p<0.001[0.6, 0.79], Gene, n=83, p<0.001[0.92, 1.0], Ouli, n=182, p=0.001,[0.55, 0.69] see Table 4.3), whereas none of the low-ranking models in the two-model groups maintained a preference for their trained method (although the low-ranker in BD only opened the box once, with her trained method, and therefore a preference could not be calculated), with one low-ranking model showing a significant preference for the non-trained method (Nkos, n=132, p<0.001). The low-ranking model in KB, where there was no dominant model demonstrating another action, showed a significant preference for her trained method (Ness, n=260, p=<0.001).

Fixed effects	β	SE	z	P
Intercept	0.81	0.66	-	-
Model rank	**-1.60**	**0.48**	**-3.35**	**<0.001**
Group (AK-BD)	**1.20**	**0.42**	**2.90**	**<0.01**
Group (AK-NH)	**2.47**	**0.67**	**3.69**	**<0.001**
Observations of other model	-0.14	0.23	-0.58	0.56

Table 4.2: Factors affecting the probability that models used their trained method in the test phase. Significant predictors are presented in bold. The final model was significantly different from the null model containing only the random effects of Test and Individual trial nested within ID (likelihood ratio test: x^2=12.2, p=0.016).

Whether or not the models used their trained or untrained method at each opening was entered into a GLMM with binomial error structure as the outcome variable with the fixed effect of model rank, group and the observations they had made of the other model in their group Individual trial number was nested within ID and entered as a random factor. Significant effects of model rank and group were found (Table 4.2); dominant models were significantly more likely to perform their trained method than low-ranking models (see Figure 4.2) and AK models were significantly less likely to stick to their trained method than NH or BD (Tukey’s post hoc test).

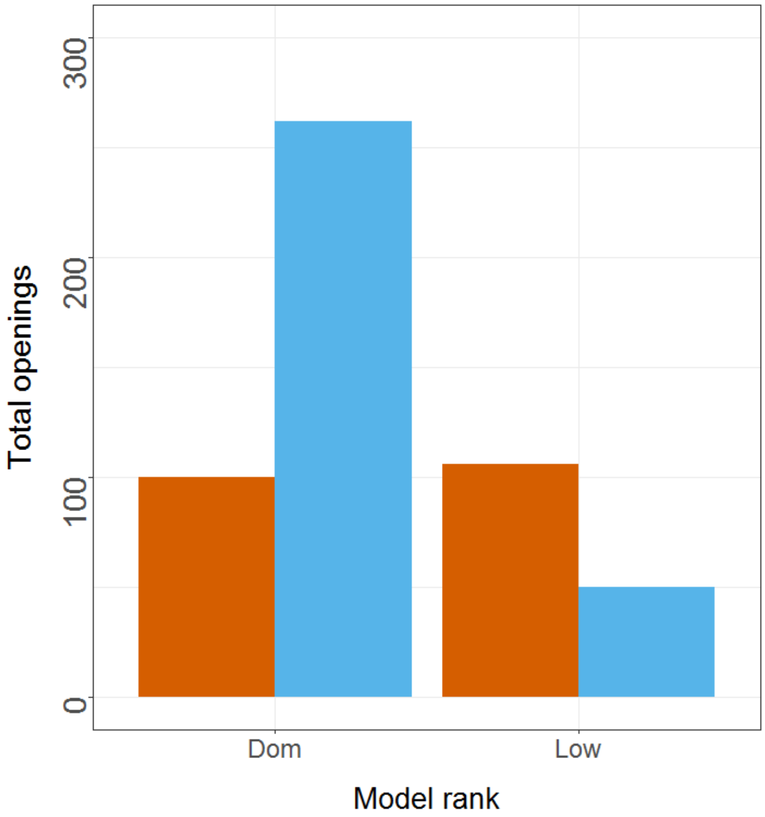

Figure 4.2: The number of box openings in which the dominant (Dom) and low-ranking (Low) models used their trained (blue) and untrained (orange) methods from the three two-model groups.

Group	Rank of model	Trained Method	No. Trained Method	No. Non-trained method	% fidelity to trained method	Significant preference
NH	Low-ranker	Push	14	9	60.9%	n.s.
	Dominant	Pivot	81	2	97.6%*	Trained
BD	Low-ranker	Pivot	1	0	100%	n.s.
	Dominant	Push	113	69	62.1%*	Trained
AK	Low-ranker	Push	35	97	26.5%*	Non-trained
	Dominant	Pivot	68	29	70.1%*	Trained
KB	Low-ranker	Push	247	13	95%*	Trained

Table 4.3: Fidelity to trained method by models showing number of each method used throughout the 10 test sessions. *= significant preference for one method, p<0.05

4.3.2: Participation

One hundred monkeys from the three two-model groups observed at least one demonstration from at least one model. Across all ten tests, 33 individuals from the three two-model groups opened the box. However, only 25 of these were successful in gaining a reward when they opened the box. The remaining eight individuals either only opened the box when it was already empty, or were unable to retrieve the reward despite having opened the box due, for example, to the pivot door closing, or food becoming trapped behind the push door.

The outcome variable of whether or not an individual participated in the test phase was entered into a GLMM with binomial error structure. The observer variables of rank, sex and age, along with the number of dominant and low-ranker demonstrations observed were entered as fixed effects. A significant effect of the number of low-ranker demonstrations seen was found along with a significant interaction between number of dominant demonstrations seen and the age of the individual (see Table 4.4); the more low-ranking demonstrations were observed, the more likely an individual was to participate (Fig 4.3) and juveniles were more likely to participate the more dominant demonstrations they had observed.

Fixed effects	β	SE	z	P
Intercept	-8.1	1.09	-	-
Dominant demos observed	-0.21	0.22	-	-
Low-ranker demos observed	**0.23**	**0.07**	**3.17**	**<0.01**
Observer variables				
Rank	0.61	1.07	0.57	0.57
Age	-1.81	0.85	-	-
Sex	-0.73	0.56	-1.30	0.19
Dominant demos observed*Age	**0.51**	**0.23**	**2.20**	**0.03**

Table 4.4: Factors affecting the probability that an individual participated in the test phase. Significant predictors are presented in bold.

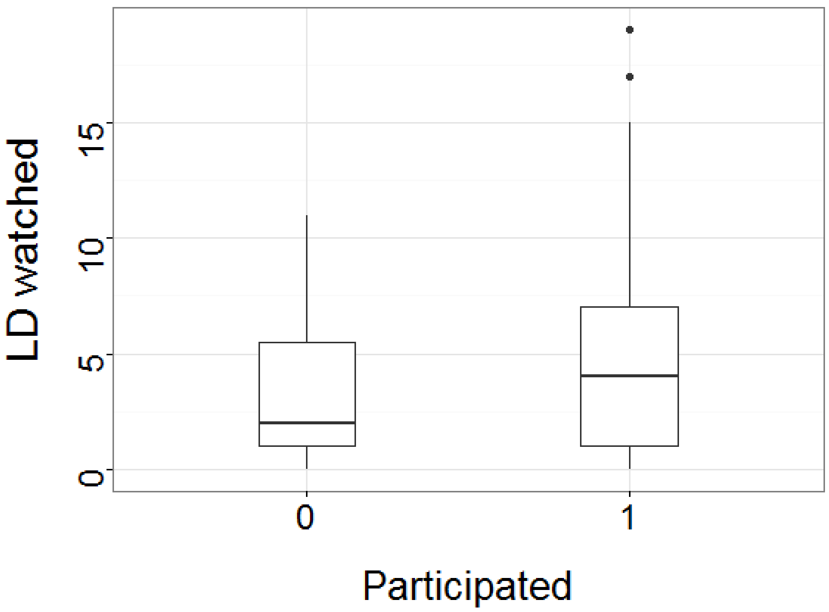

Figure 4.3: Whether or not an individual participated in the test phase (1 = participated, 0 = did not participate) by the number of demonstrations observed of the low-ranking demonstrator from within 5 metres.

Of the 33 individuals who opened the box in the three two-model groups, 19 watched demonstrations from both models, five saw demonstrations from the dominant model only, five saw demonstrations from the low-ranker only and three saw no demonstrations from either model (Fig 4.5). One individual migrated between groups during the test (Afr) and thus his data is not included.

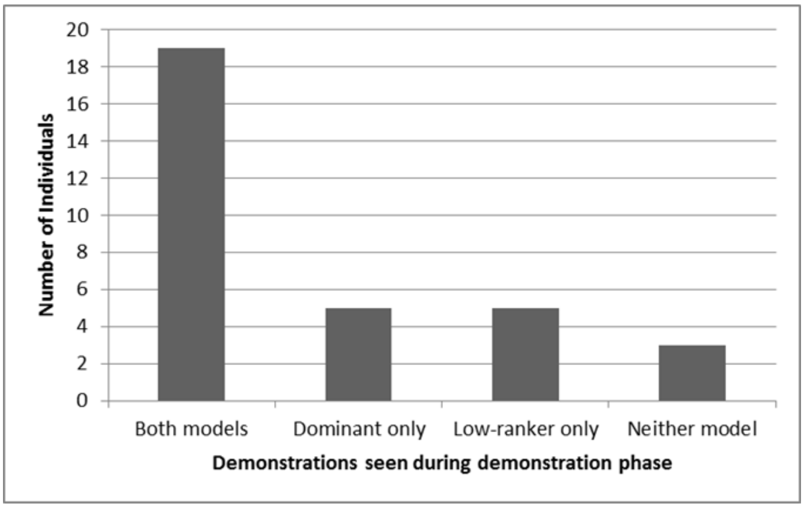

Figure 4.4: Frequency of individuals who opened the box from the three two-model groups who saw demonstrations from both models, neither model, the low-ranker only, or the dominant only during the demonstration phase.

4.3.3: Control & one-model groups

When analysing the first openings by the non-model members of the group, two separate variables were recorded; the first method by which each individual opened the box (defined as open to the point at which their hand could have fitted inside) and the first method used whereby they were successful at obtaining the reward from the box.

In the no-model control group (LT), six individuals opened the box. No significant preference for either method was found on the first method used or the first method used successfully (binomial tests, n=6, p>0.05). Of the two individuals who opened the box more than six times throughout the five tests, one (Mna) showed a significant preference for push (binomial test, n=149, p<0.001, 95% CI [0.68, 0.82]) and the other showed no preference for either method (Noa, n= 7, p>0.05).

In the one-model group (KB) only three individuals opened the box, all using the model's method of push on their first opening, all of which were successful, including the dominant female of the group (Tang). Two of the three openers also showed a significant preference for the model method over the course of the 10 tests (binomial tests; Lif, n=35, p=0.041, 95% CI [0.17, 0.49]; Tang, n=9, p=0.039, 95% CI [0.52, 0.1], see Fig 4.10), whilst the third showed no preference for either method (Avo, n=30, p>0.05). All three individuals had seen at least one demonstration by the model.

4.3.4: Two-model groups

Given the small sample sizes, Fisher's exact tests were run to assess whether the method of opening (pivot or push) differed across the conditions in the two-model groups. When the first method used was analysed there were no significant differences between the dominant-model-pivot (DV) and the dominant-model-push (DS) conditions (Figure 4.6a); however, when only the first method which was successful for each monkey was analysed, a significant difference was found between individuals in the DV and DS conditions (Fisher's exact test, n=33, p=0.03, 95% CI [0.90, 151], Figure 4.6b), revealing a preference for the dominant models' method (DMM). Percentages of individuals per group who used the DMM rather than the low-ranking models' method (LRMM) first are shown in Table 4.5.

When only the 19 individuals who observed demonstrations from both models in their group were considered, no significant difference was found between conditions (Fisher's exact test, n=19, p=0.09, 95% CI [0.44, Inf]). Again, when only the first method which was successful for that monkey was analysed, a significant difference was found between individuals in the DV and DS conditions (n=19, p=0.01, 95% CI [1.5, Inf]).

	Group	Condition	Used DMM first	Used DMM successfully first
All individuals (n=33)	AK	DV	88.89% (8)	85.71% (5)
	BD	DS	22.00% (2)	57.14% (4)
	NH	DV	93.33% (14)	90.91% (10)
Individuals who saw both demos (n=19)	AK	DV	100% (6)	100% (4)
	BD	DS	33.3% (6)	75% (3)
	NH	DV	100% (7)	100% (6)

Table 4.5: Percentage of individuals that used the method of the dominant female (DMM) first to open the box and to first successfully obtain a reward. (x) denotes actual number of individuals.

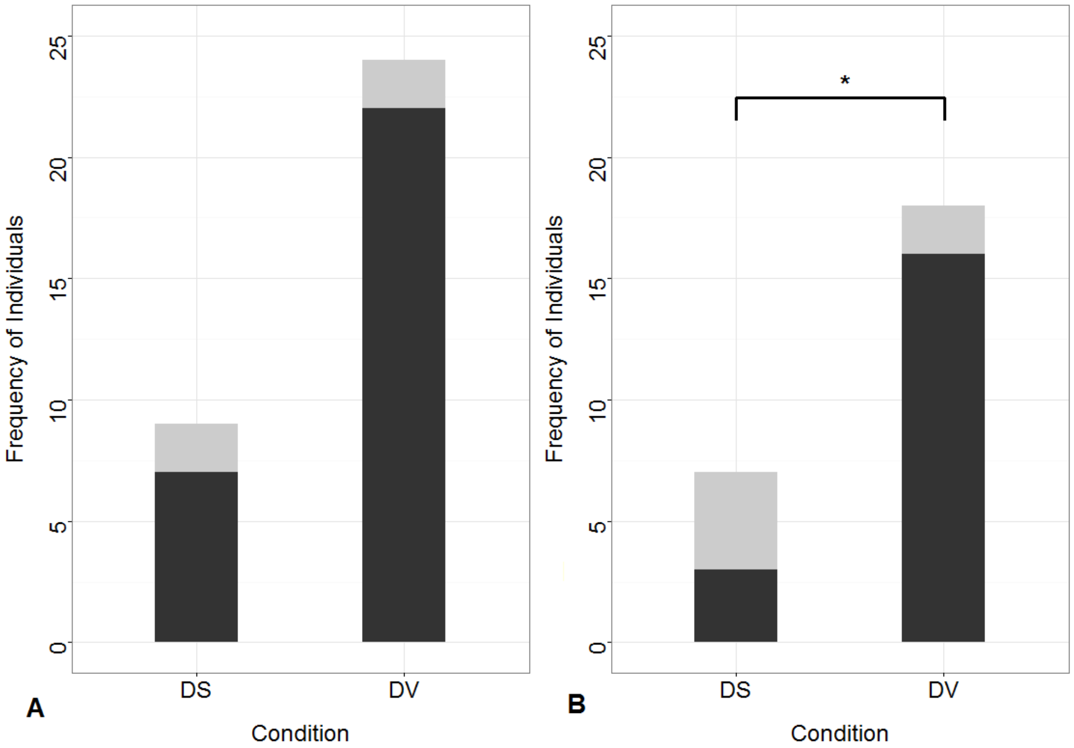

Figure 4.5: The first method (A) and first *successful* method (B) used by each individual from the three two-model groups combined (black = pivot, grey = push), as per condition (DS = dominant model pushed at demos; DV = dominant model pivoted at demos). * significant at p<0.05.

All openings made by non-models in the three two-model groups throughout the 10 test sessions were collated (n=1630) and analysed to assess whether there was an effect of condition upon the method used at each opening. As each individual opened the boxes a different number of times, a Generalized Linear Mixed Model (GLMM) with binomial error structure and logit link was used with individual trial number nested within monkey ID as a random effect. The condition and the number of demonstrations witnessed by each individual within 5 metres of both the pivot method and the push method, both at the demonstration phase and during the test phase, were entered into the model as fixed effects, with the method used at each opening entered as the outcome variable. No significant main effects of condition or observed demonstrations were found, but there was a significant interaction between condition and pivots observed, wherein for individuals in the DS (dominant method = push) condition, their likelihood of pivoting increased with the number of pivot demonstrations they observed (see Table 4.6, Fig 4.6).

Fixed effects	β	SE	z	P
Intercept	1.77	0.80	-	-
Condition	-3.53	1.28	-	-
Pivots observed	-0.02	0.06	-	-
Pushes observed	0.03	0.04	0.70	0.48
Condition*Pivots observed	**0.63**	**0.25**	**2.56**	**0.01**

Table 4.6: Factors affecting the probability that an individual used push or pivot in the test phase. Significant predictors are shown in bold. The full model differed significantly from the null model with only the random effect of trial number nested within ID (x^2= 20.17, p<0.001).

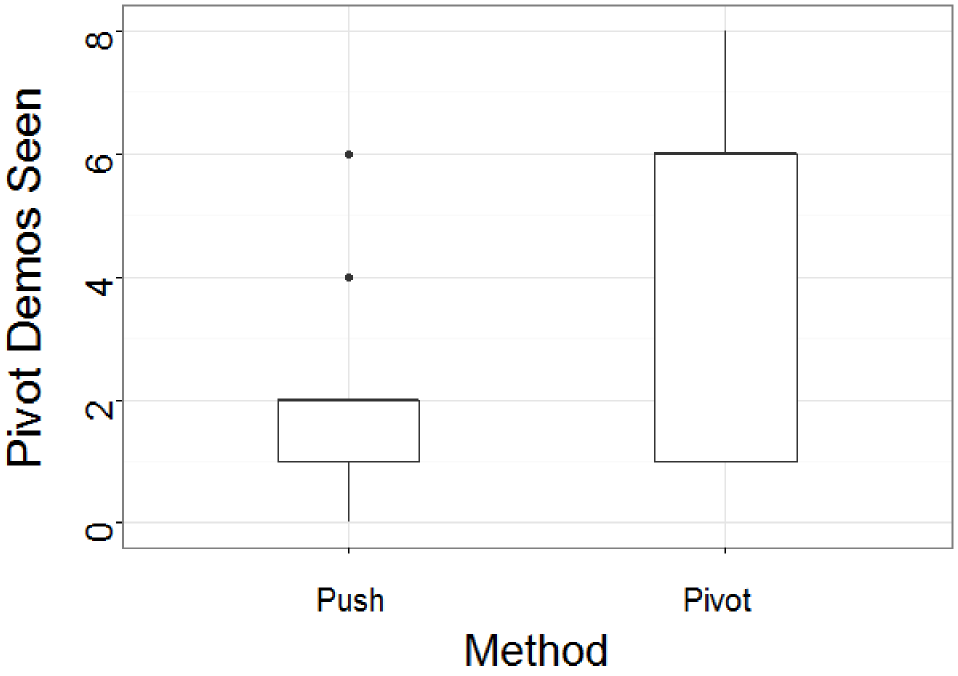

Figure 4.6: For openings in condition DS (dominant model pushed during demos) only, the method used in the test phase compared to the mean number of pivot demonstrations seen by the opener in the demonstration phase.

When the openings of only the 19 individuals who saw demonstrations from both models in their group were considered, there remained no significant main effect of condition or demonstrations seen upon the method used, but the same interaction of condition and number of pivots seen was found (Table 4.7).

Fixed effects	β	SE	z	P
Intercept	0.68	1.06	-	-
Condition	-2.74	1.30	-	-
Pivots observed	0.03	0.09	0.32	0.75
Pushes observed	0.09	0.05	-	-
Condition*Pivots observed	**0.48**	**0.23**	**2.09**	**0.04**

Table 4.7: Factors affecting the probability that an individual used push or pivot in the test phase. Significant predictors are shown in bold. The full model differed significantly from the null model (x^2=10.9, p=0.03).

A comparison of the control group, LT, with the two-model groups was conducted using a binomial error distribution, random effect of trial number nested within ID and fixed effect of condition. A significant main effect of condition was found; individuals in the DV condition were more likely to use the pivot method than individuals from the control group (Table 4.8, Fig 4.7).

Fixed effects	β	SE	z	P
Intercept	-0.34	0.82	-	-
Condition	**2.54**	**1.02**	**2.50**	**0.01**

Table 4.8: Factors affecting the probability that an individual used push or pivot in the test phase. Significant predictors are shown in bold. The full model differed significantly from the null model (x2= 8.80, p=0.01).

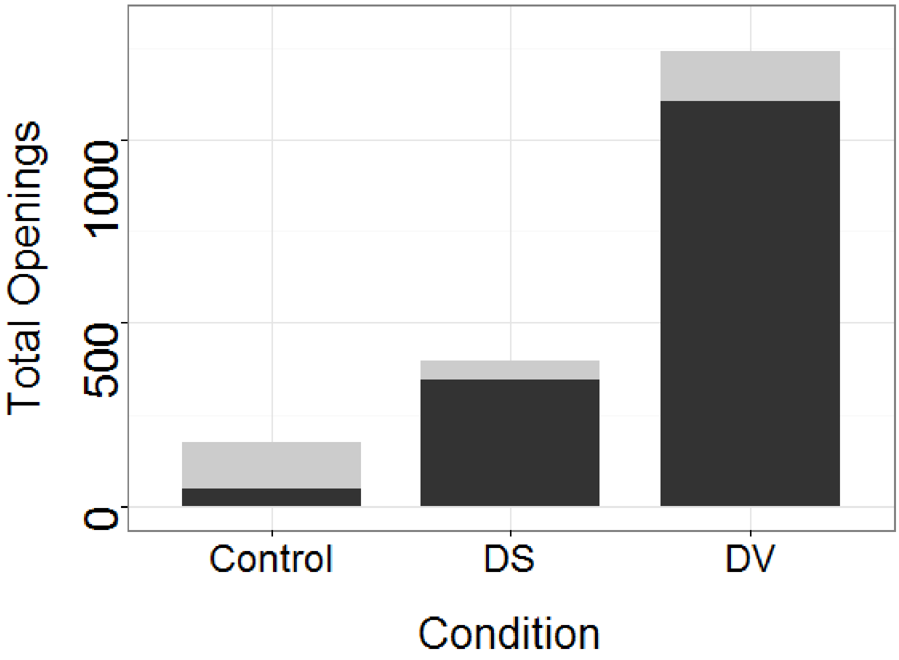

Figure 4.7: Total frequency of openings across the two-model and control conditions which used the pivot (black) or the push method (grey) throughout the 10 tests.

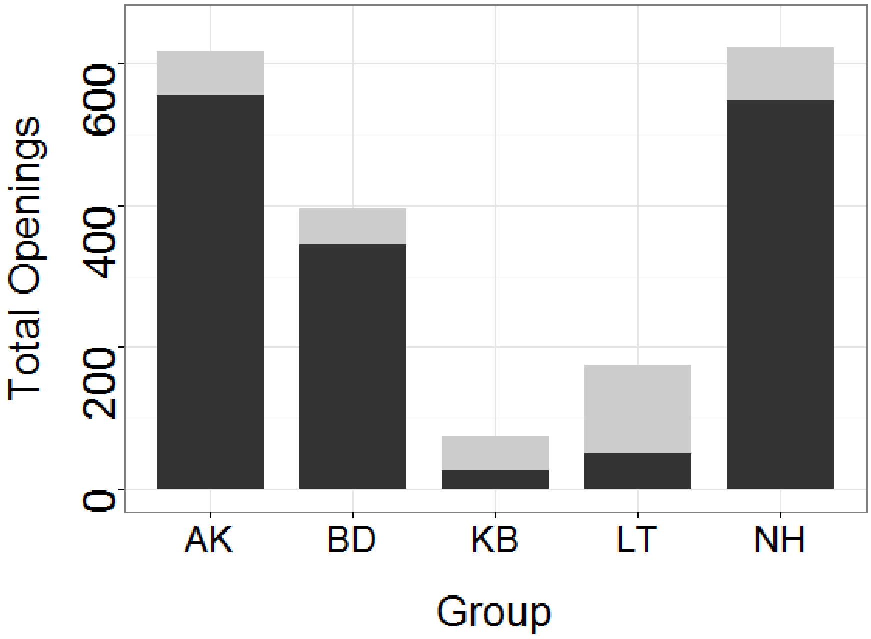

Figure 4.8: Proportions of pivots (black) and pushes (grey) used in all openings across the five groups in all test sessions. Groups were assigned to conditions as; NH and AK in condition DV (dominant model pivoted during demos), BD in condition DS (dominant model pushed during demos), KB in condition LS (no dominant model, low-ranking model pushed during demos) and LT in condition control (no models).

4.3.5: Effects of demonstrations seen, rank, kinship, age, sex and friendship

Whether or not an individual matched the method of the dominant model at each trial in the test phase was entered as an outcome variable into a GLMM with binomial error structure and logit link. Condition (DS or DV) as well as participant sex, rank, age, friendship and kinship (to the models), and the number of demonstrations they had witnessed were entered as fixed effects. As before, individual trial number nested within ID was entered as a random variable. All openings over the 10 tests from the three two-model groups (BD, AK and NH) were used. The inclusion of individual rank (rather than the other, collinear variables of kinship and friendship) led to a better-fitting model and was thus included as a fixed effect.

Fixed effects	β	SE	z	P
Intercept	1.28	0.9	-	-
Condition	**-3.91**	**0.72**	**-5.44**	**<0.001**
Dominant demos observed	-0.08	0.07	-1.23	0.22
Low-ranker demos observed	-0.02	0.07	0.36	0.72
Observer variables				
Rank	2.05	1.28	-	-
Sex	-2.61	1.36	-	-
Age	-0.24	0.76	-0.31	0.76
Rank*Sex	**5.31**	**2.06**	**2.57**	**0.01**

Table 4.9: Factors affecting the probability that individuals matched the method of their dominant female in the test phase. Significant predictors are presented in bold. The full model was significantly different from the null model containing only the random effects of individual trial nested within ID (likelihood ratio test: $x^2 = 32.3$, $p < 0.001$).

The model found a significant main effect of condition and an interaction between rank and sex. Those individuals whose dominant female demonstrated push matched her method significantly less often than those whose dominant female demonstrated a pivot (Table 4.9), thereby demonstrating a preference for pivot irrespective of condition, and rank had a significant positive relationship with the likelihood of females to match the dominant method (Fig 4.9).

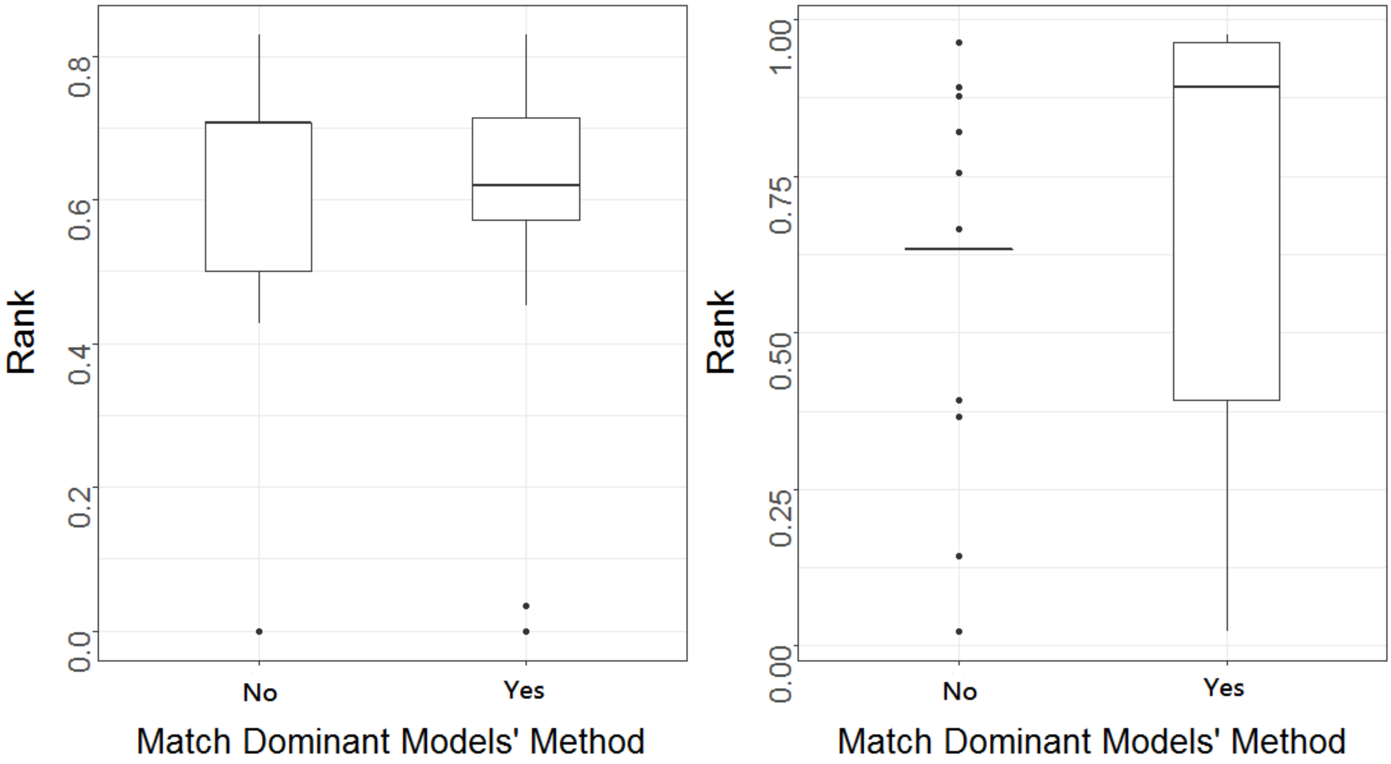

Figure 4.9: Individual rank compared to matching the dominant females' method in the three two-action groups, as split by sex: left = males, right = females.

When only data from the 19 individuals who witnessed both models in the demonstration phase were entered into the same model, significant main effects of condition, sex, age and a interaction between dominant demonstrations observed and rank were found (Table 4.10). Individuals whose dominant female pushed were less likely to match her method than those whose dominant female pushed, males were significantly more likely to match the dominant method than females and juveniles were less likely to match the dominant method than adults. Additionally, higher-ranking individuals who saw more dominant demonstrations were more likely to match the dominant model's method than lower-ranked individuals.

Fixed effects	β	SE	z	P
Intercept	3.0	1.04	-	-
Condition	**-5.3**	**0.56**	**-9.39**	**<0.001**
Dominant demos observed	-1.3	0.21	-	-
Low-ranker demos observed	0.02	0.06	0.36	0.72
Observer variables				
Rank	-0.52	1.41	-	-
Sex	**4.23**	**0.72**	**5.85**	**<0.001**
Age	**-1.94**	**0.62**	**-3.14**	**<0.01**
Dominant demos seen*Rank	**1.57**	**0.27**	**5.85**	**<0.001**

Table 4.10: Factors affecting the probability that individuals who saw both models in the demonstration phase matched the dominant method in the test phase. Significant predictors are presented in bold. The final model was significantly different from the null model containing only the random effects of individual trial nested within ID (likelihood ratio test: x^2= 38.7, p < 0.001).

4.3.6: Latency to retrieve the reward

To assess whether one method (push or pivot) could be considered 'easier' than the other, the time taken to successfully extract the food reward from the box using each method was compared using the three two-model groups (BD, AK and NH). The time taken to open the box was recorded for each opening; this was taken as the time from when the monkey first touched the box, to the moment when the apple was removed from the box. Only instances in which both the time that the box was touched and the time that the apple was removed from the box could be accurately recorded were used (n=1358, 1172 pivots, 186 pushes). The average time to open the box using the push method across all three groups with models removed was 8.25[0.82] seconds, whereas the average time to open using the pivot method was 7.62[0.25] seconds. A GLMM with Gaussian error structure and a random intercept of ID was run with fixed effect of opening method.

When the three two-model groups were analysed together there was no significant effect of method used upon the time taken to open (t=-0.88, p>0.05, as illustrated in Figure 4.11). When only the first test session was analysed, there remained no significant effect of method upon the time taken to access the reward (t= 0.69, p>0.05).

However, when individuals from the one-model group (KB) were analysed, the latency to open was significantly longer for the pivot method, which was the method not modelled in this group (estimate=-7.02[2.79], t=-2.59, p= 0.01, 95% CI [-12.6, -1.46]), as illustrated in Figure 4.12.

No significant effect of whether or not the monkeys matched the dominant method was found upon their latency to retrieve the reward (t=-0.51, p>0.05), nor was there any significant effect of group when data from all five groups were used (p>0.05).

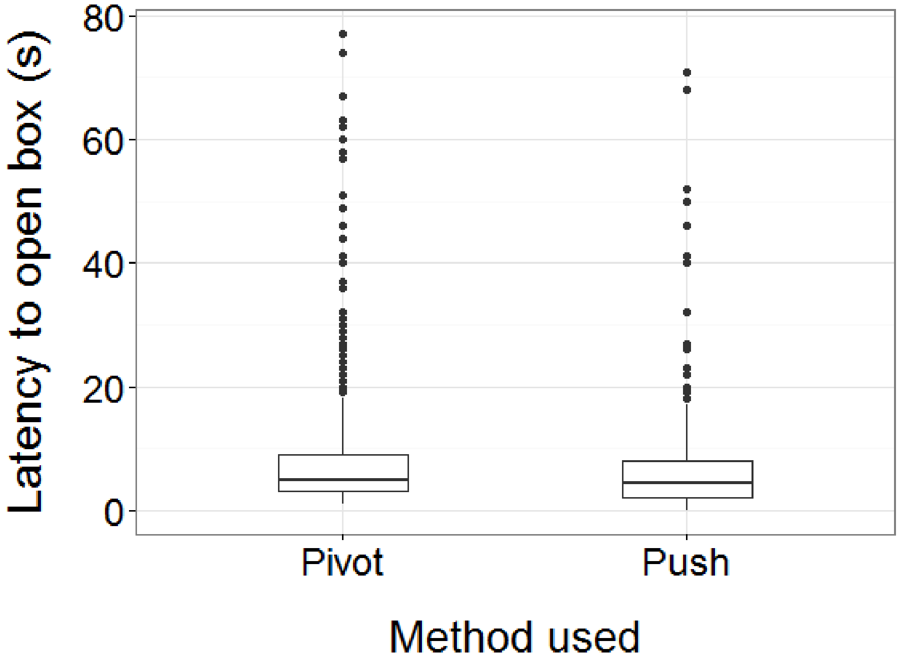

Figure 4.10: Latency (s) between touching and opening the box by individuals in the three two-model groups as per the method used to open the box.

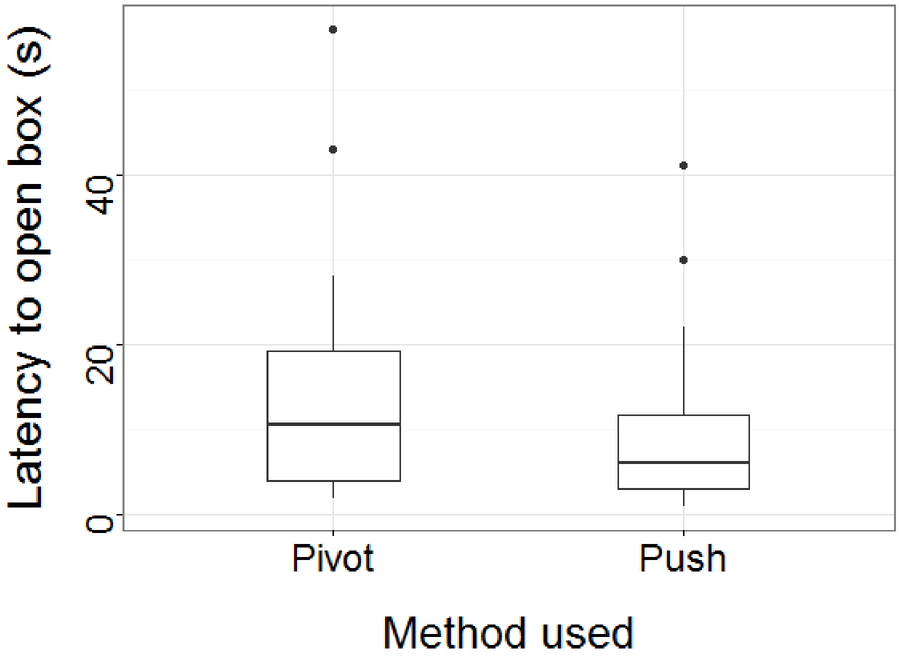

Figure 4.11: Latency (s) between touching and opening the box from individuals in the one-model group (KB) across all 10 tests, as per the method used to open.

4.4: Discussion

The primary aim of this experiment was to ascertain whether wild vervet monkeys displayed a bias to copy a dominant rather than a low-ranking model in an extractive foraging task. No significant bias towards the dominant females' versus the low-ranking females' method was exhibited in the first method used on the box by each individual, nor did a bias emerge over the course of the ten test sessions. However, there was a significant effect of the rank of the models upon the first *successful* method used to open the box with the dominant method used more; this effect became more pronounced when only the 19 individuals who had witnessed demonstrations from both models were considered. This measure does however exclude the individuals who opened the box when it had already been emptied by another monkey, which were usually monkeys of lower rank or shyer disposition coming in after the more dominant/bolder individuals had taken the reward. Therefore the first method overall should be taken as the strongest measure of method preference. There was a highly significant effect of which method the dominant female displayed upon whether individuals matched this method, thus suggesting a preference for the pivot action over the push action, regardless of the rank of the model. Therefore, whilst there was a fleeting preference for the dominant models' method in the first successful action used by individuals, this preference was not persistent and soon disappeared (unlike in previous studies whereby the model's method is preferred over the course of many openings, e.g. Whiten et al., 2005). This suggests that when both methods are demonstrated by models, the model rank has little enduring effect upon the method adopted by group members.

The lack of dominance bias found in this study is consistent with results from captive capuchins (Dindo et al., 2011), but contrasts somewhat with previous work that has found dominance-based biases in captive chimpanzees (Horner et al., 2010; Kendal et al., 2014, although see Watson et al., submitted, for new contrary data when only a low rank model is available). This may be due to species differences in social learning (e.g. Bebko & Russon, 2015), social structure and ecology. It has been shown that dominant chimpanzees are able to acquire higher quality resources than lower rankers and as such may obtain higher reproductive success (Pusey, Williams & Goodall et al., 1997; males, Wroblewski et al., 2009). However, this has not always proven to be the case for female monkeys in the vervet populations sampled thus far (Cheney et al. 1981; Cheney & Seyfarth, 1987, van Blerk, unpublished dissertation, but see Wrangham, 1981). Therefore whilst in chimpanzees, dominance might provide a useful proxy for judging success, and thus invite a bias towards copying these individuals, this may not be the case in vervets, thereby limiting the adaptive value of copying a dominant female. Additionally, a proxy strategy such as this may be too limiting; if a lower-ranking female displays an observably successful foraging behaviour, ignoring this behaviour in favour of a high-ranker's behaviour could be failing to benefit from the knowledge of a female who will have lived in the area all her life (although copying low-rankers has recently been shown in captive chimpanzees, Watson et al., submitted). Thus the lack of any enduring dominance-based bias in vervet monkeys may reflect different adaptations and lead to more flexible learning opportunities. Such flexibility might have helped this prolific species to adapt to various environments across Africa encompassing both urban and rural areas.

Alternatively, these differences could be due to environmental factors, such as the forced proximity of the captive animals studied perhaps altering the patterns of directed social learning from what may be observed in wild animals. The evidence for a *copy the dominant* bias in the Kendal et al. (2015) study came primarily from an attention bias from task naïve individuals towards higher-ranking individuals. However, a study of attention during natural foraging in vervets found no attentional bias towards high-ranking females (Reveney et al., 2013) and a similar study in the current study population by Grampp et al. (in prep.) also found no bias of attention linked to rank (although juveniles who had lost their own mother did show an attentional bias towards the dominant female), although there were strong attentional biases from juveniles towards their mothers. This therefore supports the conclusions that, unlike captive chimpanzees, vervet monkeys show only minimal and fleeting signs of a bias in social learning towards high-ranking females.

4.4.1: Evidence for social learning?

Whilst this experiment found no evidence for an enduring dominance-based bias when opening the boxes, the results do suggest that some social learning took place. When a single model demonstrates just one action to a group, past research has found that the group uses the seeded method significantly more than the alternative non-demonstrated action, both in vervets (van de Waal et al., 2015) and other primate species (Whiten et al., 2005; Claidiere et al., 2013). The same effect appeared to occur in the KB group, where only a low-ranking model was trained at the push method; all three participants used the push as their first method and two showed a significant preference for the push action. Additionally, with only one method modelled, the individuals in KB were slower to open the box using the non-modelled method (Figure 4.14). However, in the current study with two models demonstrating two different methods in the same group, it appears as though there was an underlying bias for one of the options over the other (as with the food colour study (Chapter 3) and with previous studies using artificial fruits (Dindo et al., 2011; Claidiere et al., 2013; Tennie et al., 2006), regardless of which model demonstrated it (in this case the pivot over the push action). However, this method was not preferred in the control group, LT and using time taken to obtain the reward as a proxy for difficulty, neither method was found to be significantly easier than the other. Why then was the pivot method was so preferred in the experimental groups, yet not in the LT or KB groups, as illustrated in Figure 4.10, where there either were no models, or only a push model, respectively? It appears as though there must have been a social influence upon this preference, the most plausible explanation being that the physical action of the pivot method was easier to learn socially than the push method. Whilst the push method was a somewhat discrete action in that it could not be seen clearly if the observer was behind the box and the action was mostly silent, the pivot action could be seen by observers all around the box and often made noise as the opener moved the pivot back and forth. Therefore, whilst perhaps not easier to learn through asocial learning (as per the results of the control group LT), it seems that when a model demonstrated the pivot method, regardless of the model's rank, this became the preferred method. This is suggestive of a kind of emulation learning (Tomasello, 1998; Whiten et al., 2009), whereby the vervet monkeys did not necessarily copy the actions of the demonstrator, but rather more easily learned that the pivot could be opened.

The results did reveal a significant interaction between condition and the demonstrations seen; in the DS condition only, those who had viewed more of the low-ranker’s pivot demonstrations were more likely to use the pivot in the test phase. This did not occur in the DV groups. This could potentially highlight an effect of frequency; when the frequency of pivots in a group is initially lower (due to dominant female in BD initially monopolising the boxes in the test phase and using the push), the number of pivots seen in the demonstration phase may have an effect on method used. In the DV groups wherein the dominant female and their kin initially monopolised the boxes using the pivot method in the test phase, the number of demonstrations of the pivot seen in the demonstration phase may have become diluted and unimportant.

Additionally, analyses showed that overall participation in the test phase had a significant positive relationship with the number of observations witnessed of both ranks of model. Whilst we did not set out to examine the mechanism of social learning, this could suggest a stimulus enhancement effect (Heyes, 1994), which drew the monkeys’ attention to the boxes and operated irrespective of demonstrator rank or, as somewhat supported by the preference for pivot in the two-model groups only, an effect of emulation (Tomasello, 1998). Alternatively, those present for more demonstrations may simply have more interest in the apparatus and be ‘bolder’ individuals (Carter, Marshall, Heinsohn & Cowlishaw, 2012), and thus be more likely to interact with it in the test phase.

4.4.2: Sex differences and conformity

In a past study with the same vervet population (van de Waal et al., 2013), recently-migrated male vervets abandoned their own previous individually-acquired preference for one of two alternative colours of corn, and preferentially ate the colour preferred by their new group. This displayed a remarkable level of social influence upon food choice in these monkeys. In a follow-up paper, females who had left their natal group showed a fidelity to the colour preferred by the rest of the group, despite not having eaten it themselves (van de Waal et al., in prep). The authors suggested that these effects may have been due either to conformity to the majority, or a disposition to copy particular individuals, such as high rankers in the group. The results of the present study provide no support for this latter hypothesis; there was no strong indication of the dominant female being a preferred model over another female model. Whilst vervets have been shown to copy dominant females at an extractive foraging task (van de Waal et al.,

2010) and not dominant males, that study did not test preferential copying of high over low rankers, and the current results suggest that dominance of models is not an influential factor in social learning in vervets. It could be argued that a preference for a specific technique (pivot over push) could have occluded a dominance-based bias; however, the potent social learning, including the subjugation of personal information seen in the van de Waal et al. (2013) study makes such occlusion unlikely. Therefore, these results may provide indirect support for the conformity hypothesis made by van de Waal et al. (2013); that the males who switched food colour preference in the study were conforming to the behaviour of the majority of the individuals in the group, rather than to the actions of the dominant female or other high ranked individuals. It could be argued that the strong conformity shown by the males in the van de Waal et al. (2013) study could be a unique mechanism of normative conformity (conformity for social reasons, rather than informative reasons (Claidiere & Whiten, 2012)) operating only in adult males who need to adapt to their new group to be accepted, and thus perhaps may not be seen in vervets of other age and sex classes, although the continued preference of the split group females somewhat counters this explanation (van de Waal et al., in prep). However, significant sex differences were found in the propensity for individuals to match the dominant models' method. When all participants were considered, there was a rank effect only in females (as discussed in more detail below). When just the participants who had witnessed both models in the demonstration phase were considered, males were much more likely to match the dominant than were females. Whilst only four migrated males managed to open the box during the test phases of the present study, no interaction between sex and age was found, suggesting that it was not adult males driving this effect. These results could suggest that male vervets from a young age are biased to copy the behaviour of the dominant female, as this may be adaptive when migrating to a new group and acquiring rank. However, there was no clear preference to match the dominant females' method on the first opening when all males were considered and therefore whilst they may match the method more than females, this may still not be a strong enough effect to cause observable biased learning in males.

4.4.3: Effect of participant rank and age

This experiment found a significant effect of participant rank interacting with both the number of demonstrations seen (for individuals who saw both demos) and with sex (for all individuals). For females only, high-rankers were significantly more likely to match the dominant females' trained method than lower-ranked individuals (Figure 4.10). This suggests that high-ranking females are more motivated to copy other high-ranked individuals than are lower-ranked females. It is possible that these individuals are more motivated to copy based purely upon a similarity in rank, due, for example, to a closer affiliation (Seyfarth, 1977). However, a plausible explanation for this finding also comes from kinship. Whilst no effect of kinship was found in this study, this is likely because of i) a small sample size; only a small proportion of the individuals who opened the box were classified as kin of the models, and ii) our classification of kin. Since genetic data was not available at the time of testing, kinship was defined only for those who were known to be direct offspring of the models. The groups have been followed since 2010, thus precluding any earlier offspring or siblings from being defined as kin (see Chapter 2 for further details). However, in vervet monkeys, rank is inherited maternally (Cheney & Seyfarth, 1990). Thus, high-ranking females are much more likely to be related to one another than they are to low-rankers and the finding of high-ranked females being more likely to match the method of the dominant models likely reveals a preference to copy kin. Previous research has found kinship biases in vervet monkeys, both in social learning (van de Waal et al., 2014) and in social attention (Grampp et al, in prep, and see also Chapter 6), as well as in other primate species (Dindo et al., 2011; Wrangham et al. 2016). Therefore it seems highly plausible that the rank effect seen in this is experiment is indicative of a kinship bias. It is important to note that previously only infants have been shown to exhibit a kinship bias in vervet monkeys (van de Waal et al., 2014). This study is therefore the first to suggest a kinship bias which goes beyond infancy in wild vervet monkeys (no infants opened the box during the test).

When only the 19 individuals who saw both models during the demonstration phase were considered, a significant effect of age occurred; adults were more likely to match the dominant females' method than juveniles. It has been found that adults generally have a better knowledge of the hierarchy than juveniles (Borgeaud et al. 2015) and it is possible that these observed differences might thus reflect this knowledge; the rank of the dominant female may be more salient to adults and therefore might lead to more copying of her behaviour. Indeed, research with humans has shown changing social learning biases throughout development, starting with a preference for kin, but with preferences for local experts emerging later (Henrich & Broesch, 2011). However, there was no overall preference for adults who had seen both demonstrations to prefer the dominant's method on their first choice, so more research is needed before conclusions can be drawn about age-dependent biases in vervet monkeys.

4.4.4: Model behaviour

All three dominant models in the group showed a sustained preference for their trained action, whereas none of the low-ranking models in the groups where there were two models did, with Nkos from AK even showing a significant preference for the dominant model's method of pivot (although the low-ranking model, Riss, from BD was only able to open the box once). Given that neither method was found to be more productive than the other, it is perhaps surprising that the low-ranking models did not continue to use their trained method, at which they were proficient. This suggests a social factor at work (as well as potential individual or group differences), with these models likely switching after viewing others performing the alternative action. Ness, who was the sole, low-ranking model in KB, maintained her preference for her trained, push action in the absence of a dominant model preforming the alternative action and the dominant female, Ouli, in BD maintained her trained preference for push thereby suggesting that the low-ranking models in AK and NH were not simply switching because the pivot was easier, but because of the social facilitation of witnessing the rest of the group pivoting. The lack of evidence found for a dominance-based bias in these tests suggests that the low-ranking models were not switching behaviour simply to copy their dominant female. The pivot action became the preferred method of the group in the three groups, AK, NH and BD, therefore it is possible that the low-ranking models' actions may have been affected by frequency-biased learning. Whilst the sample size here is obviously small, this finding certainly echoes that of the aforementioned migrating males and a similar experiment with great tits, both of which found that individuals abandoned their previously productive behaviour in favour of their new group's preferred (van de Waal et al., 2013; Aplin et al., 2015a). This may represent conformity to the group norm, as has been concluded for other primates (Whiten et al., 2005; Dindo et al., 2009; Luncz & Boesch, 2014, although see van Leeuwen & Haun, 2013 and Whiten & van de Waal, in press). The fact that no dominant individuals switched method is in line with similar findings that dominant individuals seem to take less account of social information than lower-ranking individuals (Kendal et al., 2015; Pongracz, Vida, Banhegyi & Miklosi, 2008; van de Waal & Whiten, in prep), perhaps due to their ability to monopolise resources and scrounge from others. This may have important implications for the study of conformity if low-ranking individuals are indeed more inclined to conform to majorities than high-rankers.

4.4.5: Conclusions

To conclude, whilst finding a weak dominance-based bias on the first successful action used, this experiment found no evidence for a persistent dominance-based bias in the social learning of an artificial fruit opening in wild vervet monkeys, in line with findings from other monkey species (Dindo et al., 2011). These findings support the findings from Chapter 3 and again demonstrate the absence of a model rank bias in a different facet of foraging behaviour. The results did reveal a bias for higher-ranked females to match the method of the dominant females, relative to that of lower-ranked females. This likely reveals a kinship bias, thus both supporting previous work and extending it to reveal a kinship bias which goes beyond infancy. The behaviour of the trained models also supports past findings that suggest more dominant individuals may put less weight on social information than lower-ranking individuals. The preference for the pivot action in the two-model groups highlights the fact that some behaviours may be more readily socially learned than other behaviours, leading to behaviour-based biases in social learning, an issue that would benefit from closer scrutiny. These results find that the behaviour of the dominant female is not preferentially copied over that of a low-ranker at the group level and thus would not lead to group-level homogeny, as has been suggested for chimpanzees (Kendal et al., 2015). Future research should therefore focus on these species-level and context differences in model-based biases in relation to social organisation and the cultural repertoire exhibited by each species in the wild.

Chapter 5: The influence of demonstrator rank upon social attention in wild vervet monkeys

Whilst social learning outcomes have been the focus of much research in recent years, relatively little empirical evidence exists for biases in social attention. This chapter analysed social attention data from the previous two chapters that detailed which individuals attended to which models during the demonstration phase of each experiment. Proximity within 5 and 10 metres was recorded in addition to visual attention, based upon head direction. These data were then analysed with respect to individual age, sex, rank, kinship and the social network of the group. No overall preference for attending to one model over another based upon rank was found; dominant females were not attended to more than low-ranking females. However, significant differences were found in the composition of the model audiences. Across several measures, higher-ranked individuals and juveniles were found to attend to more of the dominant models' demonstrations than low-ranked individuals or adults, respectively. In contrast, kin of the low-ranking models attended to more of their demonstrations. It is hypothesized that the effects of rank are indicative of a kinship bias, whilst the effects of age may reflect differing levels of tolerance towards adults and juveniles. Effects of these biases in relation to social learning outcomes are discussed.

5.1: Introduction

Social attention is intrinsically linked to social learning; in order to learn from another individual, whether it be high-fidelity copying or simple local enhancement (Heyes, 1994), an animal must first be attending to that individual to some degree. Whilst the previous chapters have focussed on the social learning outcomes of manipulating demonstrator rank, the aim of the current chapter is to assess whether attention to demonstrations varies dependent upon model rank and individual characteristics. As discussed in previous chapters, there has been a surge of interest in recent years in social learning biases, in both theoretical and empirical spheres (Boyd & Richerson, 1985; Laland, 2004; Horner et al., 2010). These studies have revealed a range of model-based biases including sex-based (Katz & Lachlan, 2003; van de Waal et al., 2010), age-based (Choleris et al., 1997) and dominance-based (Horner et al., 2010; Kendal et al., 2015) biases, among others.

However, relatively fewer studies have focussed on biases in social attention. Whilst this may be difficult to achieve in certain species that have been used for social learning studies (e.g. fish, Duffy et al., 2009), it is certainly possible in others, especially primate species. Studies of social attention are crucial to the understanding of how information may flow throughout a group and biases in social attention could lead to directed social learning (Coussi-Korbel & Fragaszy, 1995). Even more crucial are studies of social attention in wild primates, because the nature of captive conditions restricts freedom of movement and thus likely has significant effects on social attention within the group, causing animals to be in proximity to and attend to individuals that they might be farther from under natural conditions. Therefore, to understand how social learning operates in wild populations where natural instances of social learning may be hard to capture, it is useful to investigate social attention in these populations.

Social attention from infant to mother can often be inferred in primates due to the extended periods spent together and indeed recent analyses has shown that orangutan infants attend to their mothers during more difficult tasks (Jaeggi et al., 2010) and increased attention coincides with increased exploratory behaviour (Schuppli et al., 2016). However, few studies have explicitly tested biases in social attention; whether some models are attended to more than others. As the primates that exhibit the largest repertoire of cultural behaviour in the wild, chimpanzees are perhaps the most obvious species to start examining social learning biases. Data from nut-cracking in wild chimpanzees have revealed an attentional bias towards older individuals (or individuals of the same age, but not younger) in infant and juvenile chimpanzees (Biro et al., 2003) during these nut-cracking bouts.

Other studies have revealed sex-based biases in attention in captive marmosets, with individuals preferentially attending to conspecifics of the opposite sex (Schiel & Huber, 2006; Range and Huber, 2007). This latter study also found a bias (although only on some measures) of preferentially attending to affiliates over non-affiliates, thereby suggesting a role of the social network in social learning, which has previously been seen in captive studies (Claidière et al., 2013).

A primary aim of this thesis is to examine the role of dominance rank in social learning and this chapter accordingly focuses on potential associated variations in social attention. In principle, there may be a number of reasons for individuals to attend preferentially to more dominant individuals. Firstly, in groups with strict linear hierarchies, attacks are more likely to come from higher-ranked individuals and therefore it may pay for an individual to be vigilant towards those of higher rank, although as Henrich & Gil-White (2001) suggest, this may manifest as glances from a distance as opposed to sustained attention. Secondly, there may also be useful information about the environment to be gained from watching dominant individuals, because these individuals generally have access to the best food resources (Pusey et al., 1997) and therefore attending to such individuals may lead to a productive food patch.

In humans, experimental work has found that children preferentially attend to more dominant children in their group while a novel task is being tackled (Whiten & Flynn, 2012). Likewise, biases towards attending to more dominant individuals have been found in captive chimpanzees; Kendal and colleagues (2015) found an attention bias towards higher-ranking chimpanzees in an experimental context. However, it has yet to be tested empirically whether this dominance-based bias exists in wild chimpanzees, in addition to the observed age-based bias (Biro et al., 2003).

Ottoni and colleagues (2005) found that semi-free ranging capuchins selectively observed the most proficient nut-crackers in their group. Further research later revealed a preference to observe proficient, but also older and higher-ranked individuals, wherein proficiency was correlated with age, but not with dominance (Coelho et al., 2015). Contrary to these findings, Dindo and colleagues (2011) found no preference to observe dominant individuals over lower-ranking individuals in an artificial fruit experiment with captive capuchins. Similarly, no preference for observation of more dominant individuals was found in captive marmosets (Range and Huber, 2007) and two studies with wild vervet monkeys, the current study species, found no dominance-based biases in social attention during grooming (Renevey et al., 2013) and foraging (Renevey et al., 2013; Grampp et al., in prep). Renevey (2013) and colleagues found that individuals did not attend to others more based upon rank, but the monkeys did attend to females, the philopatric sex, significantly more than to males. This bias towards females was also revealed in a social learning task (van de Waal et al., 2010), wherein females were copied and males were not. Additionally, Grampp and colleagues found a bias for juveniles to attend preferentially to kin over non-kin during foraging (in prep.), a finding that has also been reflected in previous social learning outcomes where infants preferentially copy their mother’s food-cleaning techniques (van de Waal et al., 2014). These findings appear to highlight consistencies between social attention and social learning outcomes in vervet monkeys.

5.1.1: Chapter Aims

Though no previous dominance-based bias has been found in natural foraging in vervet monkeys (Renevey et al., 2013; Grampp et al., in prep), it is unclear whether this extends to experimental settings, where much of the data on social learning processes are collected. These experimental settings may differ in many important ways from natural foraging bouts, potentially by changing the spatial distribution of individuals who may otherwise spread over a hundred or more metres and by attracting attention to a novel stimulus. This chapter will examine social attention biases in monkeys who observed demonstrations of the tasks discussed in Chapters 3 and 4.

5.2: Methods

5.2.1: Study site and participants

Levels of visual attention towards dominant versus low-ranking female models were recorded during the demonstration phases of two social learning experiments run with wild vervet monkeys (see Chapters 3 and 4). For these experiments, females of differing rank were trained in each of three groups ("Noha"(NH), "Baie Dankie"(BD) and "Ankhase"(AK)) at the Inkawu Vervet Project, South Africa to perform alternative behaviours to obtain food from the same 'artificial fruit', or to choose different colours of dyed apple. All students and field assistants involved in this study were trained to identify individual monkeys using facial and bodily features and had to pass an ID test before data could be collected (see Chapter 2).

Data were collected between 26th July and 4th November 2014 (Experiment 1) and between 14th May and 29th July 2015 (Experiment 2). Group composition of participants is shown in Table 5.1. Attention data was not collected from infants as they could not be swiftly and reliably identified in all three groups at the time of test. The ranks of the six female models were determined using outcomes from dyadic conflicts; the dominant female and a low to mid-ranking female were then trained in each group (Chapters 3 and 4). The models remained the same in NH throughout the two tests, but the low-ranking models in BD and AK differed between Experiments 1 and 2, due to a disappearance and suspected change in hierarchy, respectively.

	Experiment 1			**Experiment 2**		
Group	Adults	Juveniles	Total	Adults	Juveniles	Total
NH	14	26	40	14	24	38
AK	7	19	26	8	17	25
BD	7	30	37	12	25	37
Total	28	75	**103**	34	66	**100**

Table 5.1: Group composition of participants in experiments 1 and 2. Participants in this chapter are defined as individuals who saw at least one demonstration by one model in the demonstration phase of each experiment.

5.2.2: Experiment 1:

Experiment 1 involved training the demonstrator females to choose different colours of apple, a novel food for the monkeys tested, from a foraging box. Preference for one food colour was achieved by dying slices of apple with food colouring (two of orange, green or yellow per female) and soaking one of the two colours alongside mountain aloe leaves overnight to make it unpalatable (as in van de Waal et al., 2013). The female would then quickly learn to eat one of the colours of apple whilst avoiding the other. The apple was presented in a box which was remotely controlled such that it would open only when the target female approached (see Chapter 3 for further details).

5.2.3: Experiment 2:

Experiment 2 also involved seeding contrasting behaviours in two female models, but this experiment used an artificial fruit which could be opened in either of two ways to retrieve a small piece of apple from within. One method of opening was always locked for each model, ensuring that each female demonstrated only her learned method (see Chapter 4 for further details).

5.2.4: Protocol

Demonstrations by the monkey models in both experiments were necessarily run on an opportunistic basis. The experimenter and field assistants would locate a model within the group and wait until they were within 10 metres of another individual, before placing the apparatus within 20 metres of the model and baiting it. The experimenter would then step back and allow the target female to approach the box. For each demonstration, the identities of the observing monkeys were called aloud for the video record.

In Experiment 1, those individuals within 10 metres who had a clear line of sight towards the box (i.e. no foliage obstructing their view) were considered as ‘observing’. Fifty demonstrations were conducted per model in each of the three groups. Demonstrations were recorded using a Panasonic HD (HC-X920M) handheld video camera. The addition of a Masters student assisting with Experiment 2 (Mathilde Grampp) and thus two experimenters recording attention data, allowed for head orientation to be coded in the field to obtain a more accurate measure of attention. In Experiment 2 therefore, monkeys with their head oriented towards the demonstrator during the demonstration were coded as ‘observing’. One experimenter (the roles were alternated) said ‘Touch’ for the video record when the model first touched the box and ‘Take’ when the model removed the apple from the box. All monkeys whose heads were oriented towards the model and box at any point between these two calls were coded as ‘observing’ by calling out their identities for video record. All monkeys within 5 or 10 metres, their attention states and their distance from the apparatus were narrated for the video record. One hundred demonstrations were conducted per model in each of the three groups. All demonstrations were recorded using two Panasonic HD (HC-X920M) handheld video cameras.

Attention was coded in the field as above and confirmed later using video. Both myself and MG completed the inter-observer reliability tests required by IVP to collect data (see Chapter 2), which included judging distances between individuals.

5.2.5: Data analyses

Where the outcome variables were the number of demonstrations witnessed/that animals were in proximity of, GLMMs with a Poisson error structure were fitted and estimated via maximum likelihood estimation using the package ‘lme4’ (Bates et al., 2015) in ‘R Studio’ (R core team, 2013). There were too few data points to use ID nested within group as random factors and thus ID was entered as a random intercept into the models as it led to a better fitting model (as judged by lower AIC scores, Akaike, 1974) than the inclusion of group as a random intercept. As in previous chapters, rank, kinship and friendship were collinear and could not be entered in the same model; therefore the best predictor was found (by comparing the AIC score of the full model with each predictor in turn and selecting the lowest AIC score) and included in the model, along with the fixed effects of observer, age and sex. Full models are reported in tables and interactions were only included in the model if they had a significant effect upon the outcome variable. Three different outcome variables were recorded in Experiment 2; the individuals within 10 metres of a demonstration (‘Within 10m’, which was the same measure recorded for Experiment 1), the individuals who attended to the demonstrations within 10 metres (‘Watching in 10m’) and the individuals who attended to the demonstrations within five metres (‘Watching in 5m’). These separate measures were taken to allow for differentiation between proximity and attention to the model.

5.3: Results

5.3.1: Experiment 1: Food colour preference demonstrations

Shapiro-Wilk normality tests showed the number of demonstrations observed to be non-normally distributed, therefore non-parametric tests were used for further analyses (dominant model demonstrations, W=0.81, p<0.001; low-ranking model demonstrations, W=0.84, p<0.001). In total, 91 individuals across the three groups were within 10 metres proximity with a clear line of sight during at least one demonstration. In total, 513 observations were made of the dominant model demonstrations, whilst 567 were made of the low-ranking model demonstrations. A Wilcoxon Signed-Rank test showed no significant effect of the model rank upon the total number of demonstrations observed (n=91, W=4019, p>0.05).

5.3.2: Effects of participant rank, sex, age, friendship and kinship

The demonstrations seen of dominant and low-ranking individuals were analysed as separate outcome variables. When the outcome variable was the number of demonstrations by the dominant females for which individuals were within five metres, significant effects of rank and age were found; rank had a significant positive relationship with proximity to demonstrations and juveniles were in proximity to more demonstrations than adults (Table 5.2, Fig 5.1). Only sex was a significant predictor of 5 metre proximity to low-ranking demonstrations (Table, Fig 5.1), with females being in proximity of more demonstrations than males. No significant interactions were found for either outcome variable.

Fixed effects	β	SE	z	P
Dominant demos				
Intercept	0.42	0.41	-	-
Rank	**1.14**	**0.43**	**2.63**	**<0.01**
Sex	-0.31	0.24	-1.29	0.2
Age	**0.63**	**0.28**	**2.24**	**0.03**
Low-ranker demos				
Intercept	1.18	0.43	-	-
Rank	0.4	0.47	0.85	0.39
Sex	**-0.61**	**0.26**	**-2.35**	**0.02**
Age	0.41	0.31	1.35	0.18

Table 5.2: Factors affecting the probability of individuals being within 5 metres of a demonstration, separated for the dominant and low-ranking female. Significant predictors are presented in bold.

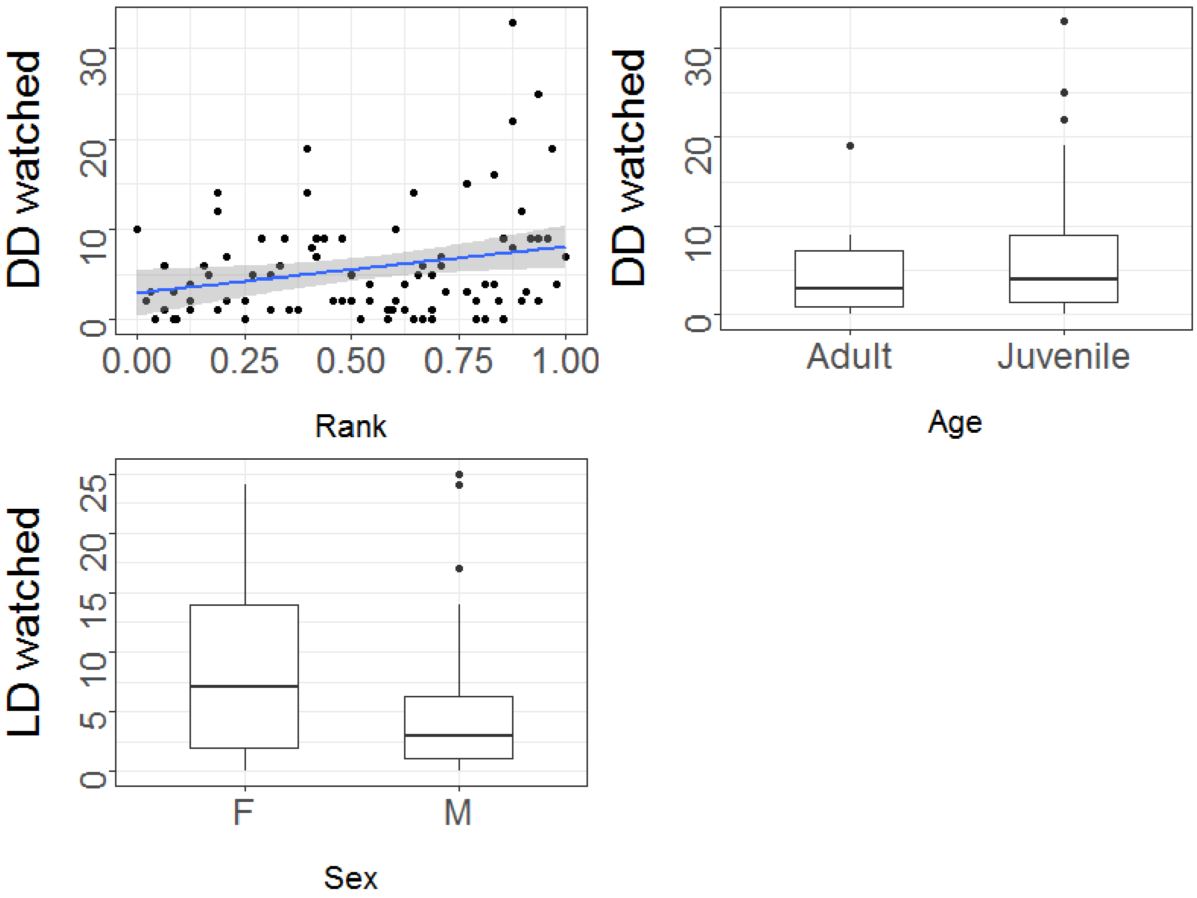

Figure 5.1: Multigraph panel illustrating the average number of demonstrations individuals were in five metres proximity for by dominant models (DD) (top) and low-ranking models (LD) (bottom) in Experiment 1 when observers are grouped by rank, sex and age.

5.3.3: Experiment 2 – Artificial Fruit Demonstrations

Shapiro-Wilk tests were run for the number of demonstrations witnessed of both the dominant and low-ranking females in all three variables (see Table 5.2); both were found to have non-normal distributions (observations of dominant female (W=0.81, p<0.001); observations of low-ranking females (W=0.84, p<0.001). Therefore non-parametric statistics were used in analyses.

A total of 107 individuals across the three experimental groups were within 10 metres for at least one demonstration of either model. The total numbers of demonstrations observed of the models (according to each measure) are displayed in Table 5.2. A series of Wilcoxon Signed-Rank Tests found no effect of model rank upon total number of observations across all outcome variables (Watching in 5, W=5028, p>0.05; Watching in 10, W=5621.5, p>0.05; Within 10, W=6302.5, p>0.05).

Measure	Dominant demonstrations	Low-ranker demonstrations
Proximity in 10m	1128	884
Watching in 10m	679	651
Watching in 5m	390	376

Table 5.3: Total number of demonstrations for which individuals were in proximity for, and observed of, the dominant and low-ranking models across the three groups

5.3.4: Effect of participant rank, sex, age, friendship & kinship

5.3.5: Watching in 5m:

When the outcome variable was the number of dominant female demonstrations viewed, rank and age were significant predictors; rank had a significant positive relationship with demonstrations viewed and juveniles observed more demonstrations than adults (Table 5.4, Fig 5.2). None of the fixed effects were significant predictors of the number of low-ranking demonstrations seen, although the variable of kinship approached significance and had a relatively large effect size and so is included in Fig 5.2. No significant interactions were found for either outcome variable. When juveniles were analysed separately, they did not watch more of the dominant models' demonstrations than the low rankers' demonstrations (Wilcoxon Signed-Rank Test, W = 2498, p>0.05)

Fixed effects	β	SE	z	P
Dominant demos				
Intercept	-0.29	0.44	-	-
Rank	**1.58**	**0.38**	**4.17**	**<0.001**
Age	**1.00**	**0.24**	**4.17**	**<0.001**
Sex	-0.13	0.21	-0.62	0.53
Low-ranker demos				
Intercept	0.39	0.55	-	-
Kinship	1.06	0.59	1.80	0.07
Sex	0.14	0.24	0.60	0.55
Age	-0.14	0.25	-0.55	0.58

Table 5.4: Factors affecting the probability of individuals observing a demonstration from within 5 metres, separated for the dominant and low-ranking female. Significant predictors are presented in bold.).

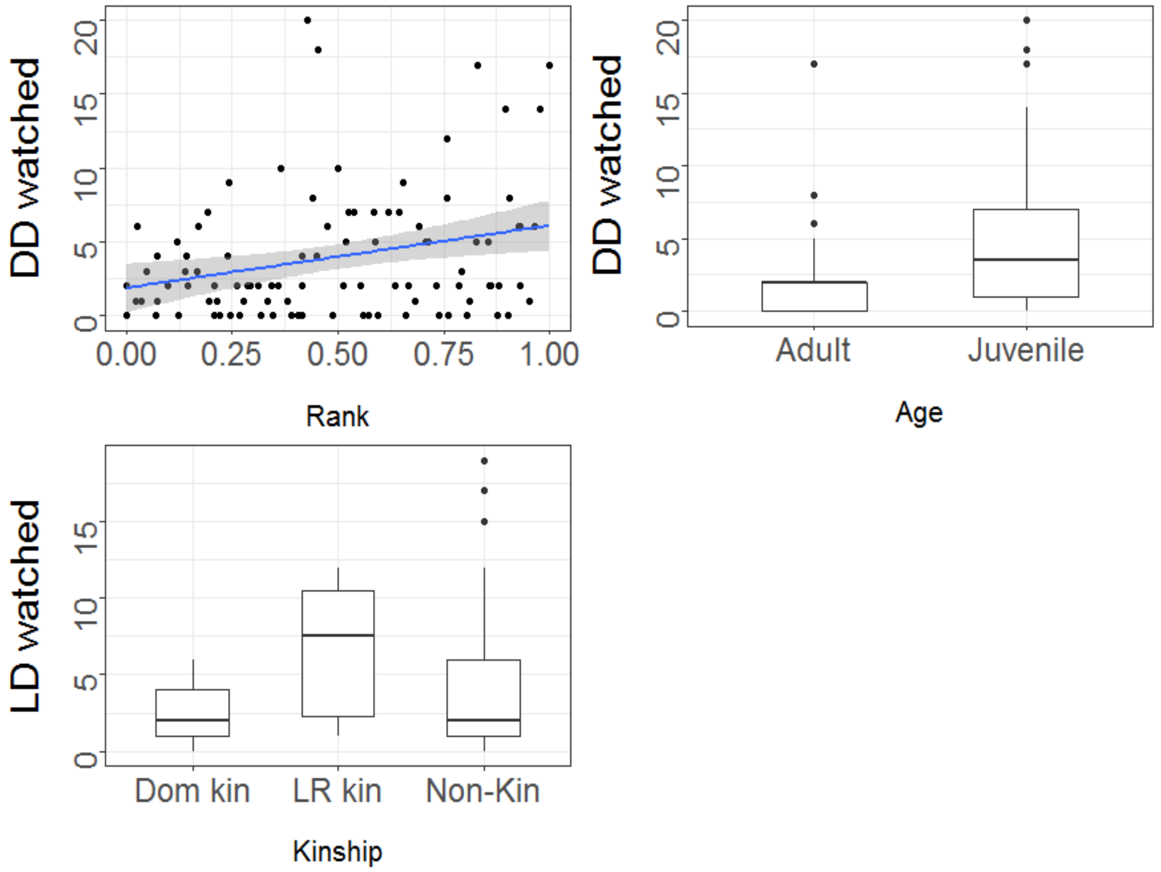

Figure 5.2: The average number of demonstrations for which the observer was watching within 5 metres of the (top) dominant demonstrators (DD) and (bottom) low-ranking demonstrators (LD) and the predictors of these outcomes in Experiment 2. Shaded area (c) represents 95% confidence interval. Note that kinship did not reach significance for the low-ranking demonstrations outcome variable (p=0.07).

5.3.6: Watching in 10m:

When the outcome variable was the number of dominant demonstrations seen, rank and age again were significant predictors; rank had a significant positive relationship with the demonstrations seen within 10 metres and juveniles saw more demonstrations than adults (Table 5.5, Fig 5.3). When juveniles alone were analysed, they did not watch more of the dominant models' demonstrations than the low rankers' demonstrations (Wilcoxon Signed-Rank Test, W = 2498, p>0.05). When the outcome variable was the number of low-ranking demonstrations seen, none of the fixed effects were significant predictors and no significant interactions were found for either outcome variable.

Fixed effects	β	SE	z	P
Dominant demos				
Intercept	0.47	0.30	-	-
Rank	**1.21**	**0.37**	**3.30**	**<0.001**
Age	**0.81**	**0.23**	**.035**	**<0.001**
Sex	-0.23	0.21	-1.08	0.28
Low-ranker demos				
Intercept	1.34	0.27	-	-
Rank	0.19	0.34	0.56	0.09
Sex	0.34	0.20	1.68	0.09
Age	-0.20	0.21	-1.0	0.33

Table 5.5: Factors affecting the probability of individuals being observing a demonstration from within 10 metres, separated for the dominant and low-ranking female. Significant predictors are presented in bold.

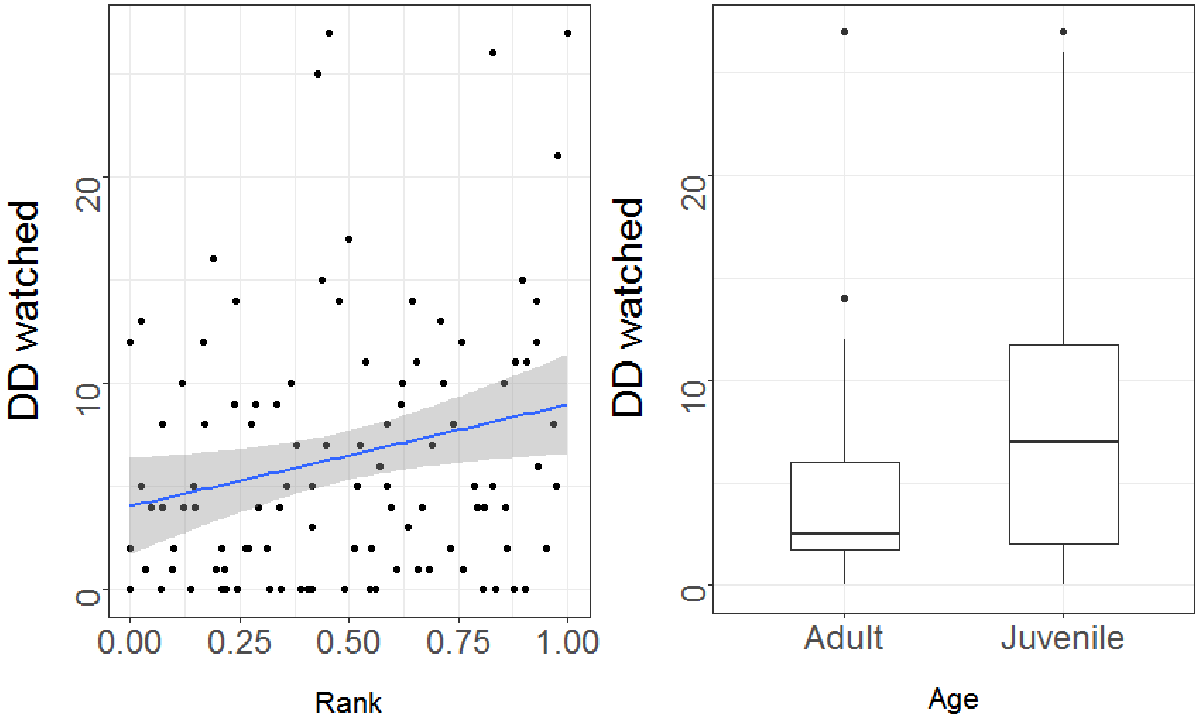

Figure 5.3: The average number of demonstrations for which observers were watching within 10 metres of the dominant demonstrators (DD) and the significant predictors of these outcomes in Experiment 2. Shaded area represents 95% confidence interval.

5.3.7: Within 10m:

When proximity to the dominant demonstrations were considered, significant effects of rank and age were found; rank had a significant positive relationship with proximity to demonstrations and juveniles were in proximity to demonstrations more than adults (Table 5.6, Fig 5.4). When the number of low-ranking demonstrations for which individuals were within 10 metres was entered as the outcome variable, only sex was a significant predictor; males were in proximity to more demonstrations by the low-ranking models than were females (Table 5.6, Fig 5.4). No significant interactions were found for either outcome variable.

Fixed effects	β	SE	z	P
Dominant demos				
Intercept	1.00	0.29	3.52	<0.001
Rank	**1.21**	**0.36**	**3.35**	**<0.001**
Age	**0.69**	**0.22**	**3.12**	**<0.01**
Sex	-0.18	0.21	-0.87	0.38
Low-ranker demos				
Intercept	1.56	0.26	6.0	<0.001
Rank	0.12	0.33	0.37	0.71
Sex	**0.44**	**0.19**	**2.26**	**0.02**
Age	-0.13	0.20	-0.64	0.52

Table 5.6: Factors affecting the probability of individuals being observing a demonstration from within 10 metres, separated for the dominant and low-ranking female. Significant predictors are presented in bold.

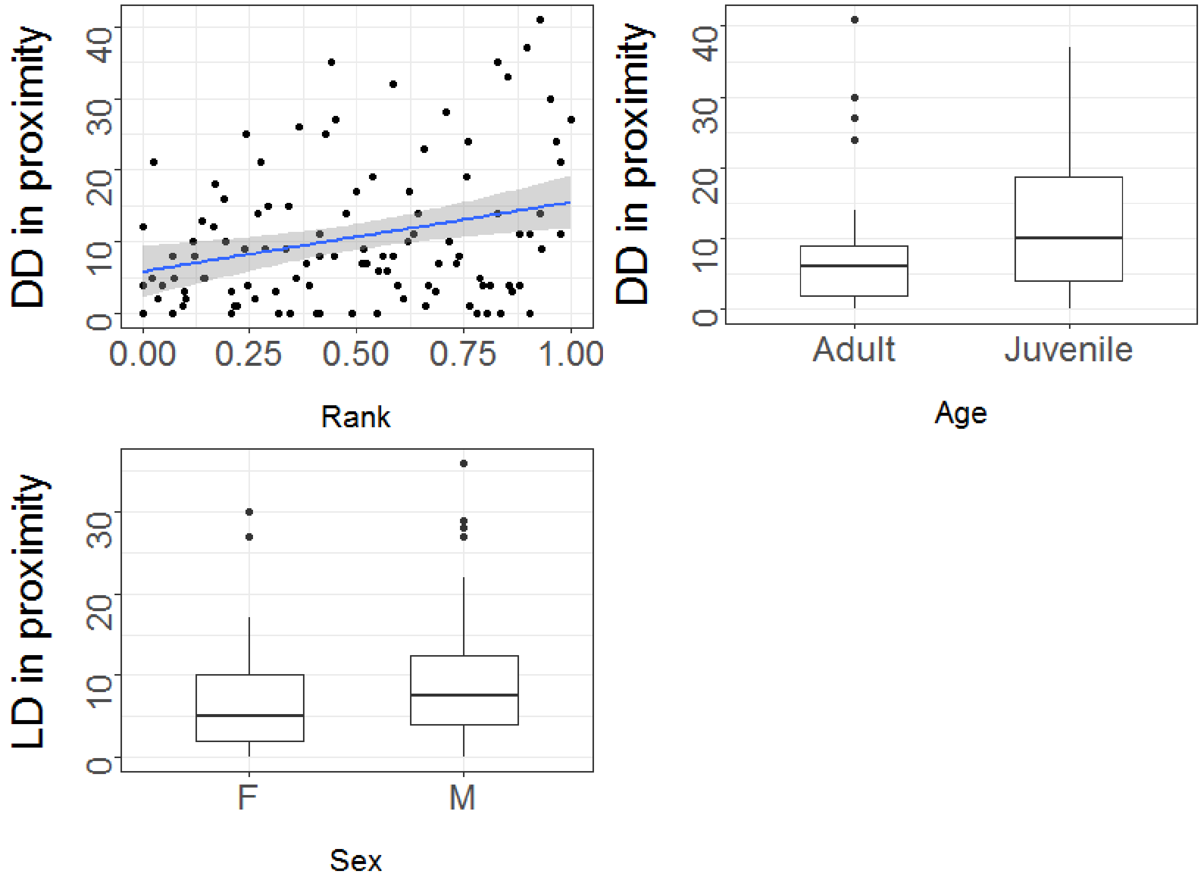

Figure 5.4: The average number of demonstrations for which observers were present within 10 metres of the (top) dominant demonstrators (DD) and (bottom) low-ranking demonstrators (LD)and the significant predictors of these outcomes in Experiment 2. Shaded area represents 95% confidence interval.

Demonstrations	**Measure**	**Experiment**	**Significant predictors**	**Description**
Dominant Demos	Proximity	Within 10 (E1)	Age, Rank	High rank > low rank Juveniles > Adults
		Within 10 (E2)	Age, Rank	High rank > Low rank Juveniles > Adults
	Attention	Watching in 10	Age, Rank	High rank > Low rank Juveniles > Adults
		Watching in 5	Age, Rank	High rank > Low rank Juveniles > Adults
Low-ranker Demos	Proximity	Within 10 (E1)	Sex	Females > Males
		Within 10 (E2)	Sex	Males > Females
	Attention	Watching in 10	-	-
		Watching in 5	-	-

Table 5.7: Significant predictors of the outcomes for the four different measures of proximity and attention across Experiment 1 (E1) and Experiment 2 (E2). Descriptions summarize the direction of the effect, (x>y denotes that class x watched, or was in proximity of, on average significantly more demonstrations than y).

5.4: Discussion

It has previously been suggested that, in primate societies with linear dominance hierarchies, lower-ranking individuals preferentially pay more attention to dominant individuals (Chance, 1967). However, in the current study wild vervet monkeys exhibited no overall social attention bias towards high-ranking individuals in two different experimental contexts; in neither experiment nor on any measure were there significantly more observations of either model based on rank. This is consistent with two other studies on vervet monkeys that found no bias towards attending to high-ranking individuals during natural foraging and grooming (Renevey et al., 2013; Grampp et al., in prep) and previous work with captive capuchin monkeys and marmosets that have shown no dominance-based attention bias in experimental settings (Range & Schuber, 2007; Dindo et al., 2011).

It can be argued that a bias towards attending to dominant individuals may be an adaptive strategy if dominance were utilised as a proxy for success, as has been suggested for biases towards other features, such as size (Duffy, Pike and Laland, 2009). A direct bias towards attending to *successful* individuals has been found in capuchin monkeys, with regards to nut-cracking proficiency (Ottoni et al., 2005) and humans have been found to copy successful individuals in experimental settings (Mesoudi & O'Brien, 2008). However, for a monkey to use dominance as a proxy for success may be risky, insofar as there may be many domains in which a dominant individual may not be successful. It has been found that vervets preferentially attend to females over males (van de Waal et al., 2010; Renevey et al., 2013), but the current findings suggest that the rank of the female is of relatively little significance to this species compared to her sex. As females are the philopatric sex in this species, all females may provide equally useful information about aspects of the habitat in which they have lived all their lives (such as foraging decisions in the present studies) and thus may render rank unimportant as compared to sex.

5.4.1: Differences in audience composition

Despite finding no overall biases in total observations, significant and interesting differences between the models were found in the composition of the audience who attended to them. On all measures, more demonstrations by the dominant female were watched by those of higher rank than by lower ranked individuals and more were watched by juveniles than by adults. In contrast, kinship appeared as a potentially important factor when predicting audiences for the low-rankers' demonstrations, although it did not reach significance (p=0.07).

5.4.2: Kinship bias

There are a number of potential explanations for these attentional biases. The non-significant trend of kin to attend to the low-rankers' demonstrations is consistent with previous work which has shown biases towards kin in vervet monkeys, both in attention during natural foraging (Grampp et al., in prep.) and in social learning during field experiments (van de Waal et al., 2014), and with other species (Schwab et al., 2007; Dindo et al., 2011).

This kinship effect was not found for the dominant models, for whose audience rank was a significant predictor instead. However, the importance of rank, rather than kinship for these models may be due to the measure of kinship that was used. As discussed in Chapter 4, in order to obtain the highest accuracy, only direct offspring known to researchers at IVP were included as kin of the model. Therefore, since rank and kinship are highly correlated in vervet monkeys due to rank inheritance (Cheney & Seyfarth, 1990), the variable of rank may have encompassed more kin of the models, such as adult offspring or siblings, than our measure of kinship, and incorporation of such information could have led to a better predictor variable for the dominant models.

5.4.3: Age bias and tolerance

I also identified a consistent age bias; for the dominant demonstrations only, juveniles attended to more demonstrations than adults. However, when juveniles alone were analysed, they did not show a significant preference for the dominants' over the low-rankers' demonstrations. Perhaps rather than an active preference towards dominant demonstrations from juveniles, this finding may be due to differences in tolerance between the dominant and low-ranking models. Social tolerance appears to be highly important in social learning (Coussi-Korbel & Fragaszy, 1995; van Schaik et al., 2003; Whiten & van Schaik, 2007) and has been suggested to be particularly important in the emergence of cumulative culture in humans (Dean et al., 2012). If a model is socially tolerant, it allows other individuals to witness a behaviour from close proximity without fear of attack and thus allows for more likely or even higher fidelity copying (van Schaik, Deaner & Merrill, 1999). Some primate species show high levels of tolerance towards even unrelated juveniles (Hirata & Celli, 2003; Boinski et al., 2003), thus it is likely that the increased levels of juvenile attention to the dominant model (when compared to adults) is a result of juveniles being more tolerated than adults by the dominant females. This lack of an age bias in the audience for the low-rankers' demonstrations is likely because the low-ranking models were unable/unwilling to chase off other adults from the demonstrations, given that the majority of other adults are above them in rank and third-party interventions in conflicts generally support the higher-ranking individual (Cheney & Seyfarth, 1990; Borgeaud & Bshary, 2015). Given that tolerance is much higher towards kin than to unrelated individuals in many species of primates (de Waal, 1986; Belisle & Chapais, 2001), it is also possible that the previously noted bias of kinship/rank, could actually be a by-product of increased tolerance to kin rather than a genuine preference in attention by the models' kin towards the models. However, for the same reasons as above, it is unlikely that a low-ranker would be able to repeatedly chase off non-kin (who are likely to outrank her) without receiving aggression in turn.

5.4.4: Implications for social learning

The biases found in the current experiment seem to point to a mixture of genuine "active choice of observational target" (Ottoni et al., 2005, pg. 217), such as from kin, and attentional biases created through increased tolerance in low-ranking compared to high-ranking females, such as for the juveniles. Future tests of tolerance in relation to kin in this species would help to elucidate this point.

Regardless of the specific mechanism, it is highly plausible that these attentional biases may lead to directed social learning in this species (Coussi-Korbel & Fragaszy, 1995). Kendal and colleagues (2015) argued that a bias towards copying dominant individuals, as found in their study with captive chimpanzees, may lead to innovations from low-rankers (Reader & Laland, 2001) being overlooked by the group and could be the reason behind the discrepancy between innovation rate and frequency of group-level traditions in this species (Nishida, Matsusake & McGrew, 2009). However, our results potentially point towards a different flow of information in vervet monkeys. If there are greater limitations on which individuals can observe the dominant female (e.g. juveniles rather than adults), than on who can observe the low-ranking female, then innovations from low-rankers may spread throughout the group, possibly at an even faster rate.

Consistent with findings with other species (Pongracz et al., 2008; Kendal et al., 2015), the behaviour of the models in the artificial fruit experiment from Chapter 4 indicated that dominant individuals may be less attentive to social information than lower-ranking individuals. Therefore it is possible that behaviours preferentially attended to by low-ranking individuals (such as the low-rankers' foraging actions in the current study) may be more likely to spread throughout the group due to increased social learning aptitude in the observers, a speculation clearly requiring further testing. In the previous chapters wherein the social learning outcomes of the demonstrations were assessed, there was no preference for copying either set of models based upon rank. However, it is possible that the experiments conducted for this thesis disrupted the natural distribution of individuals by attracting many monkeys to the apparatus at the test stage and that in a naturally occurring social learning context, these biases in social attention may be more readily obvious in the spread of a behaviour.

In addition to the aforementioned biases, the analysis also revealed some contrasting sex-based biases in the composition of the audience (see Table 5.7). However, these biases were only significant predictors for the outcome measures based on proximity (‘Within 10m’ in Experiments 1 and 2). When the attention states of the individuals were taken into account, these effects disappeared. This highlights the fact that, whilst the proximity and attention biases remained consistent for most measures, this was not the case for all. Therefore caution should be taken when inferring attention from proximity in social learning and attention tasks, particularly in field experiments where attention states may be harder to qualify. However, kinship-based attention biases found in the current study are in line with observational data from the same population during natural foraging (Gramp et al., in prep), thereby lending support to the ecological validity of field experiments.

5.4.2: Conclusions

This chapter aimed to assess whether dominance-based biases in social attention were shown by wild vervet monkeys in an experimental context. There was no effect of dominance per se in the total observations by others; no more demonstrations were witnessed of the dominant females than of the low-ranking females. However differences in attentive audience composition were found between the two ranks of model. These biases appear to stem from both preferential attention towards one’s kin and/or those similar in rank, in line with previous social attention work with these species, and are also suggestive of high-ranking females showing less tolerance towards non-kin and adults. These differences in attentive audience composition could have an impact upon the spread of innovations and lead to different outcomes depending upon the rank of the innovator.

Chapter 6: Can captive tufted capuchins (*Sapajus apella*) use social information to judge the relative quality of a foraging site?

In addition to biases based upon the characteristics of a model, individuals may also show social learning biases based upon the payoff received by a model. These payoff-based biases require that the individual be able to discriminate different levels of success achieved by different behaviours. This use of 'public information' has been found in humans, chimpanzees, fish and birds, but not in marmosets. In this chapter, I examined whether two groups of tufted capuchins at the Living Links Research Centre, Edinburgh Zoo, were capable of utilising public information to inform their own foraging decisions. Small wooden boxes painted either black or yellow were used as different 'foraging sites'. Video demonstrations were created whereby a female demonstrator from the other group appeared to feed at different rates from either the 'resource-rich' or 'resource-poor' box. These video demonstrations were presented to the group before each individual was separated for testing. When given the choice between the boxes, the capuchins failed to show a significant preference for the resource-rich box over the course of three trials. This apparent inability of capuchins to utilise public information is discussed in relation to the current literature, as are potential limitations of the study.

6.1: Introduction

The previous chapters in this thesis have been concerned with illuminating potential model-based biases which may influence how an animal might learn from its conspecifics. The social learning biases investigated in these past chapters have been based upon either stable, or relatively stable characteristics of the model, such as dominance, sex and kinship. However, additional strategies suggested by Laland (2004) include those wherein the individual may copy another individual, or not, based upon the payoff the other individual receives, 'payoff-based biases' (Boyd & Richerson, 1985), rather than more stable cues. This requires that the individual first be able to judge the payoff another individual receives, and then apply this information to its own foraging decisions. Utilizing information about the success of others' foraging is also termed 'public information use' (Valone, 1989). Whereas model-based biases such as 'copy older/dominant individuals' may act as 'shortcuts' to copying more productive behaviours, payoff-based biases operate based upon the observable success of the model. Using social information to estimate the quality of a foraging site can save an animal considerable energy and allow them to select the most productive site at which to forage (Valone &

Templeton, 2002; Clark & Mangel, 1986). Therefore being able to detect successful foraging behaviour in conspecifics could be a very adaptive trait. However, it is, as of yet, not known whether most species are capable of judging another individual's foraging success, let alone adjusting their own foraging behaviour on this basis.

Humans have been shown to use payoff-biased learning during an arrowhead-building task in which participants could engage in individual learning or a range of social learning strategies (Mesoudi, 2011), although whilst payoff-biased social learning was utilised more than other social learning strategies, this was, perhaps surprisingly only by a minority of participants; the majority of the participants predominantly used individual learning.

A small number of studies have found evidence for public information use in non-human animals, most notably in studies of fish and birds. Templeton and Giraldeau (1996) found that starlings were able to better asses patch quality when they could observe the foraging success of other individuals, and thus could use this knowledge to make foraging decisions. Examining fish, Coolens et al. (2003) found species differences in public information use in sticklebacks; whilst both nine-spined sticklebacks and three-spined sticklebacks located a feeder after conspecifics were observed feeding there, only nine-spined sticklebacks were able to differentiate between resource-rich and resource-poor patches after observing demonstrators feeding at different rates and then utilise this information by choosing the resource-rich over the resource-poor site. The nine-spined sticklebacks also displayed the same preferences when the conspecific demonstrators were replaced with three-spined sticklebacks, showing that they are also capable of cross-species public information use. Additionally, there is evidence that some species of birds and fish (as reviewed in Kennedy & Gray, 1993) distribute themselves according to the Ideal Free Distribution (Fretwell & Lucas, 1970), whereby animals distribute themselves proportionally between foraging sites based on site productivity. This implies the ability to detect the resource profitability of each site, but the role of social information in this process is unclear. However, there are also examples of some species, including baboons, not meeting this distribution (Kennedy & Gray, 1993; Cowlishaw, 1997).

Whilst there has been a surge in research into social learning in primates in recent decades, studies into public information use with regards to foraging location in non-humans primates, and indeed mammals in general (Valone, 2007) are few. In one, Voelkl & Huber (2007) tested captive marmoset pairs on a foraging task wherein a trained demonstrator who had knowledge about the resource quality of food patches foraged simultaneously with a naïve individual in an adjacent cage. Contrary to the authors' expectations, the focal marmosets did not have a significantly higher foraging success when foraging in proximity to a knowledgeable demonstrator than when foraging alone. The authors hypothesized that this could be due to restraining factors of social living, such as displacement, and propose that social information perhaps may not be exploited in a number of social and environmental conditions, despite being available (Voelkl & Huber, 2007).

In a recent paper, Vale et al. (2014) examined this issue in both chimpanzees and human children. In a similar paradigm to Coolens et al. (2003), chimpanzees were shown simultaneous video displays of a conspecific feeding from a resource-poor and a resource-rich food site. Food sites consisted of coloured, opaque boxes from which peanuts could be retrieved at a controlled rate. The video stimuli, presented to naïve individuals, showed the female chimpanzee model obtaining a peanut from the resource-rich feeder every 12 seconds, whereas she was only able to obtain a peanut every 84 seconds from the resource-poor feeder. When given the choice between the two food sites (equally baited) during a single test trial, significantly more individuals chose the resource-rich feeder first. Children also showed a significant preference for the resource-rich site in a comparable study using stickers, thereby providing evidence that both species are able to use cues from conspecifics to recognise which resource site was the most profitable.

6.1.1: Chapter Aims

The current chapter aimed to investigate public information use in captive tufted capuchins (*Sapajus apella*). Capuchins are somewhat remarkable amongst monkeys in their use of tools for extractive foraging (Ottoni & Mannu, 2001; Mannu & Ottoni, 2009) and also display traditions in social 'games' (Perry et al., 2003). There is also evidence from captive experiments that the foraging behaviour of capuchins can be socially facilitated by conspecifics foraging nearby (Visalberghi & Addessi, 2000), although this does not appear to extend to the *type* of food consumed (Fragaszy & Visalberghi, 2004). Ottoni et al. (2005) found that semi-free-ranging tufted capuchins spent more time watching individuals who were proficient at nut-cracking, rather than relatively inefficient group members. Whilst not providing information about the observer's later foraging efficiency, this suggests that capuchins are able to differentiate between successful and unsuccessful foraging behaviours in their conspecifics and preferentially direct their attention to the most successful individuals (although see Coelho et al., 2015 for data suggesting nut-cracking success may be confounded with age and hierarchy).

Bonnie & de Waal (2007) allowed brown capuchins to watch female conspecifics foraging in one of two boxes; when the authors gave the observer capuchins the choice of the two boxes they found that the observer capuchins significantly more often preferred to manipulate the box which they had seen their conspecific searching, even when no reward was gained by the demonstrator. These results suggest that capuchins are able to use the foraging behaviour of others to inform their own foraging decisions.

However, whilst these studies show an attention and utilization of foraging behaviour in conspecifics, no study has yet empirically tested whether capuchins are able to use social cues to discern the abundance of food at a foraging site and use this social information to guide their own foraging. Capuchins live in tropical forests, thus making them seasonal foragers (Fragaszy et al., 2004). Therefore, capuchins face a dynamic feeding environment and, as such, might benefit from public information use about patch location and quality.

The current study used a paradigm similar to that previously used with fish, chimpanzees and children (Coolens et al., 2003; Vale et al., 2014) to test whether tufted capuchins are capable of using public information to determine resource quality and then exploiting that information to inform their own foraging decisions. The capuchins witnessed simultaneous videos of a conspecific feeding at a fast rate from a box of one colour and feeding at a slow rate from a box of the other colour. This test was arguably more cognitively demanding than the Bonnie & de Waal (2007) study, since both sites provided rewards, but at different rates. Therefore, the capuchins had to attend to the foraging success of the conspecific in order to discern the most productive site at which to forage.

6.2: Methodology

6.2.1: Participants

Participants were 20 tufted capuchins (*Sapajus apella*) housed at the Living Links Research Centre (Macdonald & Whiten, 2011) in Edinburgh Zoo (see Table 6.1 for participant details). The capuchins are housed in two groups (“East” and “West”), who have visual, but no physical, contact with each other and have large indoor and outdoor enclosures. The enclosures are mirror images of one another to reduce environmental confounds. The capuchins are fed daily on a range of fruits, vegetables and protein. No subjects were never food or water deprived during the course of this study.

The Living Links Research Centre is fitted with test cubicles into which capuchins have been trained to enter to collect food rewards during research. In these cubicles, capuchins could be voluntarily isolated with transparent or opaque occluders and were trained to place a hand on the occluder should they want to leave, at which point any ongoing experiments were halted and the capuchin was immediately allowed to re-join the group. I was trained to operate these cubicles and research began only after cubicle training, conducted by a member of the animal care staff at Edinburgh Zoo. All food rewards and quantities were sanctioned by the animal care givers at Edinburgh Zoo.

Monkey	**Group**	**DOB (dd-mm-yy)**	**Age at test**	**Sex**
Diego	West	22-07-02	12	M
Pedra	West	16-02-08	7	F
Toka	West	29-12-04	10	M
Figo	West	01-06-06	8	M
Torres	West	08-01-11	4	M
Ximo	West	02-04-10	4	M
Rufo	West	21-10-09	5	M
Inti	West	07-09-09	5	M
Mecoe	West	23-04-08	6	M
Luna	West	02-05-11	3	F
Alba	West	18-09-11	3	F
Bear	West	27-07-13	1	M
Fudge	West	14-07-13	1	M
Pixie	West	08-09-13	1	F
Kato	East	~-08-05	9	M
Anita	East	14-11-97	17	F
Carlos	East	22-07-06	8	M
Chico	East	25-04-09	5	M
Ruben	East	17-06-10	4	M
Flojo	East	19-06-11	3	M

Table 6.1: List of all individuals with group, date of birth, age at time of testing and sex.

6.2.2: Models

The models used were one female from each group. Females were used based on ease of isolation and training and given that they were used as models in previous research (Bonnie & de Waal, 2007). Two low-ranking females (as assessed by care staff at the facility) were used due to difficulties in isolating the dominant female in one of the groups. Thus, females of similar rank were used from each group to minimise potential effects of model bias. The video demonstrations shown to each group of capuchins always featured the model from the other group to reduce any effects of kinship or affiliation.

6.2.3: Apparatus

Two wooden boxes measuring 120mm^3 were used as the food sites. The boxes were opaque and painted different colours using acrylic paints. Due to differences within the vision of New World monkeys (some individuals are dichromatic, some are trichromatic, see Waitt & Buchanan-Smith, 2006), the colours yellow and black were used, as in the Vale et al. (2014) study. The boxes had a small, circular opening in the front where the monkey was able to insert his/her hand, but unable to see whether food was baited within. The boxes had no back panel, which allowed the experimenter to re-bait the box at the appropriate rate during the video demonstrations. During the test phase, boxes were placed approximately 10cm apart upon a moveable shelf. This shelf could then be wheeled up to the cubicle door, such that circular holes in the cubicle doors aligned with the holes in the front of each box. The monkeys were then able to put their hands through the hole into the door and into the opening of the box.

6.2.4: Video stimuli

Videos were created depicting the same model feeding at different rates from each box using a handheld Panasonic HD (HC-X920M) video recorder and Windows Movie Maker software. This was achieved by the experimenter placing a raisin inside the box at predetermined intervals. The video was filmed from a side-angle, showing the female reaching into the box and retrieving a raisin, but without showing the experimenter re-baiting the back of the box (Figure 6.1). Whilst the Vale et al. (2014) study used rates of 1 per 84s versus 12s, this was considered too long for the capuchin models to remain in the cubicle without any stimulus/rewards. Therefore, rates of 1 raisin per 35s versus 5s were used, achieved through different rebaiting speed and some video editing. Each video demonstration lasted 74 seconds, such that the resource-rich box was shown to provide 15 raisins and the resource-poor box to provide 3 raisins. The software 'Windows Movie Maker' was used to edit the video such that the timings were exact. Though the raisins themselves, due to their size, were not highly visible on the video demonstration, the actions of foraging and eating from the model occurred at these rates and were clearly visible on the demonstrations. For each group, the colour of the resource-rich box was counter-balanced (as shown in Table 6.2).

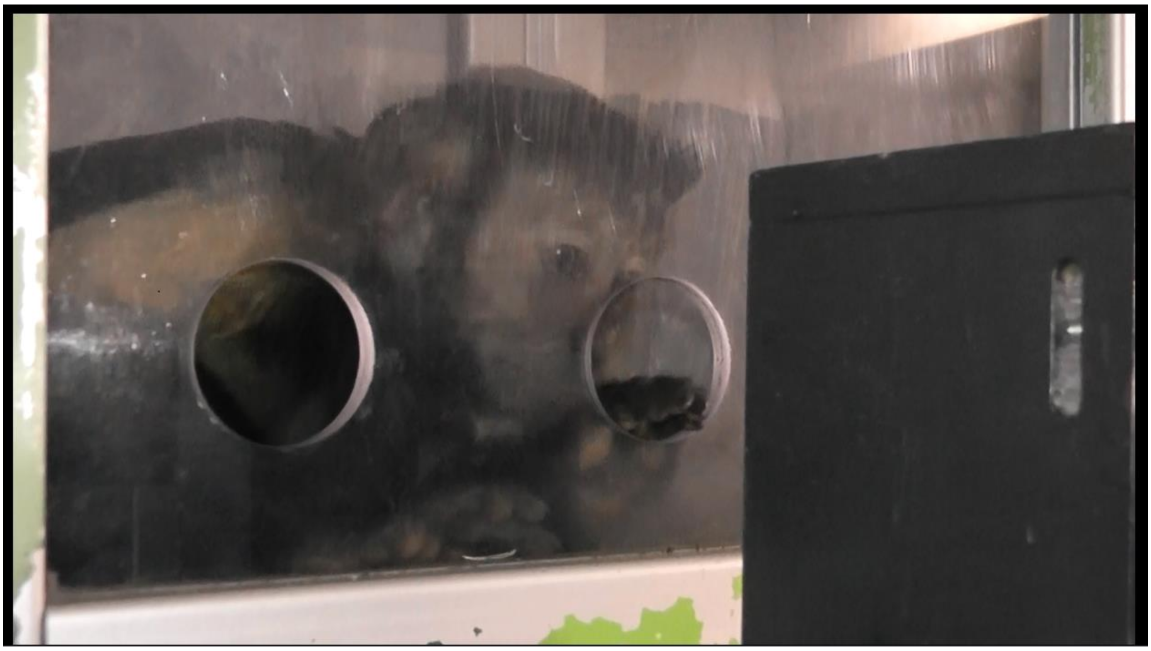

Figure 6.1: A still image taken from the stimuli video position showing the model and the black box. The observers witness the model (Sylvie) feeding at different rates from each coloured box. The back of the box is not shown on the video footage; the experimenter rebaited through the back of the boxes at pre-determined intervals. The two videos were played simultaneously and side-by-side on video screens in front of the research cubicles.

Group	**Group Size**	**Colour of resource-rich box:**	**Colour of resource-poor box:**
East	11 (6)	Black	Yellow
West	16 (14)	Yellow	Black

Table 6.2: Colour of resource-rich box presented to each group via video demonstration. Group size indicates total group size and, within parentheses, the number of individuals who entered the cubicles to take part in the experiment.

6.2.5: Video demonstration phase

Each group was shown two videos simultaneously which displayed the model feeding at the fast rate from the resource-rich box and the same model feeding at the slow rate from the resource-poor box. Two adjacent computer monitors (measuring approximately 16" x 14") were used to play the videos simultaneously from two laptops (a Lenovo ‘Thinkpad’ and a Dell ‘Notebook’). These monitors were placed on a shelf (approximately 1.5 metres high) inside the research room, which was placed up against the window to the main indoor enclosure. The boxes were placed on a lower shelf directly below whichever monitor was playing the video containing that coloured box. This was to allow the monkeys to associate the box on screen with the one they would later be tested with. For the initial phase, the demonstrations were played on loop over four sessions to each group (in blocks of, West: 1hr, 1hr, 45m, 15m; East: 1hr, 45m, 45m, 15m), totalling 3 hours (West) and 2 hours 45 minutes (East). A Panasonic HD (HC-X920M) handheld video recorder was placed beneath the screens pointing at the enclosure window. The amount of time each monkey spent attending to the demonstrations was coded from this video footage by the experimenter (myself) who could identify the individuals based on facial characteristics (as tested by the animal care staff prior to testing).

6.2.6: Test Phase

Immediately following the final 15 minute demonstration, the test phase began. For the test session, each monkey was voluntarily isolated in a central test cubicle. The other cubicles remained empty throughout the test to avoid other participants witnessing the individual’s choice and also in order to reduce distraction. Once the individual was isolated, they were given three pumpkin seeds/raisins as a reward for entering the cubicle. The shelf holding the monitors was placed two metres in front of the cubicle. One loop of the video demonstrations was then played, lasting 74 seconds. During the video demonstrations, each monkey was given a pumpkin seed/raisin approximately every 20 seconds to sustain their interest and avoid boredom.

Following the video demonstration, the moveable shelf holding the boxes was wheeled up to the cubicle with the two boxes positioned in the same arrangement as the video (with regards to left and right). To reduce any olfactory cues, neither box was baited at this stage. The monkey was then given 90 seconds to make his/her choice. A choice was defined as the first box s/he touched. Following the first touch of one box, the shelf was left in place until the monkey had touched the other box, shown a willingness to leave the cubicles or had stopped interacting with the boxes. This was to allow them to discover both boxes were empty so as not to bias their choice in the next test. Once the shelf was removed, the monkey was rewarded with three raisins and re-joined the group.

All trials were video recorded using two Panasonic HD (HC-X920M) video cameras; one angled at the front of the cubicle and a second capturing a side angle to accurately record the box touched first. When the monkey entered the cubicle, the experimenter called out their name for the video record. The first touch of each box was called aloud so as to be recorded on the video by the experimenter during the trial and later confirmed from the video footage. To counteract the small sample size, each monkey was tested three times. Tests were run from 23rd February 2015 to 19th March 2015 over seven days. Each monkey was tested only once per test session (two test sessions were conducted per day).

6.3: Results

All data were analysed using the free statistical software “R” (R Core Team, 2013), with the package ‘lme4’ (Bates et al., 2014). Seventeen capuchins (11 from the West group, 6 from the East group) participated in all three test sessions. Three juveniles participated only in the first test session and so were excluded from final analyses. All individuals clearly touched one box first in every trial. In five trials, individuals showed a desire to leave the cubicles after touching only one box and so the shelf was withdrawn and a reward given. However, for three individuals, this was on their third, and final, trial.

Individual	**Resource-rich colour**	**First choice Test 1**	**First choice Test 2**	**First choice Test 3**
Diego	Yellow	P	R	R
Pedra	Yellow	P	R	P
Toka	Yellow	R	R	P
Figo	Yellow	R	R	P
Inti	Yellow	R	P	R
Ximo	Yellow	P	R	R
Rufo	Yellow	P	R	R
Mecoe	Yellow	P	P	R
Alba	Yellow	R	R	R
Luna	Yellow	P	P	R
Torres	Yellow	R	R	R
Ruben	Black	R	R	R
Carlos	Black	R	R	R
Chico	Black	P	P	P
Kato	Black	P	P	R
Flojo	Black	P	R	R
Anita	Black	P	P	P

Table 6.3: First choice of individuals in all three test sessions. R = resource-rich box, P = resource-poor box.

Test phase	**Monkeys choosing resource-rich box first (%)**	**Monkeys choosing resource-poor box first (%)**
1	7 (41.1%)	10 (58.9%)
2	11 (64.7%	6 (35.3%)
3	12 (70.6%)	5 (29.4%)

Table 6.4: Frequency and percentages of monkeys from both groups combined choosing resource-rich or resource-poor box across the three tests.

No significant preference for either the resource-rich or resource-poor box was found in any of the three test sessions (binomial tests, n=17, p>0.05, see Table 6.4), as illustrated in Figure 6.2. The resource quality (rich or poor) of the boxes in the video stimuli was entered as a fixed effect into a GLMM with binomial error structure and logit link and first choice of box as the outcome variable. Monkey ID and group were entered as random effects (intercepts). No effect of demonstrated resource quality was found upon the first choice of box by individuals, suggesting no use of public information in foraging choice in the participants (z=0.87, p>0.05).

The outcome variable of whether they selected the resource-rich or not was entered into a further GLMM with binomial error structure and logit link in order to assess whether certain factors affected use of public information; age, sex, test session and amount of time spent watching the video stimuli were entered as fixed effects and ID and group were entered as random intercepts. None of the fixed effects had significant effects on the probability of choosing the resource rich box, no significant interactions were found and the full model did not differ significantly from the null model (see Table 6.5).

Fixed effects	β	SE	z	P
Intercept	-2.28	1.25	-	-
Age	**0.51**	**0.74**	**0.70**	**0.49**
Sex	0.82	0.87	0.95	0.34
Test session	0.72	0.41	1.76	0.08
Time spent watching video	0.01	0.01	0.66	0.51

Table 6.5: Factors affecting the probability of individuals choosing the resource rich box. No significant predictors were found and the full model did not differ significantly from the null model containing only the random effects of ID and group (likelihood ration test, x^2=6.06, p=0.2).

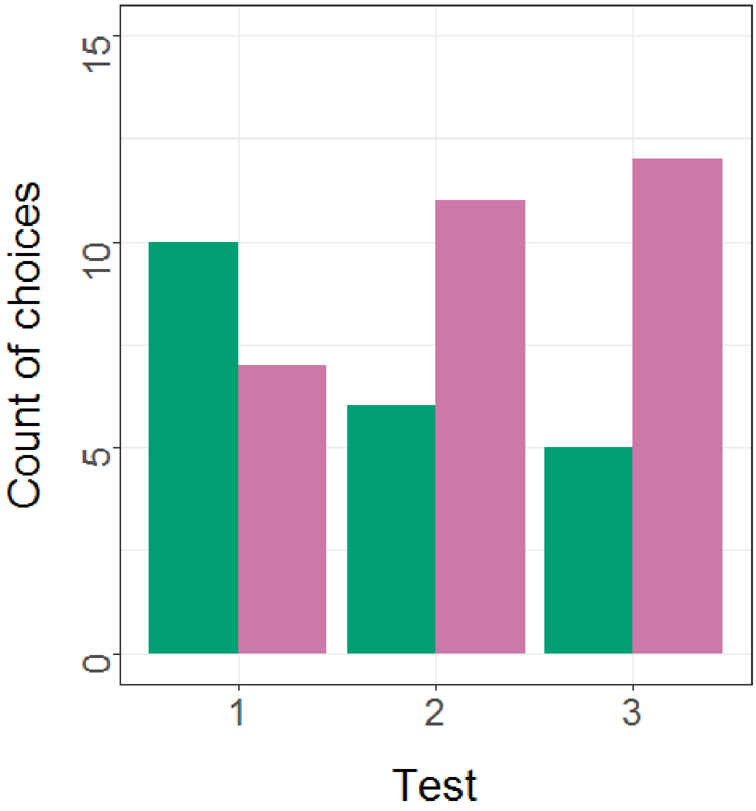

Figure 6.2: Total choices of resource-rich (pink) and resource-poor (green) boxes for all 17 individuals across the three trials.

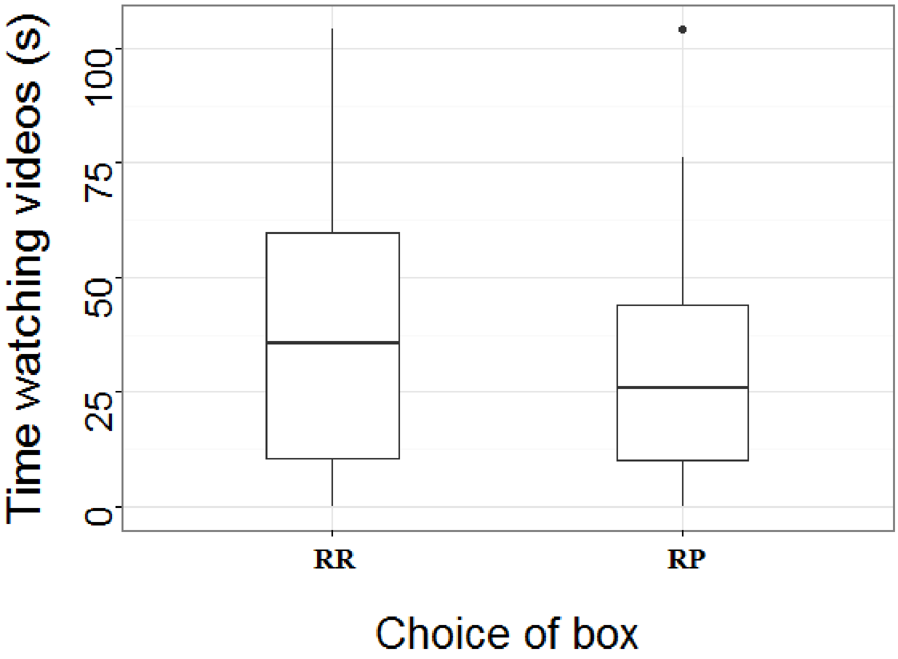

Figure 6.3: Boxplot illustrating the time spent watching the video stimuli (s) during the presentation phase and the first choice of box in the test phases. RR = resource rich, RP = resource poor.

6.4: Discussion

6.4.1: Do capuchins utilize public information?

The current experiment aimed to assess whether captive tufted capuchins would use public information about resource quality to inform their own foraging decisions. After being shown video demonstrations showing boxes of difference resource quality, as demonstrated by a conspecific, the capuchins showed no significant preference towards the resource-rich box over the resource-poor box, suggesting that they did not use the available public information to attempt to enhance their own payoff.

To choose the resource-rich box, the capuchins had to keep track of how often the conspecific on the video was eating from each box respectively. In a study assessing quantity assessment (Evans, Beran, Harris & Rice, 2009), it was found that capuchins appear to have more limited abilities at judging food quantities when presented one piece at a time when compared with chimpanzees. Thus, the way in which the information was presented may have been too difficult for the capuchins to keep track of. Nonetheless, the failure of the capuchins is somewhat surprising given that both birds (Templeton and Giraldeau, 1996) and fish (Coolens et al., 2003) have exhibited the ability to use public information and the fish were tested using a similar paradigm. Indeed, in contrast to the current results, previous research has found that tufted capuchins will preferentially choose a box based on a conspecific's exploration of it, even in the absence of food rewards (Bonnie & de Waal, 2007). However, the present task was more complex than the aforementioned study; in the current paradigm, participants witnessed food being retrieved by a conspecific from both boxes, but at a different rate and thus discriminating between these required a more finely tuned use of social information, going beyond the stimulus enhancement (Heyes, 1994) shown in the Bonnie and de Waal (2007) study.

The current findings are somewhat at odds with the findings of Ottoni et al. (2005), who found a preference of tufted capuchins to attend to the best nutcrackers in their groups, thereby implying that the capuchins were able to judge the success of these individuals. However, later research found that this nut-cracking proficiency was also correlated with age and dominance rank, with older and more dominant individuals observed more (Coelho et al., 2015). Therefore it is possible that increased attention to successful individuals in the former study may be a by-product of a model-based bias that does not require assessment of foraging success, such as copying older or more dominant individuals (e.g. Horner et al., 2010). More research is needed to disentangle these biases in free-ranging capuchins.

Somewhat surprisingly, given the traditions exhibited by wild capuchins (Panger et al., 2002; Perry et al., 2003; Ottoni & Izar, 2008), past research into food choice with captive capuchins has revealed somewhat limited social learning capabilities. A series of experiments has revealed that, whilst the presence of conspecifics eating can increase food intake (Visalberghi & Addessi, 2000), the *type* of food being eaten does not have to be the same – the mere act of co-feeding may serve to increase food intake (Fragaszy & Visalberghi, 2004). Given these past findings, it is perhaps unsurprising that the capuchins did not use social information to decide between food sources. It is also reasonable to suggest that the combination of these past and current findings indicates a very general role of social enhancement in foraging in capuchins that may not extend to judgement of the foraging success of conspecifics. This would then suggest that this ability is not necessary for the formation of the traditions shown in wild capuchins (although it has been suggested that judging others’ payoff in relation to your own is likely a critical aspect of cumulative culture (Laland, 2004)). Capuchins show a high level of social tolerance during foraging (Boinski et al., 2003), which may serve to promote the spread of foraging behaviour without the need for payoff-based judgements.

6.4.2: Potential limitations of the study

Of course, there are a number of alternative explanations which may explain the results of the current study, the first of these being lack of attention to the video stimuli. Whilst social learning research has successfully utilised video demonstrations in the past (Price, Lambeth, Schapiro & Whiten, 2009; Hopper, Lambeth & Schapiro, 2012; Vale et al., 2014; Gunhold, Whiten & Bugnyar, 2014), the extent of information which different species of primate are able to extract from video stimuli is still somewhat unclear. Indeed, after this experiment had been conducted, a study was published finding that capuchins failed to use video stimuli to locate a hidden food (Anderson, Kuroshima & Fujita, 2016). In addition, compared to the time over which the demonstrations were played to the group (2h45 – 3h), the capuchins watched the screen for a very limited time (range = 0-104 seconds, Figure 6.3), showing an apparent lack of motivation to attend to the video stimuli. The video demonstrations did not contain any auditory cues (due to the editing of the video the sounds were sometimes inconsistent and thus the video was muted). Capuchins are known to produce food calls (DiBitetti, 2003), although the exact function of these calls as referential signals is not yet clear (Gros-Louis, 2002; 2004). It is possible that the lack of auditory information may have reduced the social information available from the video stimuli, compared to that available from a live model, such as in Bonnie & de Waal (2007). However, it should be borne in mind that captive marmosets tested on a public information use task with live conspecific models also failed to utilise this information with regards to their own foraging tactics (Voelkl & Huber, 2007).

It could also be argued that animals kept in captivity compared to those tested in natural environments have different needs and motivations when it comes to foraging. Being always well fed, a captive capuchin may not have the need or motivation to differentiate between resource poor and rich foraging ‘patches’. However, whilst it is highly likely that differences in foraging motivation may be found between wild and captive animals, the chimpanzees in the Vale et al. (2014) study were also in a captive setting (as well as the capuchins in the Bonnie & de Waal (2007) study) and still utilised social information to make a beneficial foraging decision. This indicates that there are likely species differences between capuchins and chimpanzees, either in the motivation or ability to absorb information presented in video format, or in the motivation of ability to utilise public information with regards to foraging decisions.

6.4.3: Conclusions

To conclude, this experiment revealed no evidence that captive tufted capuchins utilise public information to guide their own foraging decisions, unlike chimpanzees and children tested using the same paradigm (Vale et al., 2014). These findings, taken together with previous experiments into capuchin social learning of diet (Fragaszy & Visalberghi, 2004) suggest that social influences on diet in capuchins may be limited to stimulating synchronous foraging and not using the behaviour of conspecifics to make judgements about particular food sources or items. However, the capuchins in this study exhibited very low attention to the video displays, making it possible that the public information was not utilised due to a lack of motivation to view these stimuli. Therefore a similar experiment using live models is necessary to disentangle these explanations. It should also be considered that drawing conclusions about the foraging behaviour of an entire species from a sample taken from very specific life history conditions may be problematic (Mesoudi et al., 2016). This research area would benefit from the use of field experiments (e.g. Biro et al., 2003; van de Waal et al., 2013) to examine whether wild tufted capuchins are capable of using public information in a natural foraging setting.

Chapter 7: General Discussion

The aim of this research was to investigate social learning biases in wild vervet monkeys and captive capuchin monkeys. Whilst the mechanisms of social learning have been the primary focus of much social learning research in non-humans, less is known about social learning biases in non-human primates, despite the potentially important role they have been proposed to play in information transfer (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). As such, this thesis examined dominance-based biases in wild vervet monkeys, both in social learning and social attention, and payoff-based biases in captive capuchins. This chapter discusses the findings of the current research and their implications for the field, alongside potential limitations and directions for future research.

7.1: Dominance-based biases

One of the central questions of this thesis pertained to dominance-based biases. Do wild vervet monkeys exhibit a bias towards preferentially copying, and attending to, dominant rather than low-ranking individuals when making foraging decisions? This question was asked using both food preference (Chapter 3) and manipulation of artificial fruit (Chapter 4) paradigms. In Chapter 3, no evidence for a dominance-based preference in food colour was found; the monkeys exhibited no consistent preference for either the dominant females' or the low-ranking females' demonstrated preferred colour of apple. The paradigm used in Chapter 4 allowed for more in-depth analyses. Whilst no preference to copy the dominant models was found when the first action used by each monkey was examined, when the first *successful* action used was analysed, a significant preference for the dominant models' method emerged. However, the dominance-based preference soon disappeared; when all openings were analysed, no consistent bias emerged for either method, based upon model rank. Consistent with this, Chapter 5, which analysed the attention given to each model in the course of the two experiments, found no evidence of an overall preference to attend to any of the models based upon rank during either experiment. Therefore, the conclusion of this research is that in the tested population at least, wild vervet monkeys do not exhibit a persistent dominance-based bias in their social learning of foraging behaviour.

It has been proposed that dominant primates have access to the best resources (Cheney & Seyfarth, 1990; Pusey et al., 1997) and thus may have higher reproductive success (Pusey, 1997, but see Fedigan, 1983). Therefore, dominant individuals could be seen as successful models (Laland, 2004) and copying them might be expected to be an adaptive strategy. Although the current results are to date the first and only results of such tests in this species, they suggest that such a dominance-bias in social learning has not evolved as an adaptive strategy for vervet monkeys. There are a number of possible reasons why this may be. Unlike in some other species (Pusey et al., 1997; van Noordwijk & van Schaik, 1999), dominant female vervet monkeys in tested populations do not exhibit an overall higher reproductive success (Cheney et al., 1981; Cheney & Seyfarth, 1987, but see Wrangham, 1981) and as such copying her behaviour may not necessarily increase fitness. Additionally, findings from social attention studies (Renevey et al., 2013) and social learning experiments (van de Waal et al., 2010) have previously revealed biases to attend to and learn from female vervet monkeys. This has been hypothesized to be because females are the philopatric sex and, as such, likely have the best information concerning the local environment (van de Waal et al., 2010). Given these past and current findings, it may be the case that all females are local 'experts' worth copying irrespective of rank, and that copying one female over another based upon rank yields no increased benefit.

Henrich & Gil-White (2001) have also suggested that copying based upon success should only make sense for animals that display 'infocopying' (imitation), as the details of the technique are what determines its success (they used termite fishing as an example). However, this may place too much emphasis on extractive foraging and does not take into account more subtle copying behaviour, such as socially learning which foods to eat, as in Chapter 3, or where to forage.

Similar to the results in this thesis, a study of captive capuchins also found no evidence for a dominance-based bias in social learning (Dindo et al., 2011). This may be consistent with the current results that a *copy the dominant* bias may not be adaptive for some monkeys. However, there is some evidence that males may be more attended to in semi-free ranging capuchins, due to their greater propensity to engage in nut-cracking (Ottoni et al., 2005; Coelho et al., 2015), whereas Dindo and colleagues (2011) used female models in the test (due to difficulty training the males), leading to the possibility that this failure may have been because of the sex of the model. There is also evidence that rank is related to reproductive success in capuchins (Jack & Fedigan, 2006), but again, this is in relation to males and not females (Fedigan, Carnegie & Jack, 2008). Therefore a study assessing dominance-based bias using male capuchins as models would be useful to clarify this issue.

Additionally, given the evidence that capuchins attend more to the best nut-crackers as well as older and more dominant individuals (Ottoni et al., 2005; Coelho et al., 2015), a useful direction for future research would be to attempt to disentangle the strategies of *copy successful individuals* and *copy dominant individuals* (Henrich & Gil-White, 2001; Laland, 2004). Henrich & Gil-White (2001) state that, whilst dominance (rank in competitive contexts) and prestige (high status based on deference for those with high success levels) can be correlated in individuals, they are two separate processes. In one of the two studies which may indicate dominance-based bias in chimpanzees, dominance is entangled with success on previous tasks (Horner et al., 2010). In the current studies, only one model had been previously used as a model in a social learning/object manipulation task (Nkos, low-ranking model from AK in Chapter 4); her method of opening the artificial fruit in the current experiment was not preferred by other individuals in the group, although of course with one individual no claims can be made about prior success and learning biases in vervet monkeys. Experiments manipulating success levels of individuals of different rank would allow us to differentiate between these two variables and could potentially test whether each bias was used.

Nevertheless, the results of Kendal and colleagues' (2015) experiment suggests there may be differences in social learning biases between species. This would perhaps not be too surprising given the great differences in social structure, dominance hierarchy and cultural repertoire between vervets and chimpanzees (Goodall, 1986; Cheney & Seyfarth, 1990; Whiten et al., 1999; Tournier et al. 2014). Infant survival and thus reproductive success appears to be positively linked to rank in chimpanzees (Pusey et al., 1997), resulting in dominant female chimpanzees potentially being a better proxy for success than dominant female vervet monkeys. It is difficult to evaluate the reasons for these differences in utilizing a *copy dominant* strategy with evidence from only three primate species, but it is likely that the ecology and social structure of each species plays a central role. Important differences between primate species have been observed in social learning, particularly about food (Rappaport & Brown, 2008) and it is perhaps unsurprising that species which occupy such a wide range of ecological niches should utilize social learning in a correspondingly diverse manner.

Additionally, the reasoning for the adaptive value of a *copy the dominant* bias has thus far been based on an informational function; that the dominant should provide good information on the local environment, such as foraging techniques and diet selection. Yet it could also be argued that copying a dominant individual may serve a different adaptive function; to somehow increase affiliation with the dominant individual by copying them, perhaps by coordination in time and space by matching foraging decisions, similar to de Waal's (2001) Bonding- and Identification-based Observational Learning (BIOL) hypothesis. However, Kendal and colleagues (2015) found that task naïve individuals were more likely to attend to the dominant individuals, thereby suggesting an informative function of copying the dominant individual in this case.

As a note of caution, it should be made clear that evidence for a purely dominance-based bias in chimpanzees comes from only one study in captive individuals (Kendal et al., 2015). A recent study (Watson et al., submitted) has found that captive chimpanzees learn socially from a low-ranking demonstrator, but not a dominant demonstrator when trained in separate groups. As such, further studies investigating dominance-based bias in chimpanzees would be beneficial (as discussed further below) before too many conclusions can be drawn about species differences.

7.1.1: Dominance-bias and the evolution of culture

Kendal and colleagues (2015) argued that a dominance-based bias could (perhaps in concert with conformity) lead to the between-group traditions observed in wild chimpanzees (Whiten et al., 1999; 2001); a preference to copy the dominants rather than the low-ranking immigrants who may bring with them different behaviour may allow for the maintenance of homogenous group behaviour, as well as potentially limiting the number of traditions which emerge (Kendal et al., 2015; Nishida et al., 2009; Luncz, Wittig & Boesch, 2015). Given that we see a great difference in cultural repertoire between chimpanzees (Whiten et al., 1999; 2001) and vervets, who at present have not been credited with any clear behavioural traditions (although see Tournier et al., 2014 for tentative evidence of dietary traditions), it is indeed possible that a *copy the dominant* strategy could be key in creating and maintaining homogenous group behaviour in chimpanzees. However, as noted above, Watson et al. (submitted) found that behaviours can indeed spread from a low-ranking chimpanzee in a captive setting, where that is the only model on view; a finding which is mirrored in the artificial fruit experiment (Chapter 4) wherein individuals appeared to copy the sole, low-ranking model in the KB group. Therefore the necessity of a *copy the dominant* bias in the emergence of traditions remains ambiguous. Whilst humans (Whiten & Flynn, 2012) and chimpanzees (Kendal et al., 2015) appear to share a dominance-based bias, the extent to which it is necessary for the emergence of culture remains unclear. Given that such a bias has also been revealed in domestic hens (Nicol & Pope, 1999), it may suggest a case for convergent evolution based upon the role of hierarchy in the social system of each species. Nonetheless, more data from other primate and non-primate species, as well as other populations of vervets, are needed before conclusions can be drawn about the origin and ontogeny of this dominance-based bias.

7.1.2: Captive & field experiments

Something that should also be borne in mind when comparing this research and previous work is the notable difference in the environment in which the experiments have been conducted. The current research primarily used field experiments to address its research questions (with the exception of Chapter 6) and is the first (to my knowledge) to investigate dominance-based bias in wild primates. Field experiments have provided interesting and insightful results from a range of species (e.g. Biro et al., 2003; Pesendorfer et al., 2009; van de Waal et al., 2013; Aplin et al., 2015a). Whilst it cannot be claimed that these experiments are replicating natural conditions due to the very fact they involve experimental manipulations, along with the presence of researchers themselves, what they do allow for is an examination of responses to manipulated and matched control conditions within a naturally occurring group, in their home environment. The fact that these animals have developed and learnt about their surroundings in their natural social groupings, immersed in the environment which they have evolved to live in, makes them far better models than individuals in artificial groups in a human-made environment. Indeed, notable differences in behaviours such as tool use have been found between captive and wild populations of primates (van Schaik et al., 2016). Whilst some of the stringent controls that can be put in place in captivity are obviously not possible in the wild, and this is to the detriment of the paradigm, if one wishes to get closer to the behaviour an individual actually exhibits, rather than what they are merely capable of exhibiting, then field experiments are invaluable. This may ring particularly true for studies of social learning. It is possible that artificial social groupings could have influenced the studies which found a dominance-based social learning bias in chimpanzees (Kendal et al., 2015); animals who are forced to experience a certain close proximity to group mates may exhibit different attentional biases compared to those living in their natural, fission-fusion state (Goodall, 1986; Murray et al. 2007). What is needed is a comparable experiment with wild chimpanzees, although this may prove difficult given restrictions on provisioning, as well as their increasingly endangered status. The field would greatly benefit from further studies such as that of Hobaiter and colleagues (2015), who witnessed an innovation and were able to track its spread. However, this requires a vast amount of observation time and no small amount of luck to witness such critical occurrences, and therefore cannot easily be planned.

7.2: Rank & kinship biases

Whilst an overall preference for vervets to copy dominant individuals was not uncovered in this research, the dominance hierarchy still played a significant role in social attention and the spread of behaviours. High-ranking females were more likely than lower-ranked females to match the dominant models' behaviour (Chapter 4) and higher ranked individuals were more likely to view more of the dominant models' demonstrations (Chapter 5) when compared to lower-ranking individuals. These findings reveal that the rank of learners may be a more important factor in the spread of information in wild vervet monkeys than that of potential models.

This effect could be due to an overall bias to copy the dominant which, due to the hierarchy, was only able to be expressed in high-rankers, similar to the pattern suggested for social grooming in monkeys (Seyfarth, 1977). However, if low-rankers were able to gain access to the box, which they were across the 10 tests, there is no reason to suggest they would be restricted in their choice of action. Instead I propose a different explanation: as discussed in the individual chapters, our measure of rank may have also served as another measure of kinship for our study population. Kinship was assigned based upon direct observations of maternity; only individuals who were seen as babies nursing from the mother were listed as that female's offspring. Since IVP researchers have only been observing the population for 6 years at the time of these analyses, adult offspring and siblings were likely missed out from the definition of kinship. Rank in vervet monkeys is maternally inherited (Seyfarth, 1977; Cheney & Seyfarth, 1990), meaning that those close in rank are also likely to be kin. Therefore, as shown by the fact that our kinship and rank measures were found to be collinear during analyses, rank very likely offers another, more encompassing measure of kinship in the vervets. It could be asked, when high-ranking females were found to be more likely to copy the high-ranking models, why then wasn't the converse effect found for low-ranking females if this effect is due to kinship? This could be because low-rankers opened the boxes less than high-rankers, or because the hierarchy was less accurate for lower-ranked individuals. The finding of increased social attention from high-rankers to dominant models, and increased social attention towards the low-ranking models from their kin in Chapter 5 lends weight to the hypothesis that rank may be serving as a proxy of kinship in these analyses. Kinship, and in particular the mother-infant dyad, is an extremely important aspect of social structure in most primates and extended periods of infancy in close contact with the mother allow her to act as a primary model for social learning in the infant. The findings of increased social attention and copying from kin are consistent with findings from both vervets (van de Waal et al., 2014; Renevey et al., 2013; Gramp et al., in prep) and a wider selection of species (Lonsdorf et al., 2004; Jaeggi et al., 2010; Dindo et al., 2011; Valenzuela et al., 2010; Wrangham et al., 2016), thus lending support to the contention that the effects of rank seen in Chapters 4 and 5 are likely to be veiled effects of kinship. One of the more exciting aspects of these results is that previously only infants were shown to exhibit a kinship bias in whom they prefer to learn from in vervet monkeys (van de Waal et al., 2014). Infants were not included in the analyses of Chapters 4 and 5 as they did not open the box and, in terms of attention, they could not be identified quickly and accurately enough to warrant inclusion in the data. Thus, the kinship/rank biases seen are from individuals over the age of one year and provide the first evidence that kinship-based biases in social attention and learning biases go beyond infancy in vervet monkeys. As stated, since only maternal offspring were categorized as kin, we were unable to test here whether siblings showed enhanced social learning and attention, as has been found in other species (Schwab et al., 2008).

7.3: Age bias & Tolerance

In Chapter 3, there appeared to be an age-based bias in matching the dominant females' preferred colour. However, when juveniles were analysed separately, there was no consistent bias in matching either the dominant or low-ranking models' preferred colour. Instead, it appeared to be an effect of preference for the yellow colour. However, in Chapter 4, when only the individuals who saw both models in the test phase were considered, there was a significant effect of age; juveniles were more likely to copy the dominant models than were adults. In humans, some evidence has suggested that our social learning biases change throughout our development, starting with a preference to copy our kin and then beginning to look for the experts within our groups (Henrich & Broesch, 2011; Lucas et al., in press; see also Schuppli et al., 2016 for evidence of age-dependent changes in model observation in orangutans). These result suggest that a vervet monkey's social learning biases may change as they grow older, although the findings detailed in the previous section show that a preference to copy kin seems to persist into adulthood. Conversely, the findings of Chapter 5 revealed that juveniles watched more of the dominant demonstrations than did adults (a result not found for the low-ranking models) consistently across both experiments. But when analysed alone, juveniles did not show a significant preference for attending to the dominant females over the low-ranking females. This would then suggest that, rather than a bias of attention on the juvenile's part, the differences found are due to a factor external to the juveniles themselves. Given the strict linear hierarchy of vervet monkeys (Cheney & Seyfarth, 1990), it seems likely that this factor is based on tolerance. Past research has shown that some primates are tolerant of even unrelated juveniles (Hirata & Celli, 2003; Boinski et al., 2003; Ottoni et al., 2005). However, aggressive behaviours were not recorded during the demonstration phase and therefore we cannot say with certainty that an increase in tolerance led to a higher proportion of juveniles than adults observing the dominant female. It is also possible that a direct correlation between conflicts and audience may not have been found; the hierarchy appears well known to group members, particularly adults (Borgeaud et al., 2013) and therefore the presence of the dominant female may have kept other adults away without imminent threat of attack. Whilst past research has shown dominant female vervets to be more tolerant of ‘bonded’ individuals (Borgeaud & Bshary, 2015), it is unclear if this extends to other juveniles. Research suggests that social tolerance is an important factor in social learning (Coussi-Korbel & Fragaszy, 1995; van Schaik et al., 2003; Santorelli et al., 2011; Dean et al., 2012) by allowing others close enough proximity to the behaviour to allow for detailed observation and perhaps higher fidelity copying (van Schaik et al., 1999). It is likely no coincidence that species (and populations) with higher levels of tolerance and gregariousness seem to exhibit more traditions in the wild (Fragaszy et al., 1999; Whiten & van Schaik, 2007), although the direction of this relationship is not currently clear (Whiten & van Schaik, 2007). The results presented here suggest that juveniles are able, likely through increased tolerance, to observe more of the dominant female’s actions than are adults. However, in Chapter 4, juveniles were *less* likely than adults to match the dominant models’ method. . It may be that a more naturalistic paradigm is needed to reveal any correlation between these attentional biases and social learning outcomes. It may also be the case that, whilst juveniles are tolerated more than adults, they may still not be highly tolerated in general, when compared to species such as the great apes, capuchins or spider monkeys (Fragaszy et al., 1999; Boesch & Boesch-Achermann, 2000; Boinski et al., 2003; Santorelli et al., 2011).

7.4: Majority and sex bias

Frequency-biased transmission is a much debated and quite contentious issue in current literature on social learning biases (van Leeuwen et al., 2015; 2016; Aplin et al., 2015a; 2015b, Whiten & de Waal, 2016). The current research did not set out to examine majority-based biases and therefore has limited scope in what it can contribute to this debate. However, the results may provide indirect support for a conformity bias by ruling out alternatives. Dominance-based bias was a potential alternative explanation for previous findings of apparent conformity in wild vervet monkeys (van de Waal et al., 2013; Tennie et al., 2013; van de Waal et al., in prep). When migrating males adopted the colour preference of their new group and females in a split group showed a preference for their previous group's preferred colour, the authors proposed conformity as the transmission bias. However, it is possible that individuals could have been copying the dominant female of the group, rather than a majority of individuals. Whilst, the current experiments found no overall bias in the population to copy the dominant females, a sex bias was found in Chapter 4; males were more likely to match the dominant females' method than females. This may suggest a bias in males to preferentially copy the dominant female, perhaps being adaptive when they migrate between groups and might rely on female support to acquire rank. A previous study with birds also found different biases depending upon the sex of the individual (Benskin et al. 2002). However, the food colour experiment (Chapter 3) found no significant preference for the dominant models' colour when only adult males were analysed and the continued preference of the females in the split group for their former group's preferred colour of corn (van de Waal et al., in prep) cannot be explained by this sex bias. Additionally no sex bias was found in the attention measures in Chapter 5, as one might expect if migrating males were focused on dominant females in order to assist their integration in a new group. Therefore, no compelling evidence was found to support the explanation of dominance bias over conformity, although further work examining behaviour of migrating males would be useful.

7.6: Model behaviour

In the demonstration phases of the field experiments, the models were restricted to having access to only one option; one good tasting colour of apple, or one unlocked method to open the box. During the test phase however, both alternatives became available and viable. We were unable to accurately judge how many pieces of each colour were eaten by individuals beyond the first colour chosen in Chapter 3. Thus we can only accurately say that of the six models who participated in the test phase, four chose their trained colour. The exceptions were Ouli (BD) who chose yellow instead of her trained orange and Yeni (KB) who chose yellow instead of her trained green, likely reflecting the preference for yellow that we found in the rest of the group.

In the artificial fruit experiment of Chapter 4, the three dominant females all showed a sustained preference for their trained method, whereas the low-ranking models did not show this sustained preference (other than in the KB group where, perhaps tellingly, there was no dominant model demonstrating an alternative action). This is consistent with previous research in other species which has shown that dominant individuals use less social information from conspecifics than low-ranking individuals in foraging tasks, and in this sense are more conservative to their individually learned habits (Pongracz et al., 2008; Kendal et al., 2015). This may be because of scrounging; high-rankers are able to take food from low-rankers and as such do not necessarily need to socially learn more efficient foraging techniques from others. Low-rankers however often have more restricted access to food (Cheney et al., 1981) and therefore may have to be more flexible in their foraging techniques, perhaps leading to more innovation, as has been reported for low-ranking chimpanzees (Reader & Laland, 2001). Given that no bias to copy the dominant females was found in either of the current studies, particularly in low-rankers, it does not seem likely that this switching can be attributed to the low-ranking models copying the high-ranking models. The sole model in KB, a low-ranker trained to push, maintained her preference for her trained action, unlike the low-ranking models in NH and AK. This thereby suggests that there was a social influence to this switching and that the low-ranking models, in contrast to the dominant models, switched methods after witnessing the behaviour of the rest of the group. This behaviour echoes previous studies wherein individuals have abandoned previously useful personal information in favour of a new group's preference (van de Waal et al. 2013; Aplin et al. 2015), which represents an extremely powerful effect of social influence. This may be either because of a motivation to 'conform' to the behaviour of the majority of the group (Whiten et al., 2005, although see van Leeuwen et al., 2016), or because witnessing others using the pivot action made this method more salient to them (as discussed in the next section). Regardless, the fact that only the low-ranking models switched behaviours may have important implications for the contexts in which we may expect to see conformist transmission.

Of course, there are limitations to these findings; only seven models were tested and the only low-ranking female who was trained to pivot (BD group) opened the box only once and thus a preference could not be calculated, leading to the question of whether the low-rankers in NH and AK changed because of a preference towards the pivot. However, the dominant female trained at push in BD did not change to pivot, thus suggesting that this switching behaviour was related to the females' ranks and not just the method used.

7.5: Payoff-based biases

The final experiment of this thesis was concerned with another form of social learning bias; payoff-based bias. This bias leads an individual to copy another based upon the payoff they are receiving for their current behaviour (Laland, 2004) and in terms of foraging is also referred to as public information use (Valone, 1989). It could be argued that this bias is more cognitively demanding than the others discussed here as it requires an assessment of another's current success, something which is often assumed, but for which little empirical evidence exists (Laland, 2004). Humans have been shown to utilize a payoff-based bias, though to a lesser degree than might be expected (Mesoudi, 2011). In tests of public information use with captive primates, chimpanzees have shown discrimination (Vale et al., 2014), whereas marmosets did not use public information to inform their own foraging behaviour (Voelkl & Huber, 2007).

The experiment in Chapter 6 failed to find any evidence for public information use in captive tufted capuchins. At first the findings may appear surprising given some capuchins' famous repertoire of cultural behaviours (Perry et al., 2003; Ottoni & Izar, 2008) and reports that they preferentially attend to the most proficient nutcrackers in their groups (Ottoni et al., 2005). However, further data reveals that capuchins also preferentially attend to older and more dominant individuals (Coelho et al., 2015), thus calling into question whether they actually keep track of the nutcrackers' payoffs. Indeed, the picture painted over the course of many captive studies suggests that capuchins may actually use social information in a very general manner (Fragaszy &Visalberghi, 2004). It has been found that seeing a conspecific feeding increases intake of a novel food in capuchins, even when the conspecific was eating a familiar food (Visalberghi & Addessi, 2000). In the light of this past literature, the results found here are perhaps not too surprising. These findings beg the question of whether more specific and accurate social learning processes are necessarily required to lead to the traditions that have been observed in wild capuchins (Perry et al., 2003; Ottoni & Izar, 2008). It may be that a cognitively simpler set of social learning skills are sufficient to create and maintain behavioural traditions, such as those we see in wild capuchins; a notion supported by findings of cultural transmission in insects (Leadbeater & Chittka, 2007; Alem et al., 2016).

The findings, together with those for captive marmosets (Voelkl & Huber, 2007) might suggest a phylogenetic difference between monkeys and apes (Vale et al., 2014) in their use of public information. However, given that fish (Coolens et al., 2003), birds (Templeton and Giraldeau, 1996) and bees (Leadbeater & Chittka, 2007) have been found to utilize public information in their own foraging, this perhaps instead signals multiple cases of convergent evolution. However, further tests with a greater range of species are required before any conclusions can be made.

Of course, as with any negative results there are alternative potential explanations for these findings. Perhaps the chief limitation of this study was the use of video. Whilst past studies have used video stimuli to great effect with non-human primates (Paukner & Anderson, 2006; Hopper et al., 2008; Vale et al., 2014; Gunhold et al., 2014), the extent to which each primate species is capable of using information presented via video is still somewhat unclear. Additionally, as evidenced by the time spent watching the videos, the capuchins in the study showed little attention to the video stimuli and thus may not have been able to obtain the public information necessary to show discrimination in the task. Individuals in captivity are, certainly in the Living Links Research Centre, well cared for and well provisioned. Thus, the motivation to attend to social information about the best foraging site might be somewhat diminished in these individuals. A similar experiment with live models (as in Voelkl & Huber, 2007) would help clarify whether the failure of the capuchins to select the resource rich box was due to inattention/incomprehension of video stimuli, or a failure to accurately utilize public information.

7.7: Preferred behaviours

One issue that arose in two of the experiments was that of one option being more preferred than another; both the yellow colour in Chapter 3 and the pivot method in Chapter 4 appeared to be preferred irrespective of the model. This is an issue that often arises when using multiple opening artificial fruits to test for social learning (Tennie et al., 2006; Dindo et al., 2011; Claidière et al., 2013). These pre-existing preferences can pose problems to researchers trying to find actions of equal or at least comparable preference in order to test other phenomena. However, they give us the important information that any potential bias must then be weaker than the preference if it is being occluded by it, pointing to a somewhat ‘fragile’ system of social learning (Tennie et al., 2009). Furthermore, finding two perfectly balanced alternative actions may not lead to better understanding of social learning behaviours, for when do these perfectly balanced options present themselves in the wild? Social learning does not occur in a vacuum. It has previously been argued that in cultural repertoires in wild animals, some innovations may spread differently to others due to differences in their saliency (van Schaik, Wich & van Noordwijk, 2006). In Chapter 4, the results from the control group strongly suggest that it is not the pivot method alone that is preferred, but the pivot method when performed by a model. The noisy and visually more obvious action apparently lends itself better to social learning by vervets than does the more discrete push action. Of course, the control and one-model groups show that the vervets were fully capable of learning the pivot through asocial learning, but the demonstrator seem to increase the ease with which it was learned, somewhat similar to the zone of latent solutions hypothesis (Tennie et al., 2009).

It is often the case that these preferences for certain behaviours are thought of as a confound to researchers. However, these results amongst others suggest that they could be an extremely important factor impacting which behaviours end up spreading and perhaps even becoming group-level traditions, especially when they are not simple differences in ease of learning/performing, but differences in what I will call ‘copyability’; the ease of *socially learning* an action. As such, I would suggest that this factor should instead be given more heed in this area of research. Indeed, whilst many model-based biases may have certain effects in theory (e.g. Boyd & Richerson, 1985), the inclusion of this copyability factor has the potential to dramatically alter the outcome compared to what we would expect if all options were as equally salient.

7.8: Limitations of the studies

Whilst providing valuable information about social learning biases in monkeys, particularly in the wild, the studies contained herein had a number of limitations. As already discussed, the use of video stimuli limited the conclusions that could be drawn in Chapter 6.

Given that one of the primary aims of this research was to examine dominance-based bias, the paradigms chosen in Chapters 3-5 were tailored to this in an attempt to investigate this specific issue by training different models based upon their rank. Whilst no evidence for a persistent dominance-based bias was found in these experiments, other interesting variables were highlighted. Differences in individual learner’s rank and/or kinship appear to be important factors in the choices made by monkeys in these experiments. Their contribution was elucidated through statistical techniques; however, given that the experiments were not specifically designed to assess kinship bias, this restricted the extent to which these biases could be tested.

Another limitation placed on the data obtained, particularly for the assessment of social attention, is that it was experimental data. The experimental nature of these studies may have biased the results by changing the spatial distribution of the individuals who were drawn to the stimulus and food reward of the experiments. Thus, strictly, the data herein can only tell us how vervet monkeys socially learn from, and attend to, others under these experimental contexts.

However, natural attention data taken alongside the current field experiments return similar results (Grampp et al., in prep) with regards to the effects of kinship and rank on social attention. Therefore, it appears that the results from field experiments may be reasonably representative of natural occurring social learning.

7.9: Future directions

Based upon the findings of the current research and in light of their relationship to the current literature I suggest a number of future directions for work in this field. Firstly, potential candidates for dominance-based biases among primate and non-primate species should be identified based upon their social system and ecology and tested for a range of social learning biases. Given the correlation in the present research between biases in social attention and behavioural outcomes of social learning, it would be useful to accompany these experiments with observational data of natural foraging behaviour. These are relatively simple to achieve and would benefit the experimental aspects of the research by assessing their ecological validity to the species in question. As discussed, further examining dominance-based bias in capuchins using male models could help shed light on current mixed results. Additionally, experiments which manipulate the success levels of individual of varying rank would be useful to separate the biases of prestige and dominance which are often confounded, but which represent different traits (Henrich & Gil-White, 2001; Horner et al., 2010).

Tolerance also appeared as a potential factor in the social attention of vervets, as has been suggested for other species (van Schaik et al., 1999; Santorelli et al., 2011). It would be interesting to investigate social learning biases in both more and less tolerant species to further elucidate the role of social tolerance in social learning. For instance, silverback gorillas show great tolerance towards young in the group (Stewart, 2001) and there is evidence that juveniles are often in close proximity to him (Watts & Pusey, 1993). Therefore it would be interesting to see whether juvenile gorillas display a bias towards copying their mother, or towards this tolerant male and compare these potential biases at several age intervals.

It would also be useful to have a clearer understanding of the functions behind these biases. Experiments which could ascertain whether copying biases served informational or normative functions (Claidiere & Whiten, 2012) would be invaluable for understanding these biases in evolutionary terms. This could potentially be achieved by experiments which allowed both task-naïve and task-knowledgeable individuals to witness models of differing rank and then assess their behavioural decisions when interacting with the task.

Finally, as discussed above, differences in behavioural salience, and what I have termed 'copyability', the ease with which an action is *socially* learned, should be investigated in its own right. For example, experiments could present captive individuals with behavioural variants found in wild conspecifics, as well as variants which serve a similar function but which are not found in wild animals, in order to assess whether, as might be predicted, certain behaviours lend themselves better to social diffusion.

7.10: Conclusions

To my knowledge, this research is in the first to experimentally test dominance-biased social learning in wild primates. It is important not to overstate the generality of these first findings; experimental results from local populations of animals may not be representative of the species as a whole, but products of specific environments, experimental paradigms and individual differences (Mesoudi et al., 2016). Nonetheless, I will draw some general conclusions from the experiments detailed within.

Two distinct field experiments found no evidence for a persistent bias that would lead to the preferential spread of a foraging behaviour from a dominant female, rather than a low-ranking female in our studied population of wild vervet monkeys. An analysis of social attention during these experiments further revealed a lack of preferential attention towards the dominant models. This suggests that a dominance-based bias is not inherent to all primate species, but is likely dependent upon social organization and ecology. Instead, the findings suggest that kinship, observer rank and observer age play more important roles in social attention and spread of behaviours in wild vervet monkeys. It also revealed the first tentative evidence for a kinship bias which goes beyond infancy in wild vervet monkeys.

Furthermore, an experiment with captive capuchins found no evidence for public information use in a foraging task, in contrast to results from chimpanzees, but in keeping with results from other monkey species. Whilst further testing is required to rule out potential alternative explanations, these results suggest that payoff-based strategies of social learning may require more complex cognitive skills than many primates display in experimental testing.

Finally, these findings highlight the important impact of external factors outside of individual social learning biases and suggest that factors such as the 'copyability' of the task and model tolerance may have important effects upon social learning outcomes. Overall, these findings present us with a clearer picture of social learning biases in monkeys and suggest many useful directions for future research.

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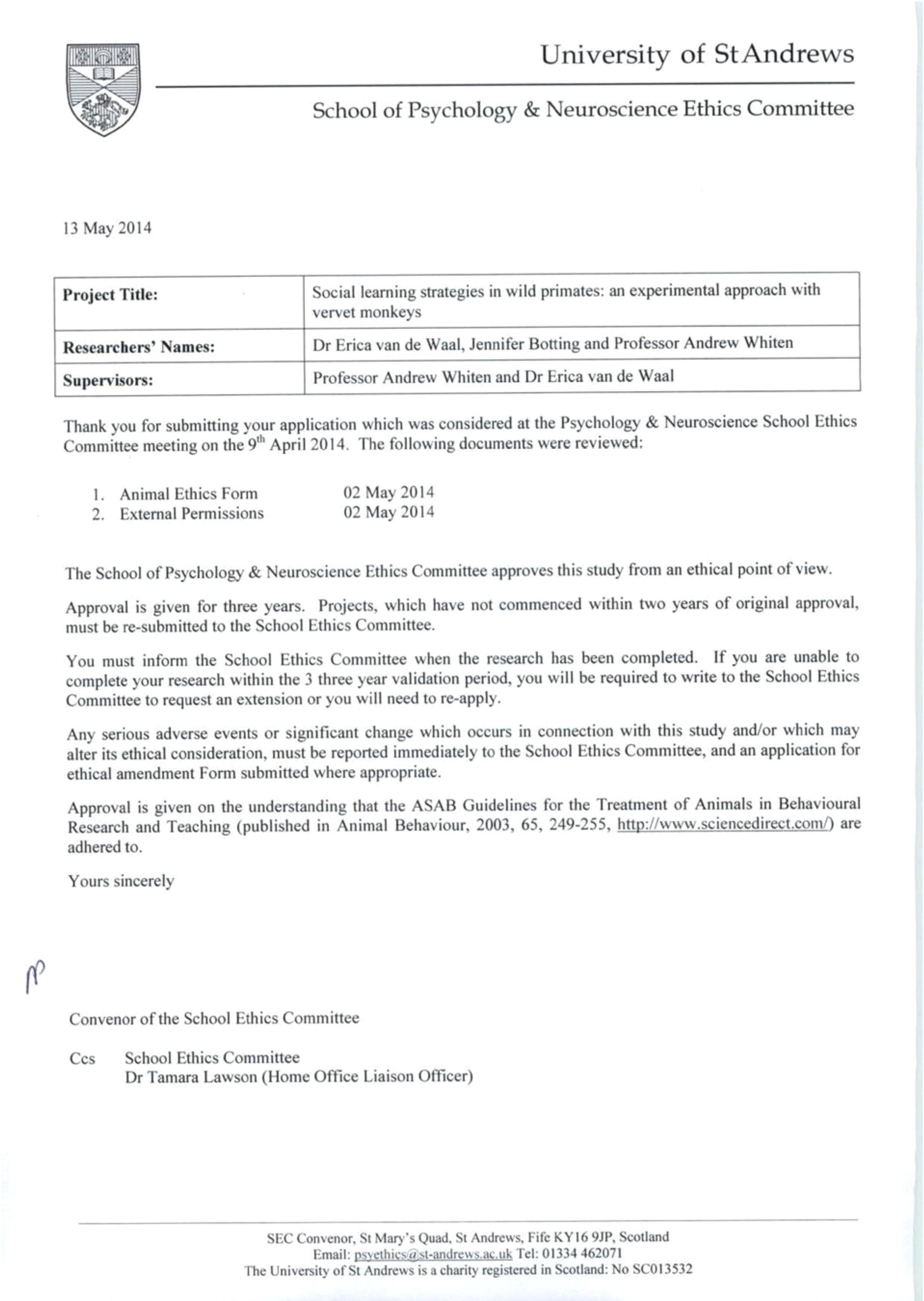
Appendices

Ethical permission letters from the University of St Andrews



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

13 May 2014

Project Title:	Social learning strategies in wild primates: an experimental approach with vervet monkeys
Researchers' Names:	Dr Erica van de Waal, Jennifer Botting and Professor Andrew Whiten
Supervisors:	Professor Andrew Whiten and Dr Erica van de Waal

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 9th April 2014. The following documents were reviewed:

1. Animal Ethics Form	02 May 2014
2. External Permissions	02 May 2014

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

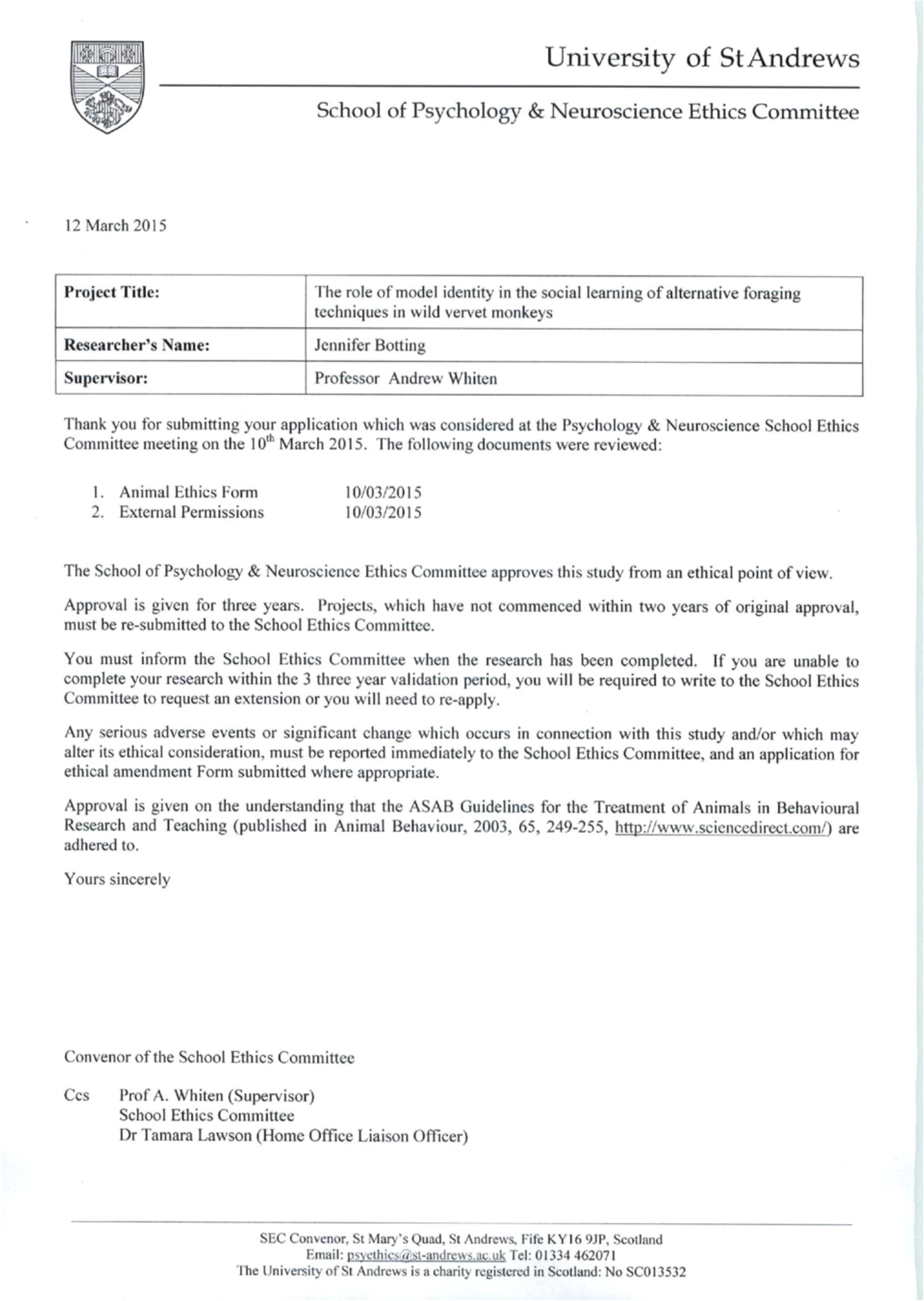
Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532



University of St Andrews

School of Psychology & Neuroscience Ethics Committee

12 March 2015

Project Title:	The role of model identity in the social learning of alternative foraging techniques in wild vervet monkeys
Researcher's Name:	Jennifer Botting
Supervisor:	Professor Andrew Whiten

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 10th March 2015. The following documents were reviewed:

1.	Animal Ethics Form	10/03/2015
2.	External Permissions	10/03/2015

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

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Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof A. Whiten (Supervisor)
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
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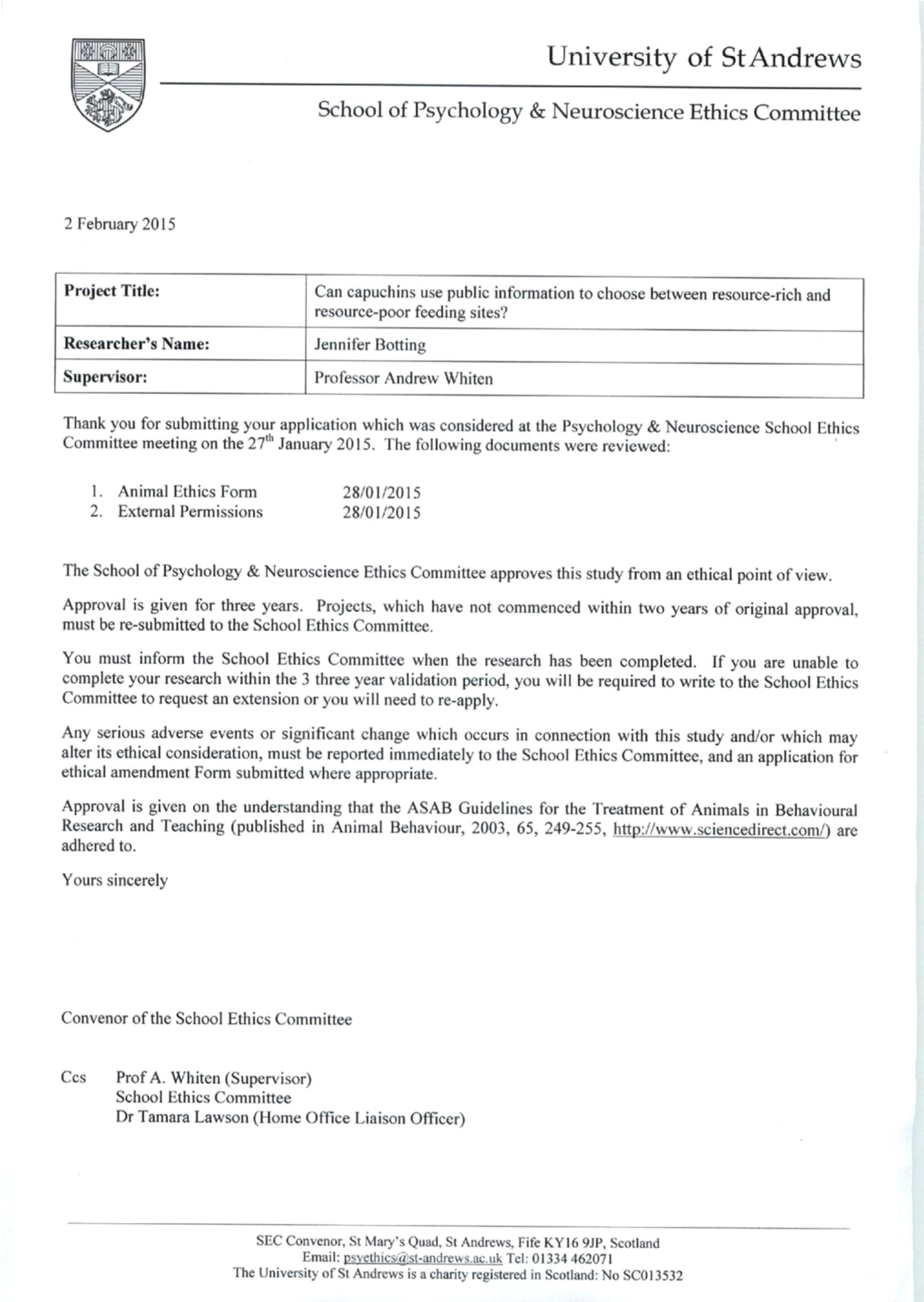

University of St Andrews

School of Psychology & Neuroscience Ethics Committee

2 February 2015

Project Title:	Can capuchins use public information to choose between resource-rich and resource-poor feeding sites?
Researcher's Name:	Jennifer Botting
Supervisor:	Professor Andrew Whiten

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 27th January 2015. The following documents were reviewed:

1. Animal Ethics Form	28/01/2015
2. External Permissions	28/01/2015

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

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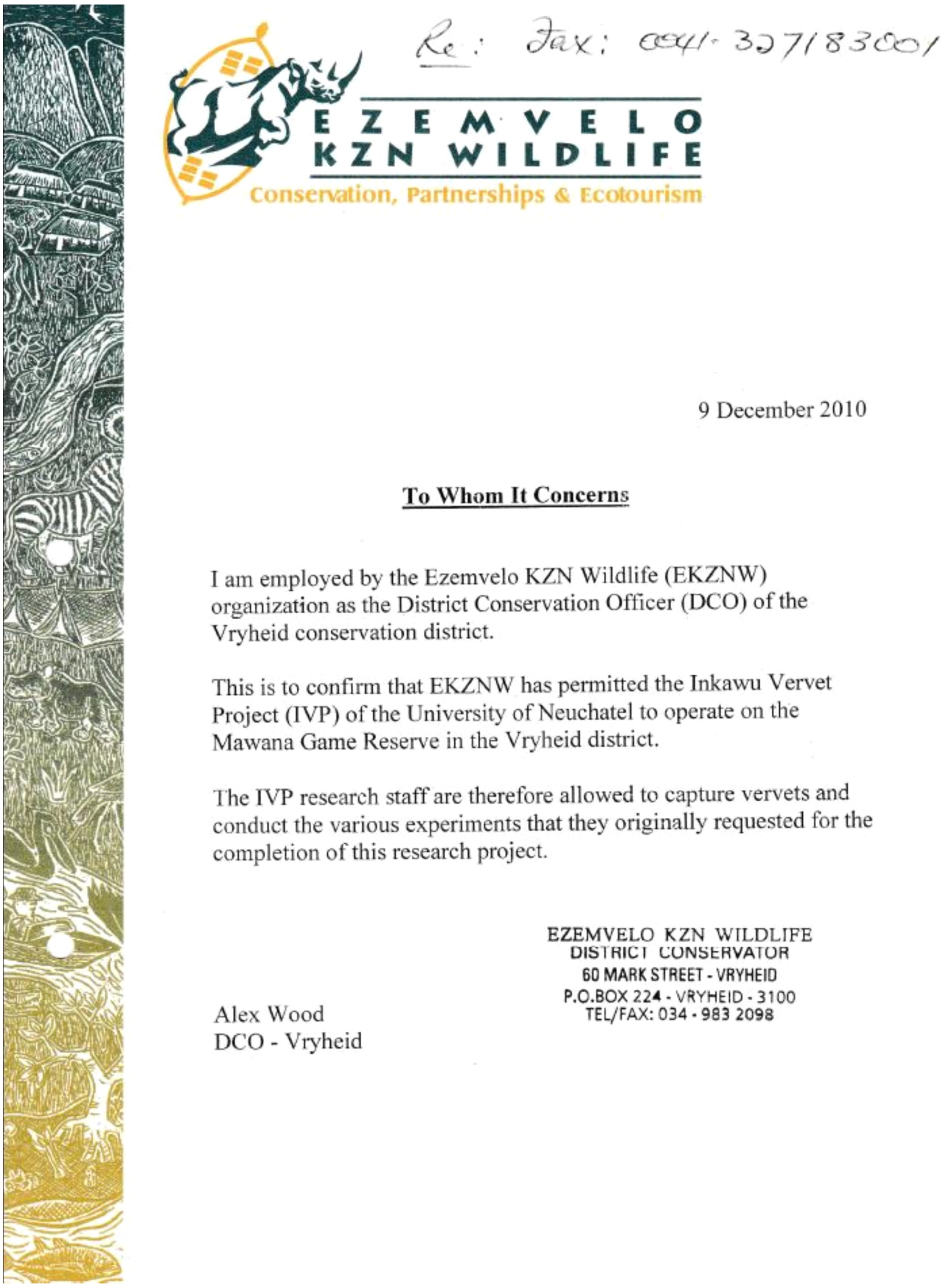
Yours sincerely

Convenor of the School Ethics Committee

Ccs Prof A. Whiten (Supervisor)
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)

SEC Convenor, St Mary's Quad, St Andrews, Fife KY16 9JP, Scotland
Email: psyethics@st-andrews.ac.uk Tel: 01334 462071
The University of St Andrews is a charity registered in Scotland: No SC013532

Permission letter from Ezemvelo KZN Wildlife (EKZNW)



Re: Fax: 0041-327183001

EZEMVELO
KZN WILDLIFE
Conservation, Partnerships & Ecotourism

9 December 2010

To Whom It Concerns

I am employed by the Ezemvelo KZN Wildlife (EKZNW) organization as the District Conservation Officer (DCO) of the Vryheid conservation district.

This is to confirm that EKZNW has permitted the Inkawu Vervet Project (IVP) of the University of Neuchatel to operate on the Mawana Game Reserve in the Vryheid district.

The IVP research staff are therefore allowed to capture vervets and conduct the various experiments that they originally requested for the completion of this research project.

EZEMVELO KZN WILDLIFE
DISTRICT CONSERVATOR
60 MARK STREET - VRYHEID
P.O.BOX 224 - VRYHEID - 3100
TEL/FAX: 034 - 983 2098

Alex Wood
DCO - Vryheid

IVP Behavioural Ethogram

Behaviour	**Definition**
Agnostic behaviours (aggressor)	
stare	Individual lifts up eyelids so white above eyes is visible and stares at another individual(s), often moving head forwards
attack	Forward motion of the body towards another individual(s)
stare attack	Combination of previous behaviours; individual moves forwards whilst staring
grab	Grabbing a part of another individual's body with hand
approach	Individual approaches another individual (more slowly than in attack)
take place	Individual takes the place recently occupied by another individual
approach and take place	Combination of previous behaviours; individual approaches another individual (who moves away) and take the place the other individual was occupying
bite	Individual bites another on body
hit	Individual hits another on body using hand(s)
hand on head	Individual places hand on top of another individual's head
kidnap baby	Individual takes infant of another individual and appears to refuse to give it back
chase	Individual runs after another individual who is fleeing
aggressive vocalisation	Individual makes a vocalisation during a conflict
feeding from mouth	Individual takes food from another individual's cheek pouches (usually using fingers)
frustrated hop	Individual (usually infants) jumps up and down on spot, usually with screaming
steal food	Individual takes food from another individual
Agnostic behaviours (victim)	
ignore	Individual carries on with previous behaviour
avoid	Individual turns head or moves body away from the aggressor, or stops previous behaviour
jump aside	Individual jumps aside to avoid something or someone
crawl	Individual moves top half of body to floor whilst facing an aggressor
stand up	Individual stands bipedal during a conflict
leave	Individual walks away from an aggressor
retreat	Individual quickly moves away from another individual (but not pursued, as in chase)
flee	Individual runs away from an aggressor as they are chased
refuse	Individual refuses to let another feed from mouth, but turning head or moving away
self-scratch	Individual scratches own body
look for support	Individual looks around for support whilst being aggressed
grunt	Individual grunts as another approaches
scream	Individual screams (high-pitch vocalisation) towards an aggressor
Affiliative behaviours	
groom	Individual grooms another individual
present	Individual presents a body part to be groomed, often following approach (ap.pr)

ignore	Individual carries on with previous behaviour
sit in contact	Individual sits next to another individual with their bodies touching
touching	Individual touches another monkey, but doesn’t groom
hugging	Individual puts arms around another individual as if hugging
infant handling	Individual is holding/manipulating the infant of another individual
nursing	Infant is suckling from its mother
mouth to mouth	Individual touches its mouth to/near another individual's
lip smacking	Individual makes a noise by repeatedly smacking it's lips or teeth together
Sexual behaviours	
presentation of sexual parts	Individual presents sexual parts to another individual
inspecting sexual parts	Individual inspects another individual's sexual parts with hands or mouth
hip grab	Individual grabs a female's hips prior to mounting
mount	Individual mounts a female
homosexual mounting	Individual mounts another individual of the same sex
complete mounting	Mounting in which the male ejaculates
masturbation	Individual manipulates own genitals with hand or mouth

Table A.1: Behavioural ethogram used by IVP members to collect data on social and sexual interactions. The ethogram was originally developed for use with vervet monkeys by C. Fruteau and then modified for use at IVP by IVP researchers. Hierarchies for Ch. 3, 4 & 5 were calculated using agnostic behaviours from the above ethogram, as detailed in Ch. 2.

Social network analyses supplementary information

Experiment 1: Feb-Aug 2014	Model	Partner	Real Association Index*
Baie Dankie (BD)	Dominant - Oulik	Che	0.989
		Lek	0.984
		Ogi	0.999
		Onb	0.999
	Low-ranking - Mooi	Mevr	0.999
		Miel	0.999
Ankhase (AK)	Dominant - Gaga	Gele	0.999
		Ghan	0.999
		Gugu	0.992
		Gho	0.981
	Low-ranking - Isil	Ilon	0.999
		Inhl	0.991
		Iji	0.992
		Idwa	0.999
Noha (NH)	Dominant - Gene	Gla	0.996
		Upps	0.999
	Low-ranking - Bogo	Zur	0.99
		Bos	0.999
		Bras	0.999
		Lhas	0.98

Experiment 2: Jan-July 2015			
Baie Dankie (BD)	Dominant Model - Oulik	Asis	0.996
		Piep	0.998
		Potj	0.998
		Prin	0.992
	Low-ranking - Riss	Roo	0.994
		Hipp	0.995
		Mad	0.987
		Rak	0.984
Ankhase (AK)	Dominant - Gaga	Gele	0.998
		Ghan	0.997
		Gugu	0.992
	Dominant - Nkos	Ndon	0.989
		Nyo	0.996
Noha (NH)	Dominant - Gene	Gaya	0.999
		Gla	0.996
		Upps	0.999
	Low-ranking - Bogo	Bela	0.982
		Bos	0.994
		Bras	0.999
		Lhas	0.98
		Yoog	0.991

Table A.1: Preferred dyads for each model in the three experimental groups, BD, AK and NH as calculated using SOCPROG 2.6 (Whitehead, 2009) for the period Feb-Aug 2014 covering the data anaylsed in Chapter 3 & 5 and for the period Jan-Jul 2015, covering the data analysed in Chapter 4 & 5. *=Preferred dyads had a real association index greater than 97.5% (Whitehead, 2009).

		Strength	Eigenvector centrality	Reach	Clustering coefficient	Affinity
NH	Group mean	1.47(0.87)	0.11(0.08)	2.89(2.04)	0.13(0.05)	1.82(0.38)
	Dominant Model (Gene)	1.85[0.29]	0.19[0.03]	4.56[1.00]	0.25[0.06]	2.47[0.18]
	Low-ranking model (Bogo)	1.54[0.28]	0.08[0.02]	2.63[0.67]	0.1[0.02]	1.71[0.15]
BD	Group mean	1.43(0.88)	0.11(0.08)	2.82(1.89)	0.16(0.05)	1.91 (0.26)
	Dominant Model (Ouli)	3.85[0.49]	0.33 [0.03]	7.96[1.63]	0.18[0.02]	2.06[0.2]
	Low-ranking model (Riss)	2.04[0.29]	0.15[0.02]	3.97[0.78]	0.14[0.02]	1.95[0.2]
AK	Group mean	1.56 (0.79)	0.13 (0.08)	3.03 (1.7)	0.16 (0.04)	1.85 (0.3)
	Dominant Model (Gaga)	1.74[0.29]	0.15[0.03]	3.51[1.02]	0.23[0.04]	2.01[0.27]
	Low-ranking model (Nkos)	2.37[0.02]	0.21[0.02]	4.77[1.27]	0.16[0.03]	2.02[0.26]

Table A.3: Social Network Analyses statistics for the period January-July 2015, including group means and individual model values.

		Strength	Eigenvector centrality	Reach	Clustering coefficient	Affinity
AK	Group Mean	1.8(0.92)	0.14(0.1)	4.05(2.39)	0.13(0.06)	2.17(0.29)
	Dominant Model (Gaga)	2.57[0.24]	0.30[0.03]	7.15[1.07]	0.31[0.04]	2.78[0.24]
	Low-ranking Model (Isil)	0.66[0.25]	0.11[0.02]	3.68[0.75]	0.14[0.02]	2.22[0.20]
BD	Group Mean	1.48(0.85)	0.11(0.07)	2.90(1.78)	0.17(0.04)	1.92(0.19)
	Dominant Model (Ouli)	3.78[0.40]	0.31[0.02]	7.76[1.3]	0.20[0.02]	2.05[0.16]
	Low-ranking Model (Mooi)	1.18[0.22]	0.09[0.02]	2.31[0.56]	0.18[0.02]	1.96[0.19]
NH	Group Mean	0.68(0.44)	0.11(0.07)	0.66(0.42)	0.10(0.10)	0.95(0.13)
	Dominant Model (Gene)	0.90(0.19)	0.17(0.05)	0.95[0.28])	0.09[0.03]	1.06[0.16]
	Low-ranking Model (Bogo)	1.07[0.27]	0.16[0.05]	0.98[0.37]	0.07[0.02]	0.91[0.15]

Table A.4: Social Network Analyses statistics for the period February-August 2014, including group means and individual model values.